

Plant Breeding

Semester III

SEC I: Agricultural Botany

Unit 3a: Plant Breeding

SELECTION IN SELF-POLLINATING CROPS

Two methods of selection are generally practiced in self-pollinating species of crop plants:

- **Mass Selection**
- **Pure Line Selection**

MASS SELECTION

- This is the method of improving a crop strain through the selection of a large number of superior plants by visual assessment, pooling of their seeds and developing a new variety from it. Selection is done for easily observable characters like plant height, nature of the panicle, grain or seed size, resistance etc.
- The population raised from the selected plants will be more uniform and superior when compared to the original population. However, the population will show considerable variations especially for quantitative characters. The variations thus produced are sometimes subjected to progeny test.
- Progeny test is the technique of assessing the performance of a crop population by analyzing the performance of its progeny.

PROCEDURE OF MASS SELECTION

The procedure of mass selection extends to 7-8 crop seasons in case of annual crops. The procedure involves identification of superior plants from a population and bulking their seeds, preliminary yield trials, multi-location trials, seed multiplication and distribution.

1. Identification of superior plants and collections of seeds

This is done in the first year of the experiment. A large number of phenotypically similar superior plants are selected and their seeds are bulked.

2. Preliminary Yield Trials

This is usually done in the second year or second crop season. The bulked seeds are grown in a preliminary yield trial. The variety from which selection is made should also be included as a check in order to determine improvement in characteristics.

3. Multi-location trials

This is usually done from the third year onwards

4. Seed Multiplication and Release

After multi-location trials, the seeds are subjected to the procedure of variety release and then multiplied and distributed to farmers.

MERITS AND DEMERITS OF MASS SELECTION

- Varieties developed through mass selection are more widely adapted than pure lines since they are developed from a large number of plants selected for their superior characteristics. The procedure of mass selection is simple and less sophisticated. Mass selection retains considerable degree of genetic variability.
- But, the varieties developed through mass selection are non-uniform in comparison to pure lines. The degree of improvement is only limited. Without progeny test, it is not possible to assess the genetic stability of the variety.

PURE LINE SELECTION

Pure line selection involves the development of a new variety from a simple homozygous self-pollinated plant. As a result, all the individuals within a pure line have the same genotype and variations, if any, are due to the environmental influences. In pure line selection, a large number of superior plants are selected from a self-pollinated crop, harvested individually, individual progenies are raised and evaluated and the best progeny is released as a variety. This technique is also called individual plant selection.

PROCEDURE OF PURE LINE SELECTION

The procedure of pure line selection involves individual selection of superior plants and collection of their seeds separately, growing individual plant progenies and rejection of undesirable progenies, preliminary yield trial and rejection of undesirable progenies, multi-location trials and release of the most adaptable and superior progeny as a new variety.

1. Selection of Superior plants and collection of seeds

A large number of superior plants are selected in the first year based on visual assessment for characteristics and their seeds are collected separately. Selection is made on the basis of easily observable characters.

2. Growing Progeny Lines of the Selected plants

Progeny lines of individual plants are grown in the second year and inferior progeny lines are rejected. Seeds of each lined are collected separately

3. Preliminary Yield Trial

Preliminary yield trial of the remaining progenies is carried out in the third year and inferior progenies are rejected. Seeds of each line are collected separately.

PROCEDURE OF PURE LINE SELECTION

4. Replicated Yield Trials (Multi-location Trials)

Replicated yield trials are carried out at several locations and inferior progeny lines are rejected. The lines are screened for resistance and quality traits. This is done from fourth to seventh years.

5. Variety Release and Seed Multiplication

This is done in the eighth year. The best progeny selected from the above is released as a new variety. The seeds are multiplied for distribution.

CHARACTERISTICS OF PURE LINES

All the plants within a pure line have same genotype, as the parent plants are homozygous and self-fertilizing. Variations, if any, within a pure line are environmental and usually non-heritable. Selection within a pure line is not effective. However, in the course of time, variations produced by mechanical mixtures, mutations and natural hybridization get incorporated into the populations and further cycles of mass selection and pure line selection may become necessary to improve the variety.

MERITS & LIMITATIONS OF PURE LINE SELECTION

- **Pure line selection brings about the maximum possible improvement over the original variety. Pure line selections are extremely uniform in their behavior. Uniform flowering, maturity etc are the characteristic adaptations of pure lines. Due to their extreme uniformity, such variations can easily be identified in seed certification programs.**
- **However, pure line varieties show very narrow range of adaptations to environmental fluctuations. Pure line breeding is a tedious technique and the varieties developed in this way, even though uniform, are short-lived.**

Inbreeding

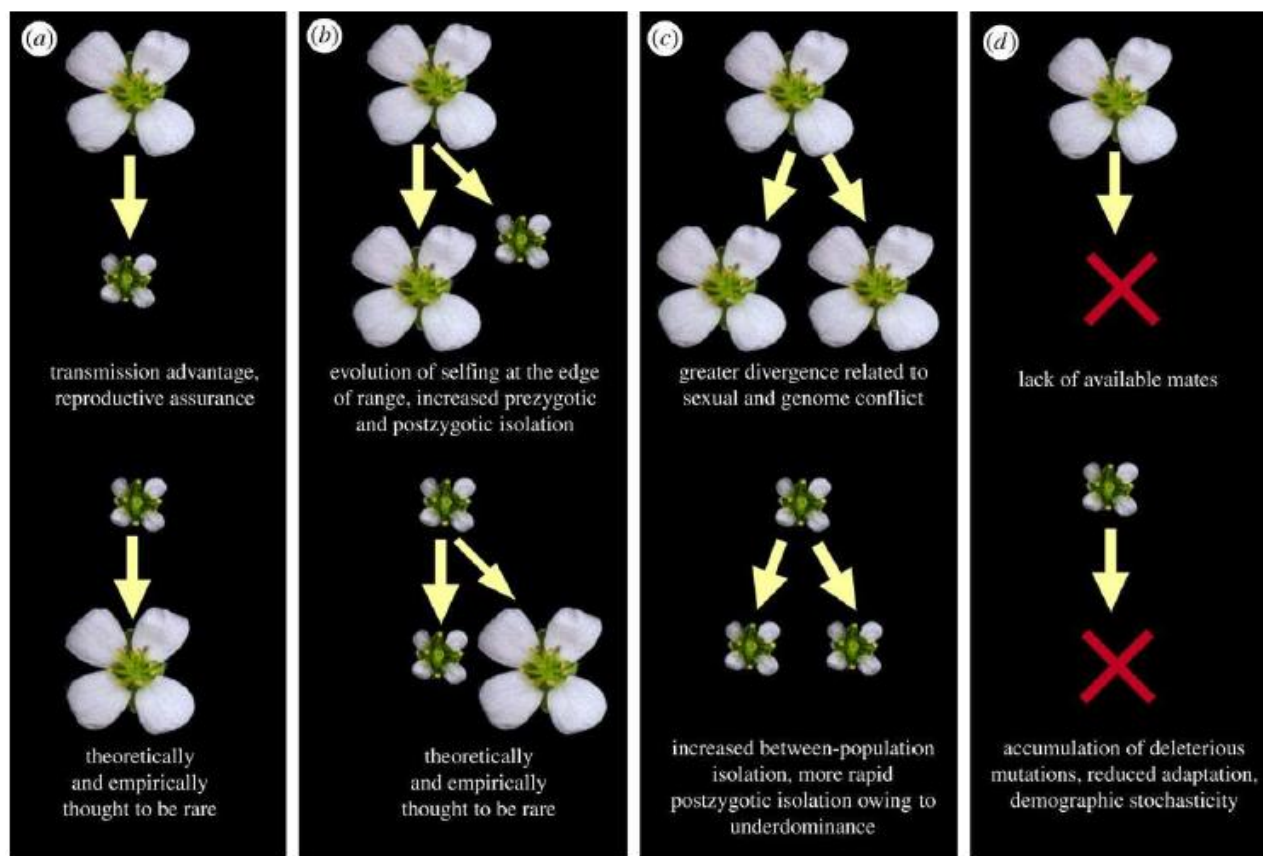
- Inbreeding = mating of related individuals
- Often results in a change in the mean of a trait
- Inbreeding is intentionally practiced to:
 - create genetic uniformity of laboratory stocks
 - produce stocks for crossing (animal and plant breeding)
- Inbreeding is unintentionally generated:
 - by keeping small populations (such as is found at zoos)
 - during selection

INBREEDING DEPRESSION:-

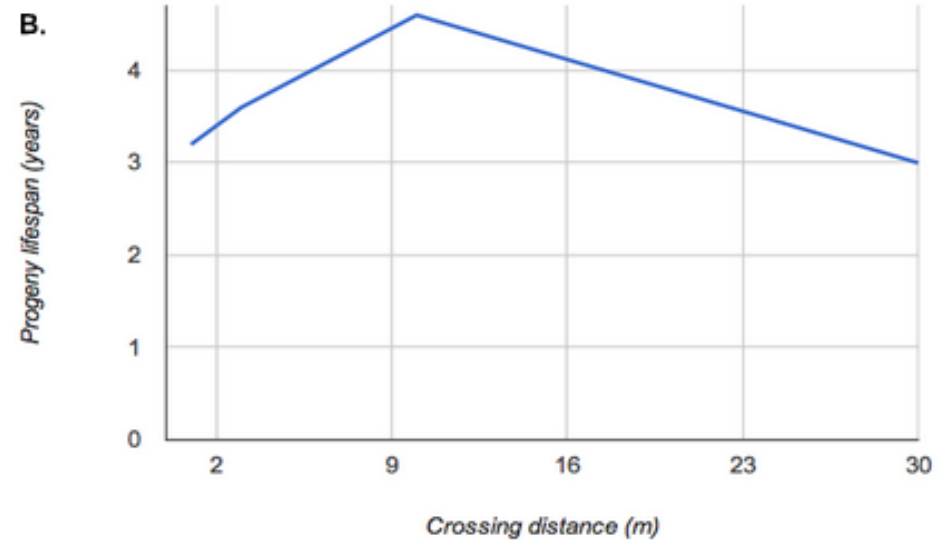
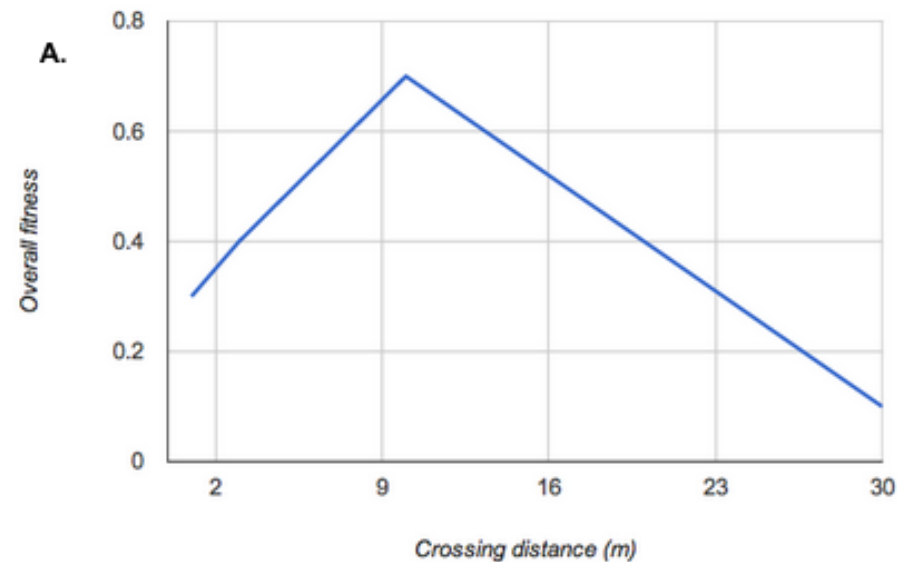
- ❖ **Inbreeding depression** is the reduced biological fitness in a given population as a result of inbreeding, or breeding of related individuals. Population biological fitness refers to an organism's ability to survive and perpetuate its genetic material. Inbreeding depression is often the result of a population bottleneck. In general, the higher the genetic variation or gene pool within a breeding population, the less likely it is to suffer from inbreeding depression.
- ❖ Inbreeding depression seems to be present in most groups of organisms, but varies across mating systems. Hermaphroditic species often exhibit lower degrees of inbreeding depression than outcrossing species, as repeated generations of selfing is thought to purge deleterious alleles from populations. For example, the outcrossing nematode (roundworm) *Caenorhabditis remanei* has been demonstrated to suffer severely from inbreeding depression, unlike its hermaphroditic relative *C. elegans*, which experiences **outbreeding depression**.

HISTORY:-

- ❖ A systematic observation on the effects of inbreeding date back to about 1700AD
- ❖ In 1876 Darwin published his book on cross and self fertilization in vegetable kingdom, Darwin concluded that progeny obtain from self fertilization were weaker than those derived from out crossing
- ❖ Darwin also reported the result from his experiments on self and cross fertilization in maize, these are the first published account of inbreeding depression
- ❖ Detail information on inbreeding in maize was published independently by East in 1908 and Shull in 1909.



Processes affecting macroevolutionary diversification of outcrossers (top panel) and selfers (bottom panel), and factors that may enhance rates of transition. (a) Transitions from outcrossing to selfing are thought to be common, while the reverse is rare. (b) Selfing may often evolve as a speciation process, where the ancestral outcrossing lineage persists. (c) Speciation rates within outcrossers can be enhanced by higher rates of sexual and genomic conflicts, whereas selfers may experience accelerated rates of speciation owing to greater mating isolation and more rapid post-zygotic isolation owing to underdominant alleles. (d) Extinction rates in outcrossers can be enhanced by the lack of available mates, whereas extinction rates in selfers may be increased by reduced adaptive potential and by the accumulation of deleterious mutations.



Inbreeding depression in [*Delphinium nelsonii*](#). **A.** Overall fitness of progeny cohorts and the **B.** [progeny lifespan](#) were all lower when progeny were the result of crosses with pollen taken close to a receptor plant.

