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Amar Telidji University – Laghouat

Faculty: Sciences
Department: Agricultural Sciences and Food Sciences
Domaine: Nature and Life Sciences
Field of study: Agricultural Sciences
Specialty: Plant Production

Course Handout
Intended for third-year students - Plant Production
Course Module:

Plant Genetic Improvement

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Course outline



1. Course information

University: Amar Telidji-Laghouat

Faculty of Sciences

Department: Agricultural sciences

Target audience: 3rd year – Plant production (L3)

Course title: Plant genetic improvement

Credits: 06

Coefficient: 03

Duration: 67h30

Schedule and rooms:

- *Course:* Tuesday 14h00 à 15h30, Room: 106
- *TD:* Tuesday 15h30 à 17h00, Room: 106
- *TP:* Thursday 11h00 à 14h00, Laboratory: 02

Instructor:

- *Course/TD/TP:* Dr. BOURAKNA Zineb
- *Email contact:* zi.bourakna@lagh-univ.dz

Availability:

- ***Office hours:*** Sunday, Monday, Tuesday, from 09:00 to 13:30
- ***Forum reply policy:*** Any question related to the course must be posted on the dedicated forum so that all students can benefit from the answer. I commit to responding within 48 hours.
- ***Email usage:*** Reserved for urgent matters only. I commit to answering immediately when possible.

2. Course overview

This course, entitled **Plant genetic improvement**, is intended for third-year undergraduate students (Level L3) specializing in Plant production.

The course is divided into a set of learning units that enable students to acquire knowledge on different strategies for creating new improved varieties across all plant groups, whether autogamous or allogamous species, as well as annual plants and fruit plants, using various selection methods. Thus, this module also covers plant cytogenetics and introduces some fundamental concepts in quantitative genetics.

Below, a figure presenting a simplified conceptual map of the module will illustrate the approach we will follow throughout the study of these topics (**Fig. 1**).

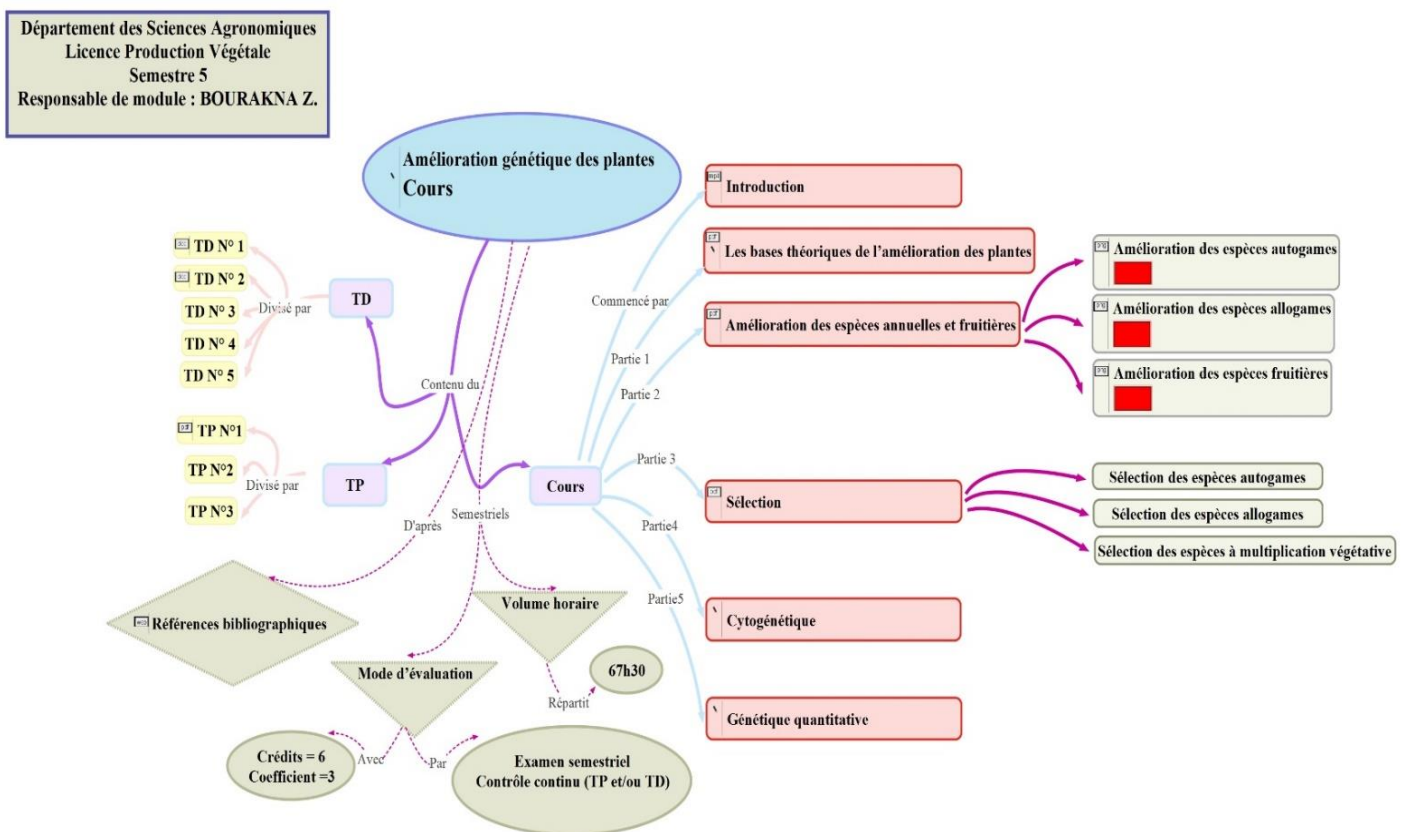


Figure 1. Simplified conceptual map of the plant genetic improvement module.

3. Course modalities

The course is organized into four types of sessions:

- **Theoretical lectures:** aimed at providing students with the essential basic concepts required to quickly understand fundamental definitions in genetics and working methods in plant breeding.
- **Tutorial sessions (TD):** scheduled after each learning unit, allowing students to apply the acquired knowledge in solving exercises.
- **Practical laboratory sessions (TP):** designed to apply and materialize the knowledge acquired during the course through practical experimentation.
- **Course hybrid mode:** The course is delivered in a hybrid format, both in-person classes (in class and in the laboratory) and online through the Moodle platform of Laghouat University. This will allow students to review or deepen the concepts presented in-person classes.

 The online platform includes spaces to:

- Download the different chapters.
- Submit individual projects in the appropriate dedicated space.

4. Prerequisites

 Before starting this module, the student must have knowledge:

- Mastery of fundamental concepts in plant biology;
- Ability to differentiate between the modes of plant reproduction;
- Mastery of Mendelian genetics.

5. Learning objectives

At the end of this course, the learner should be able to develop knowledge and understanding of the basic notions in genetics and plant improvement, and be able to connect these concepts these concepts.

 More specifically, the Plant genetic improvement course aims to:

- **Understand** the basic concepts of genetics and plant breeding;
- **Identify** the main objectives of plant breeding;

- **Explain** breeding strategies for autogamous plants, allogamous plants, and fruit species;
- **Compare** the different plant selection methods;
- **Apply** cytogenetics concepts within the framework of creating new improved varieties;
- **Master** basic notions and some calculations in quantitative genetics.

6. Assessment methods

 The final assessment is based on:

- **Continuous and regular assessment**, representing **40%** of the final grade. This allows students to accumulate points throughout the semester. This assessment is carried out through different forms, such as tutorials (TD) and practical work (TP).
- **A final semester examination**, consisting of an exam designed to evaluate the student's knowledge and competencies related to all topics covered during the semester. This exam accounts for **60%** of the final grade.

7. Content

This course of Plant genetic improvement is presented in five parts:

The first part introduces some theoretical basic concepts related to plant breeding. **The second part** deals with the different improvement strategies for annual and fruit species. **The third part** explains the selection methods for autogamous species, allogamous species, and vegetatively propagated species (clonal selection). **The fourth part** defines the main components of plant cytogenetics. **The last part** presents some concepts and certain calculations in quantitative genetics. Furthermore, each chapter is addressed through pedagogical sequences that facilitate the assimilation of the targeted concepts. This assimilation is reinforced by learning activities in which these concepts are applied to strengthen the course content. The detailed course outline is presented below:

Part 1: The theoretical foundations of plant breeding

- Modalities and significance of polygenic heritability
- Biological significance of additivity: linkats
- Heterozygosity: inbreeding and heterosis
- Breeding value of an individual in crosses
- Structure of natural populations

Part 2: Breeding of annual and fruit species

- Breeding of annual species
- Breeding of fruit species

Part 3: Selection

- Selection of autogamous species
- Selection of allogamous species
- Selection of vegetatively propagated species (clonal selection)

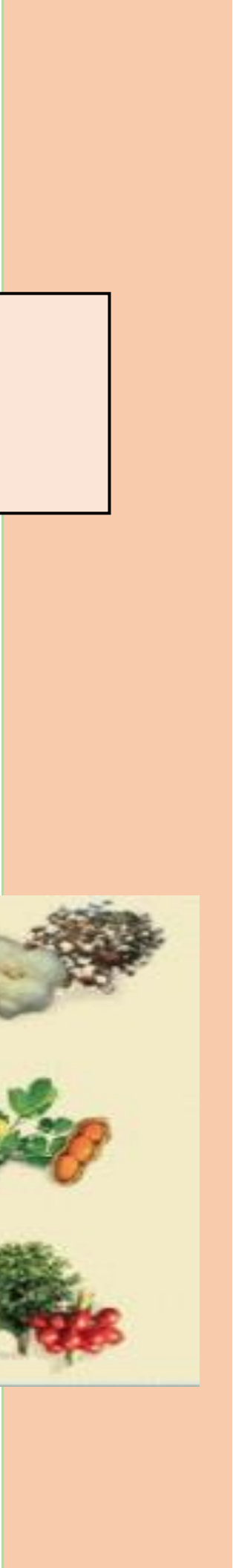
Part 4: Cytogenetic

- Types of chromosomes in Eukaryotes
- Euploidy in Eukaryotes
- Pseudopolyploidy
- Natural and artificial diploidization of polyploids
- Aneuploidy and its role in evolution

Part 5: Quantitative genetics

- Review of some statistical concepts
- Heritability of a trait
- Evolution of heterozygosity across generations
- The phenomenon of heterosis

Course content



1. Introduction

Today, the objective of agriculture is to ensure sufficient production, in both quantity and quality, in order to better feed the population, while limiting the use of inputs (fertilizers, pesticides, water) and preserving the environment as much as possible. However, populations of non-improved cultivated plants do not meet these requirements. In general, they provide limited production, are poorly adapted to cultivation conditions, are highly susceptible to diseases, and lack the characteristics required for the different uses of harvested products. The goal of plant breeding is therefore to correct these limitations.

Plant breeding can therefore be defined as the science and the art of creating new populations, called varieties, that optimally meet human needs. From a genetic point of view, it consists of assembling, within the same genotype or within a group of genotypes constituting the variety, the maximum number of favorable genes for the targeted traits. This is achieved through the combination of sexual reproduction mechanisms (selfing and crossing), the selection of the most performant plants, and, nowadays, through biotechnological tools.

The origins of plant breeding date back to about 11,000 years ago, during the “Neolithic Revolution”, when humans began cultivating plants and increasing their productivity through various improvement practices. The crop plants that exist today are therefore the result of long-term selection and produce significantly more biomass, fruits and seeds than their wild relatives. This initial phase corresponds to plant domestication, a form of selection that was both natural and human-directed, more or less consciously, which progressively modified wild plants to adapt them to cultivation and make them dependent on humans. This form of selection continued until the mid-19th century.

Since the beginning of the 20th century, the discovery of the principles and laws of genetics has opened the era of directed selection toward specific objectives, using real plant breeding techniques. Today, biotechnological tools offer the possibility to improve the efficiency of these techniques through better exploitation of genetic variability, often resulting in time-saving in the development of new varieties.

1.1. Some fundamental concepts in genetics

1.1.1. Gene

A unit of heredity that controls the expression and transmission of an inherited trait. Genes are distributed along the DNA.

1.1.2. Chromosome

A chromosome is a condensed filamentous structure formed by the association of DNA and proteins (a nucleoprotein filament). Chromosomes are located in the nucleus of cells, where they carry the **genes**.

1.1.3. Locus

A locus is the specific and fixed location of a gene on a chromosome. Plural: “**Loci**”. Each gene occupies a particular position along the chromosome.

1.1.4. Allele

Different forms that a gene can take. Alleles occupy the same position (locus) on homologous chromosomes.

A gene may exist in two or more forms called **alleles**: **homozygous (AA)** or **heterozygous (Aa)** (Fig. 2).

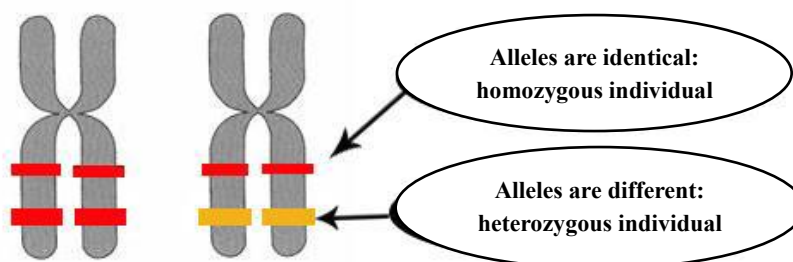


Figure 2. Gene localization on chromosomes.

1.1.5. Genotype

Allelic composition of all the genes of an individual.

1.1.6. Phenotype

The set of observable traits in an individual, resulting from the interaction between its genotype and environmental effects.

1.1.7. Homozygous

An individual carrying a gene represented by two identical alleles at the same locus. For example, **AA** or **aa**.

1.1.8. Heterozygous

An individual carrying two different allelic forms of a gene at the same locus (one dominant and the other recessive). For example, **Aa**.

1.1.9. Autogamy

Autogamy is a mode of sexual reproduction in which fertilization occurs between gametes produced by the same individual (**selfing**). **Autogamous species** naturally self-pollinate, leading to high genetic uniformity and a high rate of **homozygosity** within populations (**Fig. 3**).

Examples of autogamous species: wheat, barley, rice, soybean, pea, lettuce, bean, tomato, eggplant, chili pepper, tobacco, sorghum, peanut, cotton, coffee.

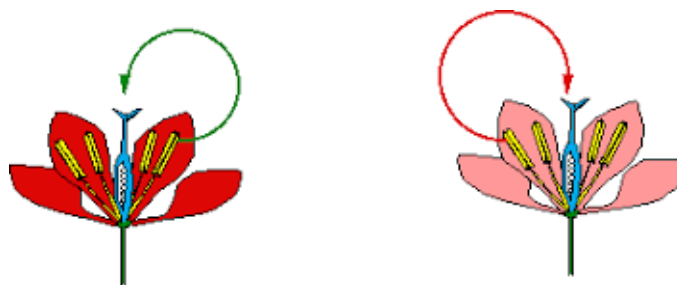


Figure 3. Autogamy.

1.1.10. Allogamy

Allogamy is a reproductive system in which individuals can only mate if they have different phenotypes. **An allogamous species** reproduces mainly by **cross-fertilization**, that is, by the union of gametes from two distinct individuals, which leads to **heterozygosity** and genetic variability (**Fig. 4**). This type of reproduction is promoted by several mechanisms, including monoecy (both sexes on the same plant), dioecy (sexes on separate plants), self-incompatibility, and pollen competition. Pollination is often facilitated by external agents such as wind or insects.

Examples of allogamous species: maize, sunflower, alfalfa, oil palm, squash, melon, cabbage, carrot, etc.

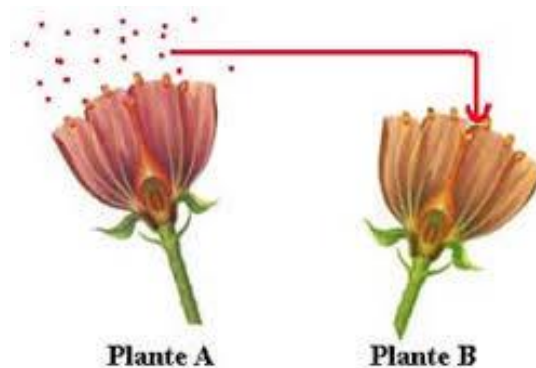


Figure 4. Allogamy.

1.2. Some concepts in plant breeding

1.2.1. Genetic variability

Genetic variability represents the totality of heritable differences existing between individuals of the same species. Genetic variability is the diversity of genes and traits within a plant species.

1.2.2. Variety

A variety is a group of plants belonging to the same species, exhibiting a set of distinct, stable, and uniform traits that can be transmitted to the offspring. It is the result of the breeder's selection work.

1.2.3. Hybridization

Hybridization is the controlled crossing between two genetically different individuals (lines, varieties, species). There are three types of hybridization:

- **Intraspecific hybridization:** between individuals of the same species.
- **Interspecific hybridization:** between different species of the same genus.
Example: crossing between two cotton varieties (*Gossypium hirsutum* × *G. barbadense*).
- **Intergeneric hybridization:** between different but closely related genera (rarer and more difficult). **Example:** crossing wheat × rye → triticale (*Triticum dicoccum*, $2n = 28$ × *Secale cereale*, $2n = 14$), resulting in an intermediate plant with 42 chromosomes.

1.2.4. Pure line

A pure line is a genetically homogeneous plant population, composed of a single genotype that is homozygous at all loci. It is usually obtained after several successive generations of selfing (generally 6 to 8 generations), which leads to a very high level of homozygosity. A pure line produces descendants that are identical to each other and identical to previous generations, therefore genetically stable.

1.2.5. Hybrid variety

Hybrid varieties result from the controlled cross between two genetically different parents. This cross can be intraspecific (within the same species) or interspecific (between different species). F1 hybrids often show hybrid vigor (heterosis).

1.2.6. Clonal variety

Clonal varieties are obtained through vegetative multiplication (cloning) of a single individual, whose genotype is reproduced identically in multiple copies. Within a clonal variety, genetic homogeneity is total.

1.2.7. Selection

Selection is the process of choosing the most productive or best-adapted plants for reproduction within a population.

1.2.8. Plant Biotechnology

Plant biotechnology includes all **modern biological techniques** that use living organisms or their components to manipulate, modify or improve plants. It mainly relies on methods such as in vitro culture, genetic transformation (transgenesis), protoplast fusion, and other molecular tools allowing direct intervention on plant cells or genetic material...

Part I

2. Part I: The theoretical foundations of plant breeding

2.1. Modalities and significance of polygenic heritability

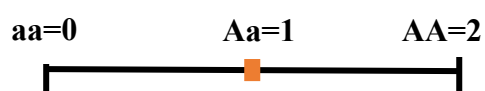
Polygenic inheritance is the phenomenon in which many phenotypic traits are controlled by a large number of genes (polygenes or polygenic systems). This type of inheritance concerns most measurable and quantitative traits such as yield, plant height, seed/grain size, fruit caliber, etc.

- The modalities of inheritance of polygenic traits depend on the relationships between genes that control them. These relationships can be of three kinds, thus defining three types of genetic effects:

- Additivity
- Dominance
- Epistasis

1.1.1. Definition of average effects (Additivity)

Additivity occurs when each additional gene contributes equally to the expression of the trait. The heterozygote (**Aa**) displays a phenotypic value that corresponds to the average phenotypic value of the two homozygotes (**AA** and **aa**). In other words: the value of **Aa** = $\frac{1}{2}$ (**AA** + **aa**). This situation corresponds to the absence of dominance. In other terms, the performance of an allele is identical regardless of the other allele present at the same locus.

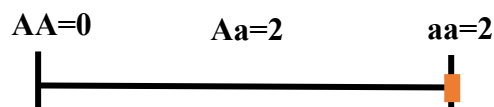


1.1.2. Dominance effects

The dominance effect describes the relationship between alleles at the same locus.

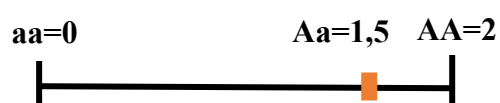
1.1.2.1. Complete dominance

When dominance is complete, the heterozygote (**Aa**) exhibits a phenotypic value identical to that of one of the parental homozygotes (**AA**). In other words, it expresses the phenotype of the dominant homozygote.



1.1.2.2. Partial dominance

In the case of incomplete (partial) dominance, the heterozygote (**Aa**) shows a phenotypic value that is closer to one of the two homozygotes (for example **AA**).



