Genetics of dairy production

E-learning course from ESA

Charlotte DEZETTER

ZBO101R11550

Table of contents

I

Genetics of dairy production

What is genetics?

William Bateson defined it as:

"Genetics is the science dealing with **heredity** and **variation** seeking to discover laws governing similarities and differences in individuals related by descent".

1. Learning objectives

At the end of this lesson, you will be able to:

- explain the difference between gene/allele, dominant/recessive, homozygous/heterozygous, genotype/phenotype;
- distinguish the keys to genetic progress;
- estimate the magnitudes of heritability and genetic variation for production traits;
- interpret the principles of genetic evaluation.

You will reach these four learning objectives through two parts:

- Part 1: Review of Mendelian Genetics
- Part 2: Principle of genetic selection

2. Review of Mendelian genetics

To reach the first objective of this lesson, you need to answer the following question:

What is the essential vocabulary about genetics?

2.1. Essential vocabulary about genetics

The genetic material is contained on **chromosomes** which are found in the nucleus of each cell. These chromosomes are paired and cows have 30 pairs of chromosomes.

From this example of an homologous pair of chromosomes, we can define four terms:

- A **gene** is a section of DNA that determines a trait.
- Since chromosomes are paired, genes are also paired.
- Therefore, these genes can have different forms which are called **alleles**.
- When the two alleles of a gene are the same (here AA), then the cow is said to be **homozygous** for the trait coded by the orange traits. However, when the two alleles are different (here Bb), the cow is said to be **heterozygous** for this trait.
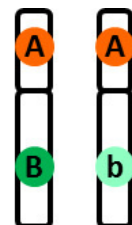
The **gene combination** of an organism defines the **genotype** of this organism. **Half of these genes** will be transfered to the offspring.

However, most of the time, we don't know exactly the gene combination of an organism. What we know is its **phenotype**, which is **the way this organism looks**. In dairy cows, we are particularly interested in the phenotype of traits that can be **recorded** such as the quantity of milk produced by a cow.

Now that we have defined the genotype and the phenotype, a new question arises:

How is the phenotype related to the genotype?

2.2. Relation between the phenotype and the genotype

### Let's start by the example of the polled gene.

If we mate an homozygous bull with two horned alleles (pp) with an homozygous cow with two polled alleles (PP), the calf will be heterozygous Pp and its phenotype will be polled.

Hence we have **three genotypes** (pp, PP and Pp) but we only saw **two phenotypes**.

Therefore, the polled allele (P) is **dominant** to the horned allele (p) and the horned allele is **recessive** to the polled allele.

When a trait is always observed in the offspring even when a recessive allele is present we speak of complete dominance.

However, we don't always observe **complete dominance**.
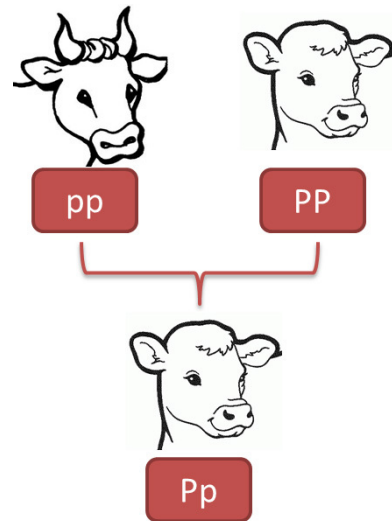
Now, let's take the example of the Shorthorn coat.

When we mate an homozygous bull with two red coat alleles (RR) with an homozygous cow with two white coat alleles (WW), the calf will be heterozygous RW and its phenotype will be roan.

Hence, the heterozygote is **different** from either of the homozygotes.

We have **three genotypes** (RR, WW and RW) and **three phenotypes**.

When both alleles are expressed equally in the heterozygous type, we speak of **co-dominance**.
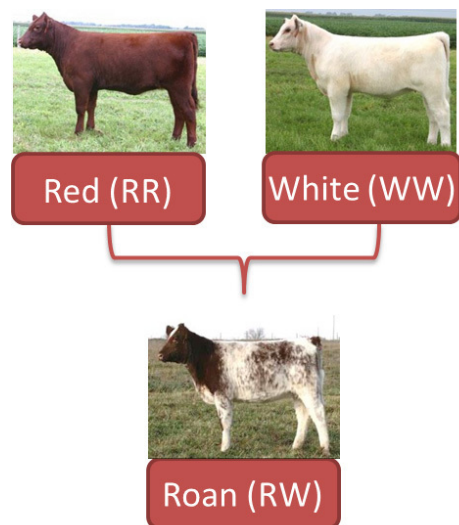
The previous examples illustrated the relation between one gene coding for one trait.

However, the phenotype is a combination of many traits. Therefore, we can arise the question:

What are the expected results for more than one traits?

## 2.3. Expected results for more than one trait

When we consider more than one trait, the expected results in the phenotype depend on the relationship between genes.

2.3.1. Independant loci

1. If the phenotype of each trait is determined separately by allelic genes and the genes determining one trait are independant of the genes for the other trait, then we speak of **independant loci**.

Homologous pair of chromosomes

No relationship => the "A" locus and the "B" locus are independant
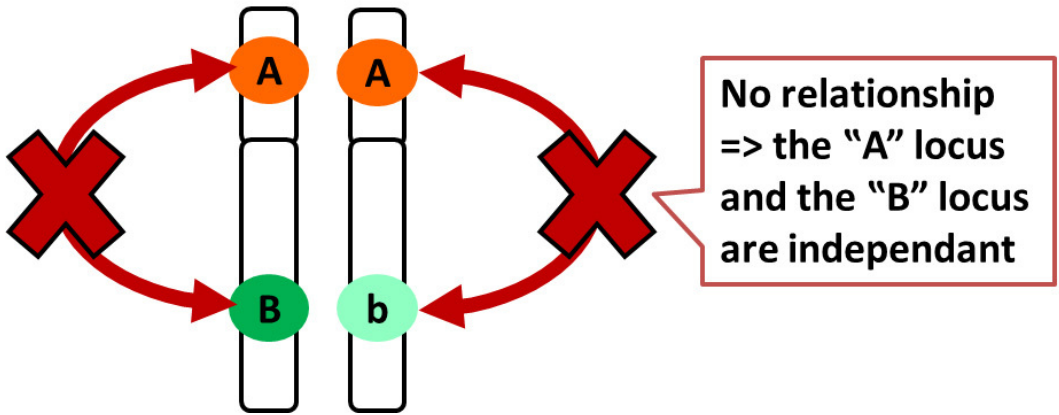
Example of independent loci: coat color and polled loci

Let's go back to the examples of the polled gene and the Shorthorn coat gene.

Now, we mate a bull homozygous with two horned alleles (pp) but heterozygous for the roan color coat (RW) with a cow heterozygous for the polled gene (Pp) and heterozygous for the roan color coat (RW).

2.3.2. Exercice

Firstly, the expected results, in the offspring, for the **"color"** locus are (?/?) (please complete the percentages of individuals of each type in the offspring) :

Roan (RW) Horned (pp) — Roan (RW) Polled (Pp)

? RR — ? RW — ? WW

2.3.3. Exercice

Secondly, the expected results, in the offspring, for the **"polled"** locus are (?/?) (please complete the percentages of individuals of each type in the offspring):

Roan (RW) Horned (pp) — Roan (RW) Polled (Pp)

? pp — ? Pp

2.3.4. Exercice

Finally, the expected results, in the offspring, for **these 2 independant loci** are (?/?) (please complete the percentages of individuals of each type in the offspring):
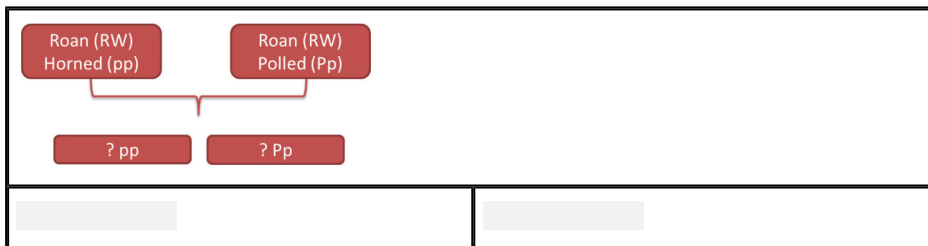
Roan (RW) Horned (pp)	Roan (RW) Polled (Pp)	
? RRpp	? RWpp	? WWpp
? RRPp	? RWPp	? WWPp

2.3.5. Epistatic effect

2. If a gene masks the effect of another gene at a different locus, it defines the **epistatic effect**.

Homologous pair of chromosomes

A A

B b

The gene "B" influences the effect of the gene "A"
➔ The gene "B" is said to be epistatic to the gene "A"
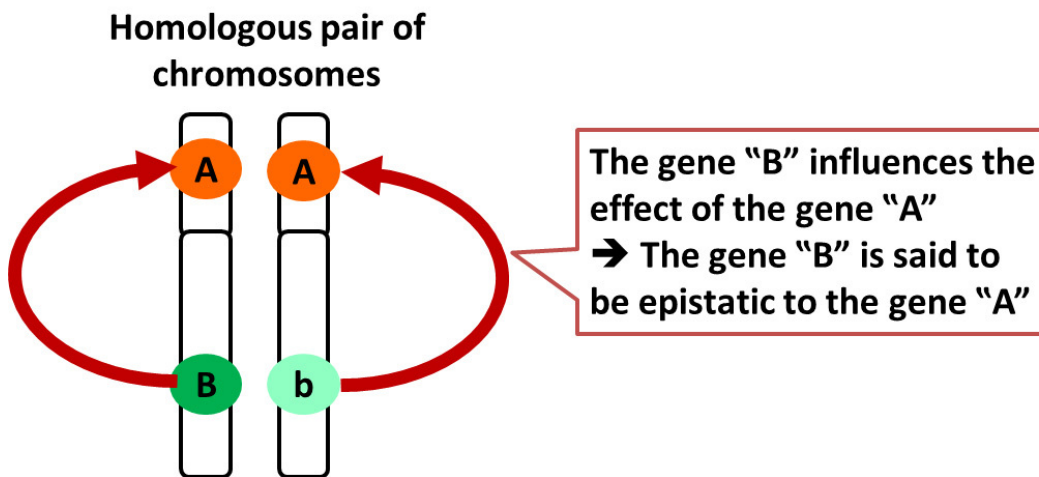
Example of epistasis: the albino gene

We mate two animals homozygous for the black and white color coat (BB) and heterozygous for the albino gene (Cc).