Inbreeding



Prepotency



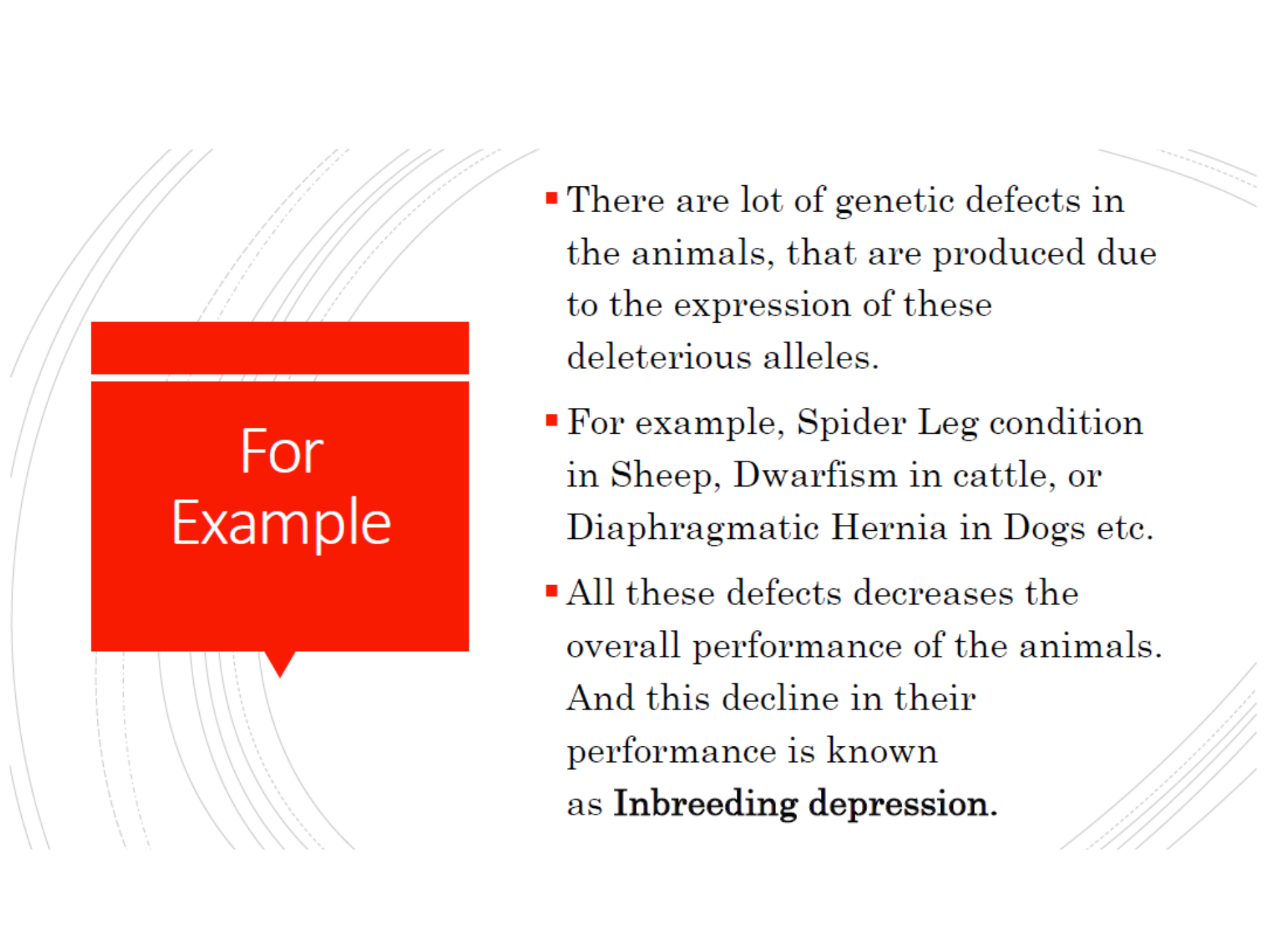
Expression
of deleterious
alleles

Prepotency

- "The ability of an individual to produce progeny whose performance is especially like its own"
- One of the consequence of inbreeding is the greater prepotency in the animals, means the performance of the offspring is similar to their parents.
- And that is why the inbreeding is performed.

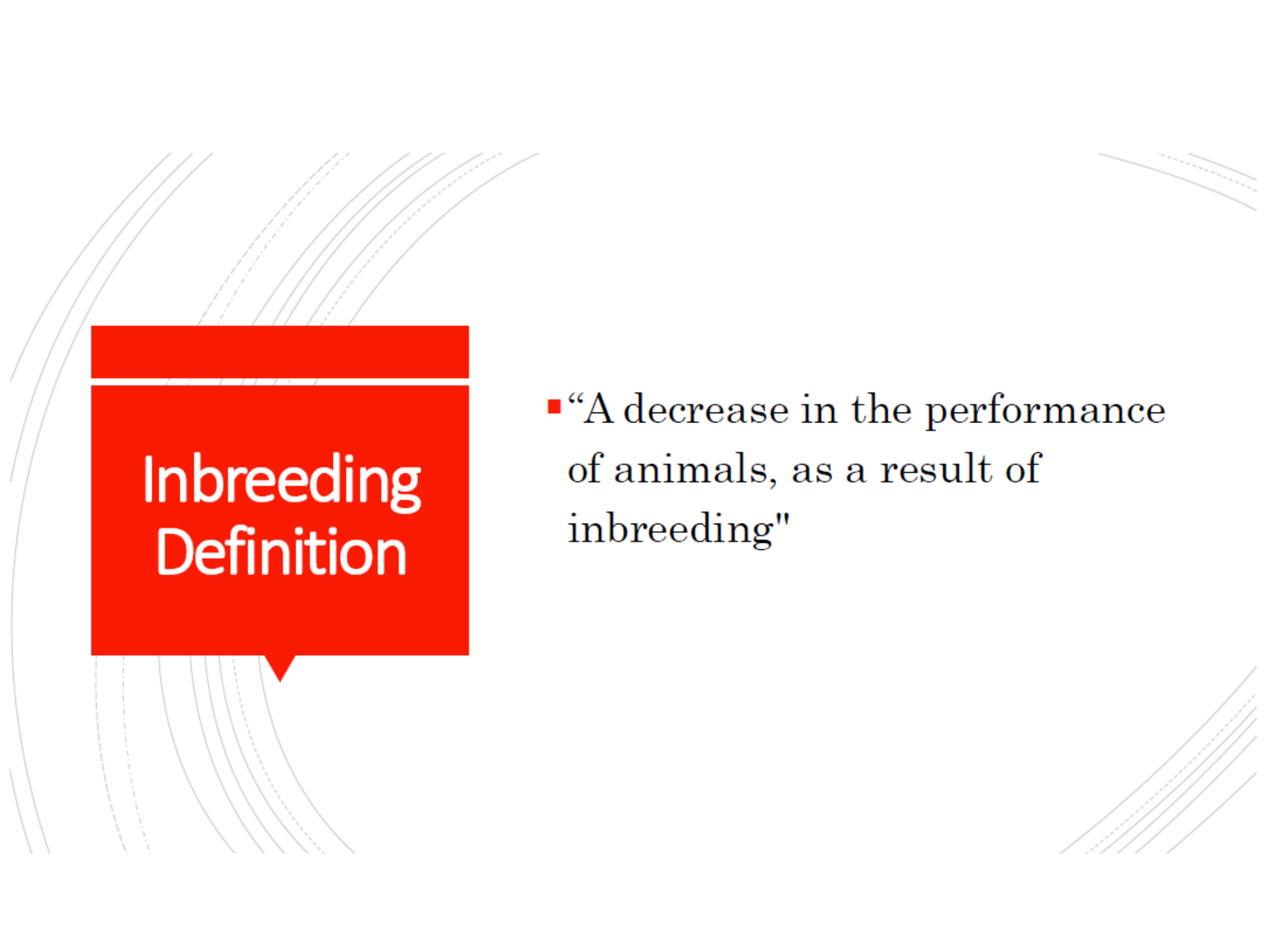
Deleterious Alleles

- "Are the damaging or defected genes produced after certain spontaneous mutation in the genotype."
- These alleles are often recessive and a heterozygous individual carrying a single recessive deleterious allele will not be affected. But if it is homozygous carrying both recessive deleterious allele will be affected by any particular defect.
- As inbreeding causes the increase in the homozygosity it causes the expression of deleterious genes.

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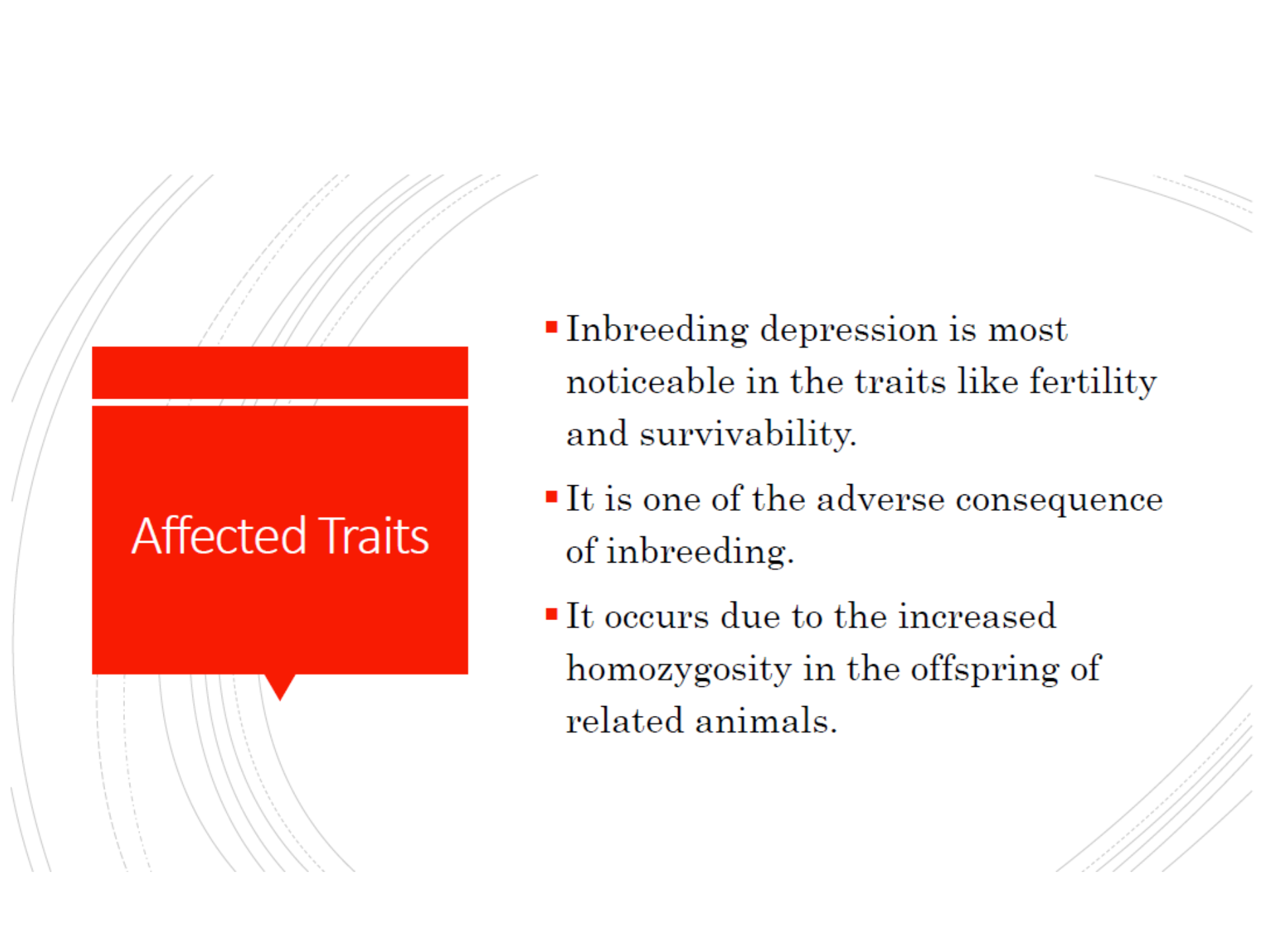
For Example

- There are lot of genetic defects in the animals, that are produced due to the expression of these deleterious alleles.
- For example, Spider Leg condition in Sheep, Dwarfism in cattle, or Diaphragmatic Hernia in Dogs etc.
- All these defects decreases the overall performance of the animals. And this decline in their performance is known as **Inbreeding depression**.

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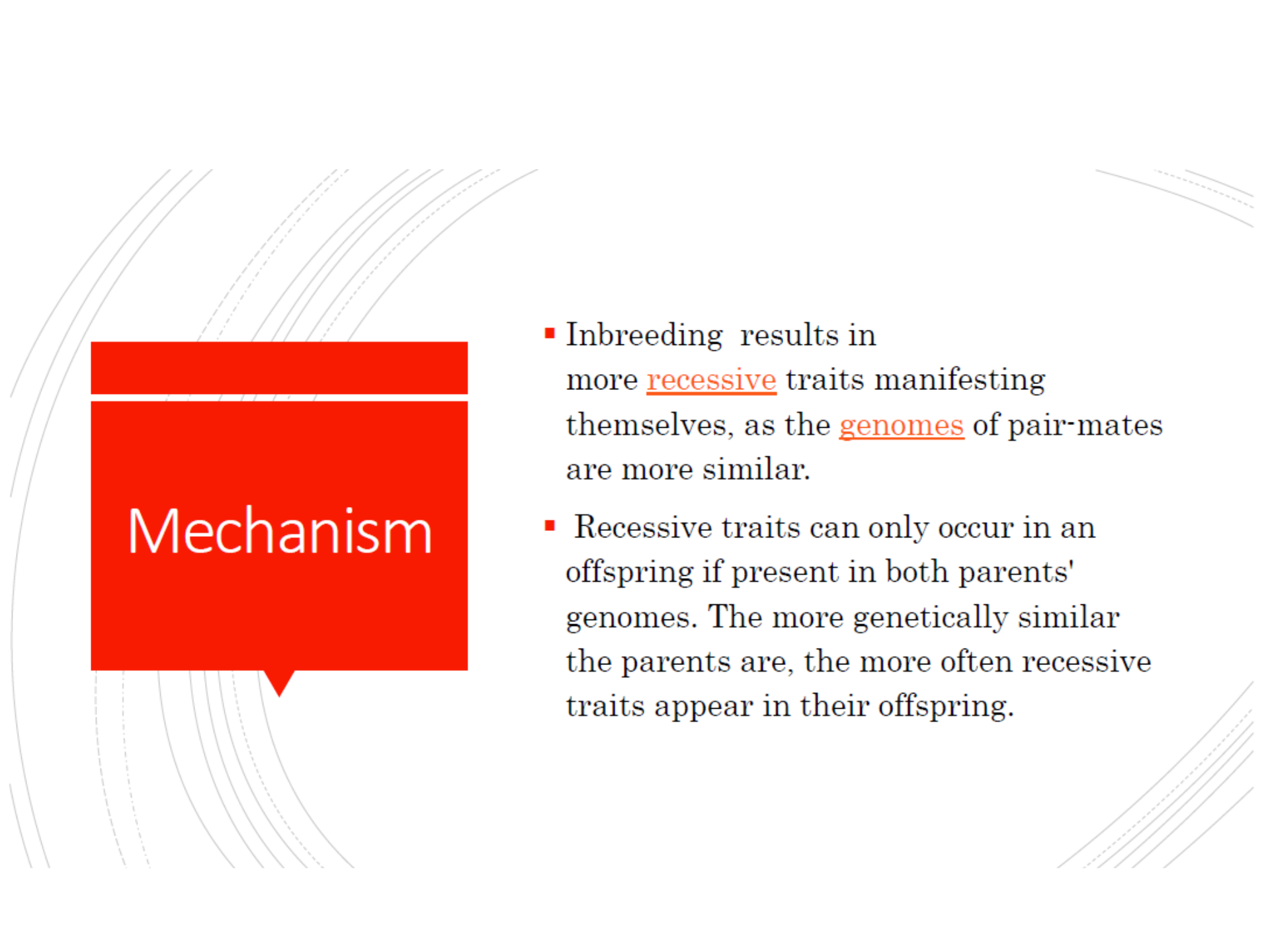
Inbreeding Definition

- “A decrease in the performance of animals, as a result of inbreeding”