1.1.2.3. Overdominance (Super dominance)

The overdominance effect occurs when each allele at a given locus produces a distinct effect on the phenotype, and their combined effect exceeds the independent effect of each allele. In this case, the heterozygote (**Aa**) has a higher phenotypic value than the dominant homozygote (**AA**).



1.1.3. Epistatic effect

Epistatic effects on qualitative traits are often described as the masking of the expression of one gene by a gene at another locus. In quantitative inheritance, epistasis is defined as a non-allelic gene interaction between genes. In this case, an allele at one locus can mask or inhibit the expression of a gene at a different locus (**Tab. 1**).

Table 1. The different types of epistasis.

Genotypes	AB	Ab	aB	ab
Classical ratios (absence of epistasis)	9	3	3	1
Dominant epistasis	12		3	1
Recessive epistasis	9	3	4	
2 dominant genes with cumulative effect	9	6		1
2 dominant genes without cumulative effect	15			1
2 recessive genes	9	7		

Example

A/a -----> **A**: brown color, **a**: yellow color (hypostatic gene).

B/b -----> **B**: color inhibition, **b**: no color inhibition (epistatic gene).

- Thus, the expected phenotypes are:

- **AABB** → no color
- **AABb** → no color
- **AaBB** → no color
- **AaBb** → no color
- **aaBB** → no color
- **AAbb** → brown color
- **Aabb** → brown color
- **aabb** → yellow color

1.1.4. Expression of variances

When studying the genetics of multifactorial traits, the main objective is to determine the respective contributions of genotype and environment.

- In any phenotypic distribution, variability results from four sources:

- Genetic variance;
- Environmental variance;
- Variance due to genotype–environment interactions;
- Variance due to genotype–environment associations.

1.1.4.1. Genetic variance

The portion of phenotypic variation that is due to differences in genotypes among individuals is called genetic variance.

1.1.4.2. Environmental variance

The portion of phenotypic variation caused by differences in the environment among individuals is called environmental variance.

Example of grain weight distributions in beans

The mean of the distribution is 500 mg and the standard deviation is 95 mg. All beans in the population are genetically identical and homozygous because they are highly inbred. Therefore, in this population, all phenotypic variability for grain weight is due to environmental variance.

- ✓ The variance of this distribution is the total phenotypic variance, denoted by (V_P). If we assume that genotype and environment have distinct and independent effects on the phenotype, the phenotypic variance is expected to be greater than the genotypic variance (V_G) or the environmental variance (V_E).

In fact:

$$P = G + E$$

$$V_P = V_G + V_E$$

- Genetic variance is decomposed into:

- Additive variance (V_A) is the genotypic variance related to the additive action of alleles at quantitative loci
- Dominance variance (V_D) is the deviation from additivity when the phenotype expressed by a heterozygote differs from the strict sum of the individual effects of the alleles of the parental homozygotes.
- Epistatic variance (V_I) is the variance due to epistasis, when two or more loci interact epistatically.

The genotypic variance can be summarized by the following equation:

$$V_G = V_A + V_D + V_I$$

1.2. Biological significance of additivity: Linkage

1.2.1. Selection values and equilibria in recombination rates between two genes

1.2.1.1. Selection values (Fitness values)

The selective value quantifies an individual's ability to survive and reproduce according to its genotype. In other words, it measures how much a gene or an individual's genome contributes to the gene pool of the following generations.

- The selective value of an individual is divided into two components:

- **Viability:** the probability of surviving to reproductive age.
- **Fertility:** the average number of descendants produced by each survivor.

1.2.1.2. Recombination rate between two genes

Genes carried on the same chromosome are said to be linked, and they can be rearranged through a mechanism called crossing-over (for recombination to occur, a **crossing-over** event must take place). These genes are linked to each other, but genetic recombination can still occur between them. At the beginning of meiosis, homologous chromosomes pair longitudinally and form a synapsis. Due to the intertwining of non-sister chromatids, breaks may occasionally occur, and their ends can be rejoined in a crossed manner. As a result, **recombinant chromatids** are formed, each composed of two segments of different origins (**Fig.5**).

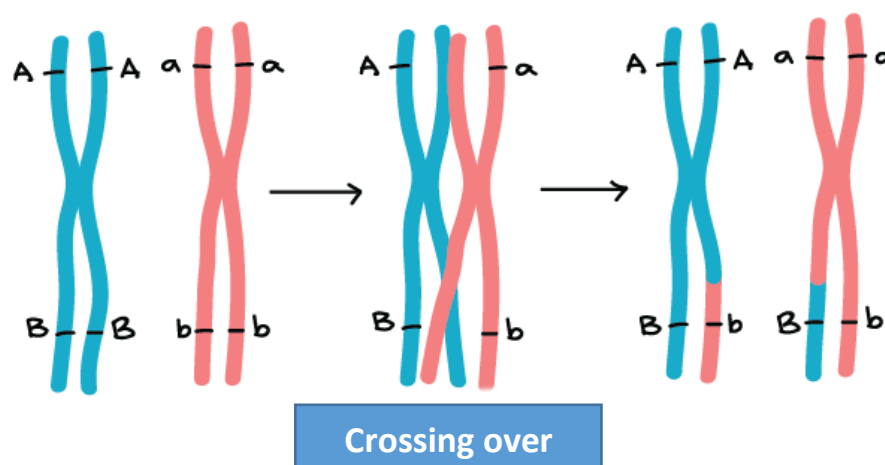


Figure 5. Recombination between two gene.

- ✓ The **recombination rate** is defined as the proportion of recombinant gametes relative to the total number of gametes produced.

$$\phi = \text{number of recombinant gametes for the genes} / \text{total number of gametes produced}$$

If certain combinations (for example A–B) confer better adaptation, selection tends to maintain these associations and reduce recombination that could break them apart. Conversely, if recombination helps eliminate unfavorable associations (such as A–b or a–B), it may be favored. Thus, under the action of selection, an evolutionary balance is established between forces promoting and opposing recombination. This balance determines the stability of the recombination rate observed in a population for these two genes.

1.2.2. Linkats

A linkat is a functional unit, and the term is used in biology to describe a specific set of genes (**gene battery**) that share certain common characteristics. These genes are composed of redundant subunits, meaning they have additional genetic elements with similar or identical functions to other elements within the same group, and this coherence can be transmitted during sexual reproduction..

- The linkat is composed of two essential levels of organization :
 - A chromosomal level, which groups together in the same region of the chromosome several loci that encode forms or functions with convergent adaptive values;
 - A second, finer level corresponds, for each of these loci, to the grouping of several coding units with roughly identical expression, forming gene battery.

Example

In maize, zein, the grain protein, is encoded by a battery of 7 genes on chromosome 7, 9 genes on chromosome 4, and a large but undetermined number on chromosome 10.

1.3. Heterozygosity: Inbreeding and heterosis

1.3.1. Consanguinity

Crosses are performed between related individuals by **self-fertilization**, generally in autogamous plants. Consanguinity (selfing) leads to an increase in the level of homozygosity within a heterozygous population.

1.3.2. Inbreeding

Inbreeding = **in**; **breeding**: crosses or fertilization.

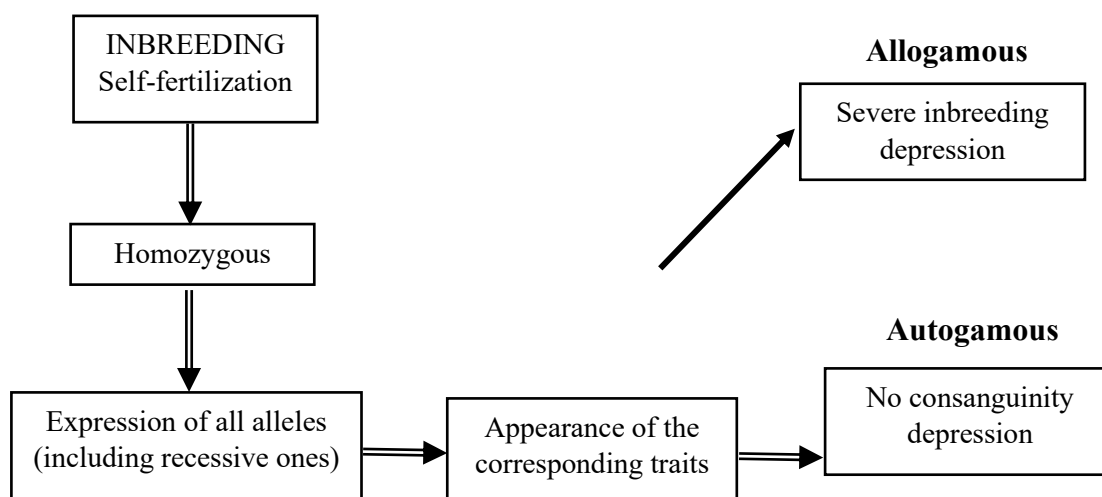


Figure 6. Inbreeding effect.

Inbreeding refers to all consanguineous crosses (self-fertilization) that lead to a progressive increase in the level of homozygosity within a heterozygous population. After each generation, the proportion of heterozygosity is reduced by half (**Fig. 6**).

In allogamous species, this inbreeding effect causes a loss or reduction of overall vigor, known as inbreeding depression. This depression is expressed as a decrease in plant size, grain yield, and fertility, as well as an increased susceptibility to diseases and sometimes the expression of lethal recessive genes.

In contrast, in autogamous species (such as wheat, barley, or rice), the inbreeding effect is practically unnoticeable, because these plants tolerate a high level of homozygosity without any loss of vigor.

- The intensity of this effect varies depending on the allogamous species. Thus, we can distinguish:

- Species **strongly** affected by inbreeding depression: **maize, alfalfa, forage cabbage;**
- Species **moderately** affected by inbreeding depression: **rye, sunflower, orchardgrass, cauliflower;**
- Species **weakly** affected by inbreeding depression: **rapeseed, fava bean.**

1.3.3. Heterosis

Outbreeding = non-consanguineous crossing; **allo-fertilization** = cross-fertilization.

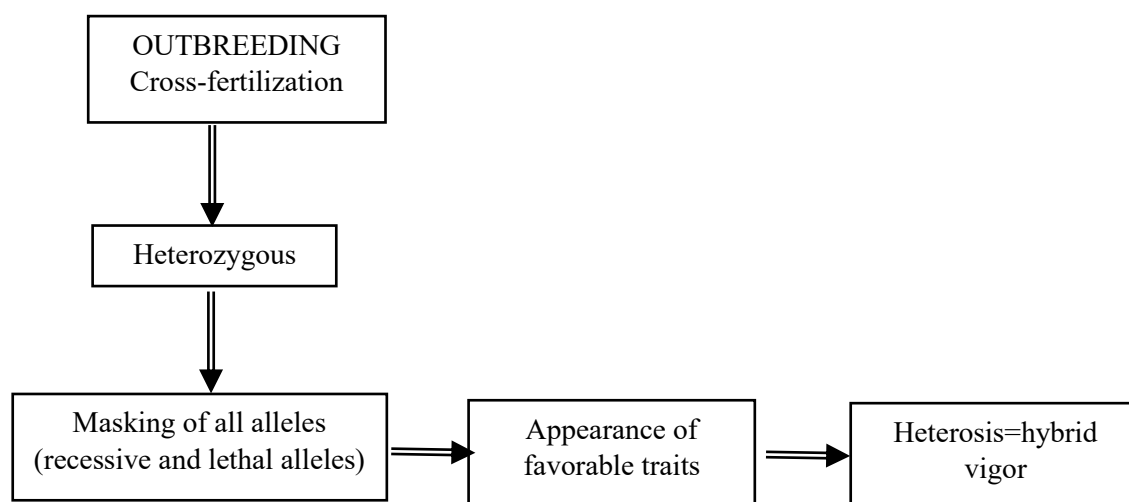


Figure 7. Heterosis effect.

Heterosis, or **hybrid vigor gains**, refers to the improvement in physiological and agronomic performance observed in hybrid individuals resulting from the crossing of genetically distinct lines. This phenomenon is the **opposite of inbreeding**, as it results from an increase in heterozygosity rather than its reduction.

Heterosis manifests as a general enhancement of vigor, often visible through faster growth, taller plants, a more developed root system, broader leaves, larger ears or fruits, an increased number of seeds, improved disease resistance, and sometimes earlier maturity (**Fig. 7**).

According to the theory of complete dominance, heterosis is explained by the accumulation of dominant genes in the F₁ generation, which mask the deleterious effects of recessive alleles, thereby giving hybrids superior vigor and performance. Practically, this

phenomenon forms the genetic basis for the development of hybrid varieties in many cultivated species. **The superiority of F₁ hybrids** over their best parents has led breeders to develop numerous high-yielding varieties, notably in **maize, sorghum, tomato**, and several other agricultural crops.

$$\text{♀ (AAbbcc)} \quad \text{X} \quad \text{♂ (aaBBCC)}$$

Value 1

Value 2

F₁(AaBbCc)

Value 3

Example 1 (Fig. 8)



Figure 8. Heterosis in maize (comparison of ears).

Example 2 (Fig. 9)



Figure 9. Heterosis in maize (vegetative development of the plant).

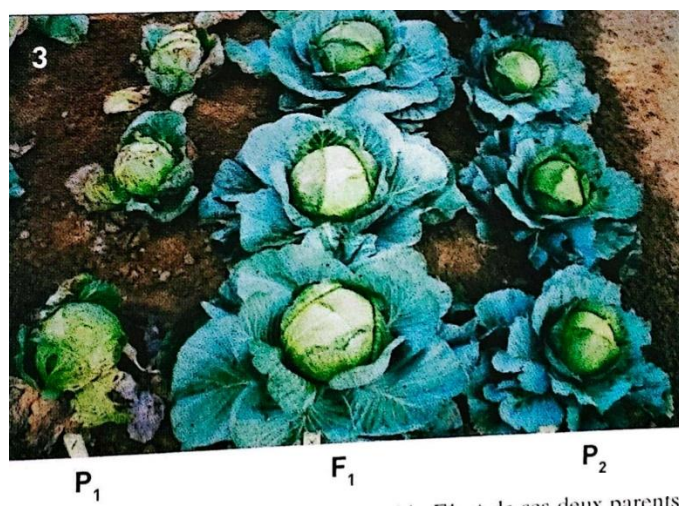
Example 3 (Fig.10)

Figure 10. Heterosis in cabbage.

1.4. Breeding value of an individual in crosses

In plant breeding, the breeder must identify which parents possess the traits of interest in order to obtain high-performing descendants. This evaluation relies on the analysis of the genetic value of individuals, determined from three fundamental concepts: **heritability**, **genetic balances**, and **combining abilities**. These parameters allow understanding and quantifying the relationships between parents (progenitor) and their descendants, thus facilitating the selection of the most promising crosses.

1.4.1. Heritabilities

1.4.1.1. Definition

In plant genetic improvement, the implementation of effective crossing programs requires a thorough understanding of the contribution of each gene to the observed variability of a given trait. Indeed, the phenotypic variability of a quantitative trait within a population can result from both genetic factors and non-genetic factors, primarily related to the environment.

The concept of **heritability** expresses the degree to which variation in a quantitative trait is transmitted from parents to their descendants. It indicates the proportion of the total phenotypic variation that can be attributed to genetic differences for a given population in a given environment.

When comparing the **heritability** of the same trait across different populations or under various environments, significant differences are often observed in the calculated heritability values. This demonstrates that heritability is not an absolute measure but a relative value, specific to each population and the environmental conditions in which it is studied.

Thus, the importance of environmental effects and the degree of genetic variability of a trait can directly influence the effectiveness of selection. For this reason, selection will be less effective when environmental variation is high, as it tends to mask the variation of genetic origin.

1.4.1.2. Estimation of heritability

Heritability represents the proportion of the total phenotypic variance that is of **genetic** origin. In other words, it measures the extent to which observed differences among individuals for a given trait are due to differences in genotype rather than environmental influences.

Broad-sense heritability (H^2)

Broad-sense heritability (H^2) expresses the proportion of the phenotypic variance (V_P) that is attributable to the genotypic variance (V_G), according to the following relationship:

$$H^2 = \frac{V_G}{V_P} \quad (V_P = V_G + V_E).$$

• The values of H^2 range between 0 and 1.

- A value **close to 1** indicates that the phenotypic variance is **mainly due to the genotype**, with little influence from the environment.
- Conversely, a **low value or one close to 0** means that non-genetic **environmental factors** account for most of the observed phenotypic differences.

Broad-sense heritability takes into account all genetic effects; it provides a general estimate of everything that is heritable. The genotypic variance (V_G) can be further decomposed into additive variance (V_A), dominance variance (V_D), and epistatic interaction variance (V_I):

$$V_G = V_A + V_D + V_I$$

Narrow-sense heritability (h^2)

Narrow-sense heritability (h^2) is the ratio of the variance due solely to additive genetic effects to the total phenotypic variance. It is expressed by the formula:

$$h^2 = \frac{VA}{VP}$$

Categories of traits according to their heritability

In plant breeding, three main categories of traits are distinguished based on the value of narrow-sense heritability (h^2):

- **Highly heritable traits ($h^2 > 0.4$):** Traits for which heritability is largely determined by genotype. These are mainly qualitative traits, which are much less influenced by environmental variations;
- **Moderately heritable traits ($0.2 < h^2 < 0.4$):** Traits for which the environment has a moderate effect;
- **Low heritable traits ($h^2 < 0.2$):** Traits strongly influenced by the environment, such as fertility and viability, disease resistance, yield, and protein content.

1.4.2. Genetic balances

A **genetic balance** reflects how well an individual's genetic makeup is adapted to a given environment. A genotype is considered **well-balanced** when the overall functioning of its genes is regarded as optimal (harmonious) (**Fig. 11**).

The nature and arrangement of alleles along a gene sequence on the chromosome thus determine the quality of this genetic balance.

A **heterozygous state** at each locus often leads to a favorable balance between alleles, reflecting optimal genome functioning and better adaptation to the environment.

- **Two types of genetic balances can be distinguished:**
 - **Internal balance:** depends on a proper linear arrangement of genes on the same chromosome, ensuring effective interactions between alleles located on the same DNA molecule;

- **Relational balance:** corresponds to an optimal interaction between homologous alleles located on homologous chromosomes.

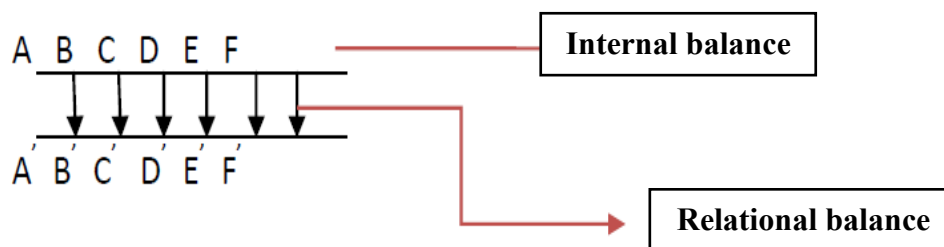


Figure 11. Genetic Balances.

1.4.3. Combining abilities

Combining ability measures the capacity of a line or an individual to produce high-performing hybrids when crossed with other genotypes. This concept is fundamental for selecting parents in breeding programs, particularly in the development of hybrid varieties.

Tests for combining ability aim to estimate the level of **heterosis** (hybrid vigor) expected when an inbred line is crossed with others. The choice of tester depends on the objective: it can be a specific plant, a line, a defined population, or any mixture.

- Two main types of **combining ability** are distinguished:

1.4.3.1. General combining ability (GCA)

General combining ability refers to the average performance of a parent when crossed with several other parents. It reflects the **additive effects of genes**, that is, the effects that are stably transmitted to the descendant.

A high **GCA** indicates that the parent carries favorable additive genes and can be used effectively in recurrent selection programs or for the development of new lines.

1.4.3.2. Specific combining ability (SCA)

Specific combining ability evaluates the performance of a particular cross beyond what would be expected from the general combining abilities of the two parents. It primarily reflects **non-additive genetic effects**, such as **dominance** and gene interactions (**epistasis**).

A high **SCA** indicates a good genetic complementarity between the two parents, often associated with hybrid vigor (heterosis).

In practice, selecting parents with high GCA promotes long-term improvement of populations, while selection based on SCA allows breeders to exploit heterosis effectively to produce high-yielding hybrid varieties.

1.5. Structure of natural populations

In nature, populations are never genetically isolated, as they are constantly influenced by factors such as **migration**, **mutation**, and **natural selection**. These processes lead to changes in **allele frequencies** over successive generations.

Such changes alter the genetic structure of the population, which can then evolve toward better adaptation to its environment.

