The homozygous and heterozygous balances are concepts of genetic organisation of populations These concepts are neither very clear nor very specific in terms of the physical bases of these genetic organisations or the types of gene combinations involved. But it may be visualised that in self-pollinated species, those gene combinations would be favoured, which show no injurious effects in the homozygous state. However, upon outcrossing, these gene combinations may show heterosis depending upon the specific gene combinations involved. In the cross-fertilized species, on the other hand, heterozygosity is the natural condition. Therefore, gene combinations that would be deleterious in the homozygous state are not selected against and are maintained in the population. Consequently, such species would show inbreeding depression. The degree of inbreeding depression in these species would be largely determined by the degree of self-fertilization occurring in the natural populations of the species. Cross-fertilized species like maize (*Z. mays*) show up to 10 per cent self-pollination and moderate inbreeding depression. Crops like alfalfa (*M. sativa*) show very little inbreeding and, as a result, a very severe inbreeding depression. Therefore, *the homozygous and heterozygous balances may be visualised as gene combinations that are adapted to heterozygosity and homozygosity, respectively.*

13.4. HETEROSIS

The term heterosis was first used by Shull in 1914. Heterosis is often called ***true heterosis*** or ***euheterosis*** to distinguish it from luxuriance. ***Heterosis may be defined as the superiority of an*** F_1 ***hybrid over both its parents in terms of yield or some other character.*** Generally, heterosis is manifested as an increase in vigour, size, growth rate, yield or some other characteristic. But in some cases, the hybrid may be inferior to the weaker parent. This is also regarded as heterosis; we shall focus on this aspect a little later. Often the superiority of F_1 is estimated over the average of the two parents, or the mid-parent. If the hybrid is superior to the mid-parent, it is regarded as heterosis (***average heterosis*** or ***relative heterosis***). This practice has found some acceptance, particularly in theoretical studies. However, in practical plant breeding, the superiority of F_1 over mid-parent is of no use since it does not offer the hybrid any advantage over the better parent. Therefore, average heterosis is of little or no use to the plant breeder. More generally, heterosis is estimated over the superior parent; such an estimate is sometimes referred to as ***heterobeltiosis***. *The term heterobeltiosis is not commonly used since most breeders regard this to be the only case of heterosis and refer to it as such i.e.,* ***heterosis***. In 1944, Powers suggested that *the term heterosis should be used only when the hybrid is either superior or inferior to both the parents.* Other situations should be regarded as partial or complete dominance. This is easily explained with the help of Table 13.1. However, the commercial usefulness of a hybrid would primarily depend on its performance in comparison to the best commercial variety of the concerned crop species. In many cases, the superior parent of the hybrid may be inferior to the best commercial variety. In such cases, it will be desirable to estimate heterosis in relation to the best commercial variety of the crop; such an estimate is known as ***economic***, ***standard*** or ***useful heterosis***. *Economic heterosis is the only estimate of heterosis, which is of commercial or practical value.*

There has been considerable confusion due to the use of various terms to describe

TABLE 13.1

Heterosis and dominance in relation to parental values

Position and mean value of the parents	*Mean value of the F_1 hybrid*	*Phenomenon*
	> 10	**Heterosis**
Parent A (10)	10	Complete dominance
	< 10 but > 8	Partial dominance
(Mid-parent) (8)	8	No dominance
	< 8 but > 6	Partial dominance
Parent B (6)	6	Complete dominance
	< 6	**Heterosis**

heterosis, and also due to the use of heterosis in different contexts. For clarity and simplicity, it is desirable to avoid the use of many terms to describe similar but somewhat different situations. For example, heterosis or euheterosis is classified as (1) mutational and balanced heterosis. ***Mutational heterosis*** results from dominance gene action, *i.e.*, masking of the deleterious affects of recessive mutant alleles by their dominant counterparts. ***Balanced heterosis***, on the other hand, arises due to over-dominance gene action, *i.e.*, superiority of the heterogygotes over both the corresponding homozygotes. In addition, several other confusing terms are employed to signify the various aspects of heterosis. These terms may be useful in discussions on some population genetic or some other phenomena, but their usefulness in plant breeding treatments is often questionable. For example, the concepts of mutational and balanced heterosis are of limited relevance since the magnitudes of these two types of heterosis can not be estimated.