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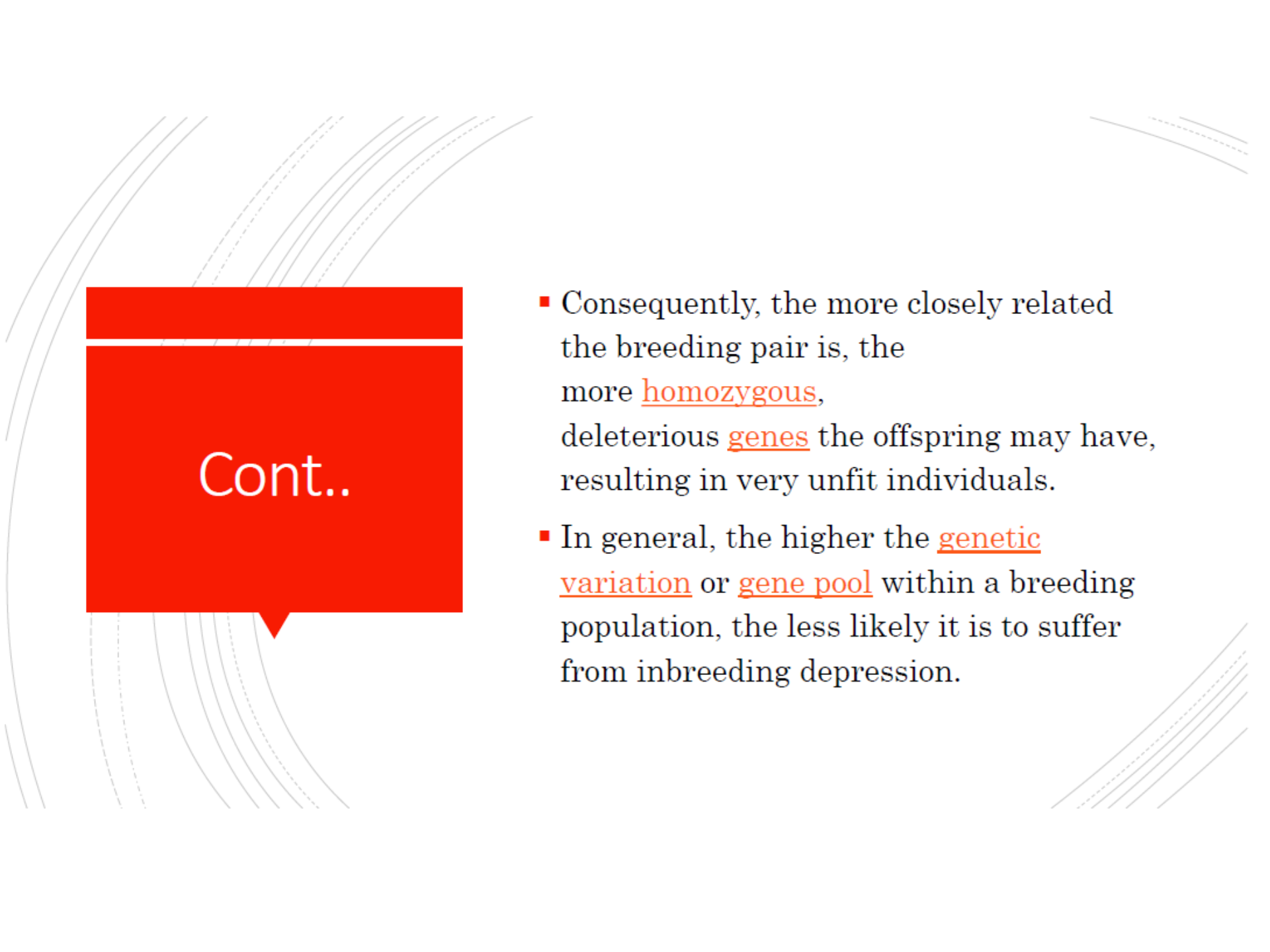
Affected Traits

- Inbreeding depression is most noticeable in the traits like fertility and survivability.
- It is one of the adverse consequence of inbreeding.
- It occurs due to the increased homozygosity in the offspring of related animals.

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Mechanism

- Inbreeding results in more recessive traits manifesting themselves, as the genomes of pair-mates are more similar.
- Recessive traits can only occur in an offspring if present in both parents' genomes. The more genetically similar the parents are, the more often recessive traits appear in their offspring.

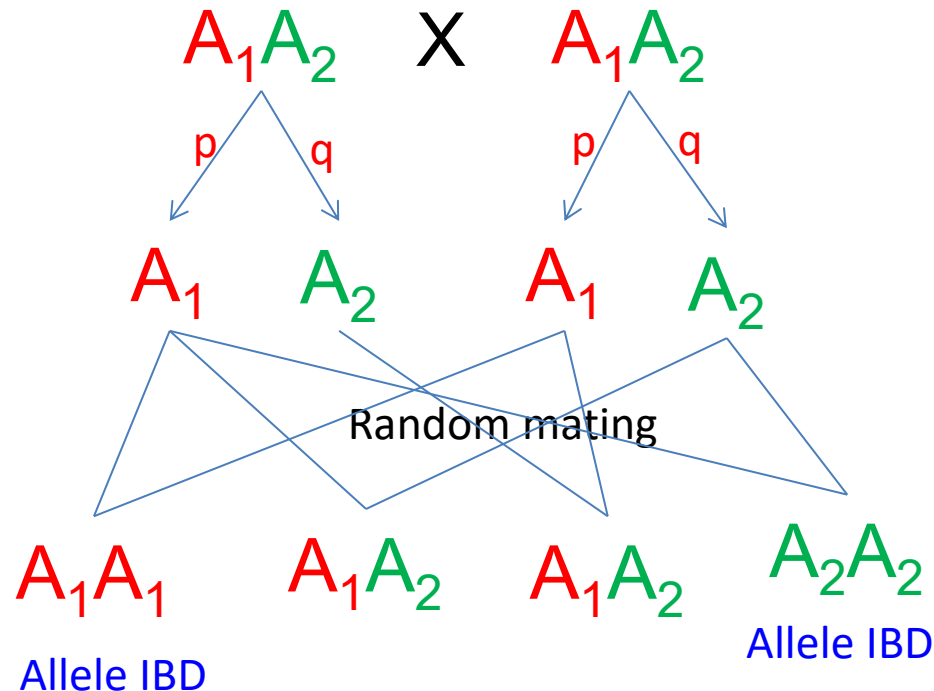
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Cont..

- Consequently, the more closely related the breeding pair is, the more homozygous, deleterious genes the offspring may have, resulting in very unfit individuals.
- In general, the higher the genetic variation or gene pool within a breeding population, the less likely it is to suffer from inbreeding depression.

NON-RANDOM MATING

- **Inbreeding:** mating between close relatives leads to deviations from H-W equilibrium by causing a deficit of heterozygotes.



$$\text{freq}(A_1) = p,$$
$$\text{freq}(A_2) = q$$

- In the extreme case of self-fertilization:

Generation	AA	Aa	aa
0	p^2	$2pq$	q^2
1	$p^2 + (pq/2)$	pq	$q^2 + (pq/2)$
2	$p^2 + (3pq/4)$	$pq/2$	$q^2 + (3pq/4)$

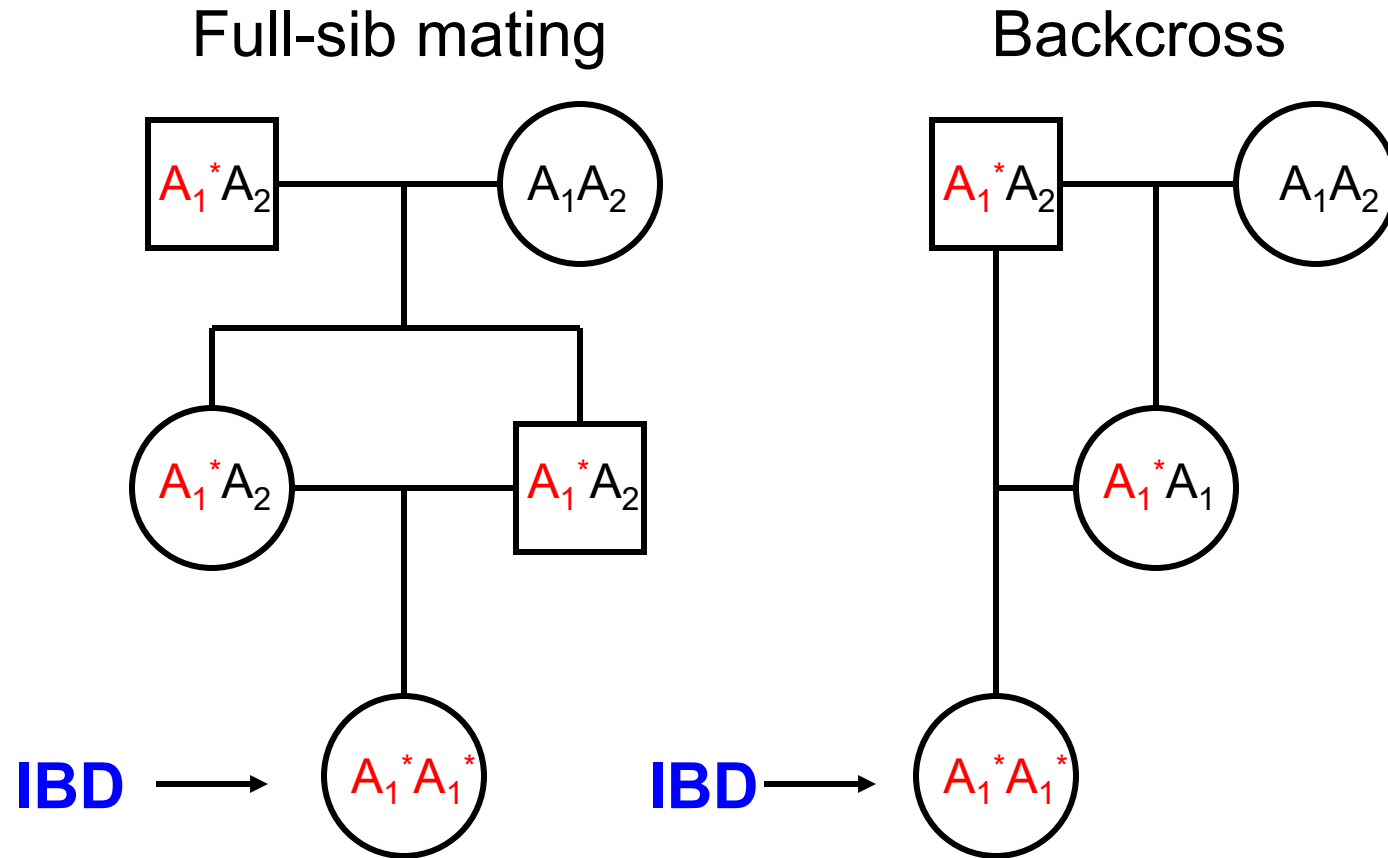
HOW CAN WE QUANTIFY THE AMOUNT OF INBREEDING IN A POPULATION?

- The inbreeding coefficient,

F

- The probability that a randomly chosen individual carries two copies of an allele that are *identical* by descent from a recent ancestor.
- The probability that an individual is *autozygous*

■ Consider two pedigrees:



AVERAGE F FROM EACH MATING IS 0.25

LOSS OF HETEROZYGOSITY IN LINE OF SELFERS

- Population Size (N) = 1

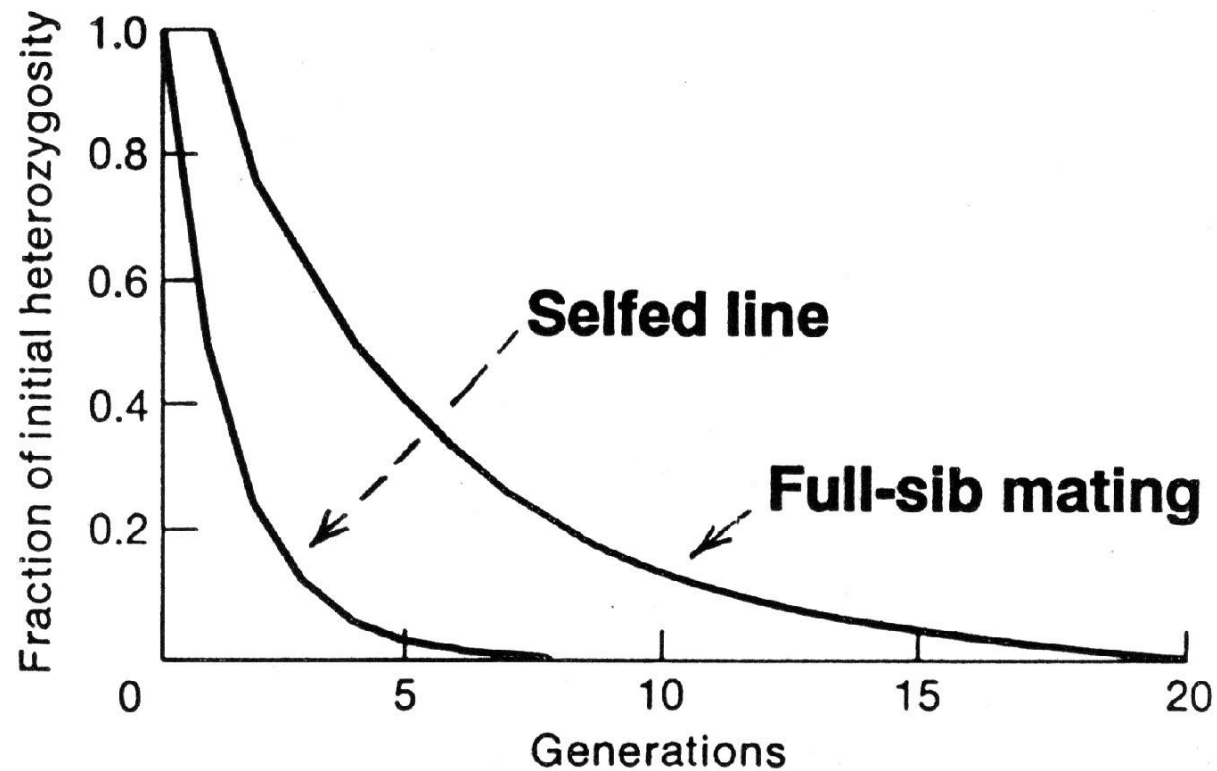
Heterozygosity after one generation, $H_1 = (1/2) \times H_0$

Heterozygosity after two generations, $H_2 = (1/2)^2 \times H_0$

After **t** generations of selfing, $H_t = (1/2)^t \times H_0$

- Example: After $t = 10$ generations of selfing, only 0.098% of the loci that were heterozygous in the original individual will still be so. The inbred line is then essentially completely homozygous.

DECLINE IN HETEROZYGOSITY DUE TO INBREEDING



HETEROZYGOSITY IN A POPULATION THAT IS PARTIALLY INBRED

- In an inbred population the frequencies of homozygous individuals are higher than expected under HWE. Thus, the observed heterozygosity will be lower than expected under HWE.

$$H_{\text{obs}} = 2pq(1-F) = H_{\text{exp}}(1-F).$$

- F ranges from 0 (no inbreeding) to 1 (completely inbred population)

Inbreeding coefficient

The inbreeding coefficient of an individual is the average probability that two genes at any given locus are identical by descent.

The average inbreeding coefficient of all individuals in a population expresses the amount of drift in allelic frequencies from a defined base population. (Falconer 2009)

If inbreeding is the only source of disequilibrium, the inbreeding coefficient (F) in a population for a given locus can be estimated from the deviation between the expected (H_e) and observed number (H_o) of heterozygotes. (Groen 1995)

F CALCULATED FROM HETEROZYGOTE DEFICIT

$$F = (H_{\text{exp}} - H_{\text{obs}}) / H_{\text{exp}}$$

Where,

H_{exp} = frequency of heterozygotes if all matings were *random*

Mean Kinship

Mean kinship is calculated by the kinship (relatedness) of that individual with the entire current population (including itself). Therefore mean kinships per individual are relative to the current population. This means that mean kinship of a specific individual might change over time when a population changes. For example mean kinship will increase each time an individual produces progeny.