The study of genetic structure aims to determine the equilibrium conditions under which allele frequencies stabilize, even though the population continues to be subject to these evolutionary forces. The genetic structure of populations is defined by the overall phenotypic, genotypic, and allelic frequencies that characterize the population.

1.5.1. Structure of a natural population in a self-pollinated species

Plants known as **autogamous** fertilize themselves (self-fertilization): the pollen from a flower fertilizes the ovary of the same plant, and pollen dispersal is very limited. These plants often have **hermaphroditic flowers** (male and female organs in the same flower), where fertilization can occur even before the flower opens. Such plants are referred to as **cleistogamous**, or capable of **automatic self-pollination**. However, strict autogamy is rare, and there is often a small degree of **residual outcrossing**, approximately 5% in wheat.

Wild populations of autogamous plants are composed mostly of homozygous individuals, as these species have developed a **tolerance to inbreeding (consanguinity)**, an adaptation acquired through natural selection. However, most autogamous plants exhibit a certain level of natural outcrossing, which leads to the presence of heterozygous loci within the population. Mutations can also contribute to heterozygosity.

The homozygous structures obtained by the breeder from such populations are called pure lines. Consequently, the selected varieties are **stable**, **uniform**, and **easily reproducible**, but they exhibit **low genetic variability**, since the gradual loss of heterozygotes occurs at all loci, leading to individuals that are homozygous with an almost complete genomic uniformity (pure lines).

1.5.2. Structure of a natural population in a cross-pollinated species

Allogamous plants reproduce mainly through **cross-fertilization**, with little or no self-fertilization. This occurs in plants that have separate male and female individuals (**dioecious**) or separate male and female flowers on the same plant (**monoecious**). In these cases, the pistil of a flower is fertilized by pollen from another flower, with pollen dispersal facilitated by wind or insects.

Some plants are **self-compatible**, meaning they can self-fertilize in the absence of foreign pollen (this is called **preferential allogamous**, e.g., sunflower). Other plants, such as cabbage, are **self-incompatible**, meaning they cannot self-fertilize because the female flower rejects its own pollen; these plants are therefore **obligately allogamous**.

In allogamous species, heterozygosity is predominant because allelic shuffling occurs at each generation of crossing. These species are sensitive to inbreeding, as natural selection can only eliminate deleterious recessive genes when they are in the homozygous state. A good variety must therefore maximize heterosis while remaining easily reproducible: this is the purpose of hybrid varieties. Allogamous generates an excess of heterozygotes, but this applies only to the loci that determine the phenotype, not to the entire genome.

Exercise: Estimation of heritability

On mesure le poids de grain par plante chez le maïs (g). L'écart-type phénotypique dans une grande population est de 15. L'écart-type phénotypique dans une lignée pure (consanguine) est de 12.

1. Calculer l'héritabilité au sens large du poids de grain par plante, (1) dans la lignée consanguine et (2) dans la grande population.
2. Expliciter votre raisonnement et souligner les réserves que ce dernier peut susciter.

Part II

3. Part II: Breeding of annual and fruit species

3.1. Definition and evolution of plant breeding

The term “**plant breeding**” or “**plant improvement**”, which refer to the set of scientific and empirical methods used to modify and direct the genetic structure of plants in order to obtain new varieties with desirable traits. These traits aim to meet human needs, such as yield, disease resistance, product quality, or adaptation to growing conditions.

It began thousands of years ago, when early humans—without being aware of it—selected the most useful plants by harvesting their fruits and encouraging the germination of their seeds near their dwellings. This unconscious domestication gradually evolved into an organized activity, shifting from simple gardening to deliberate and systematic plant selection.

In the 19th century, with the work of Louis de Vilmorin, plant breeding became a scientific discipline grounded in genetics, introducing the concept of “directed improvement” of plants. Today, it combines both science and art: it is a process that is at once rigorous and creative, aiming to develop varieties that meet human needs while adapting to their environment (Fig. 12).

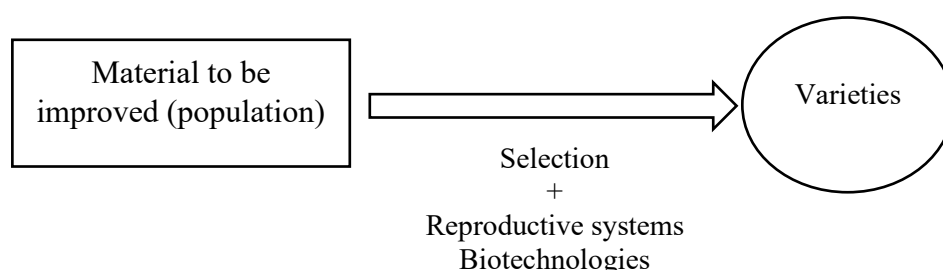


Figure 12. Illustration of plant breeding as the science and art of developing new varieties.

3.2. Objectives of plant breeding

Plant breeding aims to create new varieties that are more productive, better adapted to their environment, and endowed with qualities that meet human needs.

✚ The main objectives of plant breeding can be grouped into three categories: **productivity, adaptation, and quality.**

3.2.1. Optimization of productivity (yield)

Increasing yields is a primary objective to meet the growing needs of humanity. Higher yields can be achieved by accumulating favorable genes for this trait within a single genotype through the selection of high-performing individuals. However, yield stability is equally important; it depends on environmental adaptation, efficient use of resources (water, mineral nutrients), and resistance to stress. Thus, productivity is an overall objective resulting from the combination of genetic potential, environmental stability, and physiological adaptation.

3.2.2. Environmental adaptation

The adaptation of plants to environmental conditions is an essential factor for the sustainability and stability of production.

It includes two complementary aspects:

- **Adaptation to abiotic environment (edapho-climatic factors)**

Improving resistance to environmental factors such as drought, cold, and heavy rainfall, as well as earliness and tolerance to salinity and other climatic stresses like lodging due to wind and flooding, are key objectives for breeders in developing varieties capable of resisting or adapting to adverse environmental conditions. Indeed, various environmental influences on plants have a significant and direct impact on yield stability.

- **Adaptation to biotic environment**

It concerns **resistance to biotic stressors** (insects, pests, diseases, weeds). The development of resistant varieties allows for increasing and stabilizing production in the face of:

- Limiting the use of pesticides;
- Reducing production costs;
- Preserving the environment.

Hardiness and **biological resistance** ensure the consistency and sustainability of agricultural yields.

3.2.3. Quality

Quality criteria are multiple and closely related to the use of products for human consumption:

- **Human consumption** (baking quality of wheat, taste, color, texture, fruit size, absence of toxic compounds);
- **Animal feed** (nutritional value of fodder);
- **Industrial use** (olive oil content, sugar content of sugar beet, firmness of canned tomatoes, suitability for processing or preservation).

Thus, quality improvement aims to meet consumer expectations, industrial requirements, and marketing conditions.

3.3. Breeding of annual species

3.3.1. Properties of breeding annual species

Annual plants complete their entire life cycle in a single growing season (sowing → flowering, harvest → death).

 Their improvement presents several particularities:

- They reproduce mainly **by seeds** (rarely by vegetative means; exception: potato, through tubers);
- They have a **short reproductive cycle**, allowing rapid progress in selection and obtaining results in few generations;
- Their **spatio-temporal occupation** is **low**, which facilitates the establishment of many comparative trials in a short time;
- They do **not** exhibit **aging** of plant material, as the cycle renews every year.
- There is **no variety/rootstock association** as in perennial species (fruit trees, grapevine).

These characteristics make annual species very suitable for rapid breeding programs and allow for more dynamic genetic improvement.

3.3.2. Objectives of breeding annual species

The main breeding objectives for annual plants aim to:

- Obtain **homogeneous** and **stable** varieties, ensuring consistent production from year to year;
- Diversify the genetic material to expand the **available varietal range** (increase variability, create new varieties adapted to different contexts);
- Improve **agronomic** and **technological quality** (yield, processing quality, storage suitability, nutritional quality, etc.);
- Provide **resistance** to **biotic stresses** (pests, pathogens, weeds) and **abiotic stresses** (drought, cold, salinity, heat, wind, etc.).

According to the mode of reproduction, two main groups of annual species are distinguished: autogamous annual plants and allogamous annual plants (**Tab. 2**).

Table 2. Some annual plants (autogamous and allogamous).

Crops	Autogamous species	Allogamous species
Cereal crops	Wheat, oats, barley, rice, sorghum.	Maize, rye.
Grain legumes	Lentil, chickpea, pea, soybean, bean.	Fava bean.
Forage species	Vetch.	Dactyl, clover, alfalfa, faba bean, ryegrass.
Vegetable species	Eggplant, tomato, pepper, lettuce.	Artichoke, carrot, cucumber, watermelon, melon, zucchini.
Industrial crops	Rapeseed, coffee, cotton, tobacco, flax.	Beet, sunflower.

3.3.3. Improvement of autogamous plants

3.3.3.1. Characteristics of autogamous plants

Autogamous species are characterized by homozygosity (pure lines), homogeneity, and stability across generations.

Autogamous promotes the fixation of traits and tends to naturally reveal and eliminate deleterious recessive alleles (sterility, lethality, weakness, anomalies). Consequently, these species show fewer effects related to heterosis or inbreeding depression compared to allogamous species. Autogamous plants never suffer from vigor depression (inbreeding) and are well adapted to this mode of reproduction.

3.3.3.2. Breeding Strategies for autogamous plants

The goal of breeding is the **isolation or creation** of pure-line varieties. The objectives are to:

- Either genetically analyze natural populations to identify the best naturally occurring lines (exploitation of natural variability).
- Or create lines after inducing genetic variation through hybridization.

When a breeder crosses two plants to combine desirable traits, cross-fertilization or hybridization is performed, followed by inbreeding to obtain pure lines (**Fig. 13 and Fig. 14**).

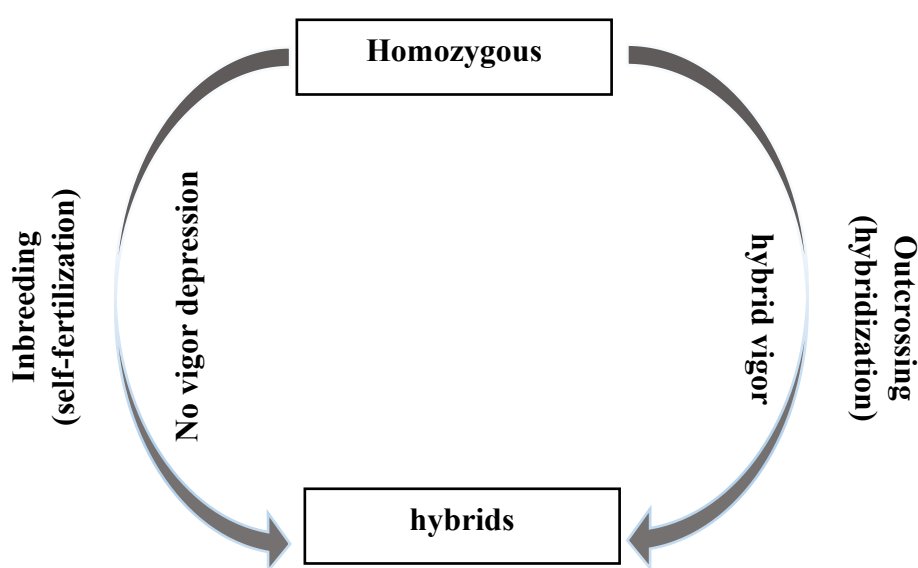


Figure 13. Breeding strategy for autogamous plants.

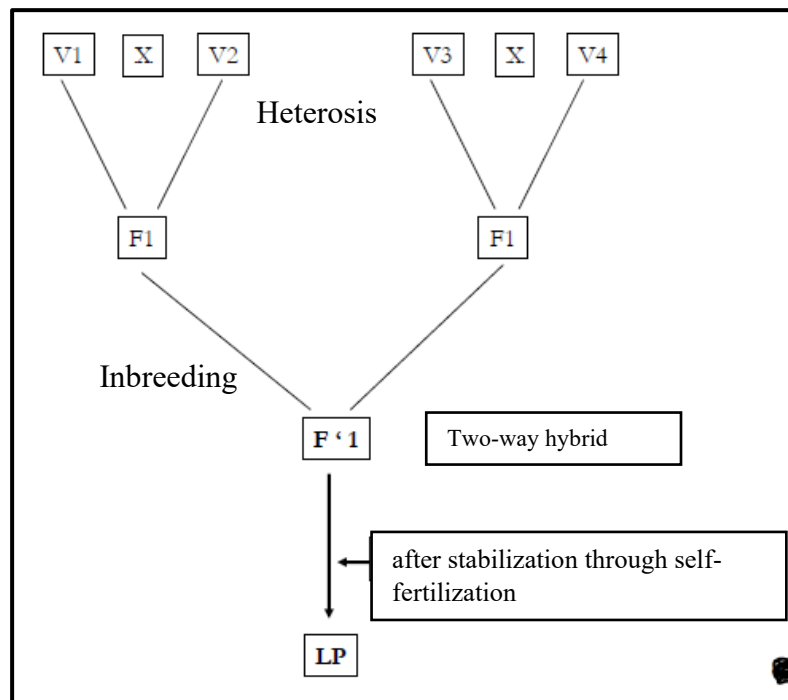


Figure 14. Hybridization and selection of autogamous plants.

Example of wheat

When the two parent plants are selected based on their traits of interest and then crossed, the breeder chooses one of the parents to serve as the female plant. On an ear of this plant, **manual emasculation** of the flowers is performed, meaning that all the stamens containing pollen are carefully removed to prevent self-fertilization.

The ear then becomes receptive only to external pollen. Next, the breeder collects pollen from the second parent chosen as the male. This pollen is taken from mature anthers and manually applied to the stigmas of the emasculated female ear. This operation ensures controlled fertilization between the two selected parents. After pollination, the ear is protected (usually by bagging) to prevent contamination from foreign pollen (**Fig. 15**).

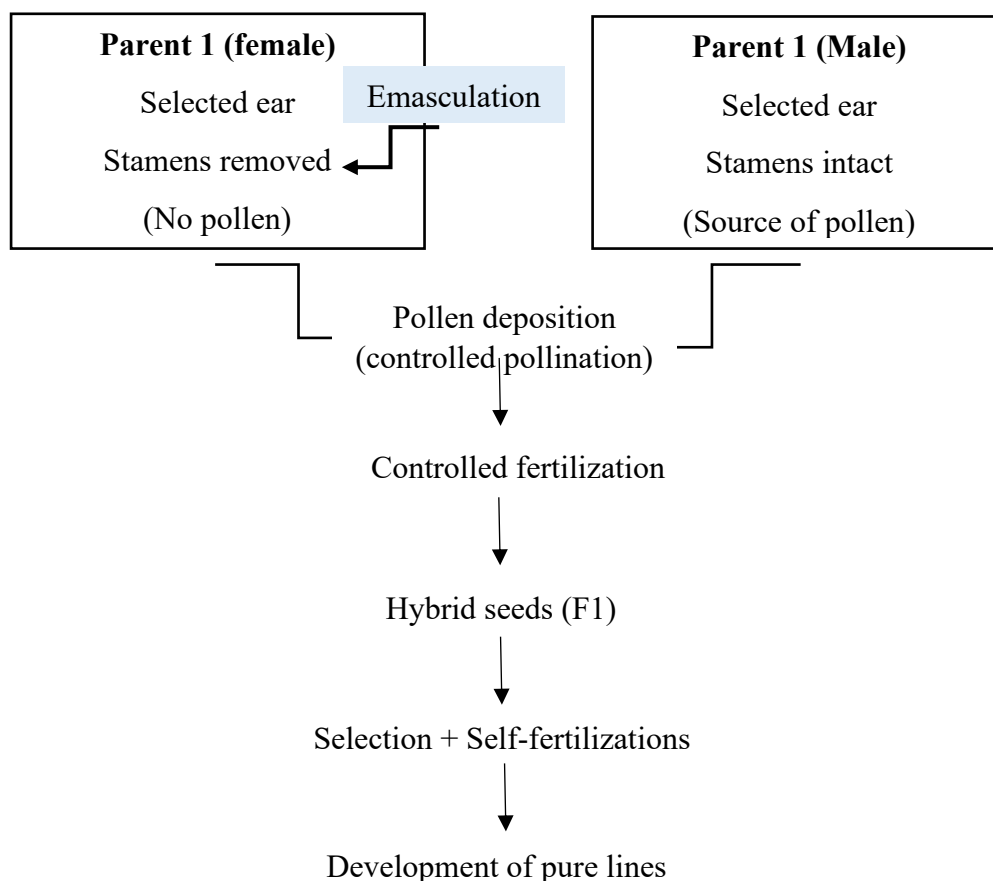


Figure 15. Breeding strategy and development of a pure wheat line.

3.3.4. Improvement of allogamous plants

3.3.4.1. Mechanisms of allogamy

Allogamous plants are generally characterized by a high level of heterozygosity, great genetic variability, and strong heterogeneity within populations. In these species, inbreeding (forced self-fertilization) results in a loss of vigor due to the expression of homozygous recessive genotypes, sometimes with harmful and unfavorable effects (inbreeding depression). This phenomenon explains why these plants are naturally adapted to cross-fertilization

✚ Cross-fertilization (allogamy) is promoted by several biological mechanisms:

- **Spatial separation of sexes**
- **Monoecy (monoecious plants)**

Male and female flowers are separate but present on the same plant: maize, melon, cucumber, etc.

- **Dioecy (dioecious plants)**

Male and female flowers are on separate plants: date palm, asparagus, etc.

- **Temporal separation of sexes**

- **Self-compatibility**

Plants can self-fertilize, but cross-fertilization is favored because the sexual organs do not mature at the same time on the same flower, and if no other pollen is available (preferential allogamy, as in sunflower).

- **Self-incompatibility**

Plants cannot self-fertilize. The female flower of a plant rejects its own pollen and favors foreign pollen (as in cabbage, etc.).

- **Morphological barrier**

In some species with bisexual (hermaphroditic) flowers, physiological or physical barriers can prevent self-fertilization, ensuring cross-fertilization (alfalfa, orchids, primrose).

3.3.4.2. Breeding strategies for allogamous plants

In an allogamous population, high genetic diversity is observed. This diversity results from a mixture of multiple genotypes resulting from continuous hybridizations between individuals within the population. This variability provides an important adaptive advantage, as it allows the population to better respond to environmental changes.

However, the breeder's goal is to exploit this variability to improve agronomic performance (yield, resistance to abiotic or biotic stresses, product quality, etc.). Thus, several approaches can be used (**Fig. 16**):

- **Creation of improved populations**

This strategy involves selecting individuals within the initial population that exhibit the most advantageous traits. After selection and multiplication, the best genotypes are recombined to obtain a new genetically improved population. This type of variety is called a **synthetic variety**. Synthetic varieties are produced by controlled intercrossing of several selected

genotypes, usually elite, and allow for maintaining a broad genetic base while improving performance.

- **Development of hybrids F1**

- **Phenotypic uniformity** in the F1 generation;
- Increased vigor, called **heterosis (or hybrid vigor)**. Heterosis manifests as a significant improvement in performance (yield, vigor, resistance, etc.) compared to the parents.

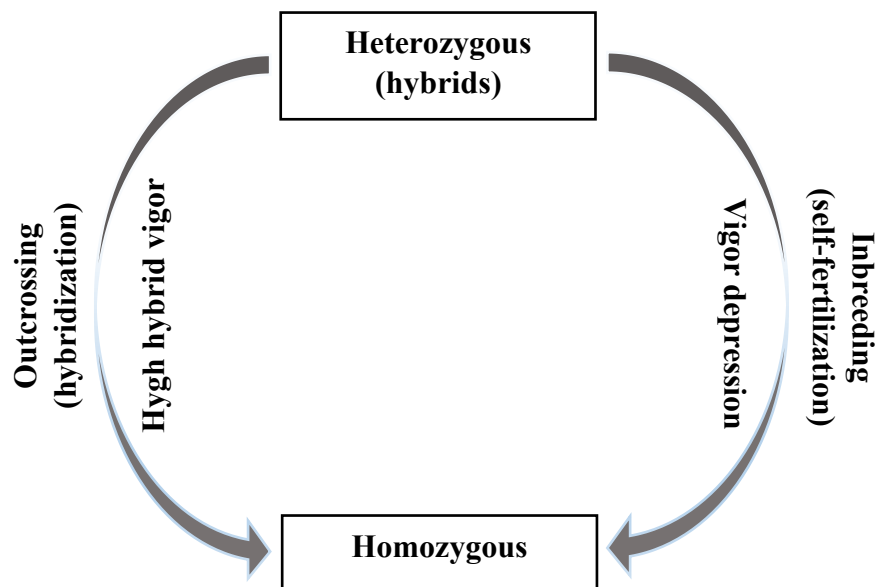


Figure 16. Breeding strategy for cross-pollinated plants.