The expected results in the offspring are:
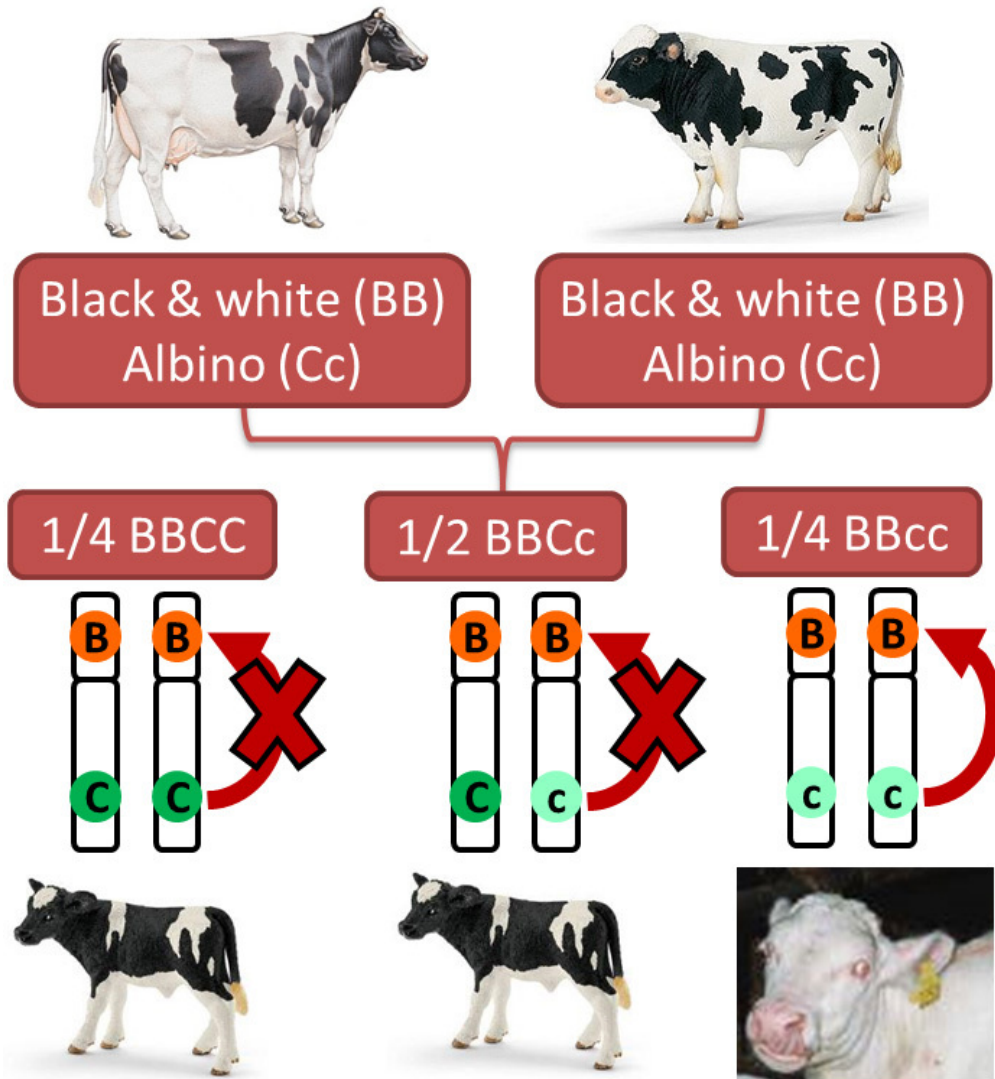
We can see that, when the offspring are homozygous with **two recessive alleles for the albino gene**, the **phenotype is albino** despite the presence of the **two dominant alleles for the black and white coat**.

Hence, the albino gene is **epistatic** to the genes for coat color.

2.3.6. Linked genes

3. If genes at certain loci tend to be inherited together, then we speak of **linked genes**. Genes are mostly linked when their loci are near each other on the same chromosome. Indeed, if the loci are linked, during meiosis, recombination gametes and non-recombination gametes are produced according to the recombination frequency, which corresponds to the distance between genes

Let's illustrate this phenomenon

When we mate 1 homozygous animal to a heterozygous animal for two different genes,	
if the loci are independent, each parent produces the expected germ cells:	Gene1 (AA) Gene2 (BB) Gene1 (Aa) Gene2 (Bb)
Therefore, in the offspring, we expect:	100% AB 50% AB 50% ab
	50% AABB 50% AaBb
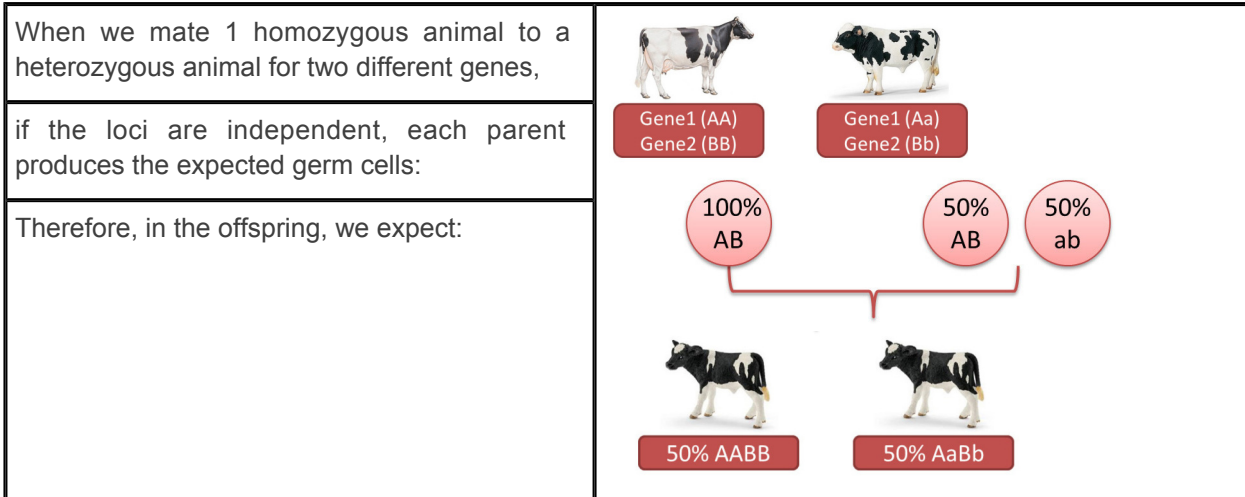
However, if the two loci **are linked**, the heterozygous parent **does not produce** 50% AB and 50% ab germ cells. Therefore, in the offspring we can't expect 50%AABB and 50% AaBb.