Relationship between Kinship (ϕ) and inbreeding coefficient (F)

$$\phi = \frac{1}{2}(1 + F)$$

Changes in the mean under inbreeding

Genotypes

A_1A_1

A_1A_2

A_2A_2

$$\text{freq}(A_1) = p, \quad \text{freq}(A_2) = q$$

Using the genotypic frequencies under inbreeding, the population mean μ_F under a level of inbreeding F is related to the mean μ_0 under random mating by:

$$\mu_F = \mu_0 - 2Fpqd$$

Where d is a change of mean value due to dominance ($d \neq 0$)

For a single locus,

if $d > 0$, inbreeding will decrease the mean value of the trait.

If $d < 0$, inbreeding will increase the mean

For multiple loci,

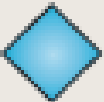
Inbreeding depression requires **directional dominance**.

The magnitude of the change of mean on inbreeding depends on gene frequency, and is greatest when $p = q = 0.5$

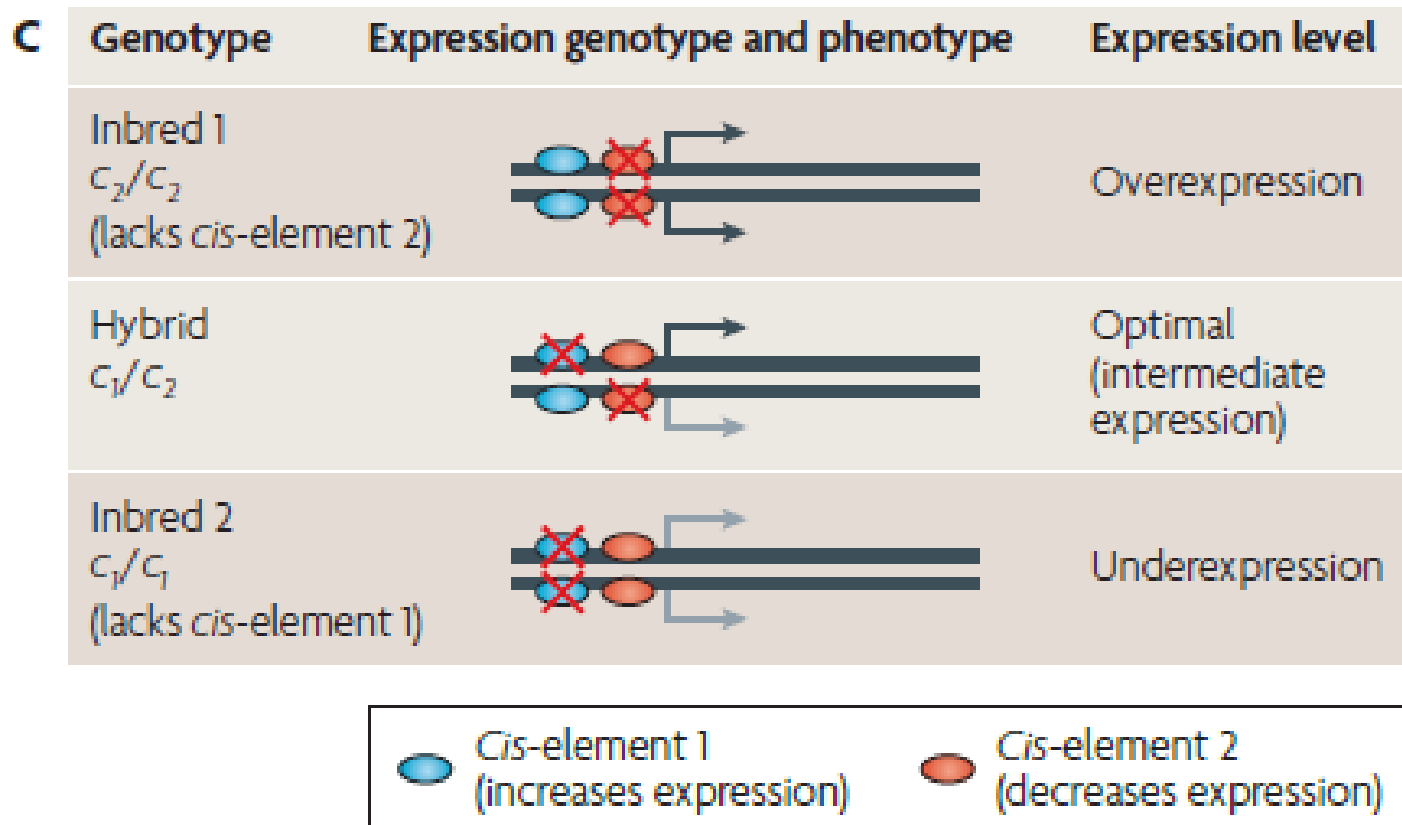
Why do traits associated with fitness show inbreeding depression?

- Two competing hypotheses:
 - **Overdominance Hypothesis**: Genetic variance for fitness is caused by loci at which heterozygotes are more fit than both homozygotes. Inbreeding decreases the frequency of heterozygotes, increases the frequency of homozygotes, so fitness is reduced.
 - **Dominance Hypothesis**: Genetic variance for fitness is caused by rare deleterious alleles that are recessive or partly recessive; such alleles persist in populations because of recurrent mutation. Most copies of deleterious alleles in the base population are in heterozygotes. Inbreeding increases the frequency of homozygotes for deleterious alleles, so fitness is reduced.

Model	Parent genotypes	F ₁ hybrid genotypes and their fitness (or quality) relative to the parent genotypes
Recessive deleterious mutations		
Dominance hypothesis		
Single locus		Intermediate fitness but above the parental average (homozygote shows inbreeding depression)
Multiple loci (effects of different mutant alleles marked in hybrids)		High fitness (heterosis and inbreeding depression)
Recessive deleterious mutations at closely linked loci		Higher fitness than the parent genotypes
Single loci with heterozygous advantage		High fitness (heterosis and inbreeding depression in homozygote)

	Gene A	Gene B	Protein produced	Functional?
				
				
				
Parent 1				No
Parent 2				No
Hybrid				Yes

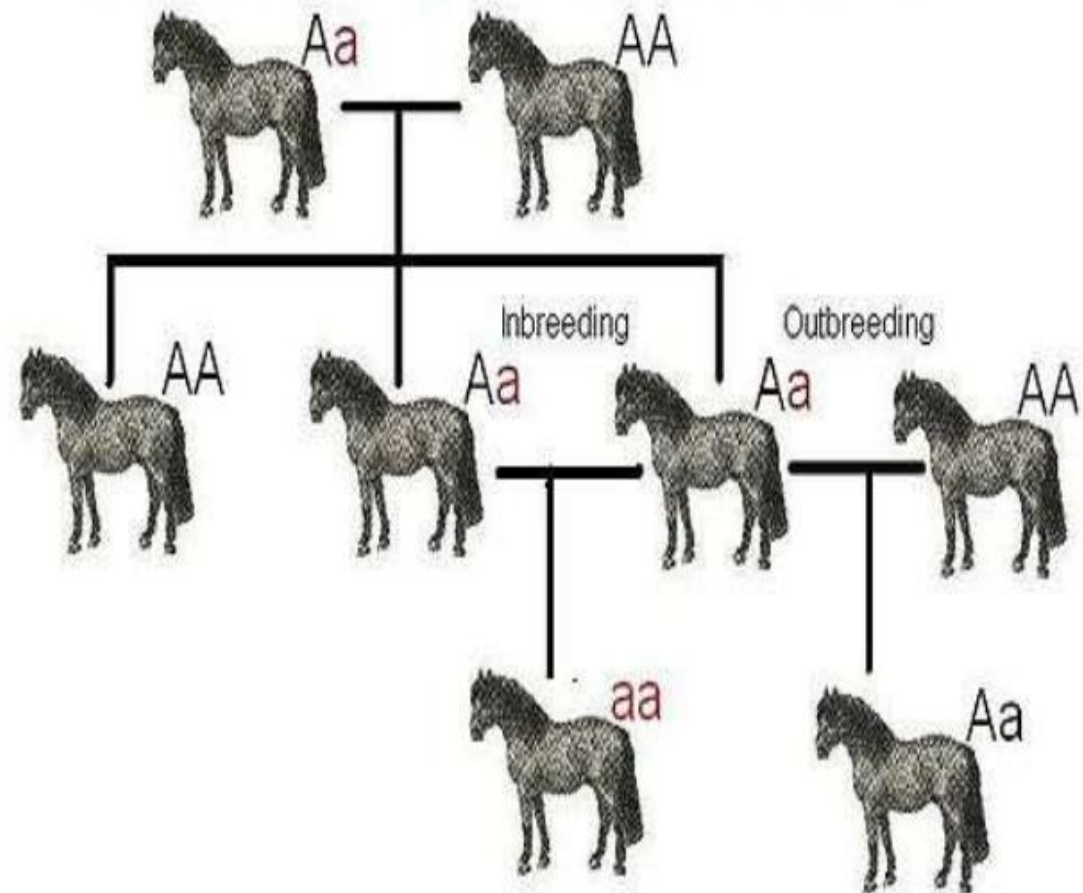
Protein complexes, including *trans*-acting transcription factors, can yield apparent overdominance. Genes *A* and *B* each encode a component of such a complex. Each parent has a mutation and lacks one component, whereas their F1 progeny receive functional alleles for both components and therefore have a functional complex (and higher fitness).



Single-locus overdominance when optimal expression is between that of the two parents⁷⁴. This might happen if one parent (inbred 1) overexpresses the gene owing to the lack of an expression-decreasing *cis*-regulatory element (*cis*-element 2; orange oval) and the other parent (inbred 2) has an allele that causes suboptimal expression owing to the lack of an expression-increasing *cis*-regulatory element (*cis*-element 1; blue oval). In the F1 hybrid, the two mutations complement one another, to give a form of pseudo-overdominance.

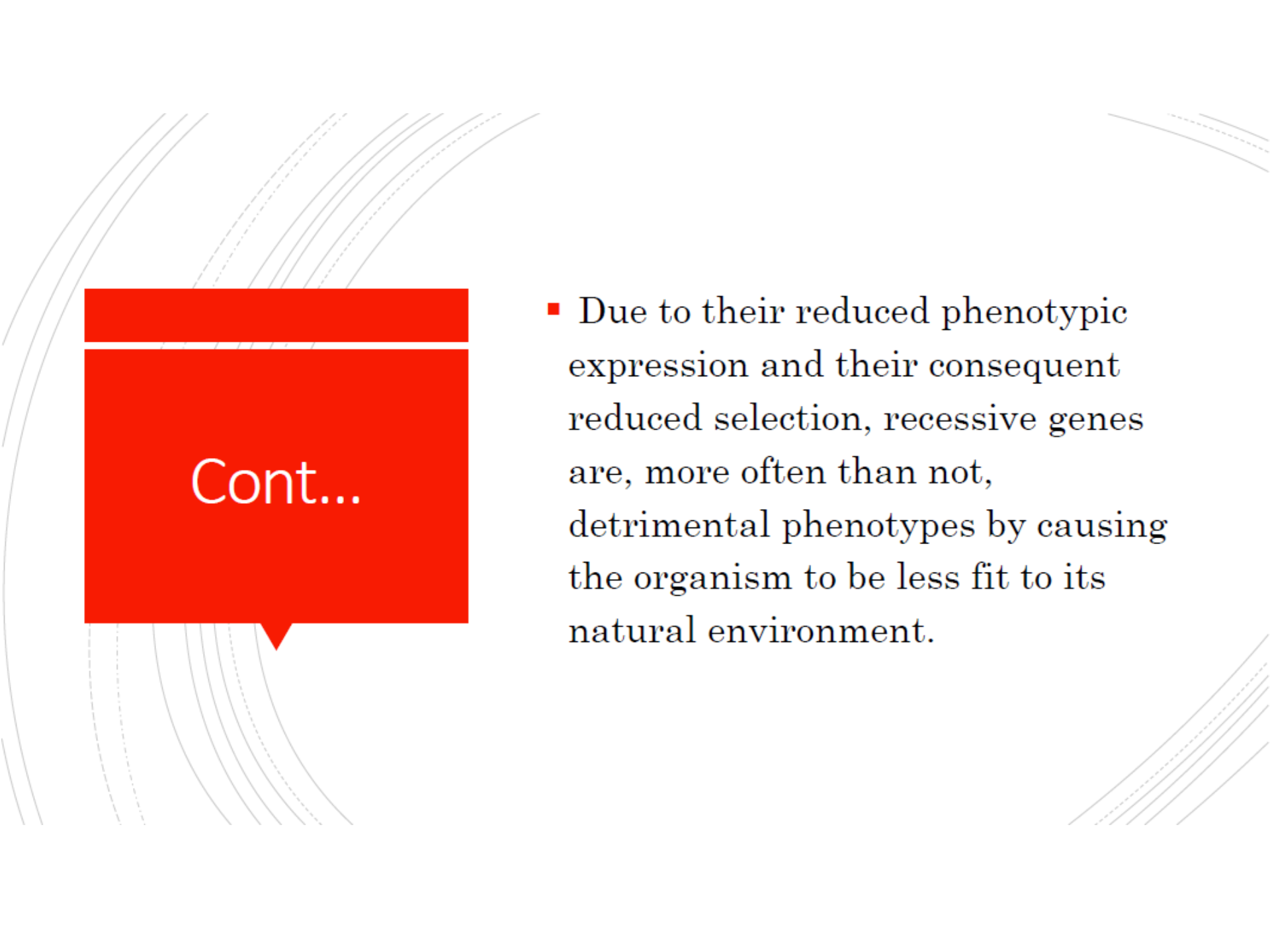
EXAMPLE

A = Dominant allele a = Recessive deleterious allele



Illustration

- In this example, a is the recessive allele which has negative effects. In order for the a phenotype to become active, the gene must end up as homozygous aa because in the genotype Aa , the A takes dominance over the a and the a does not have any effect.

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Cont...

- Due to their reduced phenotypic expression and their consequent reduced selection, recessive genes are, more often than not, detrimental phenotypes by causing the organism to be less fit to its natural environment.

How to reduce inbreeding depression ?

- **Natural Selection**:- cannot effectively remove all deleterious recessive genes from a population for several reasons. First, deleterious genes arise constantly through mutation within a population. Second, in a population where inbreeding occurs frequently, most offspring will have some deleterious traits, so few will be more fit for survival than the others.

Artificial Selection

- Introducing alleles from a different population can reverse inbreeding depression. Different populations of the same species have different deleterious traits, and therefore their cross breeding will not result in homozygosity at most loci in the offspring.

Effects of Inbreeding

- ✓ Inbreeding is due to a reduction in vigour and reproductive capacity that is fertility.
- ✓ There is a general reduction in the size of various plant parts and in yield.
- ✓ The effects of inbreeding may be summarised as under.

a) Appearance of Lethal and Sublethal Alleles:

- ✓ Inbreeding to the appearance of lethal, sublethal and subvital characteristics.
- ✓ Such characteristics include chlorophyll deficiencies E.g Albino, chlorine rootles seedlings , defects in flower structure etc. generally, plants carrying such characteristics cannot maintained and are lost from the population.

b) Reduction in Vigour:

- ✓ There is a general reduction in the vigour of the population.
- ✓ Plants become shorter and weaker because of general reduction in the size of various plant parts.

c) Reduction in Reproductive Ability:

- ✓ The reproductive ability of the population decreases rapidly.
- ✓ Many lines (plant progenies) reproduction poorly that they cannot be maintained.