Example of maize

The genetic improvement of maize is classically carried out from an initial population, following three successive phases (**Fig. 17**):

- **Development of pure lines (controlled self-fertilization)**

The breeder may induce self-fertilization to genetically homogenize the individuals. In maize, this practice is easy because male and female flowers are separate on the same plant:

- Female inflorescences (ears) are isolated in a bag to prevent contamination by foreign pollen;
- Pollen from the male inflorescence of the same plant is collected using a bag and then manually applied to the stigmas of the female flowers.

Over several generations of self-fertilization, individuals reproduce as pure lines that are **highly homozygous** for all genes. There is thus trait stability, as all male and female gametes are identical. The breeder selects the best pure lines to serve as future parents for hybrid production.

- **Evaluation of combining ability**

The obtained lines are crossed with each other according to different crossing schemes. Their general and **specific combining abilities** are evaluated, i.e., the capacity of a line to produce a high-performing hybrid when combined with other lines.

Multiple hybrid combinations are made, and those giving the best agronomic results (vigor, yield, resistance) are retained.

- **Production of F1 hybrid seeds**

Once the best parental combinations are identified, large-scale production of the first generation of hybrids (**F1**) is carried out.

 These seeds are marketed because they offer:

- High phenotypic uniformity
- High yield due to heterosis (hybrid vigor).

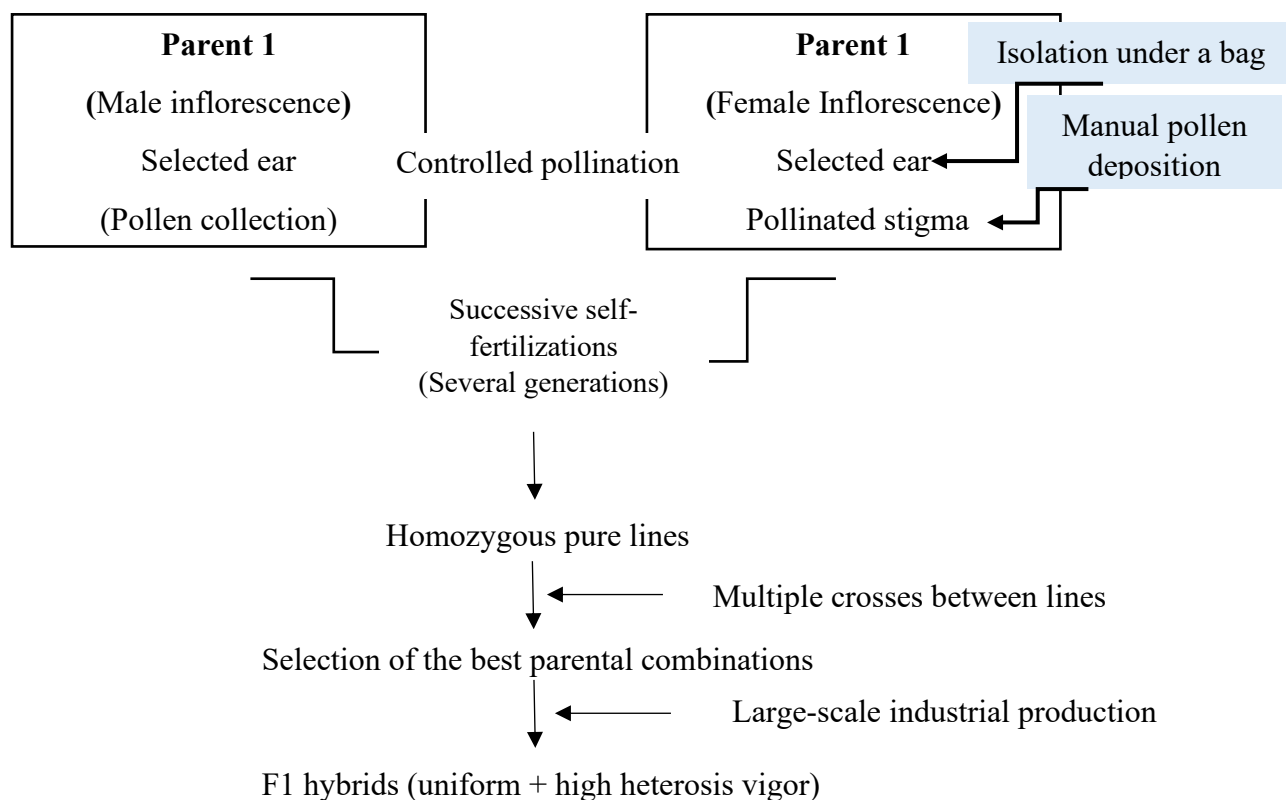


Figure 17. Maize breeding strategy.

3.4. Breeding of fruit species

Fruit species differ from annual species because they can be easily propagated vegetatively (cutting, grafting, layering, etc.) without undergoing sexual reproduction. This type of propagation allows the production of genetically identical individuals, called **clones**, which facilitates the preservation of desirable traits selected in a rare and superior genotype.

3.4.1. Properties of fruit species

3.4.1.1. Rootstock-scion association

Most cultivated fruit trees are obtained as a combination of a **rootstock** and a **scion**. The scion carries the varietal traits (cultivar), while the rootstock influences vigor, soil adaptation, stress tolerance, and more.

✚ From this situation, several implications arise for breeding:

- Selection must aim to improve both the cultivar and the rootstock;

- Rootstock/scion compatibility must be taken into account;
- Since viruses can be transmitted through grafting, sanitary selection and control are mandatory.

3.4.1.2. Long Duration of the sexual reproduction cycle

The time constraint is reflected in the long interval between two generations, which constitutes a significant handicap. It greatly slows down genetic progress because selection requires several years of observation in the orchard. This period can last 3, 4, 5 years, or even longer, depending on the length of the species' juvenile phase.

3.4.1.3. Vegetative propagation

Vegetative (clonal) propagation allows the complete transmission of the mother plant's traits to its descendent. Historically, genetic progress relied mainly on exceptional individuals found in nature and cloned, rather than on complex controlled crosses.

3.4.1.4. Space occupation

The space constraint is reflected in the fact that a fruit tree occupies a large area. Breeding programs therefore require extensive land to test, compare, and maintain several hundred or even thousands of hybrids each year. Consequently, the breeder must allocate a considerable amount of land.

3.4.1.5. Senescence (Aging)

An orchard is profitable only for a limited period. The renewal of plantings is slow and costly, which makes selection a lengthy process and requires planning over several years.

3.4.2. Objectives of breeding fruit species

Fruit species are linked both to the agronomic characteristics of the plant material and to the commercial quality of the production.

- **Agronomic aspects of the plant material**
 - Obtain vigorous plants;
 - Improve adaptation to the environment and stress (drought, cold, salinity);

- Control and optimize flowering and fruiting dates.

- **Commercial aspects of production**

- Increase fruit yield;
- Improve fruit maturity, shape, size, and visual appearance;
- Enhance organoleptic qualities (taste, aroma, sugar content, acidity, etc.).

 Thus, the objectives will differ depending on whether the focus is on improving the **cultivar (scion)** or the **rootstock**:

- **Objectives for scion (cultivar) improvement**

The scion represents the variety intended for fruit production. The objectives are:

- Reduce the juvenile period to achieve earlier entry into production;
- Increase the amount of production per tree;
- Ensure consistent production from year to year (limit alternate bearing);
- Diversify the varietal range (early/late varieties, new varieties better suited to the market);
- Improve fruit quality (shape, color, size, storage, texture, organoleptic properties);
- Introduce genetic resistance to pests, diseases, and viruses;
- Enhance tolerance and resistance to abiotic stresses (drought, cold, salinity, etc.).

- **Objectives for rootstock improvement**

The rootstock influences overall vigor, soil adaptation, and the tree's longevity. The objectives are:

- Obtain a rootstock that is easy to propagate by layering, cuttings, or produces good-quality seeds;
- Ensure the best physiological compatibility with the scion (optimal rootstock–scion affinity);
- Provide resistance to soil-borne diseases, pests, nematodes, and fungi;
- Allow good adaptation to edaphic and climatic conditions (calcareous, saline, dry, or heavy soils).

2.4.2. Methods for improving fruit species

The improvement of fruit species relies on several complementary strategies, adapted to the specific constraints of these species (long juvenile period, vegetative reproduction, large space requirements, rootstock/scion combination).

 The main strategies used are:

2.4.2.1. Study of collection

This method is based on the comparative observation of different species, varieties, cultivars, or clones (local, introduced, reference, or newly created genotypes) grouped and established in a given ecological station (experimental orchards) according to a precise statistical design allowing the study of their behavior:

- In a given ecological zone, behavior orchards of type **A** are established. In these orchards, a large number of genotypes are planted (reference genotypes, introduced genotypes, local genotypes, newly created genotypes), with approximately 10 trees per genotype following an experimental protocol. Their behavior and adaptation are evaluated over approximately 5 to 6 years.
- After these years of behavioral study, the most interesting genotypes (e.g., 15) that meet the improvement objectives are selected. The process then moves to type **B** orchards (still within the same ecological zone). In this step, the number of individuals per genotype is increased. The duration of this stage is also 5 to 6 years.
- After this period, the best among these 15 genotypes are selected and cultivated on a larger scale by farmers (0.5 ha per genotype) to verify their resistance.
- The fruits are then given to specialists for tasting and introduced into the market to obtain consumer feedback.
- Finally, after validation, the best genotypes (e.g., 3 or 4) are multiplied in nurseries and cultivated on a large scale.

The objective of this strategy is to exploit and valorize the existing diversity through repeated phenotypic selection over time and under real environmental conditions.

2.4.2.2. Controlled hybridization and selection

This method involves performing controlled crosses between compatible varieties and/or species to combine as many favorable traits as possible according to the objectives (resistance,

quality, yield, earliness, etc.). After hybridization, the most performing individuals are selected (Fig. 18).

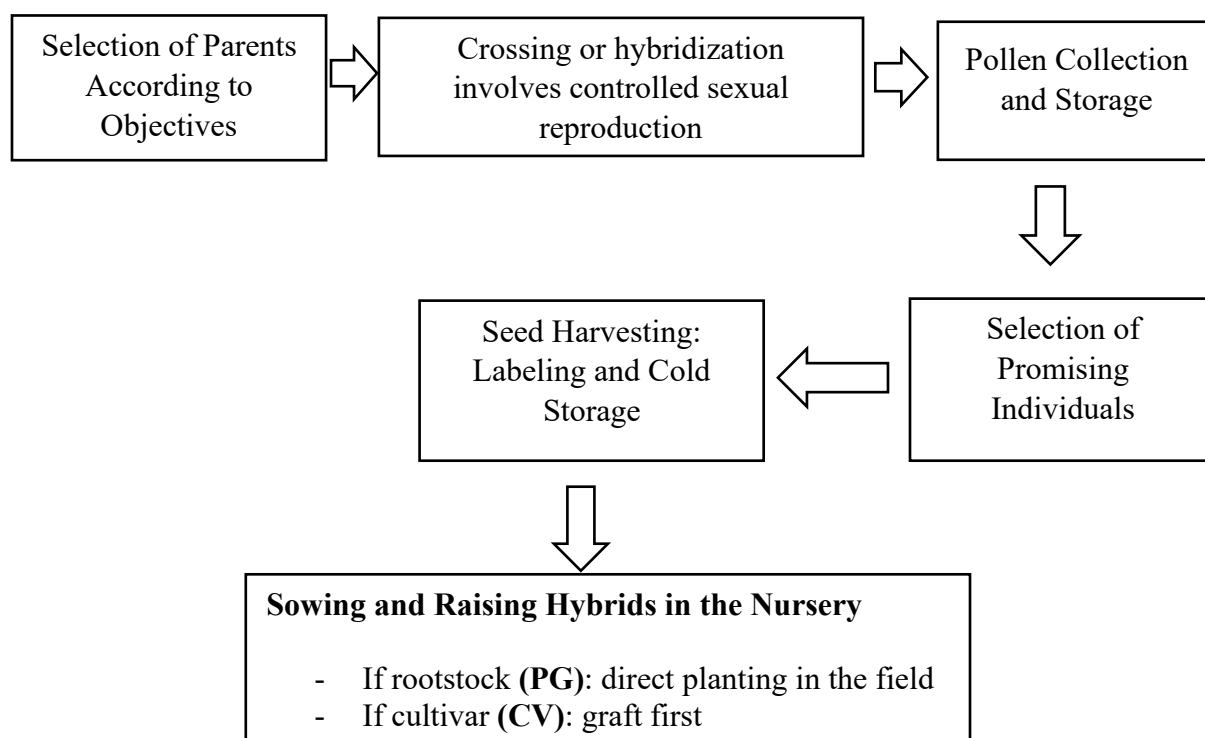


Figure 18. Improvement of fruit trees through hybridization and selection.

The objective of this strategy is to create new genetic combinations through sexual recombination and then select the best hybrids.

Example

Peach × Almond

↓
PG GF 677

Orange × Poncirus

↓
citrange

2.4.2.3. Artificial mutagenesis

Mutagenesis aims to create new genetic variations by deliberately inducing mutations through modifications of the **DNA** code using mutagenic agents (**chemical mutagens** such as colchicine or **physical mutagens** such as ionizing or UV radiation) (Fig. 19). It is applied to stems or seeds to obtain new genotypes with improved traits.

The objective of this strategy is to artificially increase genetic variability in order to generate new phenotypes, which can then be used in breeding programs.

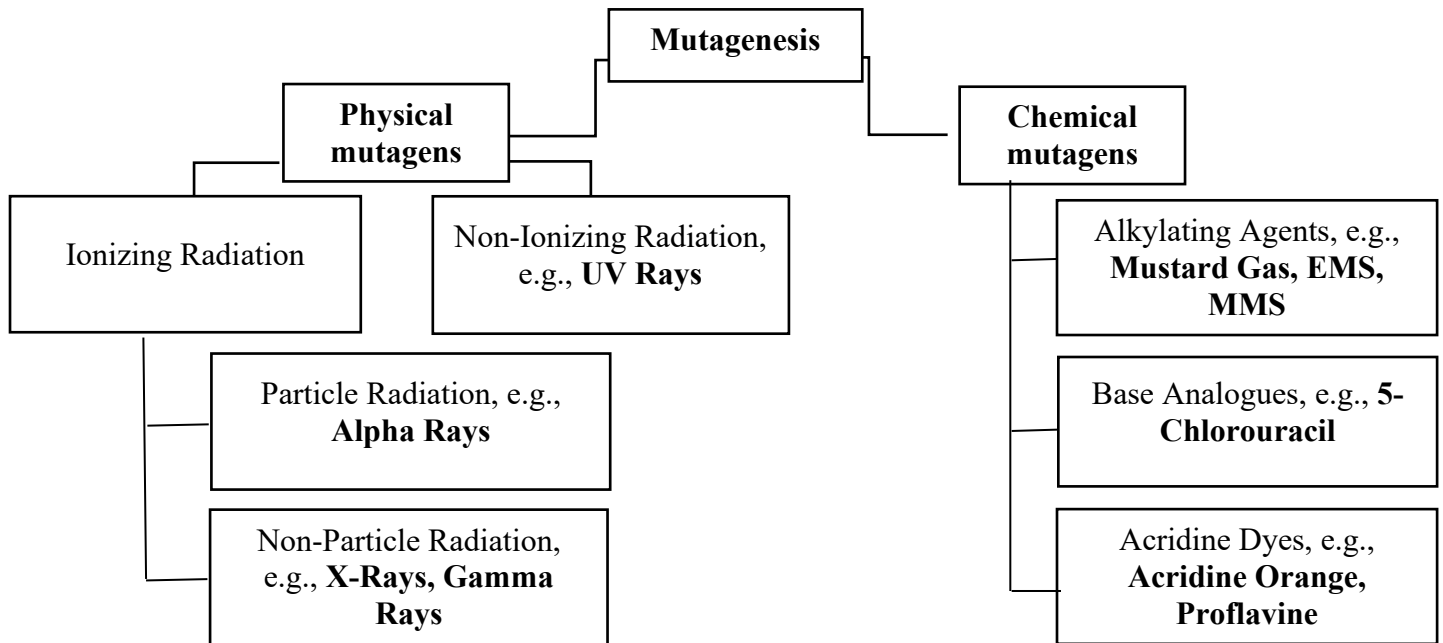


Figure 19. Common Mutagens Used for Inducing Plant Mutations.

2.4.2.4. Transgenesis

Transgenesis is a plant breeding strategy that involves introducing one or more foreign genes into a plant's genome using a genetic construct, with the aim of conferring new traits or improving existing ones. The resulting plants are called Genetically Modified Organisms (GMOs) and exhibit characteristics that could not arise naturally or through conventional breeding.

Exercise: Based on the diagram below, identify the monoecious plant.



Part III

4. Part III: Selection

4.1. Definition

Plant breeding (selection) is a set of methods used to identify, select, and propagate plants that exhibit the most favorable traits within a given population. Its ultimate goal is to obtain varieties capable of producing more, more consistently, with better quality, and with improved adaptation to biotic constraints (pests, diseases) and abiotic constraints (climate, soil).

Plant selection therefore relies on exploiting existing genetic variability, or variability intentionally created, in order to progressively improve the cultivated species.

 Selection can take two forms:

4.1.1. Conservative selection

Conservative selection is mainly applied to already established, old, or commercially released varieties. It consists of maintaining and preserving the genetic purity and original characteristics of a variety throughout many generations of multiplication.

This type of selection does not aim to create new genetic combinations but only to stabilize what already exists and prevent genetic drift, contamination through cross-pollination, or progressive degeneration.

This selection is especially important in autogamous species and in certified seed production, as it ensures that the variety remains true to its genetic identity and original description for both producers and farmer

✓ **Main methods:** mass selection and genealogic selection (pedigree).

4.1.2. Creative or improvement selection

Creative selection aims to obtain **new varieties** with improved performance through the introduction of new genetic combinations. It is an active form of selection that seeks to modify the genetic heritage by using methods that generate variability and by recombining desirable genes.

 This type of selection is mainly based on:

- **Hybridization (controlled crosses):** two parents with complementary traits are deliberately crossed with the objective of combining these traits in the same line or in the final hybrid.
- **Mutagenesis:** the voluntary use of chemical or physical mutagens to induce modifications in the DNA sequence, which may generate new exploitable phenotypes.

This type of selection is widely used in modern plant breeding programs. It offers a broader potential for innovation compared to conservative selection, because it truly creates an improvement in the genetic potential of the species.

4.2. Plant selection methods

Selection methods encompass all approaches used to select, improve, and stabilize high-performing genotypes within a population. The general principle is based on identifying, according to phenotypic or genetic criteria, the individuals that possess the desired traits, and then propagating them in order to obtain a homogeneous, stable, and productive variety. Depending on the initial material (natural population, cultivated population, hybrid line), different strategies may be applied.

 Several methods are used depending on:

- The objectives (conservation / creation);
- The type of trait (qualitative / quantitative) ;
- The mode of reproduction (autogamous / allogamous / vegetatively propagated).

 The main selection methods are:

4.2.1. Selection in heterogeneous populations

These methods are applied to an existing population that is naturally variable (local ecotype, landrace, introduced population). The best individuals are selected phenotypically or genetically within this natural variability.

4.2.1.1. Mass selection (Phenotypic selection)

Mass selection is the oldest and simplest method of plant selection. Historically, it enabled farmers to gradually domesticate wild plants, transform them into cultivated varieties, and then stabilize phenotypically homogeneous types from initially very diverse (heterogeneous) populations.

The principle consists of identifying and choosing, within an initial heterogeneous population (local varieties, traditional populations), a large number of individuals that display the best phenotypes (higher yield, vigor, earliness, drought tolerance, resistance, etc.). These superior individuals are retained and multiplied.

The seeds from these selected plants—chosen solely based on their superior phenotypes—are mixed together (in bulk) and sown collectively. The resulting descendent constitute a new population enriched with favorable genotypes compared to the original population. Selection may also consist of simply eliminating undesirable (off-type) individuals.