13.4.1. Heterosis and Hybrid Vigour

Hybrid vigour has been used as a synonym of heterosis. It is generally agreed that hybrid vigour describes only the superiority of hybrids over their parents, while heterosis describes other situations as well. But a vast majority of the cases of heterosis are cases of superiority of hybrids over their parents. The few cases where F_1 hybrids are inferior to their parents may also be regarded as cases of hybrid vigour in the negative direction. For example, many F_1 hybrids in tomato are earlier than their parents. Earliness in many crops is agriculturally desirable. It may be argued that the earliness of F_1 hybrids exhibits a faster development in them so that their vegetative phase is replaced by the reproductive phase more quickly than in their parents. *Therefore, the use of heterosis and hybrid vigour as synonym seems to be reasonably justified.*

13.4.2. Luxuriance

Luxuriance is the increased vigour and size of interspecific hybrids. The principal difference between heterosis and luxuriance lies in the reproductive ability of the hybrids. *Heterosis is accompanied with an increased fertility, while luxuriance is expressed by interspecific hybrids that are generally sterile or poorly fertile.* In addition, luxuriance may not result from either masking of deleterious genes or from balanced gene combinations

13.4.5. Manifestations of Heterosis

Heterosis is the superiority of a hybrid over its parents. This superiority may be in yield, quality, disease and insect resistance, adaptability, general size or the size of specific parts, growth rate, enzyme activity, etc. These various manifestations of heterosis may be summarised as follows.

1. ***Increased yield.*** Heterosis is generally expressed as an increase in the yield of hybrids. Commercially, this phenomenon is of the greatest importance since higher yields are the most important objective of plant breeding. The yield may be measured in terms of grain, fruit, seed, leaf, tubers or the whole plant.

2. ***Increased Reproductive Ability.*** The hybrids exhibiting heterosis show an increase in fertility or reproductive ability. This is often expressed as higher yield of seeds or fruits or other propagules, *e.g.*, tuber in potato (*S. tuberosum*), stem in sugarcane (*S. officinarum*), etc.

3. ***Increase in Size and General Vigour.*** The hybrids are generally more vigorous, *i.e.*, healthier and faster growing and larger in size than their parents. The increase in size is usually a result of an increase in the number and size of cells in various plant parts. Some examples of increased size are increases in fruit size in tomato, head size in cabbage, cob size in maize, head size in jowar, etc.

4. ***Better Quality.*** In many cases, hybrids show improved quality. This may or may not be accompanied by higher yields. For example, many hybrids in onion show better keeping quality, but not yield, than open-pollinated varieties.

5. ***Earlier Flowering and Maturity.*** In many cases, hybrids are earlier in flowering and maturity than the parents. This may sometimes be associated with a lower total plant weight. But earliness is highly desirable in many situations, particularly in vegetables. Many tomato hybrids are earlier than their parents.

6. ***Greater Resistance to Diseases and Pests.*** Some hybrids are known to exhibit a greater resistance to insects or diseases than their parents.

7. ***Greater Adaptability.*** Hybrids are generally more adapted to environmental changes than inbreds. In general, the variance of hybrids is significantly smaller than that of inbreds. This shows that hybrids are more adapted to environmental variations than are inbreds. In fact, it is one of the physiological explanations offered for heterosis.

8. ***Faster Growth Rate.*** In some cases, hybrids show a faster growth rate than their parents. But the total plant size of the hybrids may be comparable to that of parents. In such cases, a faster growth rate is not associated with a larger size.

9. ***Increase in the Number of A Plant Part.*** In some cases, there is an increase in the number of nodes, leaves and other plant parts, but the total plant size may not be larger. Such hybrids are known in beans (*P. vulgaris*) and some other crops.

These are some of the characteristics for which heterosis is easily observed. Many other characters are also affected by heterosis, *e.g.* enzyme activities, cell division, vitamin content (vit. C content in tomato), other biochemical characteristics, etc., but they are not so readily observable.

13.5. GENETIC BASES OF HETEROSIS AND INBREEDING DEPRESSION

Heterosis and inbreeding depression are closely related phenomena. In fact, they may be regarded as the opposite sides of the same coin. Therefore, genetic theories that explain heterosis also explain inbreeding depression. There are three main theories to explain heterosis and, consequently, inbreedings depression: (1) dominance, (2) overdominance, and (3) epistasis hypotheses.