2.3.7. **Exercice**

Indeed, if we consider two loci linked with a frequency of recombination equal to 20%, then in 80% of the cases there is no recombination during meiosis when in 20% of case there is. Hence, the heterozygous parent actually produces (?%):
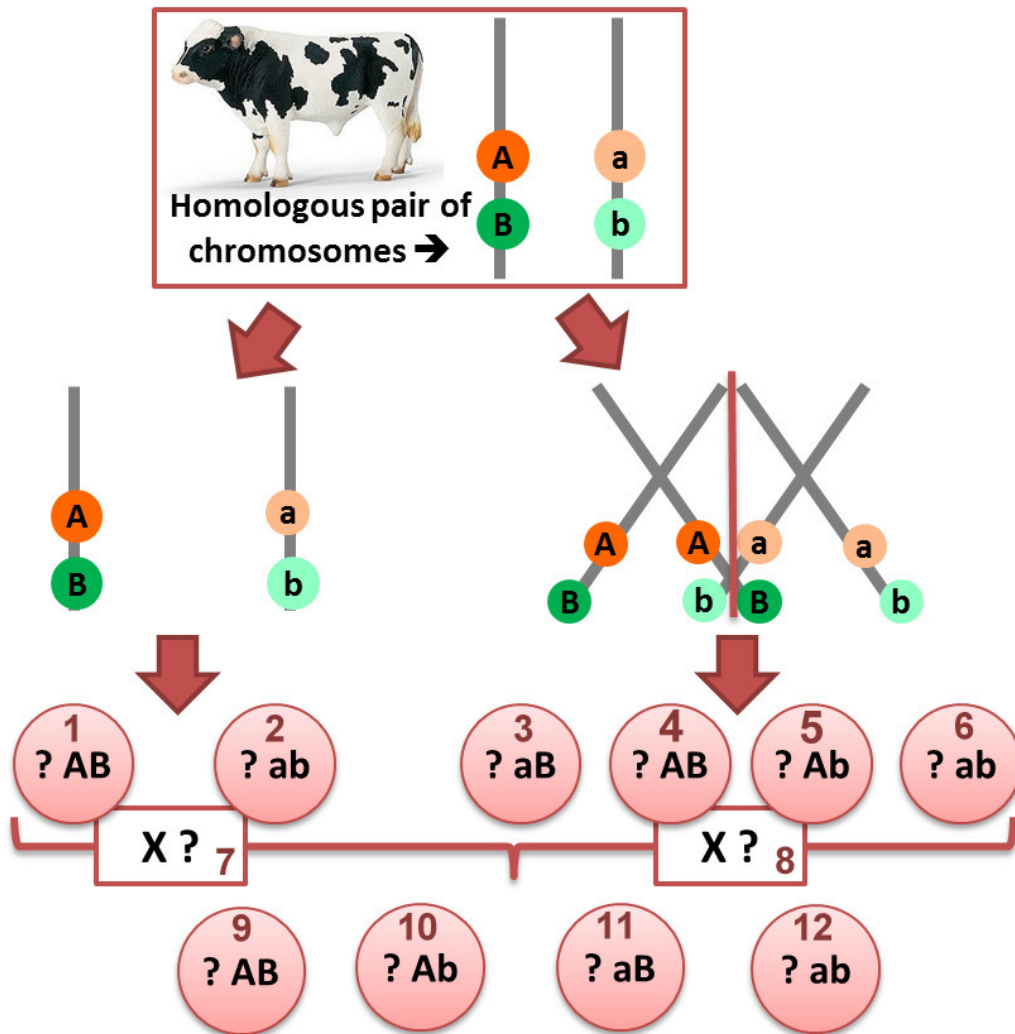
Response 1:		Response 7:	
Response 2:		Response 8:	
Response 3:		Response 9:	
Response 4:		Response 10:	
Response 5:		Response 11:	
Response 6:		Response 12:	

2.3.8. Exercice

Therefore, if we mate this heterozygous parent for two linked genes with an homozygous parent for the same loci, in the offspring we expect (?%):

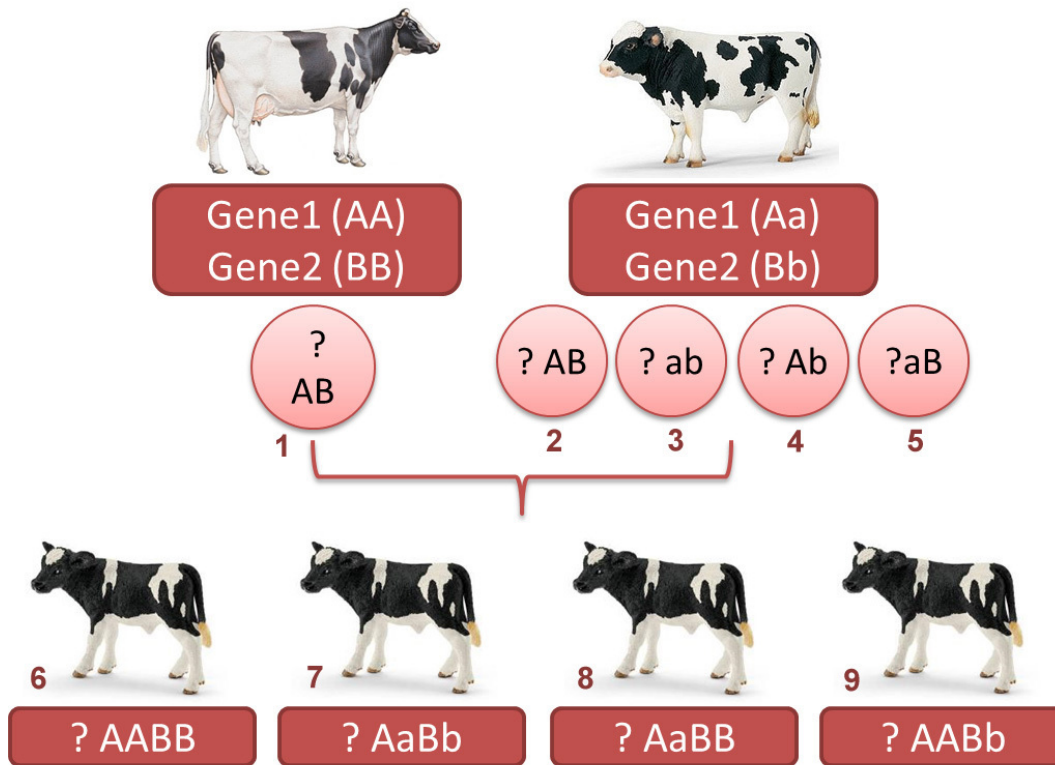|			
Response 1:		Response 6:	
Response 2:		Response 7:	
Response 3:		Response 8:	
Response 4:		Response 9:	
Response 5:			

* *

*

This objective of this part was to review Mendelian genetic concept in order to understand how it can be applied to dairy cattle genetic selection.

3. Principle of genetic selection in dairy cattle

First of all, it is important to realize that genetic improvement requires variation. Indeed, we can't select the best animals for a trait if every animal expresses the same phenotype.

3.1. Quantitative genetics

In 4.2 above, we focused on examples where one gene code for one trait **(simple genetic determinism)**. However, interesting traits for dairy production, such as yields, fertility and health are coded by many genes, are controlled by several genes, and their expression is influenced by the environment.

Quantitative genetics is the study of the inheritance of traits that show a **continuous distribution of phenotypes in a segregating population**. Traits that are controlled by many genes also exhibit quantitative inheritance as each gene segregates in a Mendelian way. Even when there are only a few genes involved, the trait variation will show a continuous distribution due to the results of measurement error and environmental effects.

Quantitative genetics is considered to have been founded in the early 20th century, notably by R.A. Fisherâs article which showed that the inheritance of continuously varying traits is consistent with Mendelian principles.

The basic principle of quantitative genetics:

Basically, the phenotypic value (P) of an individual is the combined result of its genotype (G) and the effects of the environment (E):
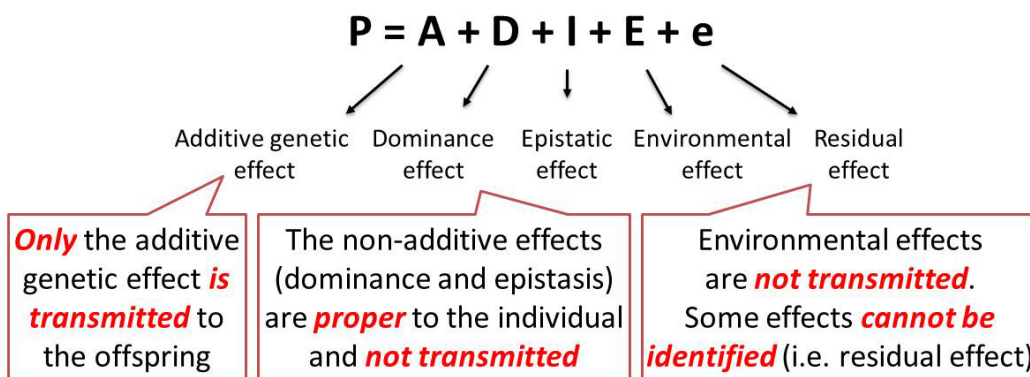
P = G + E

Genotype refers to the **total** genetic variation. This includes not only the effects of nuclear genes, but also the effects of mitochondrial genes and the interactions between genes. Genotypic variation can be partitioned into **additive and non-additive variation**. Additive variation represents the cumulative effect of individual loci, therefore the overall mean is equal to the summed contribution of these loci.

Non-additive variation represents dominance variation (interaction between alleles) and epistasis variation (interaction between genes).

Quantitatively varying traits are also affected by **environment** (E). This can be further subdivided into pure environmental effect and interaction between genes and the environment. In other words, how different genotypes respond in different environments.

So, the equation above can be better written as:

$$P = A + D + I + E + e$$

Additive genetic effect	Dominance effect	Epistatic effect	Environmental effect	Residual effect
Only the additive genetic effect *is transmitted* to the offspring	The non-additive effects (dominance and epistasis) are *proper* to the individual and *not transmitted*		Environmental effects are *not transmitted*. Some effects *cannot be identified* (i.e. residual effect)	

From the definition of the phenotype: P = G + E, we can see that there are two possible ways to improve a trait:

1. By improving the genotype through genetic selection. For example, the variation between cows for milk yield (some cows produce more milk than other), if results from genetic variation (which means that these cows will always produce more milk no matter the environment), allows genetic improvement.
2. By improving the environment through herd management.

Genetic variation is, therefore, the first component to genetic progress.

3.2. Genetic variation = component 1 to genetic progress

Previous studies showed that distribution of genetic value for a population follow a **normal distribution**:

The usual measure of variation is the **variance** which is the **standard deviation** of individual squared deviation of individual records from their population average.

The variation that is caused by genetic differences among individuals is called the **genetic variance**.