This method does not produce pure lines but rather a more phenotypically homogeneous population sharing several common traits. It is effective when the selected traits are highly heritable and easy to identify visually (flower color, fruit shape, etc.). However, it becomes much less efficient for traits that are strongly influenced by the environment (such as yield).

- ✓ **Advantages:** simple, low-cost, and easily applicable in the field.
- ✓ **Limitations:** selection is based solely on phenotype, so its effectiveness is low for traits with low heritability.
- ✓ **Example of application:** improving local durum wheat populations in arid regions by selecting plants with better drought tolerance.

4.2.1.2. Pedigree selection (Genealogic selection)

Pedigree selection, often called the “pure line method,” is based on the progressive isolation, within a highly variable (heterogeneous) population where desirable types exist, of a number of genetically homogeneous lines possessing the most interesting traits (higher yield potential and better adaptation to environmental conditions).

Genealogical selection is a method mainly applied to autogamous species, and it is most effective for traits that are little influenced by the environment. Its major advantage is that it provides pure lines for large-scale cultivation, which offer considerable benefits: uniform vegetation, stems of the same height, grains of identical size, and high yield.

 It generally follows a specific operational scheme:

- **The principle consists of selecting**, within an initial population (such as wheat, rice, or sorghum), a certain number of ears or individuals expressing the best agronomic traits (potential yield, grain size, vigor, disease resistance, lodging resistance, etc.).
- **The seeds from each ear of a previously selected plant are sown separately, line by line.** The lines are compared with each other (a comparative trial of elite lines); those showing the least favorable performances are eliminated, and only the best ones are retained.
- **At each generation, the retained lines are harvested separately** and used the following year to establish small, separate plots. Once again, the less desirable lines are eliminated.
- **This method allows, through successive self-fertilization and rigorous selection from generation to generation, the progressive development of pure (homozygous) lines**, characterized by uniform vegetation, plants of equal height, seeds of homogeneous size, and more stable yields.

- ✓ **Advantages:** allows the progressive genetic fixation of the best genotypes and the production of pure lines suitable for large-scale cultivation.
- ✓ **Limitations:** lengthy process (several years) and requires strict tracking of lineage.
- ✓ **Example:** varietal improvement of rice through genealogical tracking of the descendants of selected plants from an initial population.

4.2.2. Selection after hybridization

Selection after hybridization is based on the deliberate creation of new genetic variability through controlled crosses between carefully chosen parents (line $\times$ line, variety $\times$ variety, or even species $\times$ species). Hybridization makes it possible to recombine genes from both parents and to generate highly diversified descendants. From this newly created variability, selection is then applied to identify, isolate, and stabilize the most advantageous genetic combinations.

 This method is therefore based on two complementary steps:

- **Creation of diversity through crossing:** production of the F_1 generation, followed by a heterogeneous F_2 generation;
- **Progressive selection within the descendant:** fixation of superior genotypes to obtain new improved lines.

4.2.2.1. Pedigree selection or direct genealogical selection after hybridization

- This method consists of choosing two parents (genitors), each possessing desirable traits, and crossing them to create the desired genetic variability (**Fig. 20**). The resulting F_1 descendant is then sown to produce the F_2 generation. In this method, selection begins in F_2 to identify promising pure lines showing the best combinations of traits.
- Starting from F_2 , each selected plant is harvested separately, and its seeds are sown the following year in a distinct row (**F_3**). The least desirable plants are progressively eliminated, while the most promising lines are retained. This individual, ancestry-based tracking is maintained from generation to generation (**F_4 , F_5 , etc.**) until the lines become sufficiently homogeneous and genetically stable (homozygous).
- In the pedigree method, each generation requires one year. Selection can generally be stopped by F_5 or later, once clear phenotypic uniformity is observed.

This method requires rigor and precise tracking of the origin of each family (pedigree records), but it is highly effective for obtaining pure lines with a very specific combination of heritable traits.

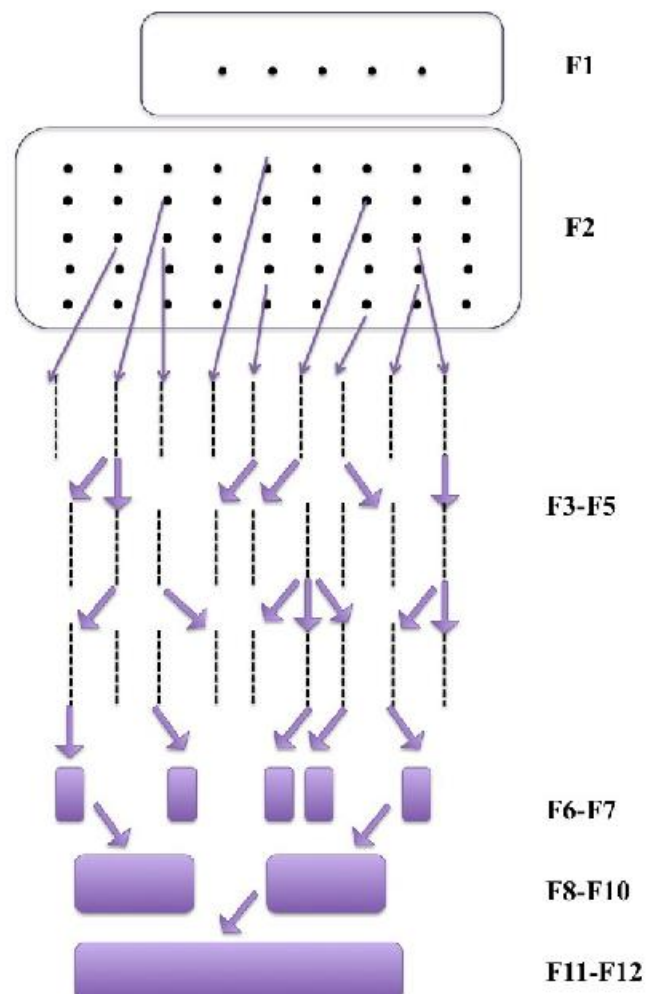


Figure 20. Direct pedigree (genealogical) selection after hybridization.

4.2.2.2. Bulk method or delayed genealogical selection after hybridization

- The Bulk method is also called "delayed genealogical selection" because, in this approach, selection occurs after the lines have stabilized (**Fig 21**). To avoid difficult choices in F₂, and to a lesser extent in F₃, the harvested seeds are mixed in bulk and sown together, without any precise pedigree-based selection at this stage. This “bulk” cultivation phase allows the plants to undergo natural competition, leading to the spontaneous elimination of the least adapted individuals (action of natural selection). This process progressively enriches the population with plants tolerant to local conditions (drought, cold, diseases, etc.).
- The principle is to wait until a certain degree of homozygosity is achieved before beginning genealogical selection to identify the best lines. By repeating self-fertilization without

selection for a total of 4 to 5 generations, generally by F_6 – F_7 , plant selection is resumed as in the pedigree method, with selected plants sown individually to produce pure lines.

- The goal is to allow successive generations to self-pollinate and genetically stabilize. After 4 to 5 generations (usually around F_6 – F_7), when the lines become sufficiently homozygous, detailed genealogical selection is then applied, as in the pedigree method. At this stage, selected plants are sown individually to produce distinct pure lines.

The Bulk method is particularly useful for traits strongly influenced by the environment, as it benefits from the natural action of stresses, diseases, and pests as biological selection agents. For example, the presence of diseases and insects helps reveal resistant plants, which are generally sought after by the breeder.

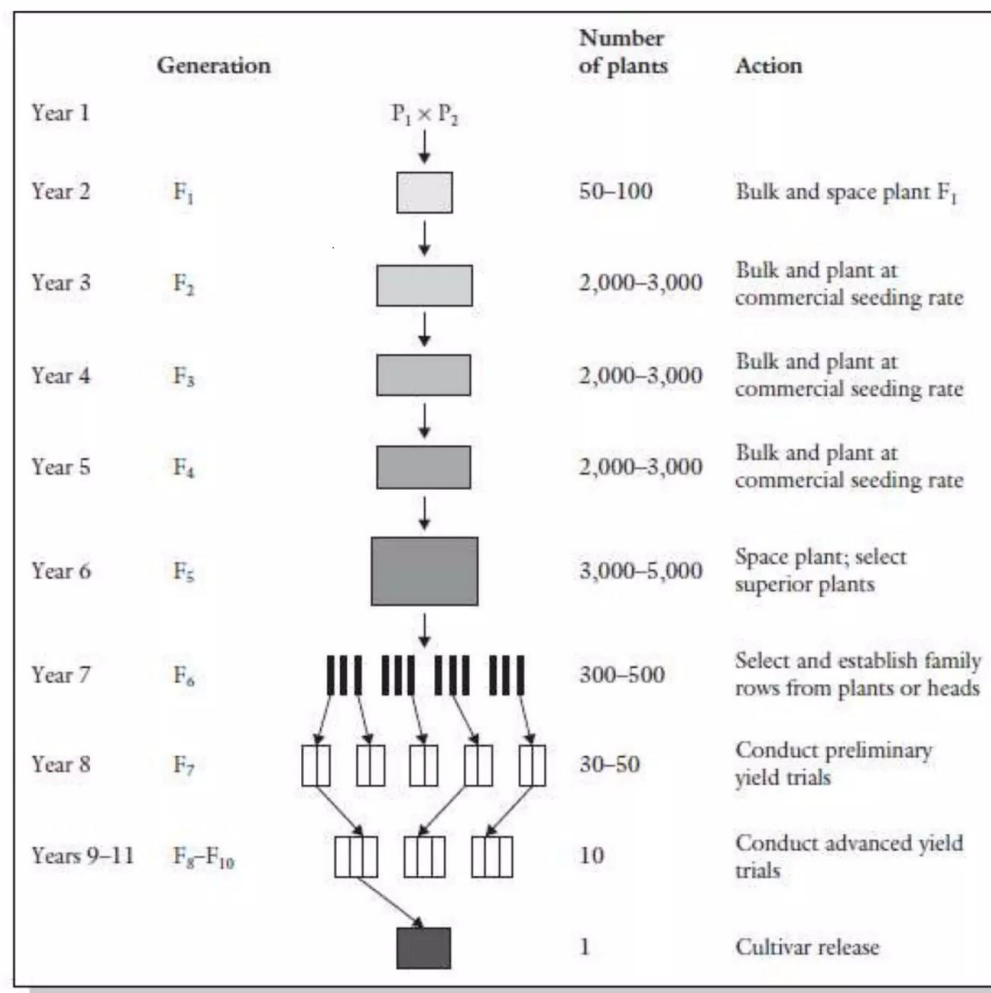


Figure 21. Bulk selection.

4.2.2.3. Selection by the SSD method (Single Seed Descent): Single-seed or single-fruit descent method

- The **SSD method**, also called "**single-seed descent**" or "**uniparental lineage**," consists of advancing generations derived from a cross by retaining only one seed (or a single fruit: ear, capsule, pod, etc.) per plant (**Fig 22**). Thus, from an F_2 plant, a single seed is harvested to form the F_3 generation; then each F_3 plant contributes one seed in turn to form F_4 , and so on.
- This process allows the representation of all genotypes present in the initial population to be maintained without imposing early selection, which is particularly useful for preserving superior genotypes, especially for traits with low heritability, such as yield.
- However, this method ignores variability within a single plant (intra-plant variance) and also requires retaining a large proportion of low-performing (undesirable) genotypes over several generations. It does not allow selection of the best genotypes among families derived from F_2 and subsequent generations. Selection begins only when the level of homozygosity is sufficiently high, resulting in so-called "fixed" genotypes (stable pure lines). The availability of highly related seed quantities allows for field trials, repeated across multiple environments.

This **SSD** selection method becomes particularly practical, efficient, and rapid when multiple generations can be produced per year, especially by using greenhouses, nurseries, or off-season cultivation to accelerate the selection cycle.

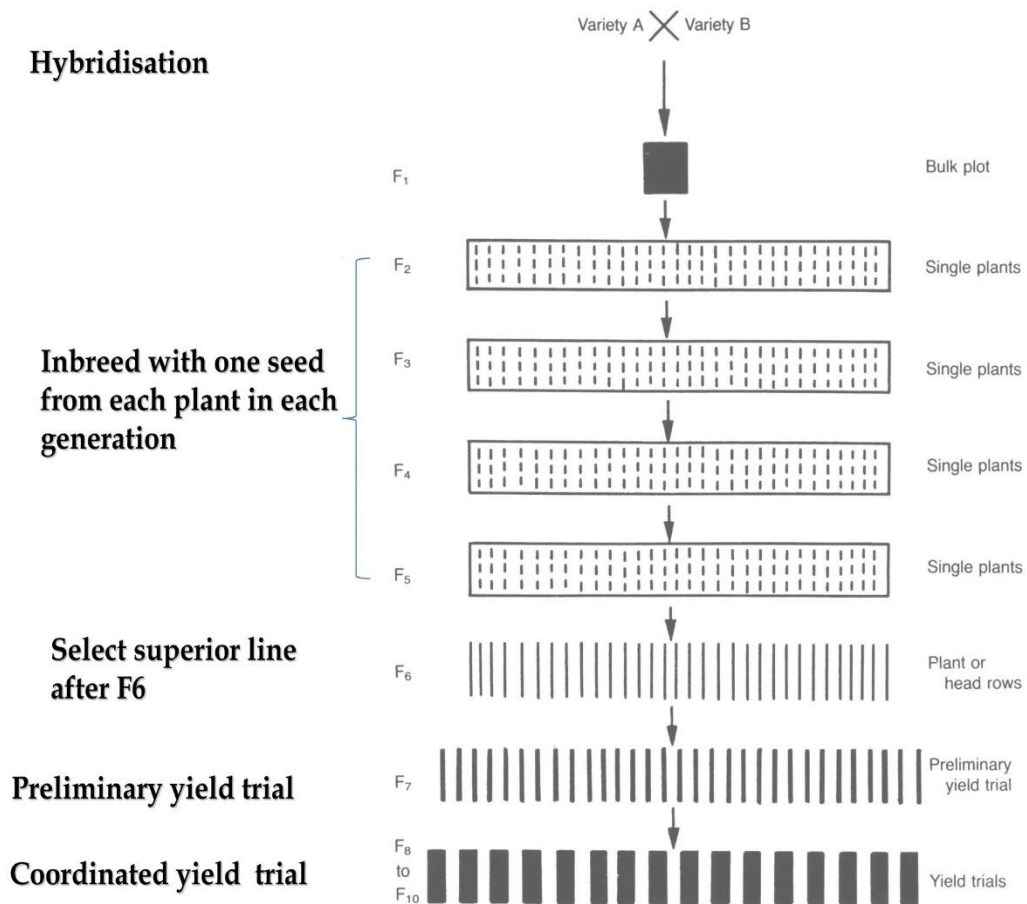


Figure 22. SSD Method (Single Seed Descent) Selection.

4.2.2.4. Backcross (Retrocross or Recurrent crossing)

Backcross, also called “**retrocross**” or “**recurrent crossing**”, is a selection method primarily used when the goal is to introduce a desirable trait (e.g., resistance to a specific disease) into an already high-performing variety (elite variety) that has a weakness (e.g., susceptibility to that disease), without altering its overall characteristics (**Fig. 23**).

 In this method, we have:

- **Recurrent parent:** an elite variety, highly productive but exhibiting a weakness (e.g., disease susceptibility).
- **Donor parent:** carries the gene of interest (e.g., a resistance gene) but usually has low agronomic performance.

 The procedure involves successive backcrosses:

1. The recurrent parent is first crossed with the donor parent to obtain F₁.

2. The F_1 is then **backcrossed** with the recurrent parent.
3. This operation is repeated for 6 to 8 generations.
4. At the end of the backcross program, the plants are self-pollinated, and genealogical selection is performed to identify the desired genotype based on the target phenotype.

During the backcrosses, the proportion of the recurrent parent's genes in the genitor increases as follows:

- 50% (first hybrid F_1);
- 75% ($= 50 + 50/2$) (first backcross F_2);
- 87.5% ($= 50 + 75/2$) (second backcross F_3);
- 93.75% (third backcross F_4);
- 96.875% (fourth backcross F_5);
- 98.43 % (fifth backcross F_6);

Meanwhile, the donor parent's genetic contribution is halved at each generation. At the end, the resulting line has a genetic constitution almost identical to that of the recurrent parent, but with the added desired trait (e.g., resistance).

The backcross method is more efficient and easier when the target trait is **dominant**, **highly heritable**, and **easily recognizable** phenotypically in the hybrid descent. It is more challenging when the desired gene is **recessive**, polygenic (**controlled by multiple genes**), or linked to undesirable genes (genetic linkage).

It is generally not necessary to test yield after the backcross method. In principle, the performance of varieties developed through backcrossing is at least equal to that of the recurrent parent. If the trait is recessive, alternating backcrossing and self-fertilization is required.

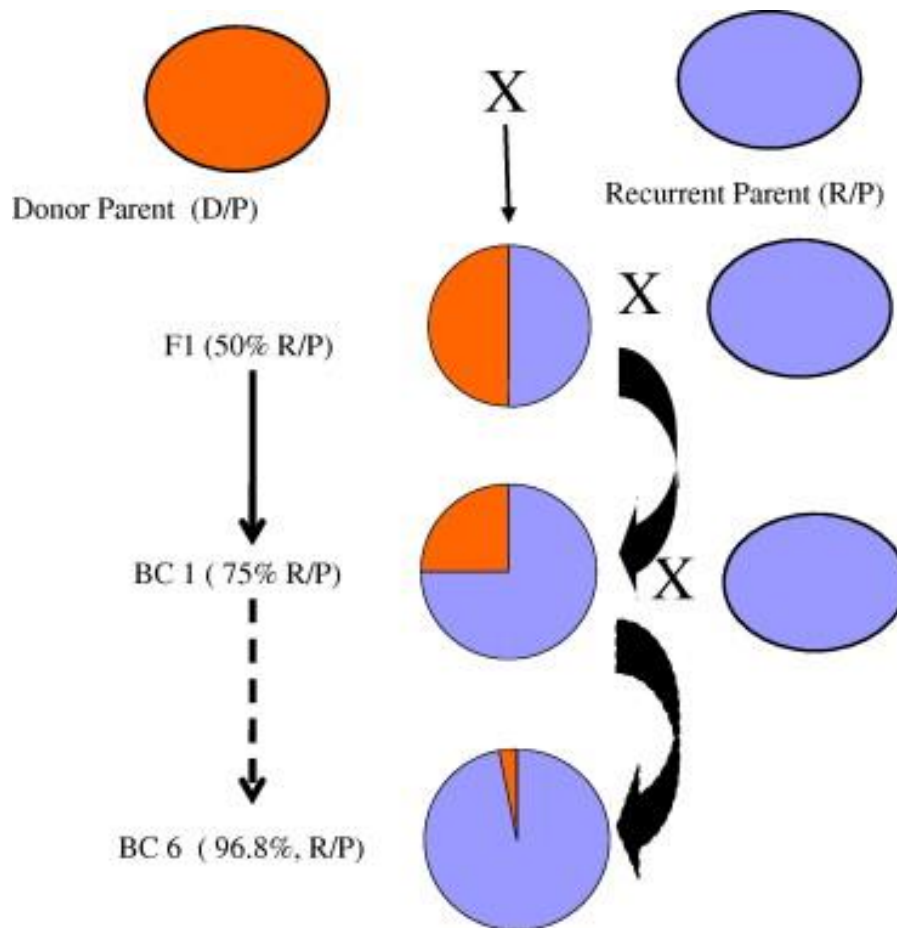


Figure 23. Backcross (retrocross).

4.2.3. Modern selection assisted by molecular genetics

Molecular tools have profoundly modernized plant breeding programs. They allow the acceleration of genetic progress by complementing classical phenotypic selection with direct genome analysis. These approaches are particularly useful for complex traits, traits with low heritability, or traits that are difficult or costly to measure in the field (e.g., resistances, tolerances, technological quality, etc.).

4.2.3.1. Marker-assisted selection (MAS)

MAS is based on the identification and use of molecular markers linked to genes of interest or chromosomal regions (QTLs) controlling the desired traits. Thus, selection can be performed not only on the phenotype but also on the associated markers in the genome. This selection method is characterized by time savings and is especially useful for complex traits with low heritability (such as disease resistance).

4.2.3.2. Genomic selection

Genomic selection relies on the use of comprehensive genetic data covering the entire genome (high-density SNPs, genomic prediction matrices). It allows the estimation of a genotype's genetic value using a statistical model constructed from reference populations. The breeder can thus predict the performance of a line even before conducting field trials. This method is widely used in major crops (maize, wheat, rapeseed) and is particularly employed in large-scale industrial breeding programs.

