21. Heterosis, inbreeding depression, various theories of Heterosis

Heterosis and Inbreeding Depression

Cross pollinated species and 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.

History of inbreeding

In breeding depression has been recognised by man for a long time. Knowing the consequences of inbreeding many societies have prohibited marriages between closely related individuals.

Darwin in 1876 published a book "cross and self fertilization in vegetable kingdom" in which he concluded that progenies obtained from self fertilization was weaker in maize. Detailed and precise information on inbreeding in maize was published by East in 1908 and Shull in 1909.

Effects of inbreeding

1. Appearance of lethal and sub lethal alleles: Chlorophyll deficiency, rootless seedlings and other malformations.
2. Reduction in vigour : Appearance of dwarf plants.
3. Reduction in reproductive ability - Less seed set, sterility
4. Segregation of population in distinct lines.
5. Increase in homozygosity
6. Reduction in yield.

Degrees of inbreeding depression

Various plant species exhibit different degrees of inbreeding depression. The depression may be from very high to nil. Based on degree of depression, the plant species can be grouped into 4 broad categories.

1. High inbreeding depression

Inbreeding leads to severe depression and exhibit lethal effects. After 3 or 4 generations of selfing it is hard to maintain lines. E.g. Lucerne, Carrot.

2. Moderate inbreeding depression

Though lethal effects are there, lines can be separated and maintained. E.g. Maize, Jowar, Bajra.

3. Low inbreeding depression

Only a small degree of inbreeding depression is observed. E.g. Cucurbits, Sunflower.

4. No inbreeding depression

The self-pollinated crops do not show inbreeding depression.

Heterosis

It is defined as the superiority of F_1 hybrid over both the parents in terms of yield or some other characters. The term heterosis was first used by Shull in1914.

Types of heterosis

1. Average heterosis

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$$\frac{\bar{F}_1 - \bar{MP}}{\bar{MP}} \times 100$$

Where,

$\bar{F}_1$ = Mean of hybrid

$\bar{MP}$ = Mid parental value

$\bar{MP}$ $(P_1 + P_2)$ Where P_1 = Parent 1

$$MP = \frac{\quad}{2} \qquad P_2 = \text{Parent 2}$$

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

ii) Heterobeltiosis : Superiority of F_1 over the better parent.

$$\frac{\bar{F}_1 - \bar{BP}}{\bar{BP}} \times 100$$

Where,

$\bar{BP}$ = Mean of better parent

iii) Economic heterosis

Superiority of the F1 compared to the high yielding commercial variety in a particular crop.

$$\frac{\bar{F}_1 - \bar{CV}}{\bar{CV}} \times 100$$

Where,

$\bar{CV}$ = Mean of commercial variety

4. Negative heterosis

Performance of F1 inferior to better parent / mid parent value. – e.g. Duration

Heterosis or hybrid vigour

Hybrid vigour is used as synonym of heterosis. Hybrid vigour refers to superiority of F_1 over better parent. In other words hybrid vigour is manifested effect of heterosis. Thus the term hybrid vigour is used to distinguish the F I superiority from negative heterosis.

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.

Genetic basis of heterosis

There are two main theories of heterosis and inbreeding depression.

1. Dominant hypothesis
2. Over dominance hypothesis.

1. Dominant hypothesis

First proposed by Davenport in 1908. It was later on expanded by Bruce, Keeble and Pellow.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.Two objections have been raised 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 vigourous as that of hybrid. However in practice such inbreds were not isolated.

b) Symmetrical distribution in F_2

In F_2 dominant and recessive characters segregate in the ratio of 3: 1. Quantitative characters, according to dominance hypothesis should not show symmetrical distribution. However, F_2 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 F_2 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 theory. According to this hypothesis, heterozygotes or atleast 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 at a2 a3 &I etc, with increasingly different functions. Heterozygotes between more divergent alleles would be more heterotic E.g. at &I will be superior to aj a2 or a2 a4.

Evidences for over dominance

In maize the maturity genes in heterozygous conditions are superior i.e. Ma ma. The heterozygote Mama is more vigorous than MaMa or mama. The human beings sickle cell anaemia is caused by ss which is lethal. But heterozygote individuals having Ss have advantage of having resistance against malaria compared to SS individuals.

Physiological basis of heterosis

Numerous studies were made to find out the physiological basis of heterosis. Earlier studies were related to embryo size, seed size, growth rates at various stages of development, rates of reproduction.

It was suggested that hybrid vigour was resulted from larger embryo and endosperm size of hybrid seeds. This was clearly demonstrated in certain cases only. In 1952 Whaley has concluded that primary heterotic effect is due to growth regulators and enzymes in the F 1. But all these studies were highly speculative. There was no evidence to point out clearly the possible reasons for heterozygote advantage.

Recent studies about heterosis

1. Reduced amount of single gene product:

In certain cases the heterozygote produces an intermediate amount of a gene product, which may lead to increased vigour and growth rate.

AA - more gene product

aa - Less gene product

Aa - Intermediate gene product.

This is seen in case of bread mold.

Neurospora crassa.

Gene Pab^{+} Produces P. amino benzoic acid.

Gene Pab Produces Less P. amino benzoic acid.

Heterozygote Pab + Pab - Intermediate amount of P amino benzoic acid which leads to faster growth of the fungus.

2. Separate gene products

AA - produce protein

aa - Produce protein which is slightly different.

Aa - will have both the Products.

This may have many advantages by having more adaptiveness. Human beings: SS Resistant to sickle cell anaemia

ss - Susceptible

Ss - Resistant to Sickle cell anaemia + malaria.

3. Combined gene product

Otherwise hybrid product. The hybrid may produce an enzyme molecule which may be somewhat different compared to enzymes produced by homozygotes. Such heterozygote enzymes are termed as *Hybrid Substance* which may be the reason for hybrid vigour.

4. Effect in two different tissues

Both homozygotes may produce high levels of an enzyme in two different tissues.

But heterozygote may produce intermediate level. E.g. Maize Adh gene for enzyme alcohol dehydrogenase in seeds.