μ = genetic mean
σ² = genetic variance

μ-3σ   μ-2σ   μ-σ   μ   μ+σ   μ+2σ   μ+3σ
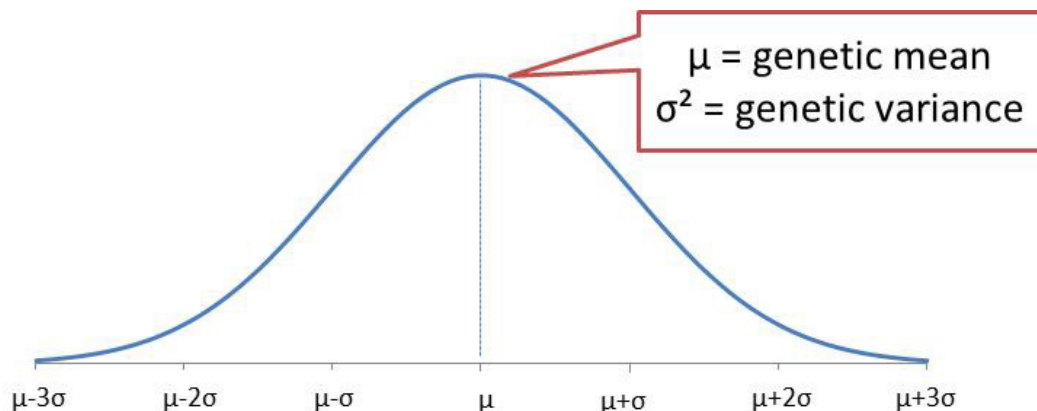
3.3. Heritability

If we go back to the formula: P = G + E, with variance properties, we can write:

Var (P) = Var (G) + Var (E)

Which is equivalent to:

Var (P) = Var (A) + Var (D) + Var (E) + Var (e)

From this formula we can define the heritability of a trait as:

$$h^2 = \frac{Var(G)}{Var(P))} = \frac{Var(G)}{Var(G) + Var(E)}$$

Finally, the expected results, in the offspring, for these 2 independant loci are:

$$h^2 = \frac{Var(A)}{Var(P)}$$

Heritability = Fraction of variation among cows caused by genetic differences. Heritability is defined **at a population level** and definitely not at individual level.
$h^2 \in [0,1]$

What is fundamental to understand and remember about heritability is that calculating heritability is important for predicting how a trait will respond to selection (*response to selection* refers to the gain in the mean of the population compared to the mean of the selected parents, see below). Hence:

- A large heritability (0.5 or greater) suggests that a record on an individual is a good indicator of that individual's genetic value → Traits with high heritability are easy to improve.
- A small heritability (0.15 or less) suggests that one record has some meaning in estimating genetic value, yet much is unknown about individual's true genetic value → A progeny test and pedigree analysis will help in predicting genetic value.

The table below gives values for heritabilities and genetic variance in the French Holstein breed for some interesting traits:

Erasmus+   UNIVERSITY OF AGRONOMIC SCIENCES AND VETERINARY MEDECINE OF BUCHAREST   eSa ECOLE SUPERIEURE D'AGRICULTURES Angers Loire   AERES HOGESCHOOL DRONTEN   GROUPE LACTALIS

Traits	Heritability	Genetic variance
Milk yield (kg)	0.30	576.081
Fat (kg)	0.30	974
Protein (kg)	0.30	518
Fat content (g/kg)	0.50	8.82
Protein content (g/kg)	0.50	2.19
Somatic cell score	0.15	0.25
Conception rate for cows (%)	0.02	0.005
Interval calving to first service (days)	0.06	60

We just saw that genetic variation is crucial to genetic progress.

The objective of genetic selection is to provide offspring which are superiors to their parents for interesting traits. Therefore, it is essential to rank and select animals based on their genetic value through genetic evaluation.

3.4. Genetic evaluation: Estimated breeding value/Definition

First, terms associated with genetic value must be described:

- **Genetic value** is the effect the genes of the animal have on its production.
- **Breeding value** has the same meaning except that it is more likely to be used to describe the effects of genes the animal can pass on to its progeny.
- **Transmitted ability** is often used as a substitute for one-half breeding value. Indeed, an animal can pass on only a sample one-half of its genes to its offspring.

True genetic value (TBV) is never known exactly, we cannot see genes and breeding values. So we must use observed phenotypes to obtain **estimated genetic value** (EBV) and **estimated transmitting ability** (ETA).

The most obvious piece of phenotypic information we can use is the animal's own phenotype. But we can also use information from relatives, such as the sire, the dam, siblings and progeny.

What is important to remember is that breeding values are estimated based on phenotypic differences between animals or more specifically, phenotypic deviation:

$$EBV = h^2 (P_i - \mu)$$

1) We use h^2 rather than h for statistical reasons.
The correlation between breeding value and phenotype is equal to h. The proportion of variation explained by breeding value is h^2.

2) How much does the individual's performance (P_i) deviate from the mean (μ).
⚠ This is not the same as phenotypic standard deviation

The principle of breeding value estimation is based on regression → We want to know differences in breeding value based on observed differences in phenotype.
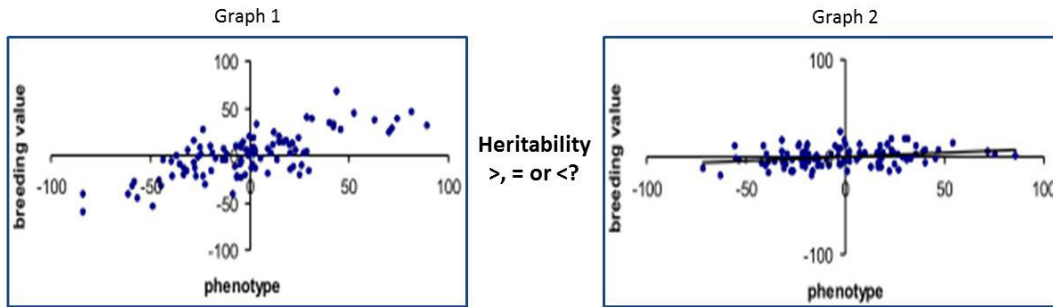
If we regress breeding values on phenotypic observations, the slope of the regression line tells us how

much difference we have in breeding values per unit of difference in phenotype.

3.5. Exercice

In the figure below, which trait has the highest heritability, the one presented in graph 1 or in graph 2?


Relationship between breeding value and phenotype, depending on heritability

3.6. Correcting for fixed effects

Estimation of breeding values should be based on fair comparisons between individual. Indeed, many environmental factors may mask the animal's genetic abilities. Systematic effects that affect phenotypes are called **fixed effects** (e.g., age and season at freshening, herds, etc.). For those fixed effects that are observable we can do correction. However, some environmental effects are not attributable to known environmental factors and cannot be corrected for. They are called **random environmental effects**.
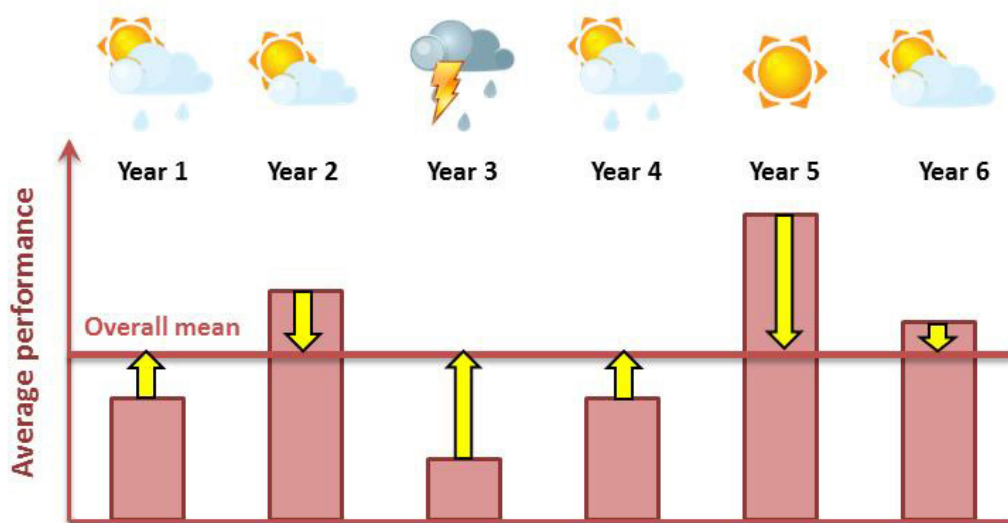
We can express the phenotype of a dairy cow as:

P = G + Fixed effects + Random environmental effects

3.7. Accuracy of EBV

As we previously see, it is quite impossible to know exactly the true genetic value of a cow. All we have is the estimated breeding value based on phenotypic or genomic information. The **accuracy** is defined as the **correlation** between true and estimated breeding value.

The main issue for dairy cattle is that usually one cow has one phenotype in one environment. Even if, we can records several performances for production, reproduction and health traits, we still have very few records per cow. Therefore, the accuracy of estimated breeding value based on the own phenotype of a cow is very low.

However, as siblings share a proportion of the same genes, it is possible to use their information in estimating breeding values.

To summarize, when we estimate breeding value of a cow:

1. The knowledge of records from close relatives increases confidence in accuracy of predicting genetic value
2. In general, as heritability increases, the accuracy of predicting genetic value of a cow also increases. The effect of heritabilities becomes smaller with more information used.
3. The accuracy of parent average depends on the parent EBV accuracy and not on heritability (but note that with low heritability it will be harder for a parent to achieve a certain accuracy).