4.3. Selection of autogamous species

Autogamous plants rapidly achieve a high level of homozygosity for all their traits within just a few generations, as each generation reinforces the fixation of existing alleles. This explains why varietal purity is excellent in autogamous species (varieties are genetically very uniform). Additionally, artificial hybridization requires delicate operations, such as flower emasculation and controlled pollination, because self-fertilization prevents the natural introduction of external pollen.

The selection techniques chosen for autogamous species first involve genetically analyzing existing populations to identify, through selfing, the best superior pure lines that have naturally arisen. When the existing genetic variation is no longer sufficient, controlled hybridization is performed to create new genetic variability. This variability obtained through crossing then serves as the starting point for establishing and studying a new line.

 The main selection methods applied to self-pollinating species are:

- Mass selection
- Pedigree (genealogical) selection within populations
- Genealogical selection after hybridization
- Backcross methods

4.4. Selection of allogamous species

In cross-pollinating (allogamous) plants, reproduction occurs mainly through outcrossing (pollination by wind, insects, or other vectors). Individuals therefore possess heterozygous genotypes, and the descendent are genetically heterogeneous.

Selection methods for these species aim to create homogeneous varieties while exploiting hybrid vigor (heterosis) resulting from crosses between complementary genotypes.

The goal of genetic improvement in allogamous species based on identification, isolation, and creation interesting heterozygous genotypes, then reproduce and stabilize the selected material. It also relies on evaluating their combining ability.

 The main selection methods applied to allogamous species are:

- **Mass selection:** a classical method for the improvement and genetic maintenance of populations.
- **Controlled hybrids:** this begins with studying the general and specific combining ability of individuals to be crossed. When combinations are promising and satisfactory, controlled hybridizations are performed between these individuals, followed by genealogical selection within the hybrid descents.
- **Creation of synthetic varieties:** these result from open (natural) pollination of an artificial population composed of a limited number of lines selected for good agronomic performance and genetic complementarity. Synthetic varieties retain a certain level of genetic diversity, providing good adaptability to different environments.

4.5. Selection of vegetatively propagated species (Clonal selection)

Vegetatively propagated species are multiplied from non-sexual organs such as cuttings (sugarcane), tubers (potato, sweet potato), bulbs (onion), stolons (strawberry), layering, grafting (citrus), or seeds produced without fertilization (apomixis).

Vegetative propagation allows the faithful preservation of the characteristics of a selected genotype (varieties or cultivars). In this case, each plant derived from the mother plant through vegetative propagation constitutes a **clone**. Genetically, clones are homogeneous and identical, although they generally remain highly **heterozygous** (because they do not undergo sexual segregation). The main advantage of cloning is the maintenance of type conformity (with very little somatic variation).

This mode of selection is particularly suitable for allogamous species that are sensitive to inbreeding, as it allows the preservation of superior genotypes without the risk of depression caused by successive self-fertilizations.

 The main selection methods applied to clonal species include:

- **Mass or pedigree (genealogical) selection in a natural population:** This method aims to eliminate degenerated clones or those carrying unfavorable mutations that accumulate over years of cultivation. Only healthy and high-performing clones are maintained.
- **Sanitary selection:** Sanitary selection aims to obtain disease-free plant material, particularly for species sensitive to viral diseases (such as potato).
- **Selection after sexual reproduction or mutation induced by radiation:** To introduce new complementary traits not present in an initial clone, controlled crosses are performed between selected clones. The flowers of the female parent are emasculated and artificially pollinated with pollen from the male plant. The resulting hybrid seeds are sown under controlled conditions, producing seedlings that form small tubers (as in the case of potato). Once a new interesting genotype appears (good productivity, resistance, technological quality, etc.), it is fixed again through cloning (return to vegetative propagation), followed by classical selection.

Exercise: Choice of an Appropriate Selection Method

For each of the following situations, identify the most appropriate selection method and justify your choice briefly.

- A local wheat population shows high phenotypic variability for grain color and plant height. The breeder aims to improve uniformity while maintaining adaptation to local conditions.
- A breeder aims to introduce a single dominant disease-resistance gene into an elite maize variety without modifying its agronomic performance.
- A potato variety with excellent yield has become progressively degenerated due to viral infections.
- A breeder works on a quantitative trait strongly influenced by the environment and wants to avoid early selection while advancing generations rapidly.

Part IV

5. Part IV: Cytogenetic

5.1. Types of chromosomes in eukaryotes

The number of chromosomes (the chromosome set) present in the somatic cells of an individual constitutes its **karyotype**, also called the **somatic number**. This number is practically constant among all individuals belonging to the same species. The genome, noted as **X**, corresponds to the **basic chromosomal number**: it is the complete set of chromosomes transmitted by a single parent, considered as a unit. In each genome, each chromosome is represented only once.

Thus, when we refer to **2n**, we designate the total number of chromosomes present in somatic cells, regardless of the number of chromosome sets (diploid: **2x**, triploid: **3x**, tetraploid: **4x**, etc.). In other words, the expression **2n** is used universally to describe the somatic chromosome number, independently of the level of ploidy.

Chromosomal notations used in plant breeding:

- **2n**: indicates the **somatic chromosome number** (the total number of chromosomes present in the somatic cells of an individual).
- **n**: indicates the **gametic chromosome number** (the number of chromosomes present in gametes, resulting from meiosis).
- **x**: indicates the **basic chromosome number**, also called the basic genome. It corresponds to the complete set of chromosomes transmitted by one parent, where each chromosome is represented only once.

However, there are exceptions to the constancy of chromosome number. Some species may include individuals with variable chromosome numbers, and sometimes even cells within the same individual may differ in their chromosome number.

Some species are represented by several **cytotypes**, having different levels of ploidy.

- Chromosomal variation may affect a limited number of chromosomes: when there are one or a few chromosomes added or missing, this is referred to as **aneuploidy** ($2n \pm 1$, $2n \pm 2$, ...). When the variation concerns the entire sets of chromosomes, this is referred to as **euploidy**.

- In many higher plants, certain tissues or cells may contain more than two sets of chromosomes (3, 4 or more). These organisms are called **polyploids** (triploids, tetraploids, pentaploids, hexaploids, etc.). Nearly one third of angiosperms (flowering plants) are polyploid.
- Polyploids whose chromosome sets are derived from the **same species** are called **autopolyploids**. However, when they originate from **interspecific hybrids** and combine chromosome sets from different species, they are called **allopolyploids**.

5.2. Euploidy in eukaryotes

Euploidy corresponds to a change in the number of chromosomes that affects a whole number of complete chromosome sets. In other words, it is a variation involving the entire chromosome complement, rather than just a few isolated chromosomes.

Thus, haploidy (x), diploidy ($2x$), as well as the different levels of polyploidy ($3x$, $4x$, $5x$, etc.) are all considered forms of euploidy (**Tab. 3**).

It is important to note that the expression **$2n$** is used universally to indicate the total somatic chromosome number, regardless of the level of ploidy (diploid $2x$, triploid $3x$, tetraploid $4x$, etc.). Therefore, the symbol $2n$ does not directly indicate the number of genomes, but simply the chromosome number of somatic cells.

Table 3. Different categories of euploidy.

Organism	monoploid	diploid	triploid	tetraploid	pentaploid	hexaploid
n. ploidy	$2n = x$	$2n = 2x$	$2n = 3x$	$2n = 4x$	$2n = 5x$	$2n = 6x$

Example:

- Common wheat (*Triticum aestivum*): basic chromosome number $x = 7 \rightarrow$ hexaploid ($6x$) $\rightarrow$ somatic number $2n = 42$ chromosomes.
- Durum wheat (*Triticum durum*): basic chromosome number $x = 7 \rightarrow$ tetraploid ($4x$) $\rightarrow$ somatic number $2n = 28$ chromosomes.

5.2.1. Monoploidy

This does not correspond to the normal haploid phase of the life cycle, during which the chromosome number is reduced from $2n$ to n .

Some lower organisms, such as fungi, possess only one set of chromosomes (n) in their nucleus. In higher organisms, monoploid individuals are usually smaller and less vigorous than normal diploids.

Known monoploid plants are generally sterile. In plants, monoploidy can be exploited in horticulture to obtain sterile seedlings.

Monoploidy is also observed in some insects (bees, wasps, ants), where males develop from unfertilized eggs and subsequently produce gametes.

5.2.2. Haploidy

Haploidy corresponds to the state of an organism whose cells, normally diploid, possess only a single genome ($n = x$). The developmental cycle of these organisms can occur in three ways: a single haploid phase (haplophase cycle), a single diploid phase (diplophase cycle), or an alternation of diploid and haploid phases (diplo-haplophase cycle).

5.2.3. Diploidy

Diploids result from the union of two haploid gametes (n) and correspond to individuals or species whose somatic set is diploid, that is, composed of two haploid sets. The majority of higher organisms are diploid and thus possess two sets of homologous chromosomes.

5.2.4. Triploidy

Triploids are formed by the union of a haploid gamete (n) from a diploid individual with a diploid gamete ($2n$) from a tetraploid parent. Triploidy is common in angiosperms: one of the haploid nuclei of the pollen grain fuses with a diploid nucleus of the ovule.

5.2.5. Tetraploidy

A diploid somatic cell ($2n$) can undergo chromosome doubling, giving rise to a tetraploid cell ($4n$). This phenomenon can occur spontaneously or be induced artificially. A tetraploid can also form through the union of two diploid gametes.

For example, if a diploid cell undergoes defective meiosis and produces diploid gametes, the selfing of these gametes will result in a tetraploid zygote.

5.2.6. Polyploidy

The term polyploid refers to any individual whose number of chromosome sets is greater than two. Some triploids and tetraploids exhibit a more vigorous phenotype than diploids, often with larger organs (grains, stems, leaves), which is exploited in agriculture to improve crop productivity and quality.

Examples in wheat:

- **Einkorn wheat (*Triticum monococcum*, diploid, $2n = 2x = 14$):** ancient cultivated wheat, low yield but tolerant to harsh conditions.
- **Emmer wheat (*Triticum dicoccum*, tetraploid, $2n = 4x = 28$):** ancient durum wheat, used for rustic bread-making and for its disease resistance.
- **Common wheat (*Triticum aestivum*, hexaploid, $2n = 6x = 42$):** derived from successive hybridizations between diploid and tetraploid species, cultivated for its high grain production.

These different ploidy levels illustrate how domestication and interspecific crosses have contributed to increased genetic variability and productivity of cultivated species.

✚ Thus, two main types of polyploidies are distinguished: **autopolyploidy** and **allopolyploidy** (Fig. 24):

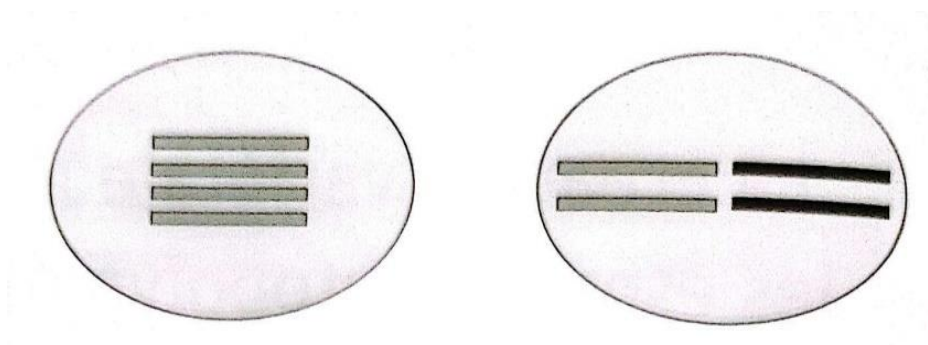


Figure 24. Autotetraploidy (left) and Allotetraploidy (right).

5.2.6.1. Auto polyploidy

Autopolyploids are obtained by multiplication of the chromosome set of a single species, that is, by doubling its basic haploid set. According to the number of copies of the basic genome:

- **Autotriploids:** 3 copies
- **Autotetraploids:** 4 copies
- **Autopentaploids:** 5 copies
- **Autohexaploids:** 6 copies

Autopolyploids can be produced spontaneously (chromosome nondisjunction during meiosis) or artificially (by colchicine treatment, or by crossing diploids and tetraploids).

- **Mechanism of autopolyploidy**

Autopolyploids can form naturally or artificially through different cytological mechanisms (**Fig. 25**):

1. **Abnormal meiotic divisions:** formation of diploid gametes; after fertilization, a tetraploid zygote can be formed.
2. **Abnormal mitotic divisions:** after chromosome duplication, a tetraploid restitution nucleus is formed, giving rise to tetraploid cells and potentially a tetraploid branch.
3. **Post-fertilization mitotic divisions:** direct creation of a tetraploid organism.

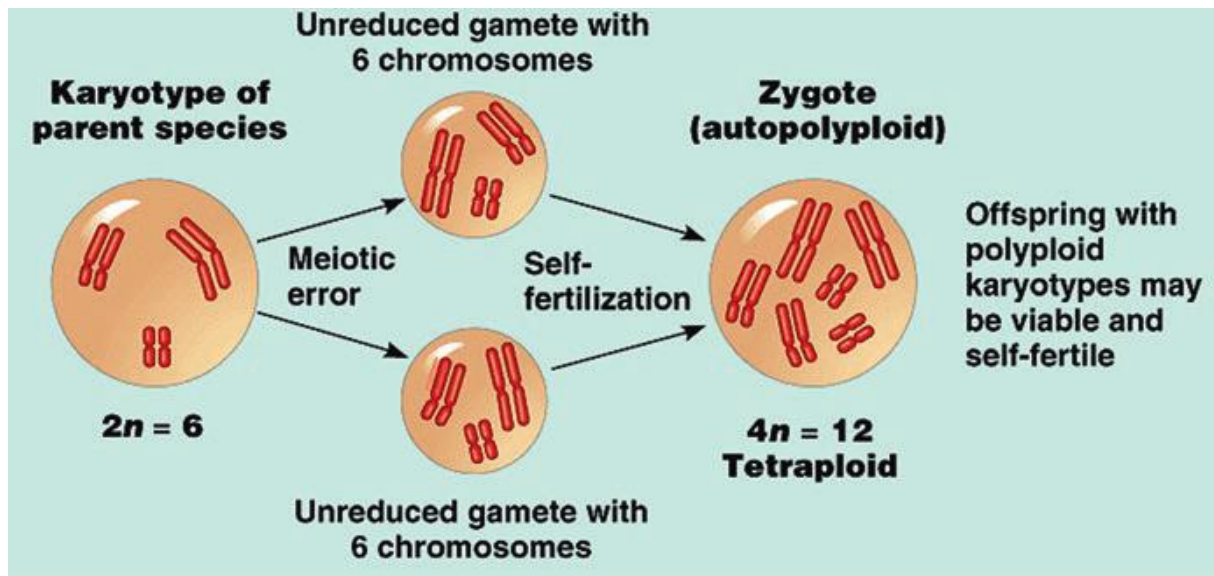


Figure 25. Mechanism of autopolyploidy.

Example:

In autotetraploids, each cell contains four copies of the same genome. For a locus with two alleles (A and a), there are more possible genotypic combinations than in diploids. While diploids only have three genotypes (AA, Aa and aa), autotetraploids can exhibit five different genotypes depending on the number of copies of the dominant allele A. These genotypes are:

- **AAAA (quadruplex)**
- **AAAa (triplex)**
- **AAaa (duplex)**
- **Aaaa (simplex)**
- **aaaa (nulliplex)**

This diversity is due to the higher number of chromosomes present in the nucleus, which increases the possible allele combinations. This increased allelic dosage has agronomic importance because it allows greater variability and modulation of trait expression. Breeders can therefore exploit more levels of expression of a single gene in autopolyploids compared to diploids.

• **Advantages of autopolyploids**

- Increased production of plant biomass (leaves, stems).
- Larger and more vigorous vegetative organs.

- Better digestibility and palatability in forage crops (higher sugar content, lower fiber content).
- Improvement of certain qualitative traits, such as root shape in sugar beet.

- **Disadvantages of autopolyploidy**

- **Reduced fertility:** pollen grains and embryos are often poorly developed.
- Some autopolyploids may be **less vigorous** than their diploid parents, especially when the basic chromosome number is already high.

Examples of autopolyploids

- Sweet potato: $2n = 6x = 90$ chromosomes (Hexaploid) (**Fig. 26**).



Figure 26. Autohexaploidy of sweet potato.

- Maize: $2n = 4x = 20$ chromosomes (tetraploid) (**Fig. 27**).

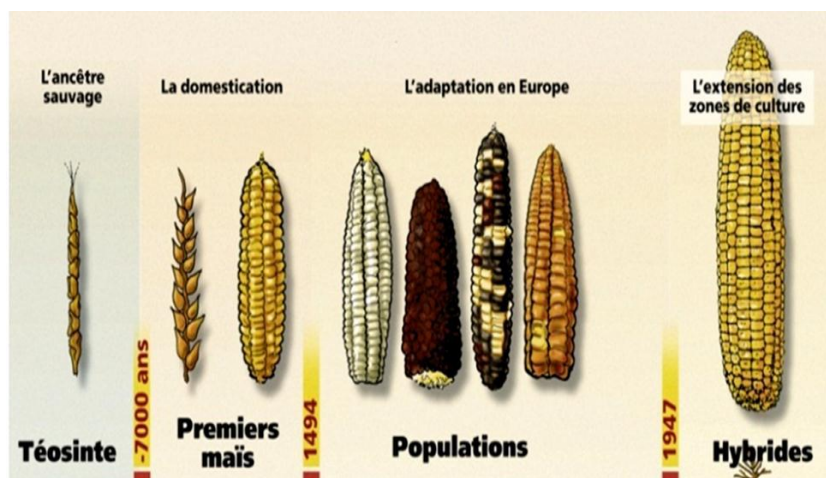


Figure 27. Autotetraploidy in maize.

- Banana: $2n = 3x = 33$ chromosomes (triploid) (**Fig. 28**).

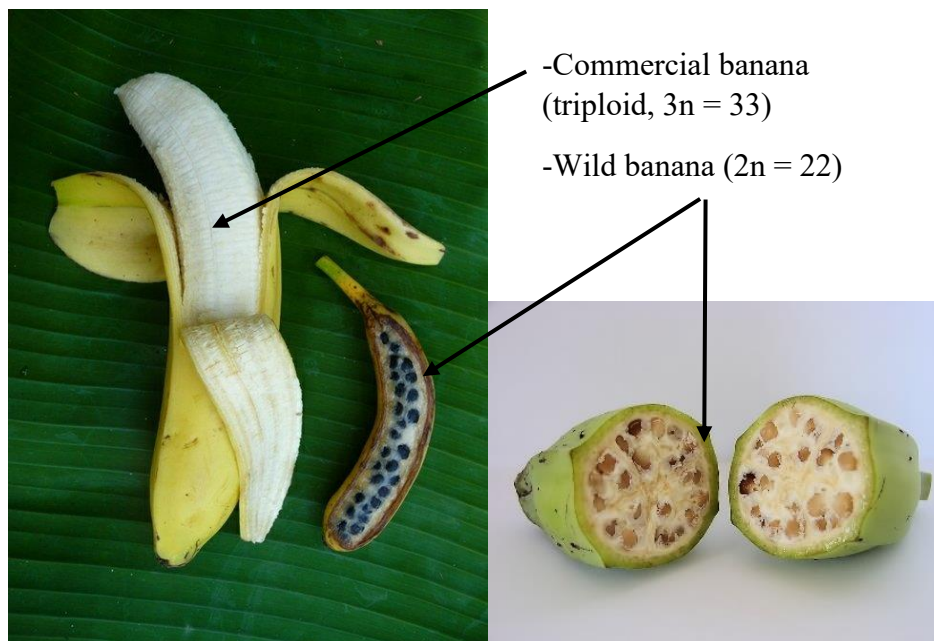


Figure 28. Autotetrapolyploidy in banana.

- Strawberry: $2n = 8x = 56$ chromosomes (triploid) (**Fig. 29**).



Figure 29. Auto-octopolyploidy in strawberry.

5.2.6.2. Allo polyploidy

Allopolyploids result from interspecific hybridization (combination of two different genomes), followed by chromosome doubling. They therefore contain chromosome sets

originating from two or more different species. They possess non-homologous diploid genomes (Fig. 30).