13.5.1. Dominance Hypothesis

The dominance hypothesis was first proposed by Davenport in 1908. It was later expanded by Bruce, and by Keeble and Pellew in 1910. In simplest terms, this hypothesis suggests that at each locus the dominant allele has a favourable effect, while the recessive allele has an unfavourable effect. In heterozygous state, the deleterious effects of recessive alleles are masked by their dominant alleles. *Thus heterosis results from the masking of harmful effects of recessive alleles by their dominant alleles. Inbreeding depression, on the other hand, is produced by the harmful effects of recessive alleles, which become homozygous due to inbreeding.* Therefore, according to the dominance hypotheses, heterosis is not the result of heterozygosity; it is the result of prevention of expression of harmful recessives by their dominant alleles. Similarly, inbreeding depression does not result from homozygosity *per se*, but from the homozygosity of recessive alleles, which have harmful effects.

This hypothesis may be further explained as follows. In open-pollinated populations, plants are highly heterozygous. As a result, they do not show the harmful effects of the large number of deleterious recessive alleles present in the population. Inbreeding increases homozygosity. As a result, many recessive alleles become homozygous. Lethal recessive alleles are eliminated by natural selection. But recessive alleles with smaller harmful effects survive in the homozygous condition. Consequently, such alleles reduce the vigour and fertility of the inbred lines that carry them in the homozygous state. Inbred lines are nearly homozygous, and different inbred lines would receive different proportions of dominant and recessive alleles. Therefore, different inbred lines may be expected to vary in vigour and yield. Thus, according to this hypothesis, it should be possible to isolate such inbreds that have all the dominant alleles present in the population. Such inbreds would be as vigorous as the open-pollinated varieties, or even more so. But such inbreds have not been isolated so far.

Similarly, heterosis in an F_1 hybrid is a result of the masking of harmful effects of recessive alleles present in one parent by the dominant alleles of the concerned genes present in the other parent and *vice versa*, Obviously, heterosis would depend upon the genotypes of the two parents. Hybrids from parents with similar recessive and dominant alleles would show little or no heterosis (Fig. 13.1, cross III), while those with different alleles would show heterosis (Fig. 13.1, cross II). In practice, some parents produce heterotic progeny, while others do not. Generally, parents of diverse origin are more likely to produce heterotic progeny than those of similar origin.

13.5.1.1. Objections. Two objections have been raised against the dominance hypothesis. The *first objection* relates to the failure in isolation of lines homozygous for all the dominant genes. The *second objection* is directed at the symmetrical distributions obtained in F_2 populations.

the increasing number of identical alleles appears to have a negative effect on vigour (see, Bichler *et al.*, 2003).

13.5.1.2. Explanations for the Objections. In 1917, Jones suggested that since quantitative characters are governed by many genes, these genes are likely to show linkage. It may be expected that dominant and recessive genes governing a character would be linked together. In such a case, inbreds containing all the dominant genes cannot be isolated because this would require several precisely placed crossovers. It would also explain the symmetrical curves obtained in F_2. This explanation is often known as the ***dominance of linked genes hypothesis.***

Later in 1921, Collins showed that if the number of genes governing a quantitative character was large, symmetrical distribution would be obtained even without linkage. Further, it is unlikely that a plant containing all the dominant genes would be recovered if the number of genes were large even if they were not linked. The distribution curve would further become symmetrical due to the effects of environment, that is, due to less than 100 per cent heritability.

13.5.2. Overdominance Hypothesis

This hypothesis was independently proposed by East and Shull in 1908. This is sometimes known as ***single gene heterosis, superdominance, cumulative action of divergent alleles,*** and ***stimulation of divergent alleles.*** The idea of superdominance, *i.e.*, heterozygote superiority, was initially put forth by Fisher in 1903; it was elaborated by East and Shull in 1908 to explain heterosis. *According to overdominance hypothesis, heterozygotes at at least some of the loci are superior to both the relevant homozygotes.* Thus heterozygote *Aa* would be superior to both the homozygotes *AA* and *aa*. *Consequently, heterozygosity is essential for and is the cause of heterosis, while homozygosity resulting from inbreeding produces inbreeding depression.* It would, therefore, be impossible to isolate inbreds as vigorous as F_1 hybrids if heterosis were the consequence of overdominance.