The table below gives accuracies of predicting value for milk production (h² = 0.3) from a cow's records and records of cow's relatives:

Number of records on cow	No other relatives	+ 1 record on dam or daugther	+ her sire's EBV (accuracy = 0.9)
0	0.00	0.25	0.48
1	0.50	0.53	0.63
2	0.57	0.60	0.66
3	0.61	0.63	0.68
6	0.65	0.67	0.71

This table shows that a **cow's records are more important** than records of many relatives. Records of daughters or dam add little accuracy unless the cow has no records. If the cow has no record, the **EBV of her sire is an important indication** of her genetic value.

The situation is different when evaluating bulls. With the use of artificial insemination, nearly perfect accuracy of predicting a bull's genetic value can be achieved if **enough daughters in many herds** are analyzed (accuracy of sire's EBV equal to 0.99 with 1000 daughters recorded in different herds). Indeed, having records of daughters in different herds allows a proper estimation of environmental effect and therefore increases accuracy of estimated breeding value of their sire.

Today, genomic test can be done early in an animal life and adds more to the accuracy when there is not much other information available:

Info used	Heritability 10%		Heritability 30%	
	no genomics	Genomics	no genomics	genomics
DNA test only	0	0.22	0	0.39
Parents records	0.22	0.31	0.39	0.51
+ 20 half siblings	0.35	0.40	0.49	0.58
+ own info	0.45	0.48	0.66	0.69
+ 20 progeny	0.66	0.67	0.84	0.85
+ 100 progeny	0.86	0.86	0.95	0.95

We just saw how to estimate breeding value and therefore how to rank cows and bulls for interesting traits with more or less accuracy. To obtain genetic improvment only the best must be selected. The extent to which selection will result in genetic improvement depends on the **intensity of selection**.

3.8. Intensity of selection

If in a population, we select the parents randomly, the genetic mean in the offspring population will be the same as the genetic mean in the parental population.

However, the results in genetic improvement will not be the same whether the best 1 of 10, the best 5 of 10, the best 9 of 10 or some other fraction are selected.
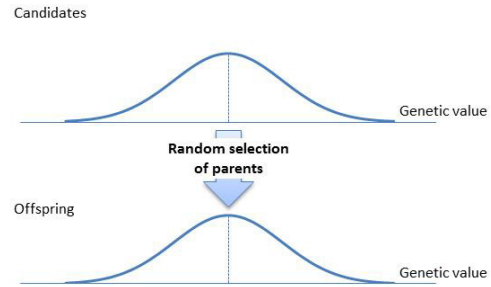
In dairy cattle, the use of artificial insemination has led to a very intense selection of bulls, as that truly herd-improving sires can be used in many herds and on many cows.

The following table gives factors associated with intensity of selection:

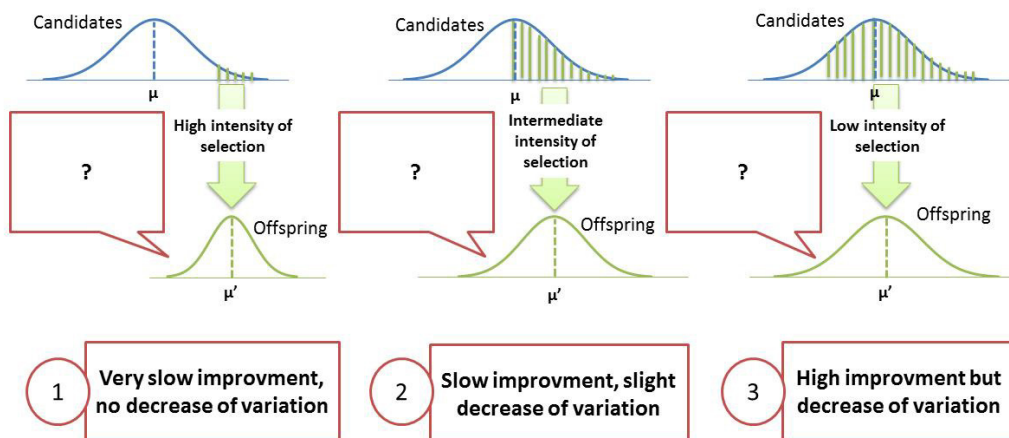| Select top percentage	Intensity factor	Comments
100	0.00	
90	0.20	Usual level for selecting cows in a herd
75	0.42	Maximum level for selecting cows in herd
50 to 10	0.80 to 1.75	Usual range for selecting dams of young bulls and of bulls out of young bulls sampled
5 to 1	2.06 to 2.67	Possible range of selection for dams and sires of young bulls

3.9. Quiz:

Question

In the figure below, which of the following statements describe the best the following charts?

1 — Very slow improvment, no decrease of variation

2 — Slow improvment, slight decrease of variation

3 — High improvment but decrease of variation

3.10. Genetic progress

Genetic improvement per generation is determined by three factors:

1. It requires **genetic variation** in order to select only the best.
2. In order to select only the best, breeders must decide which candidates are the best. Confidence on this ranking depends on **accuracy** of estimated breeding values of candidates.
3. The extent to which selection will results in genetic improvement depends on the **intensity of selection**.

We can summarize genetic improvement per generation by the following equation:

$$Genetic\ gain/generation = Genetic\ variation \times accuracy \times intensity$$

Because herd owners are usually interested in genetic progress per year, a fourth factor is quite important in determining the rate of genetic improvement. Genetic progress per generation divided by the number of years per generation gives genetic progress per year. Thus **generation interval** is important. The generation interval is the average time between birth of an animal and birth of its replacement.

We can therefore write:

$$Genetic\ gain/year = \frac{Genetic\ variation \times accuracy \times intensity}{Years\ per\ generation}$$

3.11. Simultaneous improvement of several traits

Most of the time, we want to select animals on more than one trait. For dairy cattle genetic selection focused on milk yields but also on contents of milk (fat and protein), reproduction and health. However, it can be really complex because those traits are not independent. The genetic dependence between traits is called **genetic correlation**, which defines the correlation between breeding values of two traits in the same individual. This genetic correlation can be positive or negative.

The following table gives some values for genetic correlation between traits of interest in the French Holstein population.

Traits	Fat content	Protein content	Conception rate for cows (%)
Milk yield (kg)	-0.40	-0.40	-0.23
Fat content (g/kg)		0.60	0.10
Protein content (g/kg)			0.10

As we can see that correlation between milk yield and protein content is negative, we can assume that choosing bulls for selection might be complex.

Let's illustrate this complexity. The following graph illustrates the distribution of EBV of dairy bulls on milk yield (kg/lactation) and protein content (g/kg). Each point represents an individual.
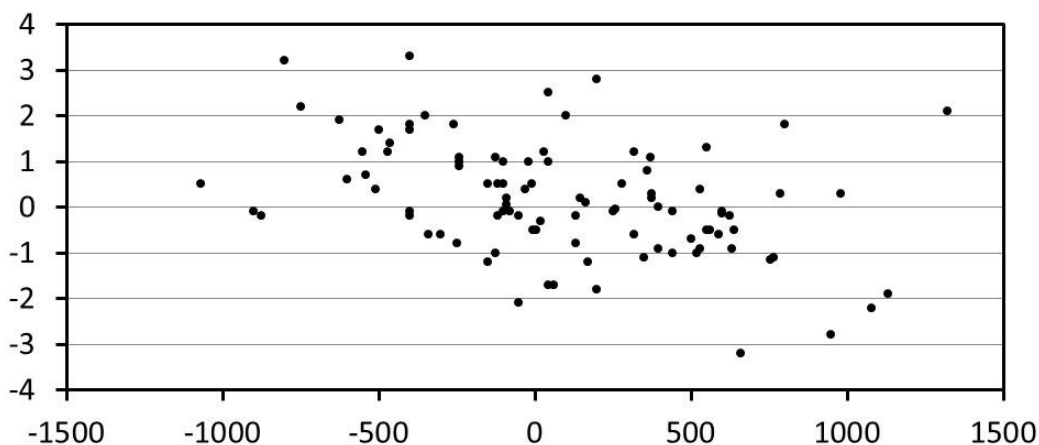
In this example, we have 40 candidates characterized by:

	Milk	Protein content
1	-750	2.2
2	-540	0.7
3	-500	1.7
4	-465	1.4
5	-400	1.7
6	-400	-0.2
7	-340	-0.6
8	-300	-0.6
9	-250	-0.8
10	-240	1.1
11	-240	0.9
12	-150	-1.2
13	-125	1.1
14	-90	0.2
15	-90	0.05
16	-80	-0.1
17	-50	-0.2
18	30	1.2
19	45	2.5
20	45	1
21	100	2
22	370	1.1
23	395	0
24	395	-0.9
25	500	-0.7
26	530	0.4
27	550	1.3
28	550	-0.5
29	560	-0.5

30	600	-0.1
31	590	-0.6
32	625	-0.2
33	755	-1.15
34	765	-1.1
35	800	1.8
36	1130	-1.9
37	320	1.2
38	950	-2.8
39	260	-0.05
40	1080	-2.2

3.12.
Quiz:

Suppose that we have to select 10 bulls among those 40 candidates. We can choose to select the 10 best bulls on milk yield or the 10 best bulls on protein yields or the 10 best bulls for a combination between milk yield and protein content.