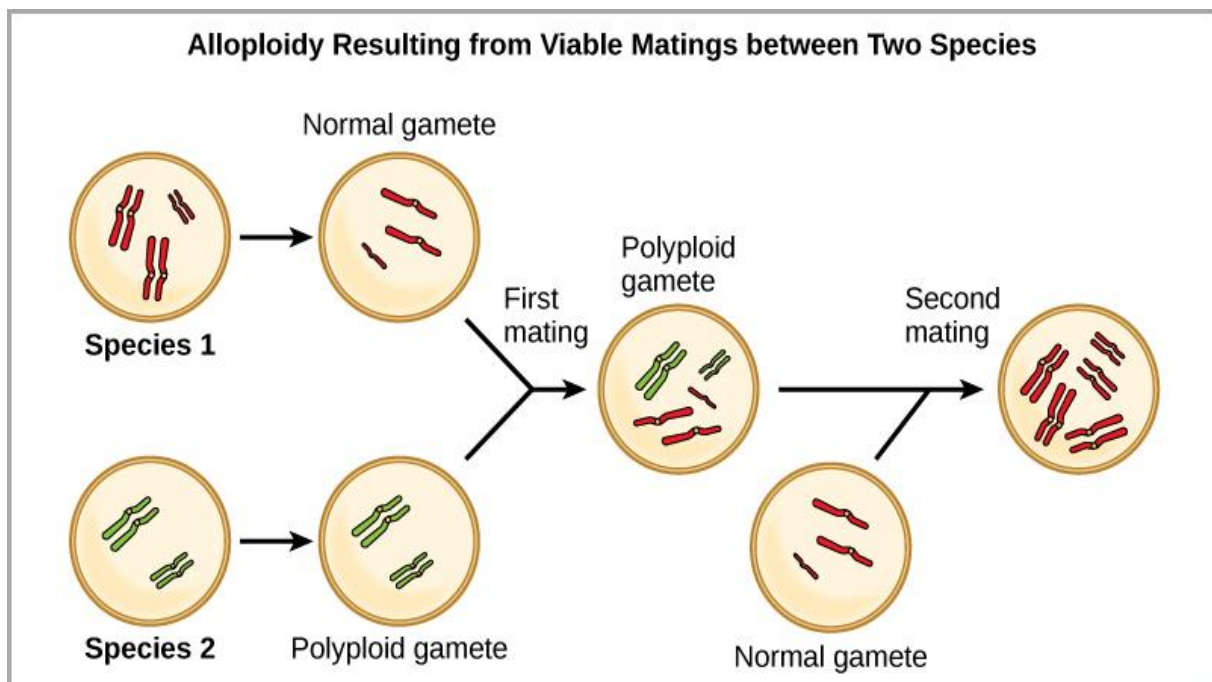


Figure 30. Mechanism of allopolyploidy.

Examples of allopolyploids

1. **Tobacco (*Nicotiana tabacum*, $2n = 4x = 48$):** a spontaneous hybrid originating from hybridization between two species *Nicotiana sylvestris* and *Nicotiana tomentosiformis* ($2n = 24$), followed by chromosome doubling (**Fig. 31**).

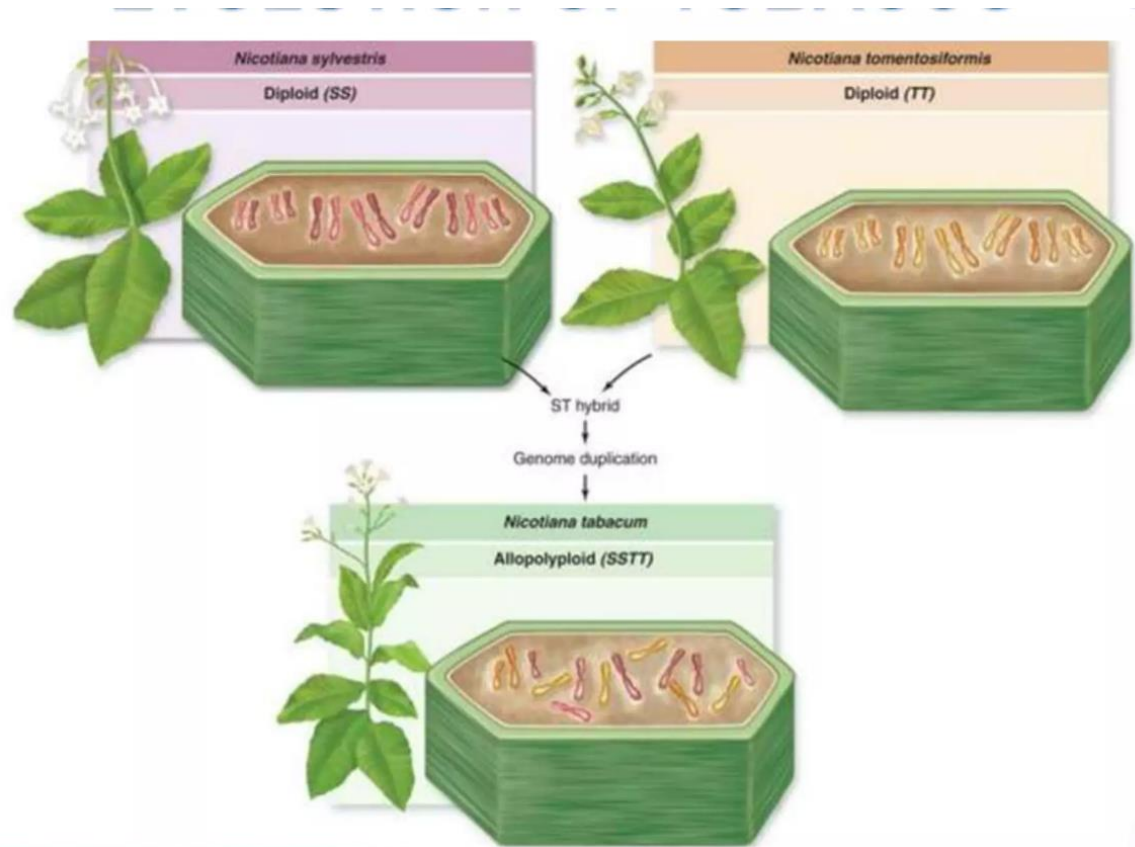


Figure 31. Allopoloidy in tobacco.

2. **Bread wheat:** The different wheat species were generated through successive polyploidization events following interspecific hybridizations between three ancestral diploid species. **The first polyploidization**, involving *Triticum monococcum* and *Aegilops speltoides*, occurred about 500,000 years ago and led to the appearance of the tetraploid durum wheat: *Triticum turgidum subsp. dicoccum* (or pasta wheat) ($2n = 4x = 28$). **The second polyploidization** occurred during domestication, around 9,000–12,000 years ago, between cultivated tetraploid wheat and another diploid species *Aegilops tauschii* (Syn: *Aegilops squarrosa*), resulting in *Triticum aestivum* ($2n = 6x = 42$), the modern bread wheat. It is hexaploid, meaning it contains six sets of chromosomes (**Fig. 32**).

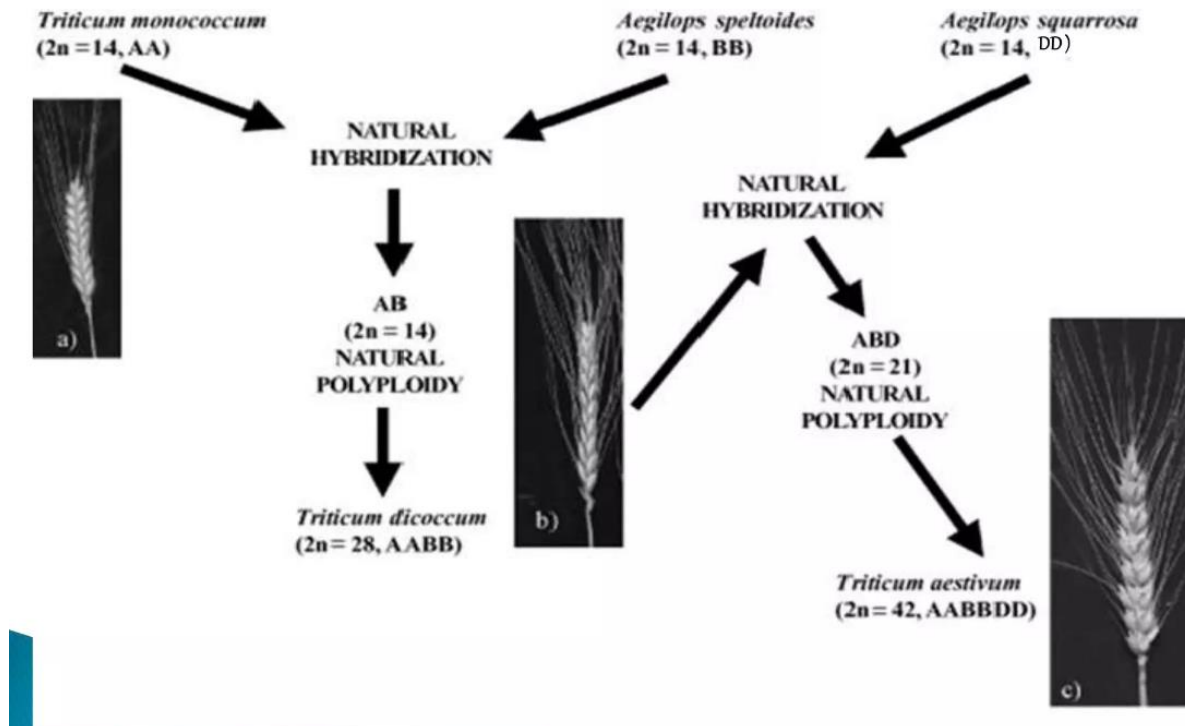


Figure 32. The Evolution of allohexaploidy in wheat.

5.3. Pseudopolyploidy

Pseudo-polyploidy is the phenomenon of genome multiplication without a corresponding increase in DNA content.

The mechanism of pseudo-polyploid formation involves transverse and general fragmentation of chromosomes, especially those with multiple centromeres, leading to apparent polyploidization. Pseudo-polyploid species have a greater number of chromosomes, but they are smaller than those of the original species.

Example: In the genus *Luzula*, the octoploid species *L. sudetica* ($2n = 48$) originates from pseudo-polyploidy. *L. campestris* ($2n = 12$) has larger chromosomes than *L. sudetica*.

5.4. Natural and artificial diploidization of polyploids

Diploidization is the process by which a polyploid organism (which possesses more than two sets of chromosomes) gradually acquires a genetic behavior similar to that of a diploid. In other words, although multiple homologous chromosome copies are present initially, the polyploid eventually organizes its chromosomes into homologous pairs like in diploid

organisms during meiosis. Therefore, diploidization allows polyploid organisms to become evolutionarily stable, fertile, and valuable for plant breeding. This phenomenon explains why many cultivated polyploid species (e.g. wheat, cotton, rapeseed) are now genetically stable and behave functionally like diploids, despite having originated from multiple ancestral genomes.

5.4.1. Natural diploidization

Natural diploidization can occur spontaneously in some polyploid species through several natural mechanisms, such as:

- **Chromosomal rearrangements:** deletions, duplications or translocations may reorganize chromosomes, leading to diploid-like pairing during meiosis.
- **Formation of bivalents:** in certain polyploids, homologous chromosomes preferentially pair as bivalents rather than forming multivalents, which facilitates balanced chromosome segregation.
- **Natural selection:** polyploid individuals that exhibit a stable diploid-like meiotic behavior have a higher likelihood of survival and reproduction, which promotes diploidization over successive generations.

5.4.2. Artificial diploidization

In laboratory conditions, diploidization can be induced in order to stabilize artificially created polyploids or to improve certain agronomic traits:

- **Chemical treatment:** the use of substances such as colchicine blocks the formation of the mitotic spindle, causing chromosome doubling. This can subsequently be followed by diploidization, which restores proper chromosome pairing.
- **Selection and self-fertilization:** in experimental polyploids, selecting plants that show a stable diploid-like behavior and selfing them over several generations allows diploidization to be fixed.

5.5. Aneuploidy and its role in evolution

Aneuploidy consists of the loss or gain of one or more chromosomes or chromosome fragments ($2n \pm 1$, $2n \pm 2$, etc.). Thus, an aneuploid plant is an organism that may carry a chromosome number higher or lower than that of the wild-type (diploid). Individuals that have

lost chromosomes are **hypo-aneuploids**, while those with additional chromosomes are **hyper-aneuploids**.

Several meiotic abnormalities can lead to aneuploidy, with **non-disjunction of chromosomes and/or chromatids during meiosis** being the main source (Fig. 33).

Aneuploidy is poorly tolerated in animals. In humans, it is often associated with developmental delays, such as trisomy 21, and certain cancers. Plants appear to be more tolerant to aneuploidy. Aneuploid individuals can arise spontaneously within diploid populations.

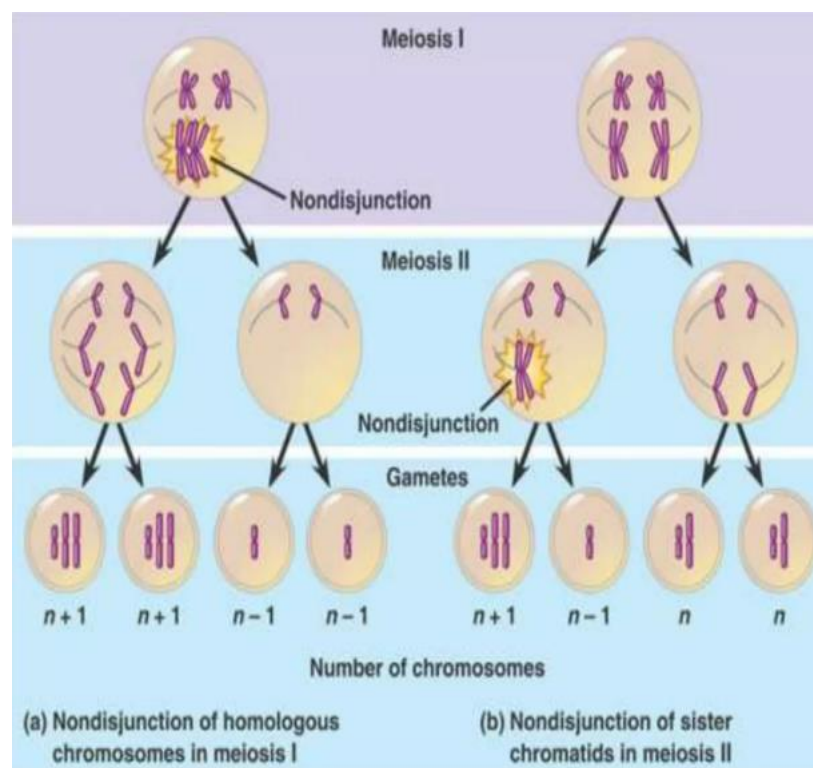


Figure 33. Mechanism of Aneuploidy.

5.5.1. Classification and historical discovery of aneuploidy

Aneuploid individuals can be classified according to the type of chromosomes affected: **autosomes** or **sex chromosomes (heterosomes)**.

 There are :

- **Autosomal aneuploidy:** one or more autosomes are present in excess or are missing compared to the normal diploid type.
- **Sex chromosome aneuploidy:** the number of sex chromosomes (X, Y, etc.) is affected, e.g., normal XX or XY; aneuploids include XO, XXX, XYY, XXXX, etc.

 The main types of aneuploidy are:

- **Monosomy:** absence of a single chromosome ($2n - 1$, called monosomic);
- **Nullisomy:** absence of a pair of homologous chromosomes ($2n - 2$, called nullisomic);
- **Trisomy:** one additional chromosome ($2n + 1$, called trisomic);
- **Tetrasomy:** one additional pair of homologous chromosomes ($2n + 2$).

For an organism with $2n = 2x = 6$, with three chromosome pairs AABBCC, the main types of **hypoploid aneuploids** are:

- **Monosomic ($2n - 1$)**

- AABBC
- AABCC
- ABCC

- **Nullisomic ($2n - 2$)**

- AABB
- AACC
- BBCC

- **Double monosomic ($2n - 1 - 1$)**

- AABC
- ABBC
- ABCC

Hyperploid aneuploids include:

- **Trisomic ($2n + 1$)**

- AABBBCC

- AABBBCC
- AAABBCC

- Tetrasomic ($2n + 2$)

- AABBBCCC
- AABBBBCC
- AAAABBCC

Example:

The presence of aneuploids has been reported in the progeny of **natural or artificial polyploids**. In a study of a **tetraploid rye** population, among 808 plants, only 77.25% were **eutetraploids** with $2n = 4x = 28$, while all others were **aneuploids** with $2n = 25, 26, 27, 29, 30, 31$, etc. The same situation has been observed in other cultivated species, including *Hordeum vulgare*, *Zea mays*, *Beta vulgaris*, and *Trifolium pratense*.

Exercise: Chromosomal Notation and Ploidy Level ($2n$, n , x)

For each of the following species, determine:

- a) the basic chromosome number (x),
- b) the ploidy level,
- c) the somatic chromosome number ($2n$).

A plant species has $x = 9$ and is tetraploid.

A crop plant has $2n = 30$ and $x = 5$.

Bread wheat (*Triticum aestivum*) has $x = 7$.

Part V

6. Part V: Quantitative genetics

Quantitative genetics is the branch of genetics that studies traits that can be measured, whether they show continuous or discontinuous variation, and that result from several genetic or non-genetic factors. Quantitative genetics is an extension of **Mendelian genetics**, still **based on Mendel's laws**. It relies on principles from **population genetics** and **statistics**.

This chapter introduces the fundamental concepts and tools of quantitative genetics by integrating **basic statistical principles** with **genetic interpretations**, in order to provide the theoretical framework required for plant breeding applications.

6.1. Review of some concepts of descriptive statistics

The **phenotypic variability** of a quantitative trait can arise not only from the effect of genes, but also from the environmental component, which contributes to this phenotypic variation. This can be assessed using **mathematical tools**, and more specifically **statistical methods**.

6.1.1. The normal distribution

The study of a quantitative trait in a large population generally shows that very few individuals exhibit extreme phenotypes. In contrast, as we approach the mean value of the population, a greater number of individuals is observed.

This type of symmetrical distribution has a characteristic bell-shaped form (Gaussian curve) and is referred to as the **normal distribution (Fig. 34)**.

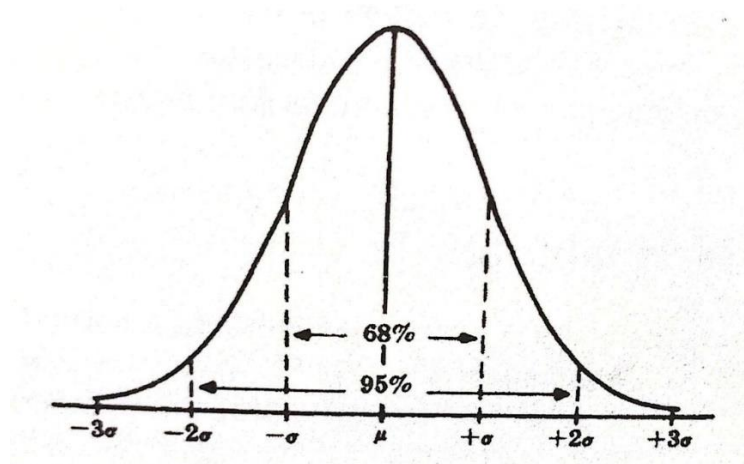


Figure 34. Shape of the normal distribution: Bell curve.

6.1.2. Measurement of the mean

The mean of the phenotypic values of a trait following a normal distribution is given by the arithmetic mean ($\bar{X}$). The mean value of a population is the sum of the values of all individuals divided by the total number of individuals (N).

$$\bar{X} = \sum X_i / N$$

where X_i is the value of individual i in the population, and N is the total number of individuals.

6.1.3. Measurement of variability

In genetics, the most commonly used measure of variability within a population is the **standard deviation**, denoted σ for an entire population. This measure indicates how far individual values deviate from the mean.

Let us consider three normal distributions (**Fig. 35**).

- Distributions **A** and **C** have the same mean, but **C** is more spread out than **A**.
- Distributions **A** and **B** have different means but the same level of dispersion.

Therefore, to properly describe a normal distribution, one must know **its mean** as well as **its dispersion**.

 The standard deviation is represented by:

- σ when referring to the entire population;
- S when referring to a sample taken from that population.