In 1936, East proposed that at each locus showing overdominance, there are several alleles, *e.g.*, a_1, a_2, a_3, a_4 ......, etc., with increasingly different functions. He further proposed that heterozygotes for more divergent alleles would be more heterotic than those involving less divergent ones. For example, a_1a_4 would be superior to a_1a_2, a_2a_3 or a_3a_4. It is assumed that the different alleles perform somewhat different functions. The hybrid is, therefore, able to perform the functions of both the alleles, which is not possible in the case of two homozygotes.

13.5.2.1. Evidence for Overdominance. There are not many clear-cut cases where the heterozygote is superior to the two homozygotes; in fact, overdominance has not been demonstrated unequivocally for any polygomic trait (see, Banga and Banga, 1998). This has been the biggest objection to the general acceptance of overdominance hypothesis. But there is no doubt that in the case of some oligogenes, heterozygotes are superior to the homozygotes. 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*. 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. Similarly, heterozygotes for the hooded gene in barley show a higher rate of photosynthesis than the two homozygotes.

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. 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 $pab^+ pab^+$.

But the number of such genes where heterozygote superiority has been established beyond doubt is limited. There is a large number of cases, however, where heterozygotes for chromosome segments, *e.g.*, inversions, etc., or complex loci are known to be superior to the homozygotes, 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.

Molecular studies suggest that most regulatory genes exhibit some measure of dosage-dependence (overdominance), whereas house-keeping genes usually show dominance. In case of yeast, loci that tend to have significant haplo-insufficient effect on growth in diploid yeast encode polypeptides that are involved in molecular complexes. In multicellular organisms, products of regulatory genes usually function as parts of complexes. It may, therefore, be expected that quantitative traits would be largely controlled by several dosage-dependent regulatory loci. Therefore, it is likely that heteroris is the result of different alleles being present at loci that contribute to the regulatory pathways involved in the development of the concerned quantitative traits. Results from several studies tend to support this suggestion. For example, the levels of mRNAs transcribed from 10 genes encoding zein were analyzed in two inbred lines and their reciprocal hybrids in maize. In the case of only one gene, the mRNA level in the hybrid was comparable to the mid-parent value; in the case of remaining 9 genes, the levels were either up to two-fold higher or lower. It is interesting that heterotic characteristics seldom show greater than two-fold effects in terms of the change in biomass or fertility, although spectacular exceptions exist. The experimental findings indicate that bringing together divergent regulatory elements will cause global modulation of gene expression that may lead to heterosis.

13.5.3. Comparison between Dominance and Overdominance Hypotheses

The two hypotheses lead to similar expectations, but they do differ from each other with respect to some expectations. The similarities and differences between them are listed below (Table 13.2).

13.5.3.1. Similarities. The two hypotheses have the following similarities.

1. Inbreeding would produce inbreeding depression.
2. Outcrossing would restore vigour and fertility.
3. The degree of heterosis would depend upon the genotypes of the two parents. In general, the greater the genetic diversity betwcen the parents, the higher the magnitude of heterosis.

13.5.3.2. Differences. The chief differences between the two hypotheses are as follows.

1. Heterozygotes are superior to the two homozygotes according to the overdominance hypothesis, while according to the dominance hypothesis they are as good as the dominant homozygote.
2. Inbreds as vigorous as the F_1 hybrid can be isolated according to the dominance hypothesis, but it will be impossible according to the overdominance hypothesis.
3. According to dominance hypothesis, inbreeding depression is due to homozygosity of harmful recessive alleles, while as per overdominance hypothesis, it is due to homozygosity itself.
4. According to the overdominance hypothesis, heterosis is the consequence of heterozygosity *per se*. But as per dominance hypothesis it is the result of dominant alleles masking the deleterious effects of their recessive alleles, and heterozygosity itself is not the cause of heterosis.

TABLE 13.2

A comparison between dominance and overdominance hypotheses of heterosis

Feature	*Hypothesis of heterosis*	
	Dominance	*Overdominance*
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