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Heterosis & inbreeding depression

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Introduction

- ❖ Cross pollinated species & species reproducing asexually are highly heterozygous. When these species are subjected to selfing or inbreeding they show severe reduction in vigour and fertility.
- ❖ This phenomenon is known as **inbreeding depression**.

Inbreeding

It is mating between individuals related by descent or having common ancestry. (Brother- Sister mating or sib mating). The highest degree of inbreeding is obtained by selfing.

Heterosis

- ❖ The term heterosis was first used by **Shull in 1914**.
- ❖ It is defined as the superiority of F1 hybrid over both the parents in terms of yield or some other characters.
- ❖ It may be **true heterosis or euheterosis** to distinguish it from luxuriance.
- ❖ Can be occurred in all types of species i.e. self-pollinating, **cross-pollinating** and vegetatively propagated.
- ❖ Koelreuter (1673) in tobacco, Darwin (1876) in several vegetable crops were studied about hybrid vigor.
- ❖ But our present knowledge on heterosis comes from the work on **maize**.

Types of heterosis/ Estimation of heterosis

1. **Average heterosis or Relative heterosis:** It is the heterosis where F1 is superior to mid parent value. In other words superior to average of two parents.

$$\text{Average heterosis} = \frac{\overline{F1} - \overline{MP}}{\overline{MP}} \times 100$$

Where, $\overline{F1}$ = Mean of hybrid, \overline{MP} = Mid parental value

This type of heterosis is of no use in agriculture since the superiority is below the better parent value.

2. Heterobeltiosis: Superiority of F1 over the better parent.

$$\text{Heterobeltiosis} = \frac{\overline{F1} - \overline{BP}}{\overline{BP}} \times 100$$

Where, \overline{BP} = Mean of better parent

3. Economic or useful heterosis: Superiority of the F1 compared to the high yielding commercial variety in a particular crop.

$$\text{Economic heterosis} = \frac{\overline{F1} - \overline{CV}}{\overline{CV}} \times 100$$

Where, \overline{CV} = Mean of commercial variety

4. Standard heterosis: Sometime heterosis worked out over the standard commercial hybrid.

$$\text{Standard heterosis} = \frac{\overline{F1} - \overline{SH}}{\overline{SH}} \times 100$$

Where, \overline{SH} = Mean value of standard (local commercial) hybrid

5. Negative heterosis: Performance of F1 inferior to better parent / mid parent value. - e.g. Duration (earliness), height in cereals, micronaire value in cotton, and toxic substances like neurotoxin in *Lathyrus sativus*.

Heterosis and hybrid vigour

- ❖ Hybrid vigour is used as **synonym** of heterosis.
- ❖ Hybrid vigour only refers to superiority of F1 over better parent, while heterosis describes other situation as well.
- ❖ In other words hybrid vigour is manifested effect of heterosis. Thus the term hybrid vigour is used to distinguish the F1 superiority from negative heterosis.

Luxuriance vs Heterosis

- Luxuriance is the increased vigour and size of interspecific hybrid.
- The principal difference between heterosis and luxuriance lies in the reproductive ability of the hybrid.
- Heterosis is accompanied with an increased fertility, while luxuriance is expressed by interspecific hybrid. That are generally sterile or poorly fertile.

Manifestation of heterosis May be in the following form.

1. Increased yield.
2. Increased reproductive ability.
3. Increase in size and vigour.
4. Better quality
5. Greater adaptability.
6. Earlier flowering and maturity
7. Greater resistant to disease and pest
8. Faster growth rate
9. Increase in the number of a plant part

Genetic basis of heterosis and inbreeding depression

There are three main theories of heterosis and inbreeding depression.

1. Dominant hypothesis
2. Over dominance hypothesis.
3. Epistasis hypothesis.

1. Dominant hypothesis

- ❖ First proposed by **Davenport in 1908**. It was later on expanded by **Bruce, Keeble and Pellow (1910)**.
- ❖ According to this hypothesis at each locus the dominant allele has favourable effect, while the recessive allele has unfavourable effect. In heterozygous state, the deleterious effect of recessive alleles are masked by their dominant alleles. Inbreeding depression is produced by the harmful effects of recessive alleles, which become homozygous due to inbreeding.
- ❖ Therefore according to this hypothesis heterosis is not due to heterozygosity rather it is the result of prevention of effect of harmful recessive by their dominant allele.

Objections against the dominant hypothesis

a) Failure of isolation of inbreds as vigorous as hybrids:

According to dominance hypothesis it is possible to isolate inbreds with all the dominant genes E.g. AA. This inbreed should be as vigorous as that of hybrid. However in practice such inbreds were not isolated.

b) Symmetrical distribution in F2

In F2 dominant and recessive characters segregate in the ratio of 3: 1. Quantitative characters, according to dominance hypothesis should not show symmetrical distribution. However, F2 nearly always show symmetrical distribution.