Question 1

For the **first strategy**, the differential of selection will be: (?) kg for milk yield and (?) g/kg for protein content.

Question 2

For the **second strategy**, the differential of selection will be: (?) kg for milk yield and (?) g/kg for protein content.

Question 3

Finally, for the **third strategy**, the differential of selection will be: (?) kg for milk yield and (?) g/kg for protein content.

* *

*

In this course, we have seen that the phenotype of an animal is expressed as an interaction between the genotype and environmental effects. Hence if we want to improve the genotype of an animal we need to have records about:

1. Phenotypes for different traits (in that case, milk, fat and protein yields records, reproductive records, health records, etc.)
2. Phenotypes of daughters must be recorded in different environments.

Hence, having genetic gains for interesting traits requires an implementation of specific breeding programs according breeds or selection cores.
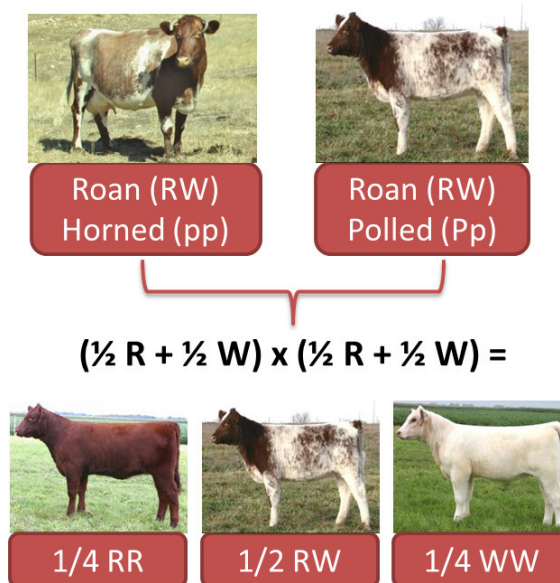
Exercises solution

> Solution n°1

Firstly, the expected results, in the offspring, for the **"color"** locus are (?/?) (please complete the percentages of individuals of each type in the offspring) :

Roan (RW) Horned (pp) — Roan (RW) Polled (Pp)		
? RR	? RW	? WW
1/4	1/2	1/4
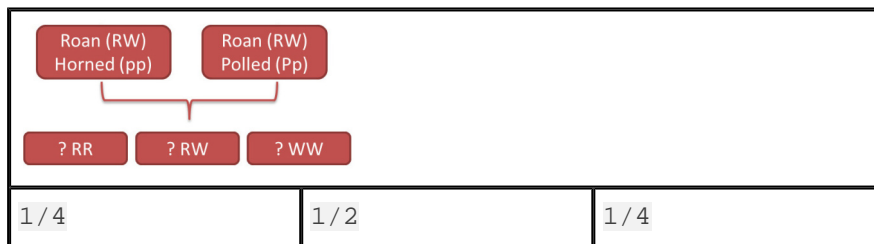
Explanation:

For the color gene, both parents transmit to their offspring the allele R with the frequency of ½ and the allele W with the frequency of ½. Hence, the frequencies of both alleles in the offspring are:
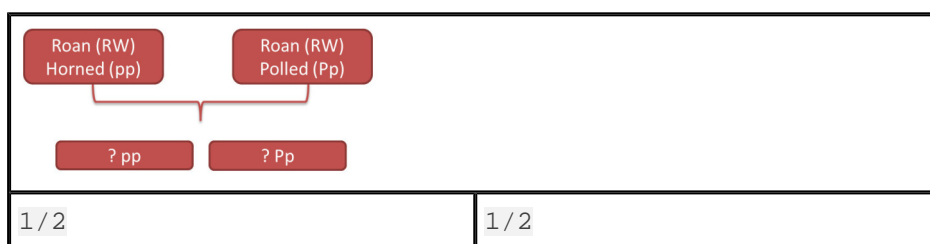
(½ R + ½ W) x (½ R + ½ W) =

Roan (RW) Horned (pp)   Roan (RW) Polled (Pp)

(½ R + ½ W) x (½ R + ½ W) =
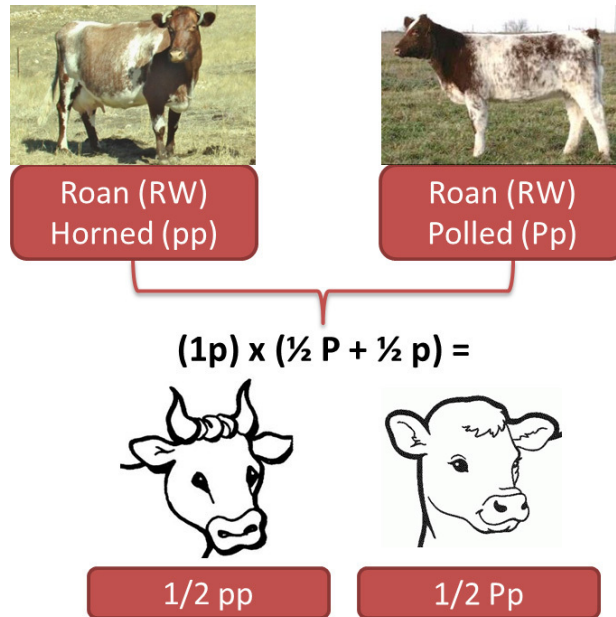
1/4 RR   1/2 RW   1/4 WW

> Solution n°2

Secondly, the expected results, in the offspring, for the **"polled"** locus are (?/?) (please complete the percentages of individuals of each type in the offspring):

Roan (RW) Horned (pp) — Roan (RW) Polled (Pp)	
? pp	? Pp
1/2	1/2

Explanation :

For the polled gene, the horned parent (pp) transmits to its offspring the allele p with the frequency of 1. The polled parent transmits to its offspring the allele P with the frequency of ½ and the allele p with the frequency of ½. Hence, the frequencies of both alleles in the offspring are:

(1 p) x (½ P + ½ p) =

| Roan (RW) Horned (pp) | Roan (RW) Polled (Pp) |

(1p) x (½ P + ½ p) =
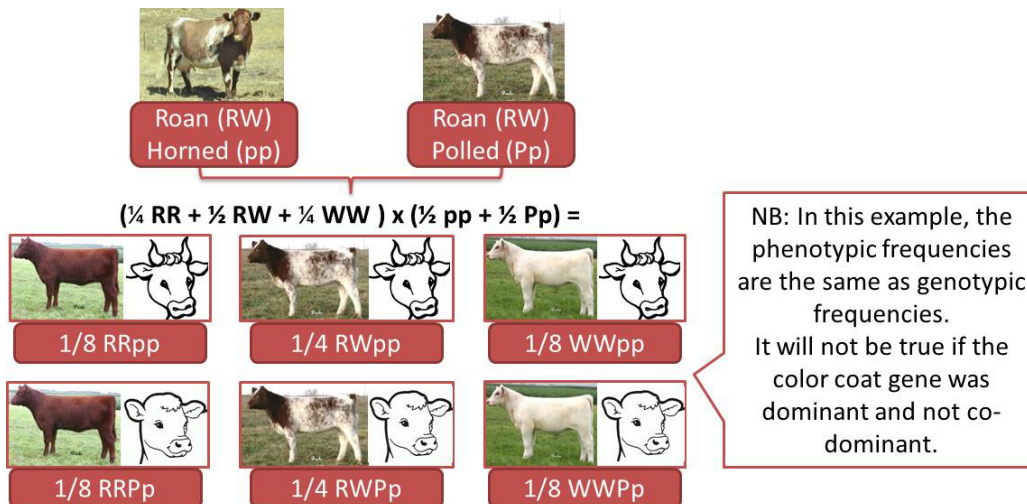

| 1/2 pp | 1/2 Pp |

> Solution n°3

Finally, the expected results, in the offspring, for **these 2 independant loci** are (?/?) (please complete the percentages of individuals of each type in the offspring):

Roan (RW) Horned (pp)		Roan (RW) Polled (Pp)
? RRpp	? RWpp	? WWpp
1/8	1/4	1/8
? RRPp	? RWPp	? WWPp
1/8	1/4	1/8

Explanation :

The proportion of genotypes in the offspring is a multiplicative effect!