Effects of Inbreeding cont...

d) Separation of the Population into Distinct Lines:

- ✓ The population rapidly separates into phenotypically distinct lines.
- ✓ This is because of an increase in homozygosity due to which there is random fixation of various alleles of different lines.
- ✓ Therefore, the lines differ in their genotype and consequently in phenotype.

e) Increase in Homozygosity:

- ✓ Each line becomes increasingly homozygous following inbreeding.
- ✓ Consequently, the variation within a line decreases rapidly.
- ✓ Ultimately, after 7 to 8 generations of selfing, the lines become almost uniform.
- ✓ Since they approach complete homozygosity (> 99 percent homozygosity).
- ✓ The lines, which are almost homozygous due to continued inbreeding and are maintained through close inbreeding, are known as inbred lines or inbreds.

i) Reduction in Yield:

- ✓ Inbreeding generally leads to a loss in yield.
- ✓ The inbred lines that is able to survive and be maintained yield much less than the open pollinated varieties from which they were derived.
- ✓ In maize, the best - inbred lines yield about half as much as the open pollinated varieties from which they were produced.
- ✓ In alfalfa and carrot, the reduction in yields is much greater, while in onions and many cucurbits the reduction in yield is very small.

Inbreeding Depression and Fitness traits



Degree of Inbreeding Depression

- The various plant species differ considerably in their responses to inbreeding.
 - Inbreeding depression may range from very high to very low or may even be absent into the following four broad categories.
- 1) High inbreeding depression,
 - 2) Moderate inbreeding depression,
 - 3) Low inbreeding depression, and
 - 4) Absence of inbreeding depression.

High Inbreeding Depression:

- Several plant species, Eg. alfalfa (*M. sativa*) carrot (*D. carota*) , hayfield, tarweed etc show very high inbreeding depression.
- A large proportion of plants produced by selfing shows lethal characteristics and do not survive.
- The loss in vigour and fertility is so great that very few lines can be maintained after 3 to 4 generation of inbreeding.
- The line shows greatly reduced yields, generally less than 25 percent of the yield of open - pollinated varieties.

Moderate Inbreeding Depression:

- Many crops species, such as maize, jowar, bajara etc. shows moderate inbreeding depression.
- Many lethal and sublethal types appear in the selfed progeny, but a substantial proportion of the population can be maintained under self- pollination.
- There is appreciable reduction in fertility and many line reproduce so poorly that they are lost.
- However, a large number of inbred lines can be obtained, which yield upto 50 percent of the open- pollinated varieties.

Low Inbreeding Depression:

- Several crop plants, E. g onion (*A. cepa*), many cucurbits, rye (*S. cereale*), sunflower (*Hannus*), hemp etc show only a small degree of inbreeding depression.
- Only a small proportion of the plants show lethal or subvital characteristics.
- The loss in vigour and fertility is small; rarely a line cannot be maintained due to poor fertility.
- The reduction in yield due to inbreeding is small or absent.
- Some of the inbreds lines may yields as much as the open pollinated varieties from which they were developed.

Lack of inbreeding Depression:

- The self- pollinated species do not show inbreeding depression although they do not show heterosis.
- It is because their species reproduce by self - fertilization and as a result, have developed homozygous balance.
- In cost of the cross- pollinated species exhibit heterozygous balance.

Minimizing the Rate of Inbreeding

- Avoid mating of relatives
- Maximum effective population size N_e
- N_e maximized with **equal representation**
 - Contribution (number of sibs) from each parent as equal as possible
 - Sex ratio as close to 1:1 as possible
 - When sex ratio skewed (r dams/sires), every male should contribute (exactly) one son and r daughters, while every female should leave one daughter and also with probability $1/r$ contribute a son

Are genetic drift and inbreeding the same thing?

- Genetic drift and inbreeding are associated with changes in allele frequencies and heterozygosity, and are particularly important in small populations.
- The problem is that at small population sizes, the combined effect of genetic drift and inbreeding leads to increased homozygosity and fixation of alleles, including deleterious alleles. Sometimes these processes are described as independent forces operating at the same level, while elsewhere inbreeding tends to be addressed as a result of genetic drift.
- there is not just one way of defining N_e and in association with genetic drift and inbreeding described variance (N_{eV}) and inbreeding (N_{eI}) effective sizes, respectively (Crow 1954).

$$N_{eV} = \frac{4N_t - m_k}{2(1 + V_k/m_k)}.$$

$$N_{eI} = \frac{N_{t-1}m_k - 1}{m_k - 1 + V_k/m_k}$$

...unless the population size remains constant, and then they can be both reduced to:

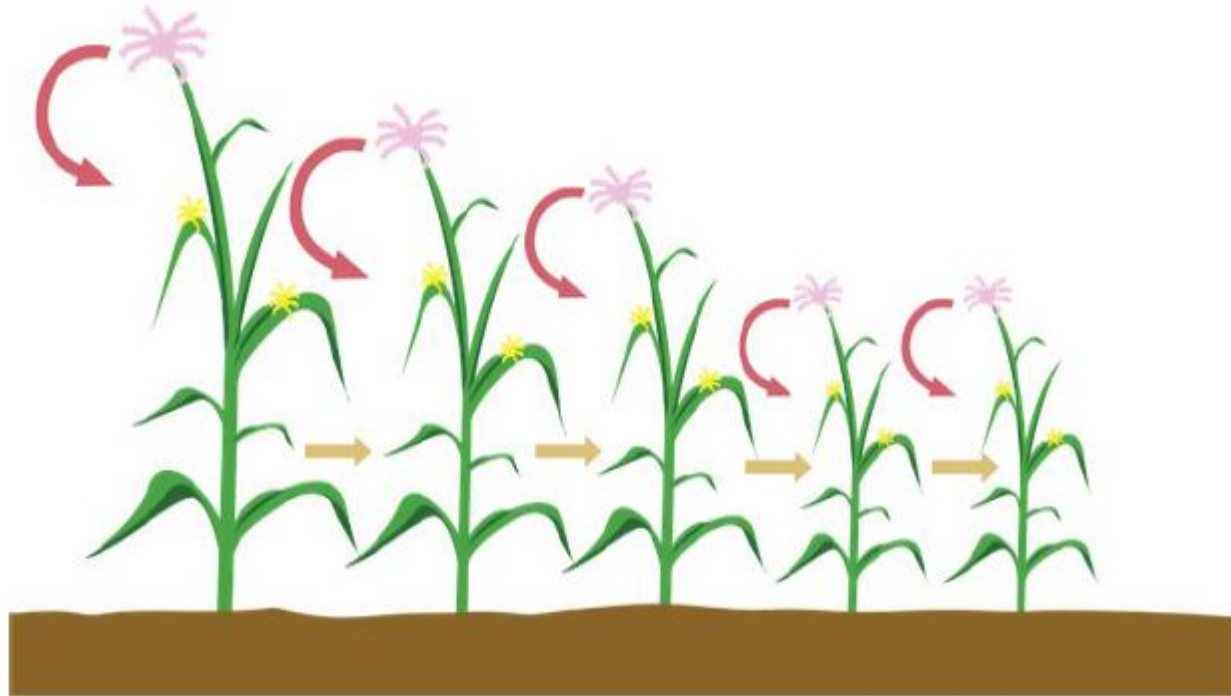
$$N_e = \frac{4N - 2}{2 + V_k}$$

Inbreeding in practical plant breeding

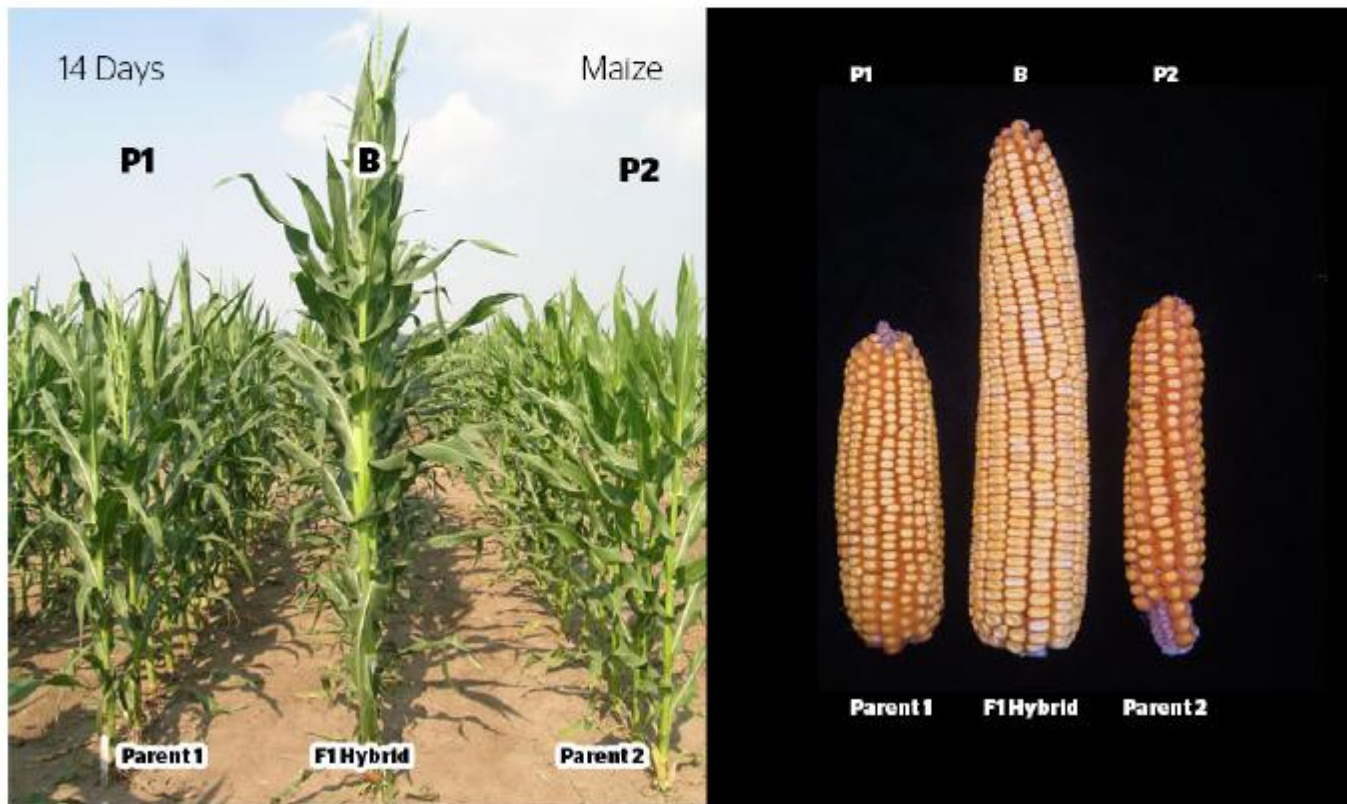
Positive use in production of F1-hybrids in maize



Continuous self-fertilization lead to fully homozygous plants called inbred lines.



If members of two inbred lines are mated,
the offspring display heterosis.



Definitions

- Heterosis or Hybrid Vigour Outbreeding:
“ Is the phenomenon that causes crossbred individuals to have an increased level of performance for certain traits over and above the average performance of their straightbred parents. “

Clarification

b/w 'Heterosis, & Hybrid vigour

- **Hybrid vigour:**

According to Shull

The developed superiority of the hybrids is the 'hybrid vigour.

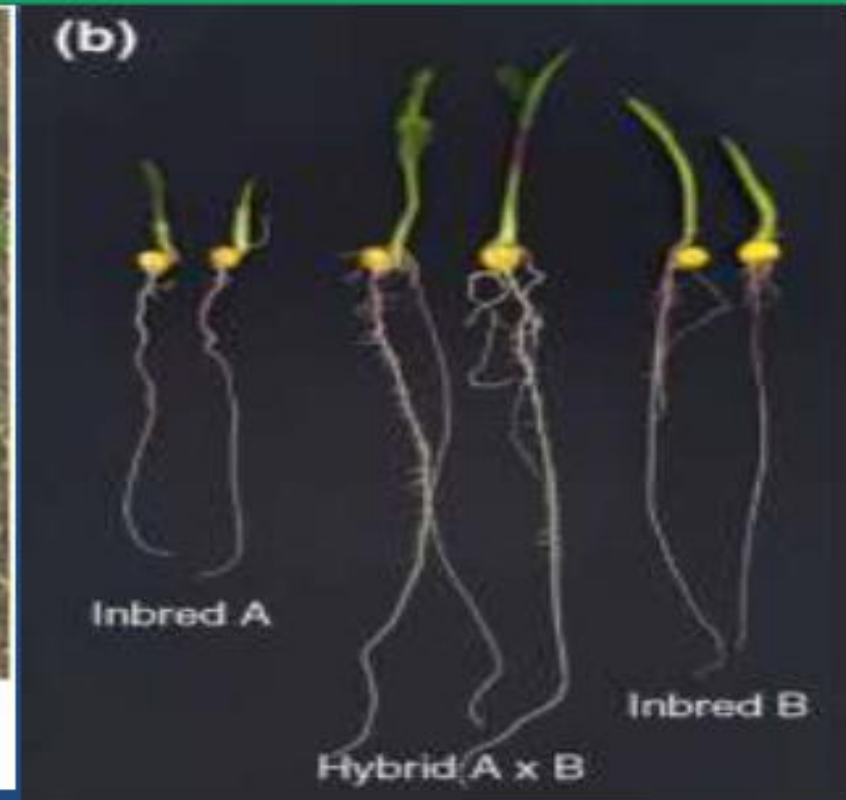
- **Heterosis:**

The mechanism by which this superiority is developed

Manifestation of Heterosis

- Heterosis is manifested in many ways.
 1. It may be either morphological or physiological in nature.
 2. Earlier maturity of F1 hybrids than in either parent is another manifestation of heterosis

Phenotypic manifestation of heterosis.