Explanation for the two objections

In 1917 Jones suggested that since quantitative characters are governed by many genes, they are likely to show linkage. In such a case inbreds containing all dominant genes cannot be isolated. So also the symmetrical distribution in F₂ is due to linkage. This explanation is often known as **Dominance of Linked Genes Hypothesis.**

2. Over dominance hypothesis

- ❖ This hypothesis was independently proposed by East and Shull in 1908. It is also known as single gene heterosis or super dominance or cumulative of divergent alleles or stimulation of divergent alleles.
- ❖ According to this hypothesis, heterozygotes at least some of the loci are superior to both the homozygotes.
- ❖ Thus heterozygote Aa would be superior to AA and aa .
- ❖ In 1936 East proposed that at each locus there are several alleles e.g. $a_1, a_2, a_3, a_4...$ etc, with increasingly different functions. So heterozygotes between more divergent alleles would be more heterotic E.g. $a_1 a_4$ will be superior to $a_1 a_2, a_2 a_3$ or $a_3 a_4$.

Evidence for Overdominance hypothesis

There are not many clear-cut cases where the heterozygote is superior to the two homozygotes; but there is no doubt that in the case of some oligogenes, heterozygotes are superior to the homozygotes.

1. In case of **maize**, **gene ma** affects maturity. The heterozygote $Ma\ ma$ is more vigorous and later in anthesis and maturity than the homozygotes $Ma\ Ma$ and $ma\ ma$.
2. **Gustafsson** has reported two chlorophyll mutants **in barley** that produce larger and more number of seeds in the heterozygous state than do their normal homozygotes.
3. Similarly, heterozygotes for the **hooded gene in barley** show a higher rate of photosynthesis than the two homozygotes.

4. In human beings (*Homo sapiens*), **sickle cell anaemia** is produced by a recessive gene s which is lethal in the homozygous state. In Africa, the heterozygotes Ss are at a selective advantage over the normal SS individuals because they are more resistant to malaria.
5. Another case of heterozygote advantage is reported in ***Neurospora crassa*** (bread mold). Gene pab is concerned with the synthesis of **p-aminobenzoic acid**. The heterozygote $pab^+ pab$ is more vigorous and shows a faster growth rate than the two homozygotes $pab pab$ and pab^+pab^+ .

However, the superiority of heterozygotes need not be a result of overdominance. It could more easily be due to linkage in the repulsion phase or epistatic effects, i.e., an interaction between two or more nonalleles.

A comparison between dominance and overdominance hypotheses of heterosis

<i>Feature</i>	<i>Hypothesis of heterosis</i>	
	<i>Dominance</i>	<i>Overdominance</i>
Similarities		
Inbreeding leads to	Reduced vigour and fertility	Reduced vigour and fertility
Out-crossing leads to	Heterosis	Heterosis
Degree of heterosis increases with	Genetic diversity between parents	Genetic diversity between parents
Differences		
Inbreeding depression is the results of	Homozygosity for deleterious recessive alleles	Homozygosity itself
Heterosis is the result of	Masking of the harmful effects of recessive alleles by their dominant alleles.	Heterozogosity itself
The phenotype of heterozygote is	Comparable to that of the dominant homozygote	Superior to both the homozygotes
Inbreds as vigorous as the F_1 hybrid	Can be isolated	Can not be isolated

3. Epistasis Hypothesis

- ❖ In 1952, **Gowen** had suggested that influence of one locus on the expression of another may be involved in heterosis.
- ❖ Theoretically, epistatic interactions will lead to the maximum heterosis when the following two conditions are met with.
 - (1) First, the epistasis should be **predominantly of complementary type**, i.e., the estimates of h (dominance effects) and i (dominance x dominance interaction effects) have the same sign so that they do not cancel each other out.
 - (2) Second, the interacting pairs of **genes should be dispersed in both the parents**.
- ❖ It has been suggested that in the absence of overdominance, dispersion (between the two parents of hybrids) of genes showing complementary epistasis seems to be the major cause of heterosis.

Fixation of heterosis

1. **Asexual reproduction:** easily conserved in vegetatively propagated crops.
2. **Apomixis:** Seeds develop without fertilization. Apomictic seeds generally developed from maternal diploid cell and hence identical to mother plants. Citrus, blackberry, many flowering plants, Hieracium (Hawck weed) are the examples where heterosis can be fixed by apomixis.
3. **Balance Lethal System:** Homozygotes are lethal and hence die, only heterozygotes survive. E.g. Evening primrose (*Oenothera* spp.), BLS developed due to complex translocation.
4. **Polyploidy:** By chromosome doubling or polyploidy, especially interspecific and intergeneric hybrid. E.g. wheat-rye cross