(¼ RR + ½ RW + ¼ WW) x (½ pp + ½ Pp) =

Roan (RW)
Horned (pp)

Roan (RW)
Polled (Pp)

(¼ RR + ½ RW + ¼ WW) x (½ pp + ½ Pp) =

1/8 RRpp

1/4 RWpp

1/8 WWpp

1/8 RRPp

1/4 RWPp

1/8 WWPp

NB: In this example, the phenotypic frequencies are the same as genotypic frequencies.
It will not be true if the color coat gene was dominant and not co-dominant.
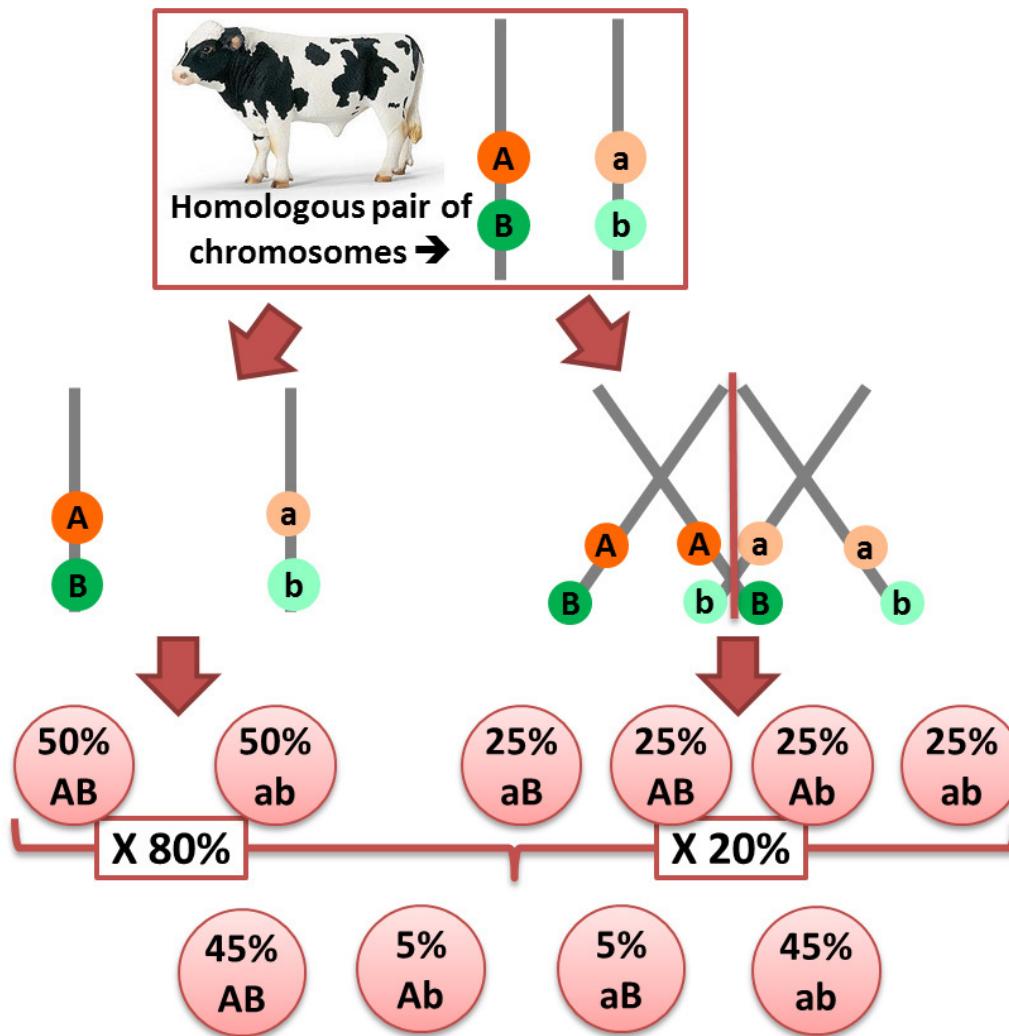
> Solution n°4

Indeed, if we consider two loci linked with a frequency of recombination equal to 20%, then in 80% of the cases there is no recombination during meiosis when in 20% of case there is. Hence, the heterozygous parent actually produces (?%):

Homologous pair of chromosomes ➔

| 1 ? AB | 2 ? ab | 3 ? aB | 4 ? AB | 5 ? Ab | 6 ? ab |

X ? 7   X ? 8

| 9 ? AB | 10 ? Ab | 11 ? aB | 12 ? ab |
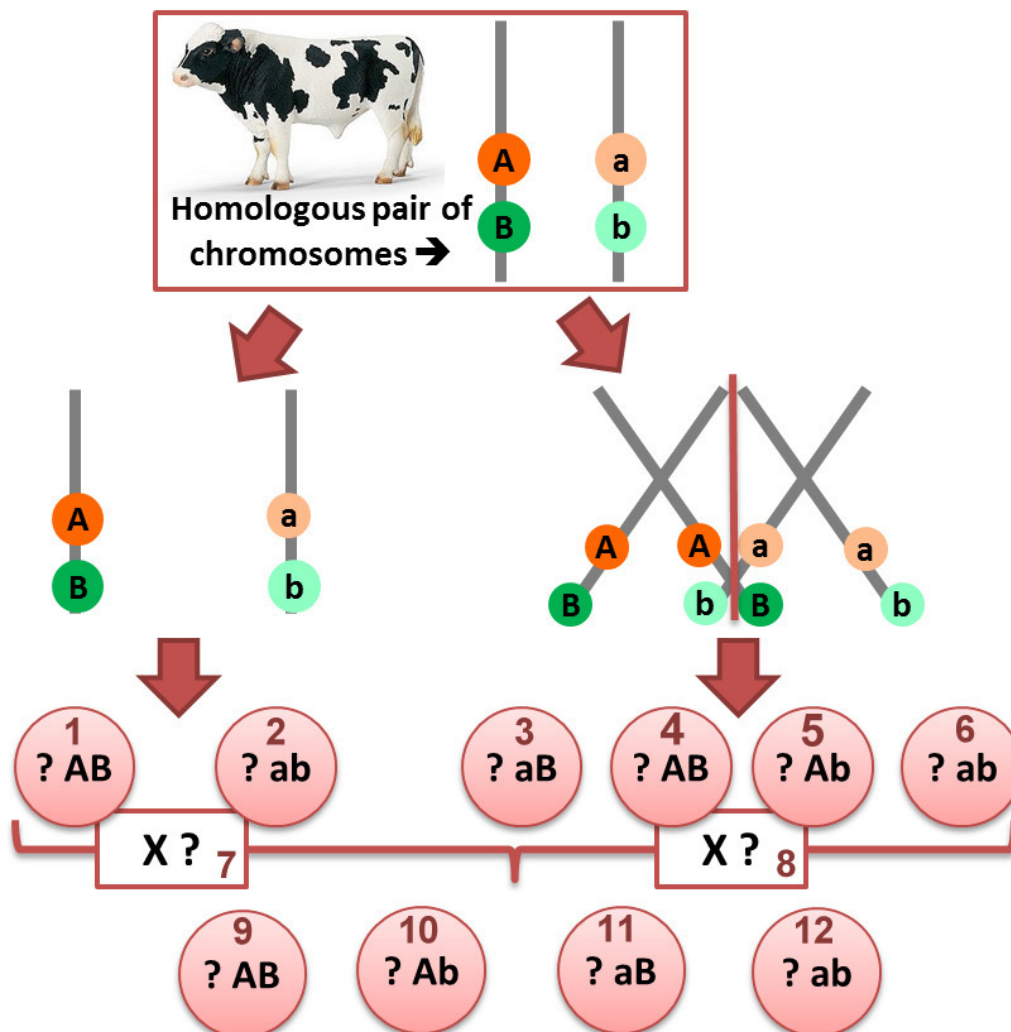
Response 1:	50%	Response 7:	80%
Response 2:	50%	Response 8:	20%
Response 3:	25%	Response 9:	45%
Response 4:	25%	Response 10:	5%
Response 5:	25%	Response 11:	5%
Response 6:	25%	Response 12:	45%

Explanation :

In 80% of cases, there is no recombination. It means that the parent transmits the chromosome AB or the chromosome ab with the frequency of ½ each. In 20% of cases, there is recombination. It means that there is a crossover between the two chromosomes (cf figure below) to produce germ cells with alleles aB or AB or Ab or ab with the frequency of ¼. Hence, the parents produces the following germ cells:
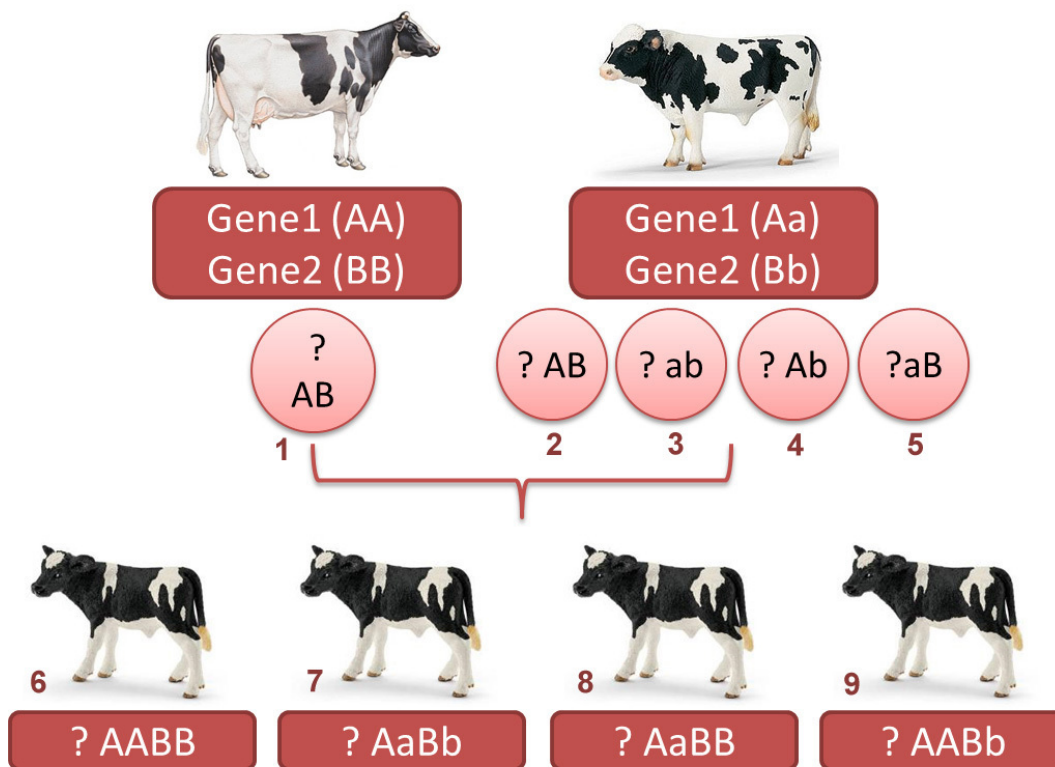