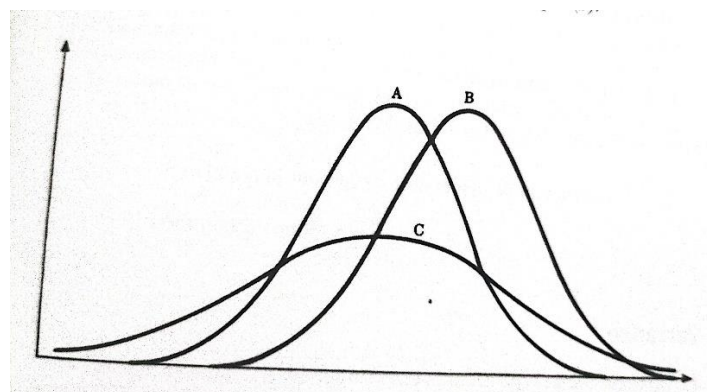


Figure 35. Measurement of variability.

The formulas are:

$$S = \sqrt{(\sum X_i - X)^2 / (n-1)}$$

$$\sigma = \sqrt{(\sum X_i - \mu)^2 / N}$$

Where:

- **n**: sample size;
- **N**: population size.

6.1.4. Coefficient of dispersion or variation

It makes it possible to compare the **relative variability** of different traits.

- **CV**= σ/μ (for a population);
- **CV**= S/ X (for a sample).

Where:

- **CV**: coefficient of variation
- σ : population standard deviation
- μ : population mean
- **S**: sample standard deviation
- $\bar{X}$: sample mean

6.1.5. Variance

The variance of a population (σ^2 or S^2) is the square of the **standard deviation**. For a given trait in a population, the total phenotypic variance (σ_p^2) can be statistically decomposed into a genetic variance (σ_G^2), a non-genetic (environmental) variance (σ_E^2), and a variance due to genotype-by-environment interactions (σ_{GE}^2). Thus:

$$\sigma_p^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2$$

6.2. Heritability of a trait

Heritability is a fundamental concept in quantitative genetics. It is defined as a fraction or proportion used to measure the phenotypic variability of a trait: the ratio between the genetic variation and the total variation (including both environmental and genetic variations).

6.2.1. Relationship and heritability

Heritability expresses the degree of resemblance between ancestors (parents) and descendants for a quantitative trait. It indicates the proportion of phenotypic variability that can be attributed to genetic variation, within a given population and environment.

To better understand heritability, we can say that a strong phenotypic resemblance between parents and descendent reflects high heritability (a strong influence of genes), whereas a weak resemblance indicates a major contribution of the environment.

6.2.2. Calculation of heritability

Heritability is a property of the trait, the population, and the environment. A change in any of these factors leads to a different estimate of heritability. If heritability is measured for the same trait in several populations living in different environments, the calculated heritability values often show high standard deviations. Therefore, the heritability of a trait is a concept relative to a studied population in a given environment; that is, it is not an absolute (constant) measure for a particular trait.

In plant breeding, three main categories of traits are distinguished according to the heritability value:

- **Highly heritable traits ($h^2 > 0.4$):** Heritability is mainly determined by the genotype. These are essentially traits related to qualitative characteristics, which are much less sensitive to environmental variation.
- **Moderately heritable traits ($0.2 < h^2 < 0.4$):** The environment can exert a moderate influence.
- **Low heritability traits ($h^2 < 0.2$):** These are traits strongly influenced by the environment, such as fertility and viability, disease resistance, yield, and protein content.

For a quantitative trait, there are two different estimates of heritability:

6.2.2.1. Broad-sense heritability (denoted by H^2)

It is the proportion of the phenotypic variance (V_P) that is estimated from the total genetic variance (V_G).

✚ Mathematically, it is expressed as follows:

$$H^2 = \frac{V_G}{V_P}$$

Where:

$$V_G = V_A + V_D + V_I$$

$$V_P = V_G + V_E$$

The genotypic variance can be further decomposed into **additive variance** (V_A), **dominance variance** (V_D), and **epistatic interaction variance** (V_I), while the phenotypic variance is decomposed into **genotypic variance** and **environmental variance** (V_E).

6.2.2.2. Narrow-sense heritability (denoted by h^2)

It is the proportion of the phenotypic variance (V_P) that is estimated **only from the additive genetic variance** (V_A), that is, the portion directly transmissible from parent to descendent.

✚ It is expressed as follows:

$$h^2 = \frac{V_A}{V_P}$$

6.2.3. Determination of the number and location of genes

Quantitative traits (such as yield, size, fruit weight, etc.) are often **polygenic**, controlled by a large number of genes called **polygenes**, each having an effect too small to be distinguished individually. Each of these genes contributes a small portion to the total variation. This polygenic variation results from the large number of segregating loci and their interactions, but the phenotypic expression of quantitative traits can also be significantly influenced by environmental variation.

Many of these genes have economic importance, making it necessary to determine their number and location in the genome. Estimating the number of genes involved relies on **biometric methods**, which analyze means and variances from crosses to distinguish the genetic component from the environmental component in the observed phenotypic variation.

Regarding gene localization, modern **Quantitative trait loci (QTL) mapping** approaches and **genome-wide association studies (GWAS)** associate molecular markers with the studied traits to identify the chromosomal regions responsible. The term **Quantitative trait loci (QTL)** refers to the multiple genes involved in the formation of a given quantitative trait, and mapping reveals whether the QTL associated with a trait are clustered on a single chromosome or dispersed throughout the genome.

These approaches provide breeders with valuable information for the targeted improvement of cultivated plants.

6.2.4. Detailed analysis of variance

Variance is often used to express variability, and one important aspect of variance is its **additive property**. Indeed, when considering two independent random variables, the variance of their sum is equal to the sum of their variances:

$$\text{Var (X+Y)} = \text{var X} + \text{var Y}$$

This property is fundamental in quantitative genetics, particularly for understanding how multiple genes contribute to the overall phenotypic variance of a trait.

6.2.4.1. Total phenotypic variation (σ^2)

The observed variability for a given trait in a population (σ^2) is not due to a single cause, but can be partitioned into three components:

- **Genetic variance (σ_G^2):** corresponds to the portion of variation attributable to genetic differences among individuals.
- **Environmental variance (σ_E^2):** represents the portion of variation caused by differences in environmental conditions (climate, soil, nutrition, etc.).
- **Genotype $\times$ environment interaction variance (σ_{GE}^2):** reflects the fact that the effect of a genotype can vary depending on the environment.

✚ Thus, the total phenotypic variance can be expressed as:

$$\sigma_p^2 = \sigma_G^2 + \sigma_E^2 + \sigma_{GE}^2$$

6.2.4.2. Using variance to estimate the number of genes

A population, like a line or a variety, consists of individuals whose genotypes are less diverse than those of the species as a whole. However, even within a genetically homogeneous group, such as a pure line, some variability can appear solely due to environmental factors.

Crossing two pure lines produces an **F1** generation that is genetically uniform in its heterozygosity. The phenotypic variability of such an F1 is therefore not genetic in origin but is mainly due to the environment. In contrast, in the **F2** generation, segregation and recombination of genes produce a large diversity of new genotypic combinations. Consequently, the F2 is more variable than the F1 from which it derives.

For any trait with a normal distribution, the means of the F1 and F2 populations tend to be intermediate between the two parental lines. If there is no change in environmental conditions from one generation to the next, the environmental variability of the F2 will be approximately the same as that observed in the F1. Any increase in phenotypic variance in the F2 compared to the F1 can therefore be attributed to genetic causes.

Thus, the **genotypic variance of the F2** (σ_{GF2}^2) is equal to the total phenotypic variance of the F2 (σ_{PF2}^2) minus the phenotypic variance of the F1 (σ_{PF1}^2):

$$\sigma_{GF2}^2 = \sigma_{PF2}^2 - \sigma_{PF1}^2$$

✚ The genotypic variance of the F2 can be expressed as:

$$\sigma_{GF2}^2 = (a^2N)/2$$

Where:

- a represents the contribution of each active allele,
- N is the number of gene pairs involved in the measurable trait.

✚ The estimate of a is obtained by the formula:

$$a = D/2N$$

Where:

- **D** is the numerical difference between the two parental means.

✚ From this, the number of gene pairs **N** can be deduced:

$$N = \frac{D^2}{8(\sigma^2_{PF2} - \sigma^2_{PF1})}$$

This formula is highly simplified. It assumes that all genes contribute to the quantitative trait, have identical cumulative effects on the phenotype, and that there is no dominance, no linkage, and no interactions.

6.2.5. Use of heritability in breeding and improvement

Heritability measures the proportion of phenotypic variability of a trait that is attributable to genetic differences among individuals in a given population. It therefore serves as an essential indicator for evaluating the effectiveness of selection.

Quantitative traits are more difficult to select in a breeding program because they are more strongly influenced by the environment than qualitative traits. If two plants are randomly selected from a mixed population, the observed difference in a specific trait may be due to the average effects of genes (heritable differences), differences in the environment in which the plants were grown, or both. The average effects of genes determine the **degree of resemblance between parents and descendants** and are thus transmitted to the descendants of the selected plants.

Consequently, when a breeder chooses individuals based on their phenotypic performance to use as parents in a cross, the success of this selection—aimed at changing traits in the desired direction—can only be predicted by knowing the degree of correspondence (genetic determination) between phenotypic values and genetic values. Heritability measures this degree of correspondence. It does not directly measure genetic control but rather the extent to which this control is expressed in a given population and environment

In plant breeding, some traits, such as yield, are typically measured at the plot level (rather than at the level of individual plants), which affects heritability estimates. The **genotypic variance** available in a population determines the magnitude of expected genetic progress.

In summary, **heritability** is a central tool for predicting the efficiency of selection and optimizing parental choice: the higher the heritability, the greater the expected genetic response in the descendent.

6.3. Evolution of heterozygosity across generations

Heterozygosity refers to the proportion of loci at which an individual carries two different alleles. In a population, it serves as an important indicator of genetic diversity. The evolution of heterozygosity over generations depends on several processes: it can increase through inter-varietal or interspecific hybridization, mutations, gene flow (migration, introgression), or balancing selection. Conversely, heterozygosity can decrease due to inbreeding, genetic drift, or directional selection.

6.3.1. Mechanisms that increase heterozygosity

6.3.1.1. Mutations

Genetic mutations create new alleles, even if they occur at low frequency. They enrich allelic diversity within a population and prevent the complete depletion of genetic variability.

Example: the emergence of a new allele conferring resistance to a pathogen in a wheat line.

6.3.1.2. Gene flow (migration, introgression)

When individuals from another population (or a closely related species) enter a population, they bring new alleles. This increases genetic diversity and heterozygosity within the population.

Example: transfer of drought-tolerance alleles from a local variety to an improved variety through introgression.

6.3.1.3. Inter-varietal or interspecific hybridization

Crossing two different varieties or two compatible species causes gene mixing. It strongly increases heterozygosity (e.g., hybrid maize). The new hybrid generation often benefits from **heterosis (hybrid vigor)**.

Example: hybrid maize → F1 hybrids are much more heterozygous than the parental pure lines.

6.3.1.4. Balancing selection

When heterozygous individuals have a selective advantage over homozygotes, the population maintains a high level of heterozygosity.

Example: some disease-resistance genes confer an advantage in heterozygous state.

6.3.1.5. Panmixia (random mating)

If mating occurs randomly (without preference), heterozygosity is better maintained than in self-fertilizing systems (autogamy).

Example: allogamous plants (e.g., maize, rye) maintain a high level of heterozygosity, unlike autogamous species such as wheat or rice.

6.3.1.6. Maintenance by the breeder

In plant selection, heterozygosity can be deliberately preserved to maintain diversity using several methods:

- **Synthetic populations:** multiple crosses among several lines.
- **Composite varieties:** deliberate genetic mixing to maintain diversity.
- **Management of consanguinity in breeding programs:** avoiding mating of closely related parents to preserve genetic vigor.

6.3.2. Mechanisms that decrease heterozygosity

6.3.2.1. Effect of self-fertilization

In a population subjected to **repeated self-fertilization**, heterozygosity decreases rapidly. At each generation of selfing, the average proportion of heterozygotes is **reduced by half**.

✚ Thus, after n generations of self-fertilization, the proportion of heterozygosity is given by the formula:

$$H_n = H_0 \times \left(\frac{1}{2}\right)^n$$

Where:

- H_n : heterozygosity after n generations,
- H_0 : initial heterozygosity.

Example: after 6 generations of selfing, only about **1.56%** of the initial heterozygosity remains. This principle is fundamental for creating pure lines in plant breeding.

6.3.2.2. Effect of inbreeding

Inbreeding corresponds to an increase in the probability that two alleles are identical by descent. It leads to a **progressive reduction of heterozygosity**.

✚ The inbreeding coefficient F quantifies this loss, and the expected heterozygosity in an inbred population is given by:

$$H_n = H_0(1 - F_n)$$

Where:

- H_n : heterozygosity after n generations,
- H_0 : initial heterozygosity,
- F_n : inbreeding coefficient at generation n .

6.3.2.3. Effect of genetic drift

In a small population, some alleles disappear by chance, even if they are not disadvantageous. Heterozygosity decreases over generations due to **genetic drift**. In the long term, an allele may become fixed (present in all individuals) or lost, purely by chance effect.

✚ The expected loss of heterozygosity per generation is:

$$H_{n+1} = H_n \left(1 - \frac{1}{2N_e}\right)$$

Where:

- H_n : heterozygosity at generation n ,

- H_{n+1} : heterozygosity at the next generation,
- N_e : effective population size (the number of individuals that actually contribute genes to the next generation).

The smaller the N_e , the faster heterozygosity is lost. Conversely, when N_e is large, genetic diversity is maintained much better.

Example

- If the population is **small** (e.g., $N_e=10$):

$$H_{n+1} = H_n \left(1 - \frac{1}{20}\right) = H_n \times 0.95$$

The population loses **5% of its heterozygosity per generation**.

- If the population is **large** (e.g., $N_e=1000$):

$$H_{n+1} = H_n \left(1 - \frac{1}{2000}\right) = H_n \times 0.9995$$

The loss of generation heterozygosity is minimal (**0.05% per generation**).

6.3.2.4. Effect of directional selection

Directional selection tends to reduce heterozygosity because it favors the fixation of one allele and the disappearance of others.

6.4. The phenomenon of heterosis

6.4.1. Definition

Heterosis is the increase in vigor observed in the descendent resulting from the cross between two genetically distant individuals. More precisely, it refers to the superiority of the hybrid (for example the F1) compared to the best parent. It is a universal biological phenomenon in higher organisms, reflecting an advantage of genome-wide heterozygosity.

Various definitions have been proposed to quantify the expression of heterosis (**Fig. 36**). Plant breeding geneticists have defined heterosis, for a given trait, as the superiority **HP_{max}** of

the hybrid compared with its best parent (a phenomenon called **heterobeltiosis**). This is the “best-parent heterosis,” and it is expressed as:

$$HP_{max} = F1 - P_{max}$$

Where:

F1 représente la valeur de l’hybride.

P_{max} est la valeur du meilleur parent.

Cependant, en génétique quantitative, on mesure l’hétérosis comme la supériorité de l’hybride (F1) par rapport à la moyenne des deux parents. C’est l’hétérosis « parent-moyen », est exprimée par :

However, in quantitative genetics, heterosis is measured as the superiority of the hybrid (F1) over the mean of the two parents. This is called “mid-parent” heterosis, and it is expressed as:

$$HP_{moy} = F1 - (P1+P2) / 2$$

Where:

P1, P2 represent the values of the parents.

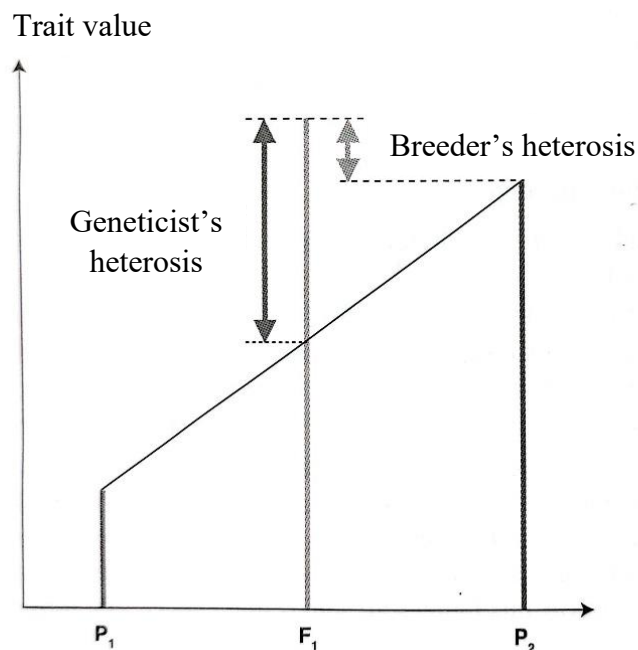


Figure 36. Best-parent heterosis (heterobelitosis), also known as breeder's heterosis, and mid-parent heterosis, also known as geneticist's heterosis.

6.4.2. Hypotheses or mechanisms

Two major mechanisms related to the complementation of genetic contributions can explain heterosis: **intralocus** complementation between alleles (overdominance) and **interlocus** complementation for favorable dominant genes (dominance, epistasis, pseudodominance).

6.4.2.1. The super-dominance mechanism

At a given locus, the heterozygote may show superiority over both homozygotes (example: $Aa > AA$ or aa). This mechanism reflects complementation between two alleles and explains only a limited part of heterosis, since it is rarely observed for complex traits.

6.4.2.2. The dominance of favorable genes

Under the hypothesis of the dominance of favorable genes, heterosis results from the complementation of parental contributions in favorable dominant alleles.

For example, with alleles **A/a** at one locus and **B/b** at another, crossing two complementary parents **AAbb** and **aaBB** produces a double heterozygote **AaBb**, which is

superior to both parents AAbb and aaBB. If values are given to each genotype at each locus "for simplicity, $AA = Aa = BB = Bb = 4$, and $aa = bb = 2$ " and assuming additivity of locus effects (absence of epistasis), the parents each have a value of **6**, while the **F1** has a value of **8**.

This mechanism appears very common. It explains the large difference between self-pollinated (autogamous) and cross-pollinated (allogamous) species. Natural populations of allogamous plants tend to accumulate, in the heterozygous state, highly deleterious recessive mutations forming what is called the **genetic load**. Inbreeding exposes these mutations in the homozygous state, which can be highly detrimental (e.g., a mutation affecting chlorophyll function disrupts expression of many other genes).

Lines of allogamous plants thus carry such genes and are very "depressed." Crossing unrelated lines masks these unfavorable genes, restoring vigor and resulting in heterosis. In contrast, in autogamous species, natural selection tends to eliminate deleterious mutations as soon as they appear in the homozygous state. Therefore, they remain at very low frequencies. As a result, crossing two random lines gives little chance of complementation and therefore weak heterosis.

- **Pseudodominance**

In the previous example illustrating the dominance mechanism, if there is very strong linkage between the two loci, recombination between them is very low, and the parental allele combinations (in repulsion) **Ab** and **aB** behave like alleles exhibiting overdominance. This situation is called **pseudodominance**.

- **Fixable and non-fixable heterosis**

1. **If heterosis is based on superdominance**, it is not possible to obtain a homozygote as performant as the heterozygote, and the heterosis is said to be **non-fixable**.
2. **Under the dominance mechanism**, it is theoretically possible to obtain a homozygous genotype with the same value as the F1 (e.g., for two loci, $AABB = AaBb$). In this case, heterosis is said to be **fixable**. However, as the number of loci involved increases, the probability of fixation becomes extremely low. In practice, heterosis remains difficult to fix for complex traits.

6.4.3. Evolution of heterosis across generations

Heterosis evolves in a characteristic way across generations. It reaches its maximum in **F1**, when two pure lines or genetically distant parents are crossed, because the hybrid combines a high level of heterozygosity and allele complementarity.

From **F2 onward**, heterosis decreases due to segregation and recombination, which cause a progressive loss of heterozygosity and therefore a reduction in the heterosis effect. In later generations (**F3, F4... Fn**), this decline continues until stabilization at a low level, close to that observed in panmictic populations.

 Thus, the evolution of heterosis is marked by:

- a **peak in F1**;
- a **rapid decline in F2**;
- and a **partial disappearance in advanced generations**.

For this reason, many economically important crops, such as **maize**, are exploited as **F1 hybrids**, ensuring the stability and intensity of heterosis.

Exercise: Descriptive statistics of a quantitative trait

A population of wheat plants shows the following grain weight values (g): 32, 35, 30, 38, 40, 36, 34, 37.

1. Calculate the mean grain weight.
2. Estimate the standard deviation.
3. Interpret the biological meaning of the variability observed.

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