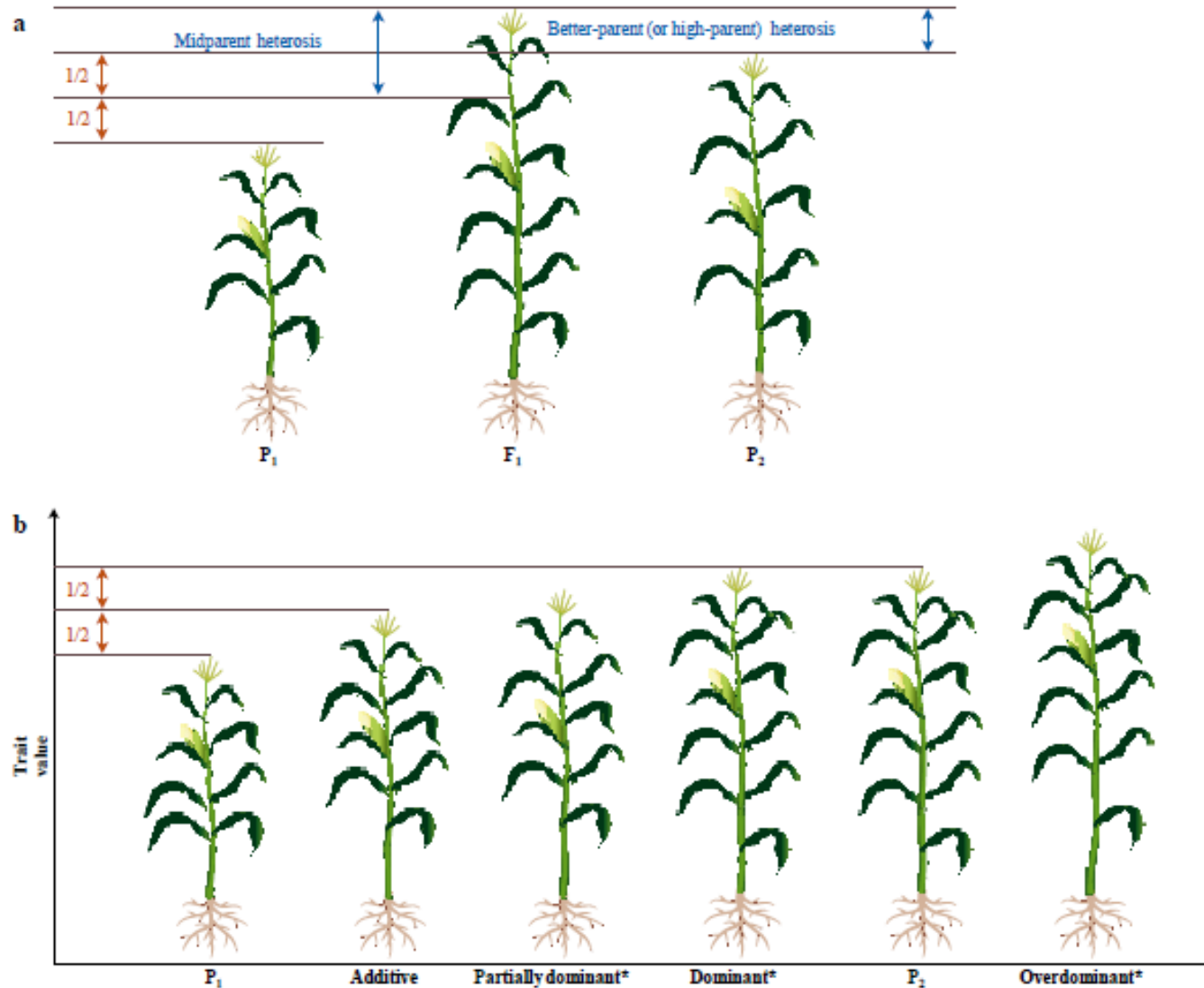


Superior performance of heterozygous F_1 hybrid plants in terms of increased biomass, size, yield, speed of development, fertility, resistance to disease and insect pest, or to climatic rigors of any kind compared to the average of their homozygous parental inbred lines (Shull, 1952 & Falconer, 1996)

History

- ❖ Heterosis was first described by Charles Darwin (Darwin 1876) and independently rediscovered by Shull (1908) and East(1908).
- ❖ Term coined by "SHULL" in (1952) as " stimulation of heterozygosity".
- ❖ After maize hybrid was first utilized in field on a large scale in USA in 1930s.
- ❖ 1st Hayes and Jones (1916) reported hybrid vigor for cucumber mainly contributed to notable increasing of fruit size and number.
- ❖ F1 hybrid of brinjal was utilized before 1925 in Japan (Kakizaki , 1931)

QUANTITATIVE DEFINITION

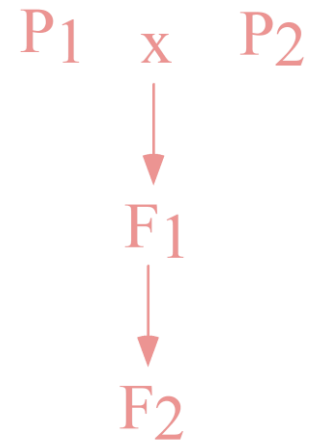


Line Crosses: Heterosis

When inbred lines are crossed, the progeny show an increase in mean for characters that previously suffered a reduction from inbreeding.

This increase in the mean over the average value of the parents is called **hybrid vigor** or **heterosis**

$$H_{F_1} = \bar{s}_{F_1} - \frac{\bar{s}_{P_1} + \bar{s}_{P_2}}{2}$$



A cross is said to show heterosis if $H > 0$, so that the F_1 mean is average than the average of both parents.

Expected levels of heterosis

If p_i denotes the frequency of Q_i in line 1, let $p_i + \delta_i$ denote the frequency of Q_i in line 2.

The expected amount of heterosis becomes

$$H_{F_1} = \sum_{i=1}^n (\pm p_i)^2 \delta_i$$

- **Heterosis depends on dominance:** $\delta_i = 0$ = no inbreeding depression and no heterosis as with inbreeding depression, directional dominance is required for heterosis.
- **H is proportional to the square of the difference in gene frequency Between populations.** H is greatest when alleles are fixed in one population and lost in the other (so that $|\delta_i| = 1$). $H = 0$ if $\delta = 0$.
- **H is specific to each particular cross.** H must be determined empirically, since we do not know the relevant loci nor their gene frequencies.

Genetical Basis of Heterosis

- A. Dominance hypothesis of heterosis.
- B. Over dominance hypothesis of heterosis.
- C. Epistasis hypothesis for heterosis
- D. Hemizygous complementation
- E. Epigenetics as a cause of heterosis
- F. Organellar heterosis

A: Dominance hypothesis of heterosis.

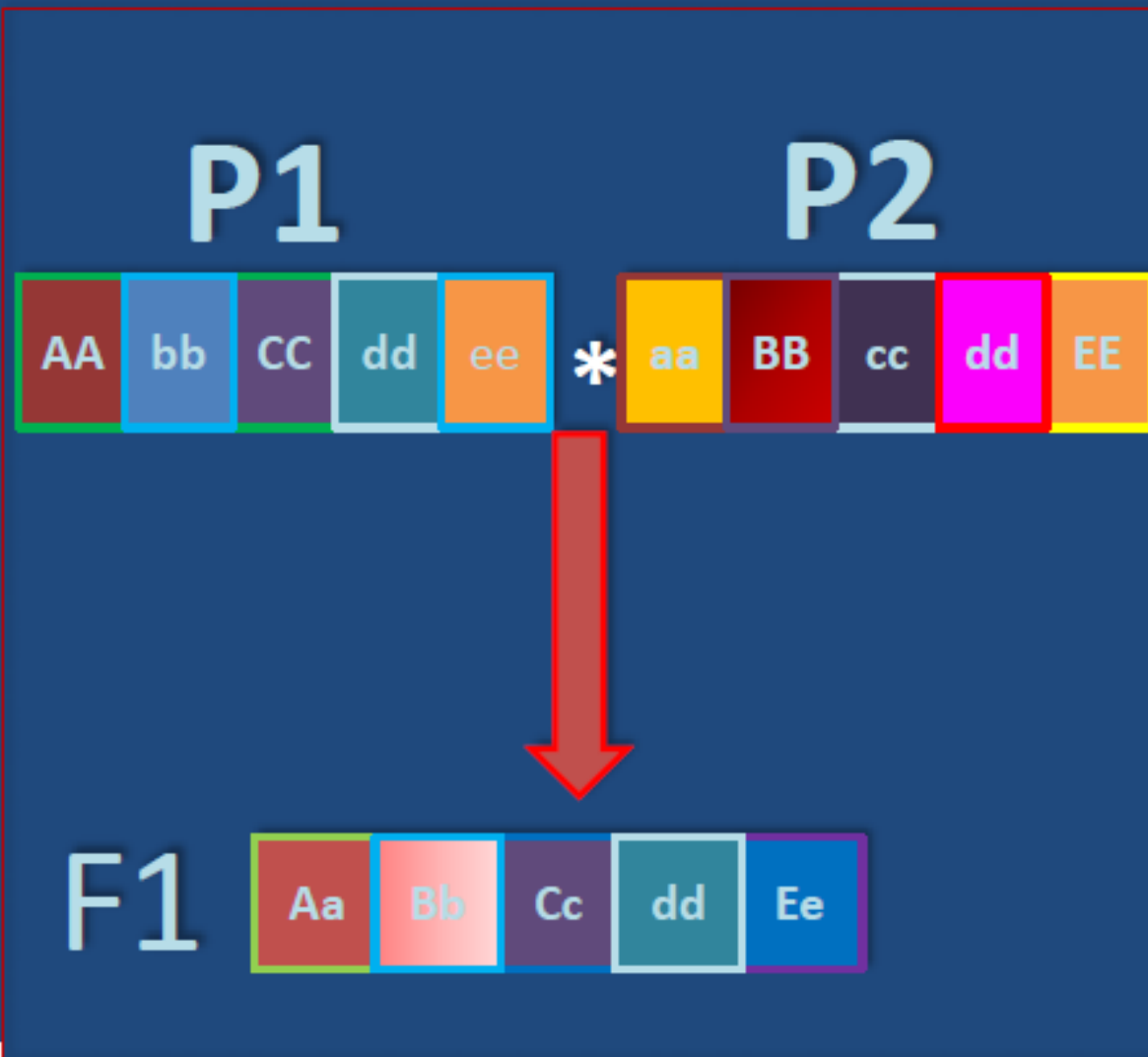
- Holds that increased vigour and size in a hybrid is due to combination of favourable growth genes by crossing two inbred races.
- In other words, the hybrid vigour is a result of action and interaction of dominant or fitness factors or cumulative (polygenic) effect of dominant genes.

A: Dominance hypothesis of heterosis

Example;

Parent :	AA bb CC dd	×	aa BB cc DD
Phenotypic value :	$2+1+2+1=6$	↓	$1+2+1+2=6$
F ₁ :	Aa Bb Cc Dd		
	$2+2+2+2=8$		

Discussion on dominance model



- Cancellation of deleterious or inferior alleles
- Heterosis depends on number of dominant genes.
- Both parents should differ in dominant genes.
- Complementation across loci must be cumulative. (Coors and Panday, 1999), to produce a superior phenotype.
- Dominance is considered more popular one (Charlesworth and Willis, 2009).

Dominance may be insufficient

Rapid rate of inbreeding depression in tetraploids
(Dudley, 1974)

The progressive heterosis in tetraploids
(Groose, et al.1989)

Is the simple complementation responsible for heterosis

Several evidences suggest that mechanisms beyond simple complementation may be important in heterosis.

The absence of a decline in the magnitude of heterosis from improved inbred parents
(Duvick 2001)



B: Over dominance hypothesis of heterosis.

Example:

Parents :	AA BB cc dd	×	aa bb CC DD
Phenotypic value :	$1\frac{1}{2} + 1\frac{1}{2} + 1 + 1 = 5$	↓	$1 + 1 + 1\frac{1}{2} + 1\frac{1}{2} = 5$
F ₁ :	Aa Bb Cc Dd		
	$2 + 2 + 2 + 2 = 8$		

Is over-Dominance sufficient to explain heterosis

EVIDENCES

- Heterozygous individual may have an advantage due to the combination of both allozymes (Falconer and Mackay, 1996)
- Role of single genes in the manifestation of heterosis for various traits in Arabidopsis and Tomato (Redei, 1962; Semel *et. al.*, 2006; Krieger, 2010)

❖ EXAMPLES OF ODO GENES

- SFT Gene in Tomato
- Erecta mutant in Arabidopsis

LIMITATIONS

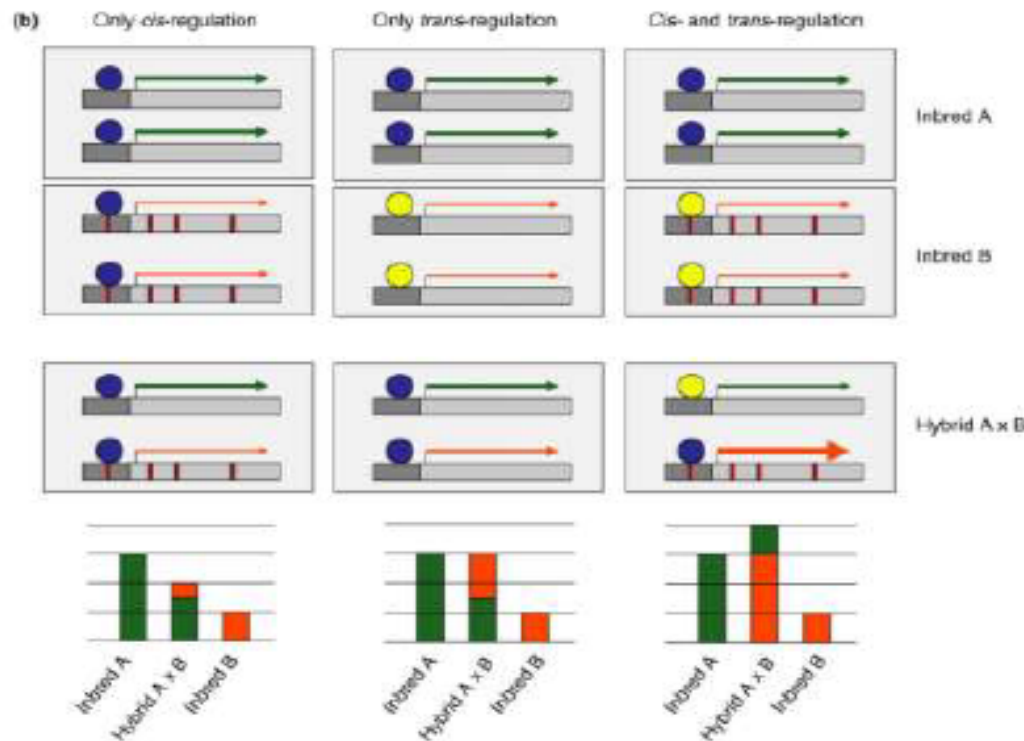
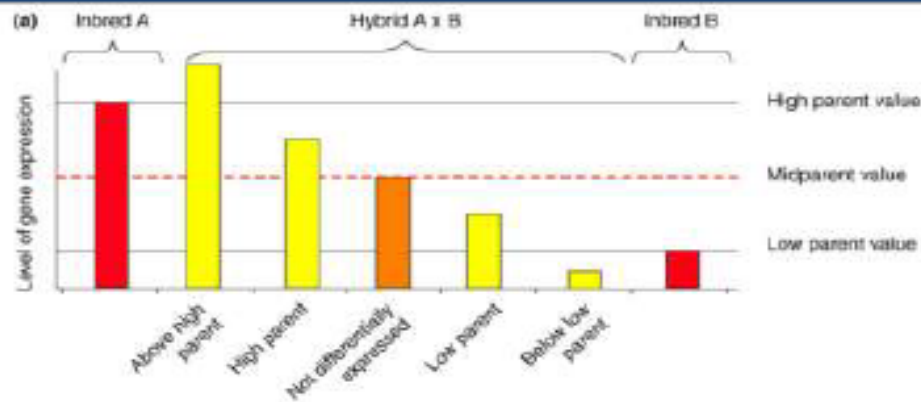
- For ODO to produce superior phenotypes, single gene or small genomic regions are needed which seem contradict to the hybrid performance of many agronomic important traits controlled by multiple genes (Lippman and Zamir, 2007)
- Though evident as examples of overdominance, it is possible that they involve dosage effects on regulatory networks (Birchler, 2010)

Epistatic model for heterosis

The epistasis hypothesis considers epistatic interactions between nonallelic genes at two or more loci as the main factor for the superior phenotypic expression of a trait in hybrids

(Powers 1945).

Relative gene expression levels in hybrids and regulation of allele-specific gene expression in hybrids



.cis-regulation reflect the relative expression levels of the parental inbred lines in the allelic ratio of gene expression in the hybrid.

- trans-acting factors show equal expression of the two alleles in the hybrid.