> Solution n°5

Exercice p. 10

Therefore, if we mate this heterozygous parent for two linked genes with an homozygous parent for the same loci, in the offspring we expect (?%):

| Gene1 (AA) Gene2 (BB) | Gene1 (Aa) Gene2 (Bb) |

| ? AB (1) | ? AB (2) | ? ab (3) | ? Ab (4) | ?aB (5) |

| 6 ? AABB | 7 ? AaBb | 8 ? AaBB | 9 ? AABb |

Response 1:	100%	Response 6:	45%
Response 2:	45%	Response 7:	45%
Response 3:	45%	Response 8:	5%
Response 4:	5%	Response 9:	5%
Response 5:	5%		

Explanation :

The homozygous parent transmits exclusively the chromosome AB. Hence, by multiplying with the frequencies of alleles transmitted by the heterozygous parent, the expected results in the offspring are:
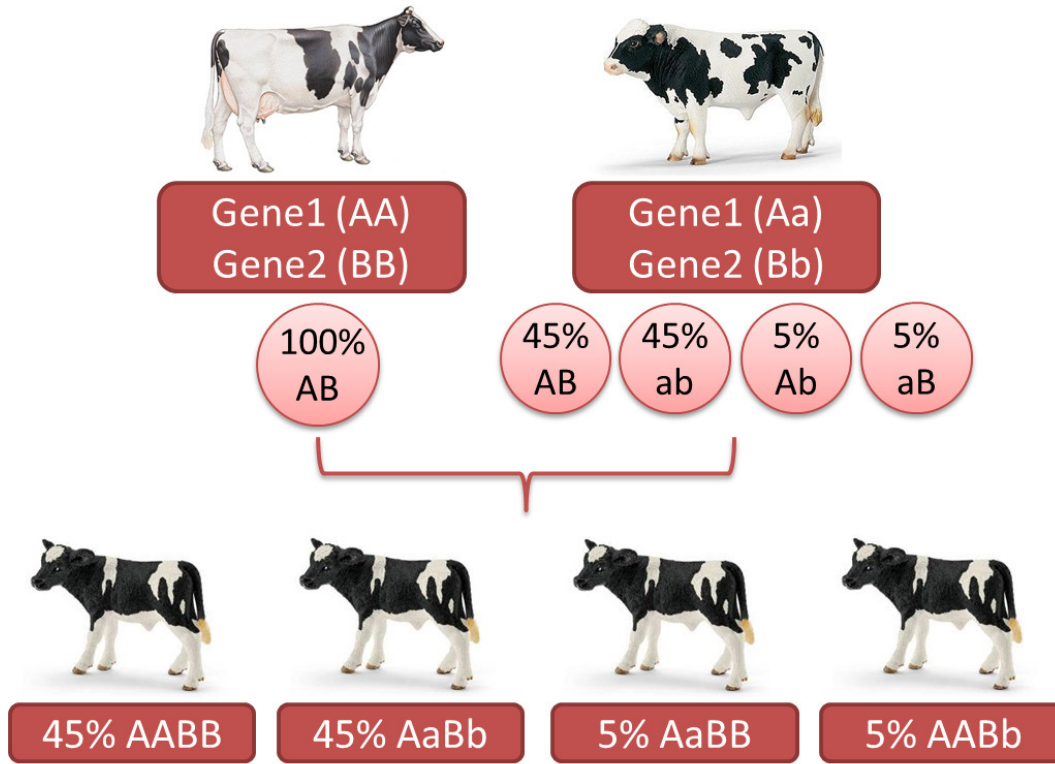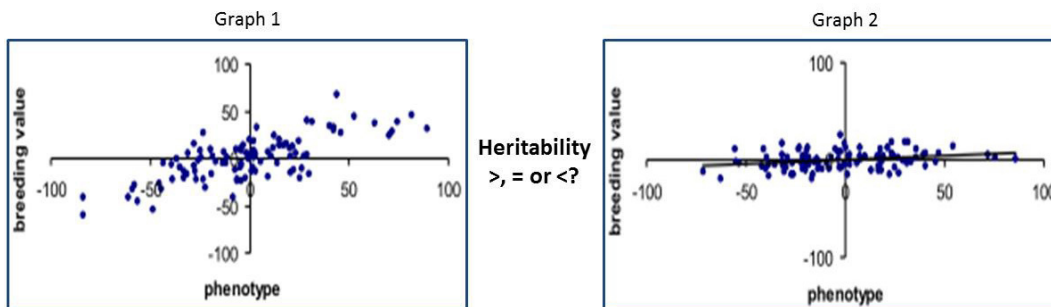
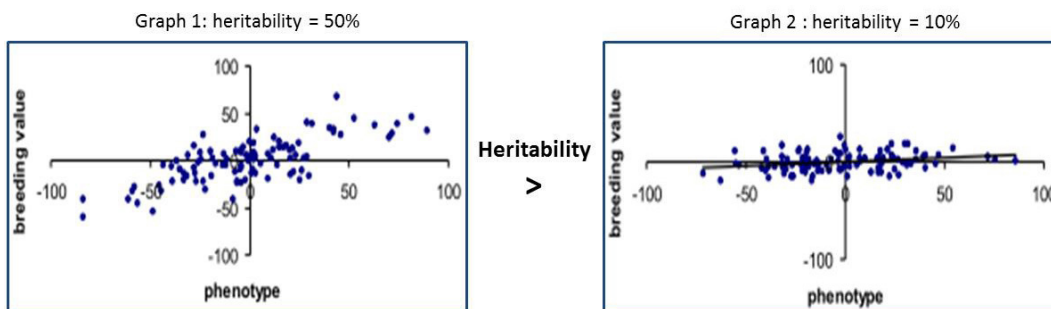| 45% AABB | 45% AaBb | 5% AaBB | 5% AABb |

> ## Solution n°6

In the figure below, which trait has the highest heritability, the one presented in graph 1 or in graph 2?

Relationship between breeding value and phenotype, depending on heritability

Heratibility >

Explanation :

Relationship between breeding value and phenotype, depending on heritability
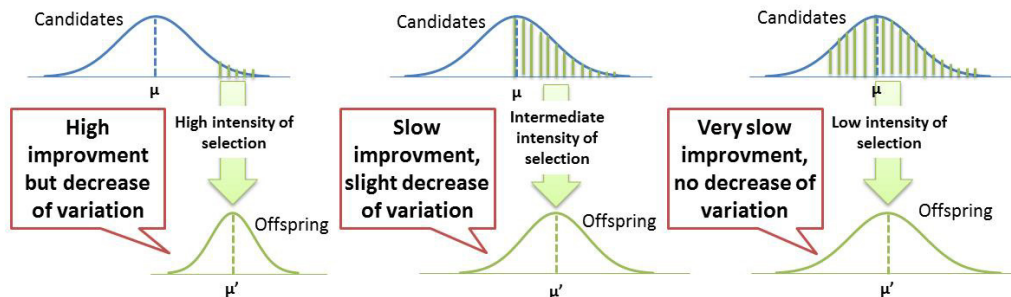
From this exercise, we note that:

1. The higher the heritability is, the larger the part of phenotypic difference is attributed to breeding value.
2. The slope of regression line between breeding values and phenotype is equal to the heritability.

> Solution n°7

The solution is:

What is important to understand and remember from this illustration is:

Fundamental

When there is selection, the variability in the population decrease. Hence, in order to maintain choices for reproducers in next generations, **intensity of selection** should result from a compromise between genetic gain expectation and preservation of genetic variation.

> Solution n°8

For the first strategy, the differential of selection will be: **+785.5 kg** for milk yield and **-0.875 g/kg** for protein content.

Here are the bulls selected:

	Milk	Protein content
36	1130	-1.9
40	1080	-2.2
38	950	-2.8
35	800	-1.1
34	765	2.5
33	755	-1.15
32	625	-0.2
30	600	-0.1
31	590	-0.6
29	560	-0.5

> Solution n°9

For the second strategy, the differential of selection will be: **-27 kg** for milk yield and **+1.7 g/kg** for protein content.

Here are the bulls selected:

	Milk	Protein content
19	45	2.5
1	-750	2.2
21	100	2
35	800	1.8
5	-400	1.7
3	-500	1.7
4	-465	1.4
27	550	1.3
37	320	1.2
18	30	1.2

> Solution n°10

Finally, for the third strategy, the differential of selection will be: **+305 kg** for milk yield and **+1.2 g/kg** for protein content.

Here are the bulls selected:

	Milk	Protein content
18	30	1.2
19	45	2.5
20	45	1
21	100	2
22	370	1.1
26	530	0.4
27	550	1.3
35	800	1.8
37	320	1.2
39	260	-0.05

Fundamental

What is important to remember from this example is that:

1. When we only consider one trait in selection, traits genetically negatively correlated will be deteriorated.

2. When we consider both traits, we will be able to have genetic gain for both traits. However, the gain for each trait will be lower than when we only considered one trait.
3. For traits with lower heritability, improvement of negatively correlated traits will be even more complex.