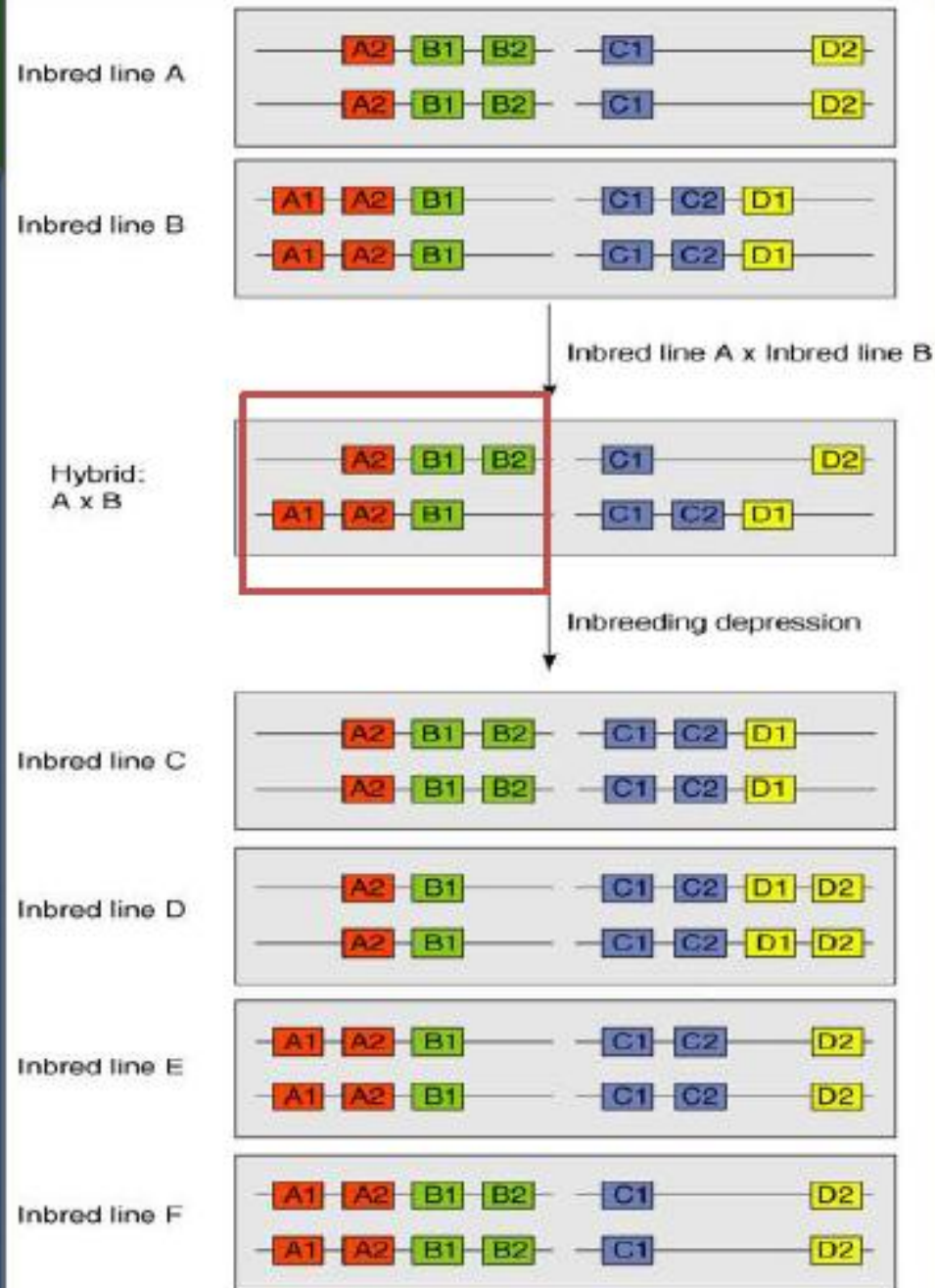
EPISTASIS AS GENETIC MODEL FOR HETEROSIS

- The interaction of favorable alleles at different loci contributed by the two parents, which themselves may show additive, dominant and overdominant action (Powers, 1945, Yu *et. al.*, 1997; Monforte and Tanksley, 2000; Li *et. al.*, 2001; Luo *et. al.*, 2001)
- The genetic background and allelic interactions can have an effect on the heterotic contributions of individual loci
- Recently demonstrated in tomato introgression lines that heterosis is manifested even in the absence of epistasis (Semel, *et al.* 2006)

Hemizygous complementation

Complementation of present-absent genes

• Hemizygous complementation of many such genes with minor quantitative effects in hybrids might thus lead to a significantly increased performance of hybrid plants.

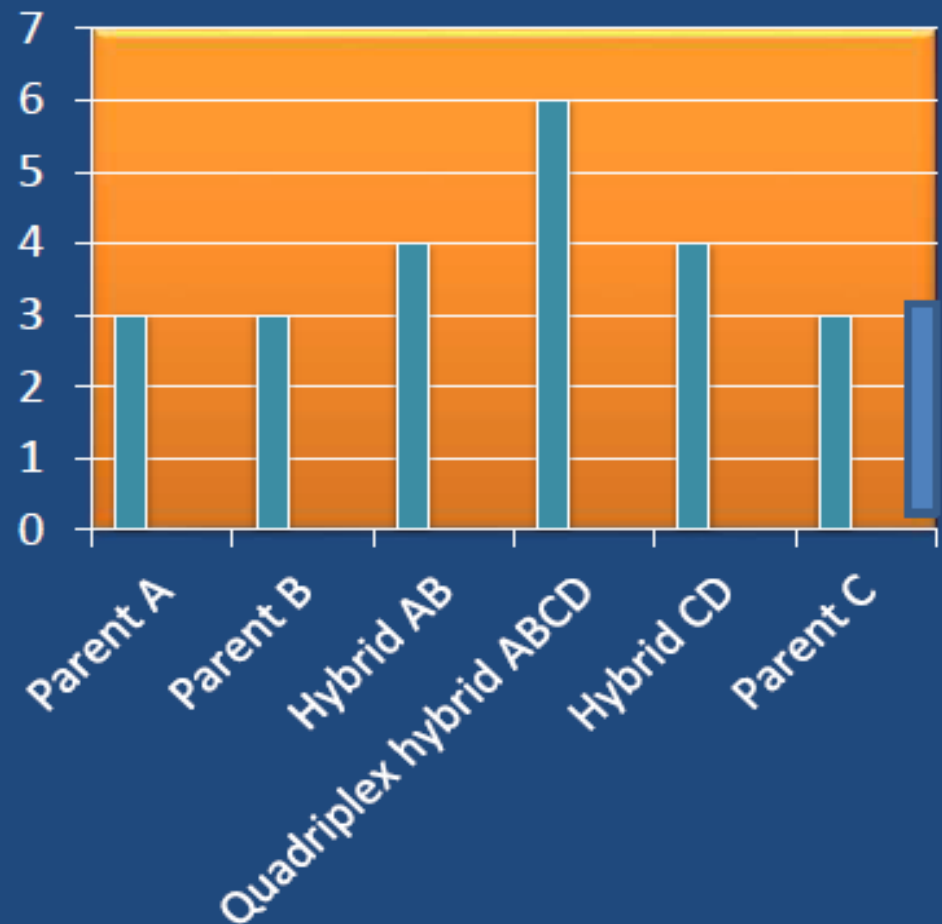


Progressive heterosis

Progressive heterosis refers to the fact that double cross hybrid autotetraploids (ABCD) typically show greater vigor than single cross hybrids (AABB; CCDD and so on).

➤ Increased allelic diversity creates a more robust heterotic response.

➤ Quadruplex hybrid, which contains potentially four different alleles per locus, exceeds even that of the hybrids A-B and C-D.



There is a genomic dosage effect operating on heterosis

Epigenetics as A cause of heterosis

TYPES

□ "Epigenetics" refers to heritable (through mitosis or meiosis) alterations in gene expression that are independent of DNA sequence: different epigenetically regulated forms of a gene are known as epialleles.

□ Chromatin status, mediated through epigenetic modification, can potentially affect gene expression in cis (at the gene itself) or in trans (by regulating loci indirectly).

**DNA
METHYLATION**

**HISTONE
MODIFICATION**
CHROMATIN REMODLING

**RNA
INTERFERENCE**
siRNAs,
miRNAs etc

DNA methylation and heterosis

- Conversion of cytosine to 5 methyl cytosine.
- Could generate epigenetic variation/ Epialleles and creation of hybrid vigour.
- DNA methylation does not change the DNA sequence and its function, but does change its expression level, referred as an epigenetic change.
- Associated with gene silencing, and genes with abundant 5-methylcytosine in their promoter region are usually transcriptionally silent. (Jones and Takai, 2001; Dong et al, 2006)
- It can be suggested that inbreeding depression partly or primarily results from lower levels or fewer genes expressed simply due to homozygosity of methylated DNA in regulating factors.
- Heterosis is from higher levels or larger number of genes expressed simply due to heterozygous conditions between methylated and non-methylated DNA in the F1 hybrid.

RNA Interference

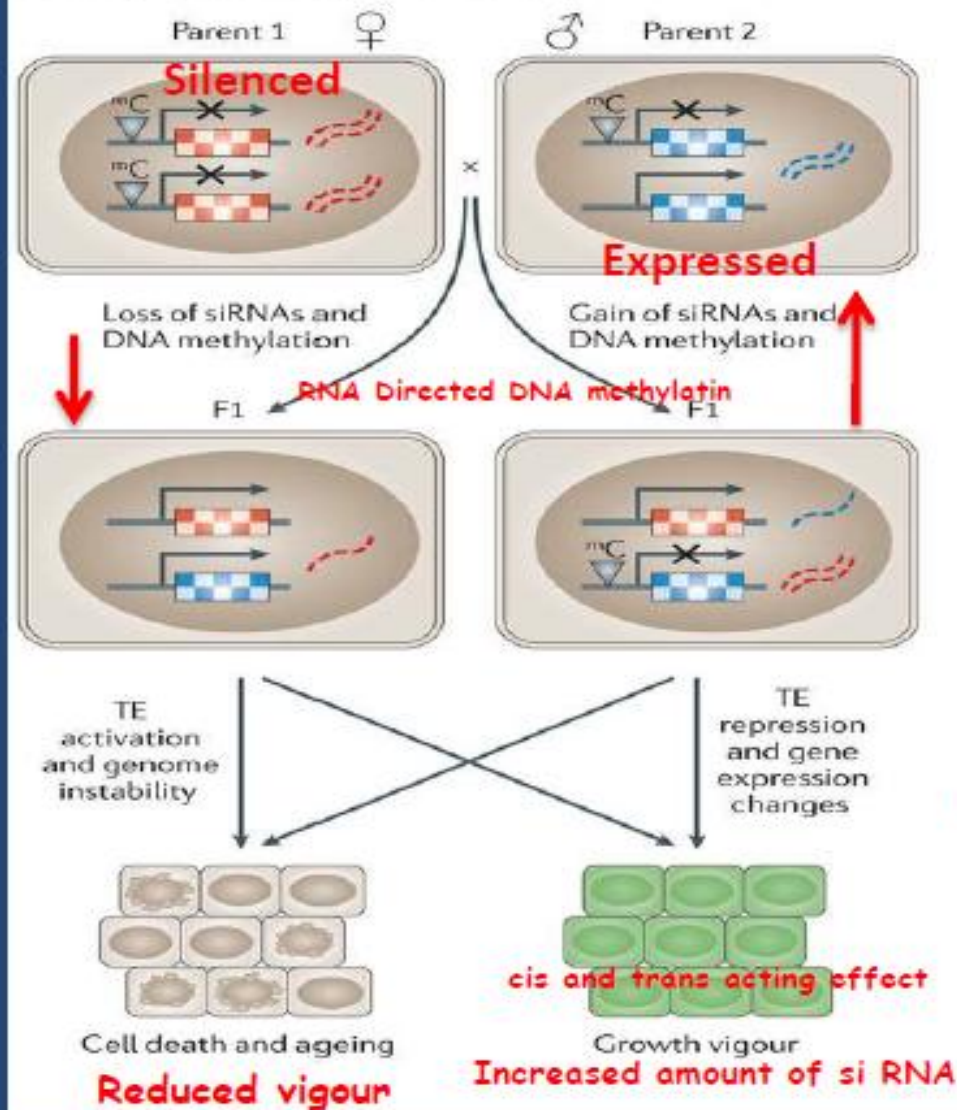
Small RNAs

small interfering RNAs (siRNAs)

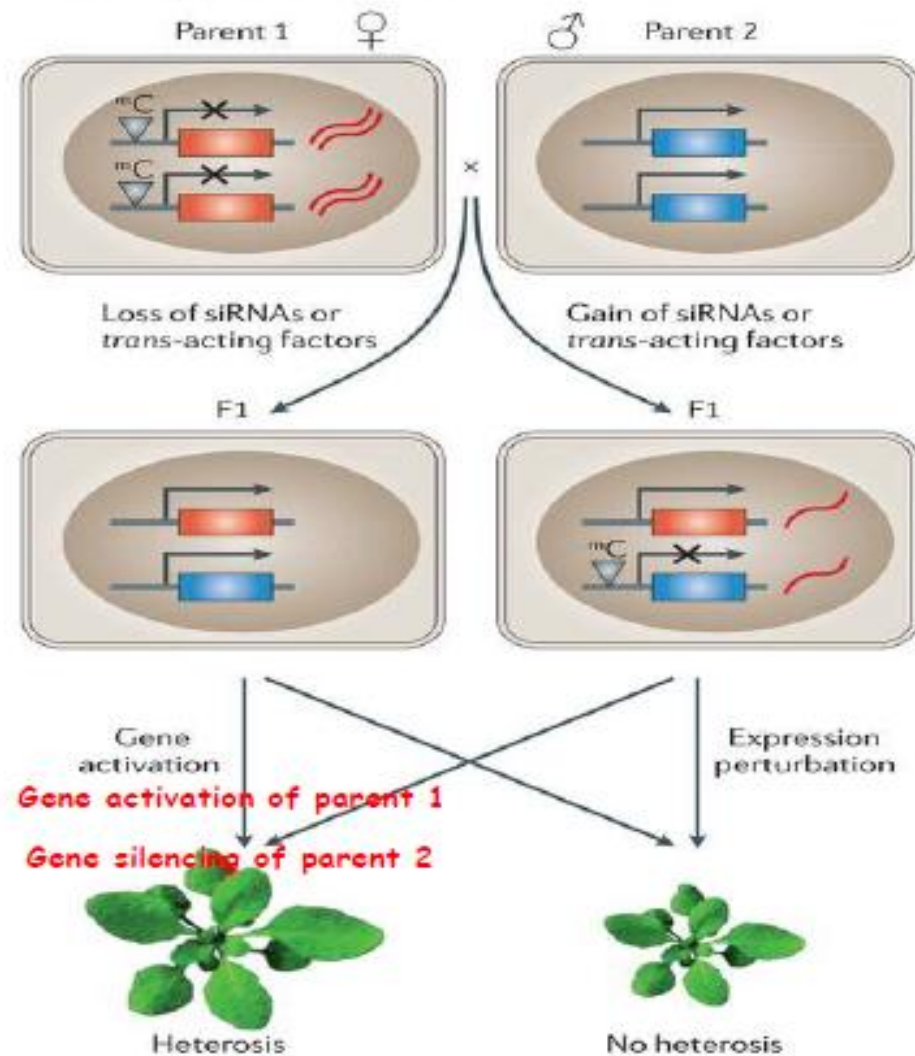
- ❖ Mediate post-transcriptional gene silencing, RNA-directed DNA methylation, and chromatin remodeling.
- ❖ These RNAs are negative regulators of target transcript accumulation (Allen et al., 2005).
- ❖ miRNAs and siRNAs are differentially expressed between hybrid and its parental inbred lines (Mica et al., 2006).

A model for small RNAs in the allelic expression of genes and transposable elements in hybrids and allopolyploids.

a TE regulation and genome stability

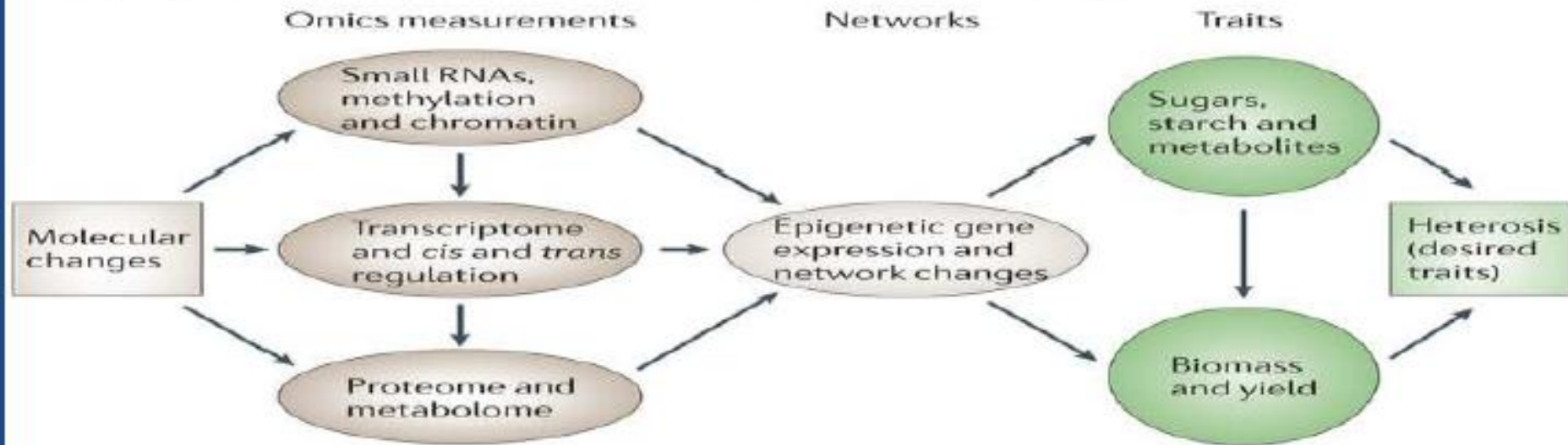


b Gene expression and heterosis

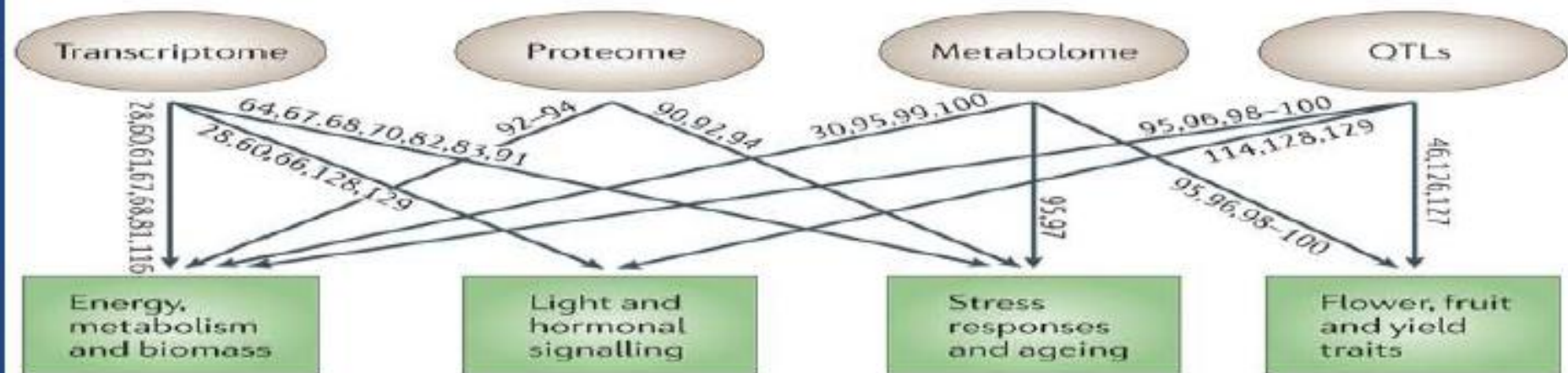


Molecular changes at epigenetic, genomic, proteomic and metabolic levels lead to heterosis traits

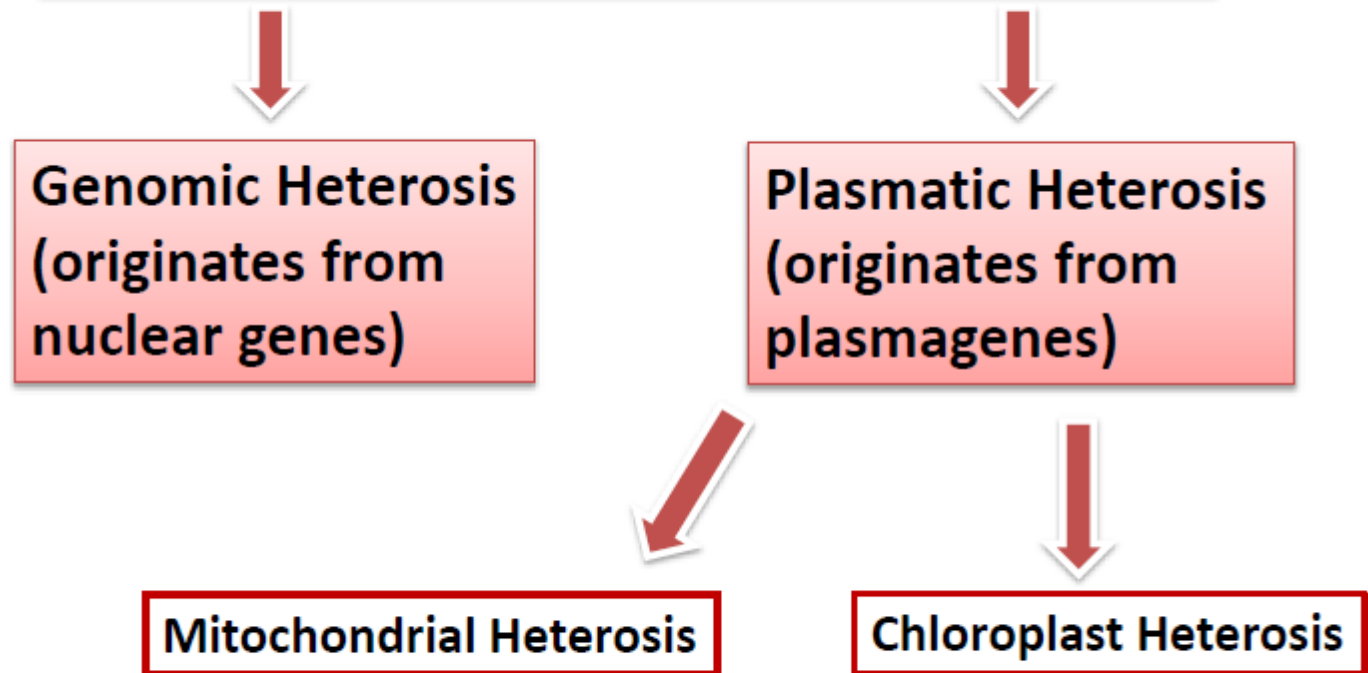
a Reprogramming of genetic, epigenetic and expression networks



b Genome-wide studies showing links between biological pathways and traits



Mac Key (1976) classified Heterosis



Organelle Heterosis and Complementation – Mitochondrial Heterosis

- The involvement of mitochondria in heterosis is judged by **respiratory function** and **higher enzyme activities** in the hybrids.
- Mitochondrial complementation- the enhanced **oxidative phosphorylation** efficiency of artificially mixed mitochondria of certain inbreds (in maize seedlings).
- The more vigorous varieties of **maize and soybean** have more tightly coupled mitochondria than the less vigorous varieties.
- Mitochondrial ATP:O ratios in wheat seedlings are correlated to seed metabolism, which is in turn determined by the metabolic activity of the plant during formation and maturation of the seeds.

- Positive correlation between **seed and oil yield** and mitochondrial activity in oil palm has been observed.
- Hybrid mitochondria possess an **abundance** of lipid-phospholipid, linoleic acid in their fatty acid fraction and a higher amount of internal “bound” water during heterotic expressions.
- Mitochondrial complementation and grain yield in **hybrid wheat** showed correlation between F1 yield heterosis and mitochondrial efficiency.
- All these observations are in accordance with the view that mitochondria plays a significant role in the manifestation of heterosis.

Chloroplast Heterosis

- Chloroplast heterosis i.e. **higher photosynthetic rates**, have also been observed in the seedling stages.
- The term “chloroplast complementation” is generally used to indicate the greater activity of **1:1** parental mixture of isolated chloroplasts when compared to the mid- parental values.
- **Hybrids** are characterized to possess **highly developed fine** structure of mitochondria and chloroplast than their respective parents.
- The **increase in size** of the lamellae and thylakoid membrane structure in the chloroplast of the hybrid was directly **correlated** with their chlorophyll contents.

- The enhanced activities of the **key enzymes** of the Calvin cycle in hybrid chloroplasts, heterosis in chlorophyll content in maize and sorghum has been reported.
- The enhanced activities due to chloroplast complementation were also found to be closely associated with the degree of **grain yield heterosis**.
- These observations on chloroplast heterosis and complementation, just like mitochondrial complementation, suggest that hybrids are endowed with **efficient conservation** of energy in their organelles.

Organelle Heterosis and Complementation in Higher plants

Parameters	Plant species
Cytochrome oxidase	Wheat (<i>Triticum aestivum</i>)
Oxidative phosphorylation (ADP: O ratio)	Wheat (<i>Triticum aestivum</i>) Maize (<i>Zea mays</i>)
Respiratory control index (State 3 / state 4 oxidation ratio)	Maize (<i>Zea mays</i>) Barley (<i>Hordeum vulgare</i>) Soybean (<i>Glycine max</i>) Pea (<i>Pisum sativum</i>)
Cytochrome and phospholipid contents	Wheat (<i>Triticum aestivum</i>) Chloroplast heterosis and complementation
Ribulose biphosphate Carboxylase/oxygenase	Maize (<i>Zea mays</i>) Sorghum (<i>Sorghum vulgare</i>) Barley (<i>Hordeum vulgare</i>)
Photophosphorylation	Maize (<i>Zea mays</i>) Cotton (<i>Gossypium hirsutum</i>)
Chlorophyll content	Wheat (<i>Triticum aestivum</i>) Soybean (<i>Glycine max</i>) Maize (<i>Zea mays</i>)

Intergenomic Interaction and Organelle Complementation

- Intergenomic interaction between nuclear and organelle genes is a **dominant theme** in heterosis
- Organelle heterosis is the result of **complementation** between polymorphic mitochondria and chloroplast, which may be transmitted **biparentally** in the F1 hybrid.
- Mechanism of heterosis at the level of mitochondria and chloroplast would involve complementation of **proteins or polypeptide** subunits encoded by both nuclear and organelle genes having non-additive gene effects instead of unique nuclear genome.
- The resulting **products** due to intergenomic interaction in organelles of hybrid organisms ensure for **enhanced** structural and catalytic functions of these organelles.

Interspecific Complementation and Heterosis

- Organelle polymorphism can result from **recombination** between organelle genomes derived from the paternal and maternal sources due to biparental transmission.
- In **parasexual** hybrids, chloroplasts from both parents may stay together and be distributed to daughter cells, with one type of chloroplast dominating the other.
- Mitochondria isolated from the seedlings of the hybrids and their parents showed different efficiencies of **oxidative phosphorylation** during ATP synthesis.
- The mitochondria from the non-heterotic hybrids had the **same** phosphorylative efficiency as that of the parents was considered as an expression of heterosis.

Examples

Numerous QTLs with different levels of dominant, over dominant, and epistatic effects have been mapped for heterosis in

Tomato (Semel et al., 2006),

A. thaliana (Hua et al. 2003;Kusterer et al., 2007; Melchinger et al., 2007;Meyer., et al 2010).

Besides the involvement of various gene actions found in these studies, all the three gene actions may condition heterosis in crops (Li et al, 2008; Swanson-Wagner, et al 2006).

Types of heterosis

A. On the basis of origin and nature have 2 types:

1. Euheterosis or true heterosis

a) Mutational heterosis

b) Balanced heterosis

2. Pseudoheterosis

B. On the basis of types of estimation :

1: Average or Relative heterosis

2: Heterobeltiosis

3: Useful or standard or Economic heterosis

Types of heteros

A) Euheterosis or true heterosis .

a) **Mutational Heterosis**

Lethal (mostly), recessive, adaptively unfavorable mutants are either eliminated or sheltered by their non-lethal, dominant and adaptively superior alleles in cross pollinated crops. This is termed as mutational heterosis.

b) **Balanced Heterosis**

Well balanced gene combinations which are more adaptive to environmental conditions and useful from the agriculture point of view result in balanced heterosis.

Types of heterosis

Pseudoheterosis:

- Also termed as luxuriance. Progeny possess superiority over parents in vegetative growth, but not in yield and adaptation, usually sterile or poorly fertile. This concept cannot be utilized in hybrid varieties production.

Types of heterosis

B. On the basis of types of estimation :

a): **Average or Relative Heterosis:**

When heterosis is estimated over mid parental value i.e. average of two parents it is referred as average or relative heterosis.

b): **Heterobeltiosis**

When heterosis is estimated over better parent it is called as heterobeltiosis.

c): **Standard Heterosis**

When heterosis is estimated over standard commercial hybrid it is called as standard heterosis. It has practical importance in [plant breeding](#). It is also referred as useful or economic heterosis.

Factos Affecting Heterosis

1) Geographical and Genetic Diversity:

In upland cotton, a close relationship is observed between the genetic diversity of parental varieties and performance of their hybrids for lint yield. In intra and interspecific hybrids of cotton, the highest heterosis is observed in the cross combinations involving ecologically distant parents. High heterosis is observed in crosses involving local x exotic lines.

Factors Affecting Heterosis

2) Agronomic Performance:

High heterosis can be obtained from the crosses of two low yielded inbreds but absolute yield of such hybrids is lower than the adapted varieties. To produce good hybrids, varieties with high per se performance must be chosen. There is a high positive correlation between parental performance and hybrid vigour. The performance of any trait in a hybrid is dependent upon the relative performance of its parental varieties.

Factors Affecting Heterosis

3) Adaptability:

A close association is observed between the adaptability of the hybrids and their parents. In India, several hybrids have been developed at intra and interspecific levels especially in tetraploid cotton. Highly heterotic combinations involve at least one of the parents with wider adaptability.

4) Genetic Base:

Genetic base of parental lines is found to play an important role in the manifestation of heterosis in their hybrids as there is a close relationship between the genetic base and adaptability of varieties. Hybrids with high levels of heterosis involve at least one of the parents with a broad genetic base.

Application of Heterosis

- increasing yield and nutritive value of crop plants
- Increasing the growth rate
- Increasing the meat production
- Enhancing the milk yield,& egg production.
- Improving the performance of various animals i.e: races horses,& domestic pigeons.
- Production of new combination of colours and scents in garden flowers

Agricultural importance of heterosis

Crosses often show **high-parent heterosis**, wherein the F_1 not only beats the average of the two parents (**mid-parent heterosis**), it exceeds the best parent.

Crop	% planted as hybrids	% yield advantage	Annual added yield: %	Annual added yield: tons	Annual land savings
Maize	65	15	10	55×10^6	13×10^6 ha
Sorghum	48	40	19	13×10^6	9×10^6 ha
Sunflower	60	50	30	7×10^6	6×10^6 ha
Rice	12	30	4	15×10^6	6×10^6 ha

