CHAPTER NINE

# Heterosis

Hybrid cultivars are used for the commercial production of a number of plant species. They are a desirable type of cultivar because of their ability to capitalize on heterosis. Heterosis is the superiority in performance of hybrid individuals compared with their parents. The occurrence of heterosis is common in plant species, but its level of expression is highly variable.

## MEASUREMENT OF HETEROSIS

The performance of a hybrid relative to its parents can be expressed in two ways. Mid-parent heterosis is the performance of a hybrid compared with the average performance of its parents. High-parent heterosis is a comparison of the performance of the hybrid with that of the best parent in the cross.

Heterosis usually is expressed as a percentage and computed as follows:

$$\text{Mid-parent heterosis (\%)} = \frac{F_1 - \text{MP}}{\text{MP}} \times 100$$

$$\text{High-parent heterosis (\%)} = \frac{(F_1 - \text{HP})}{\text{HP}} \times 100$$

where $F_1$ = performance of hybrid

MP = average performance of parents per se (parent 1 + parent 2)/2

HP = performance of best parent

For example, assume that the yield of a hybrid is 90 units, that of parent 1 is 60 units, and that of parent 2 is 80 units. The average performance of the parents would be 70 units.

$$\text{Mid-parent heterosis} = \frac{90 - 70}{70} \times 100 = 28.6\%$$

$$\text{High-parent heterosis} = \frac{90 - 80}{80} \times 100 = 12.5\%$$

## GENETIC BASIS OF HETEROSIS

Heterosis can be expressed when the parents of a hybrid have different alleles at a locus and there is some level of dominance among those alleles (Falconer, 1981). There has been extensive debate concerning the relationship between level of dominance and expression of heterosis. The two hypotheses that have received the most attention are the dominance hypothesis and the overdominance hypothesis. According to the dominance hypothesis, heterosis is caused by complete or partial dominance. In the overdominance hypothesis, the value of the heterozygote is considered superior to the value of either homozygote.

The difference between the two hypotheses can be illustrated with the cross *AAbbCC* × *AABBcc*. Assume that the amount of performance contributed by the *A* allele is 10 units, that of *B* is 12, that of *b* is 6, that of *C* is 8, and that of *c* is 4. By substituting these values for each allele, the average of the alleles *AA* would be 10, of *BB* would be 12, of *bb* would be 6, of *CC* would be 8, and of *cc* would be 4. The performance of the *AAbbCC* parent would be $10 + 6 + 8 = 24$, and that of *AABBcc* would be $10 + 12 + 4 = 26$. The performance of the hybrid will be unaffected by the *A* allele because this allele contributes equally to the expression of both parents and the hybrid. If there is no dominance, the value for the *Bb* and *Cc* loci will be the average of the two alleles, $Bb = (12 + 6)/2 = 9$ and $Cc = (8 + 4)/2 = 6$, and no heterosis will be expressed in the hybrid: $AABbCc = 10 + 9 + 6 = 25$. If partial or complete dominance is present, as is assumed by the dominance hypothesis, the value of the heterozygote will be greater than the average of the two alleles at a locus. For example, assume that there is partial dominance for *Bb*, which gives it a value of 10, and for *Cc*, which has a value of 7. The hybrid would express both mid-parent and high-parent heterosis: $AABbCc = 10 + 10 + 7 = 27$. The maximum values for the heterozygous loci *Bb* and *Cc* under the dominance hypothesis are those achieved with complete dominance, $BB = Bb = 12$ and $CC = Cc = 8$. In this case, the hybrid would express even greater heterosis than with partial dominance: $AABbCc = 10 + 12 + 8 = 30$.

For the overdominance hypothesis, the value of the heterozygote exceeds that which is possible with complete dominance. The value of *Bb* would be greater than that of *BB* or *bb* ($Bb > 12$), and the value of *Cc* would be greater than that of *CC* or *cc* ($Cc > 8$). If $Bb = 13$ and $Cc = 9$, the *AABbCc* hybrid would have a value of $10 + 13 + 9 = 32$.

There are arguments for and against both of the hypotheses. The dominance hypothesis was proposed by Bruce (1910) and received strong support from Jones and others (Jones 1917,1945,1958). It is considered a reasonable explanation of heterosis because it is based on levels of dominance that have been widely observed for qualitative characters. In contrast, evidence for the expression of overdominance for qualitative characters is limited.

Several arguments against the dominance hypothesis have been presented (Hallauer and Miranda, 1981). If complete dominance is the maximum expression of a heterozygote, it should be possible to develop a homozygous segregate from a cross that is equal in performance to the hybrid. For example, the cross of *AAbbCC* × *AABBcc* should produce $F_2$ progeny with the genotype *AABBCC* that are equal in performance to the hybrid *AABbCc*. In crops such as maize, inbred lines have not been identified that are equal in yield to the best hybrid. This inability to obtain inbreds that are equal in performance to hybrids is cited as evidence against the dominance hypothesis. In rebuttal of this argument, it has been pointed out that the probability of recovering all favorable dominant alleles in one homozygous individual is limited when parents differ for a large number of alleles controlling a quantitative character (Collins, 1921).

If complete or partial dominance is present, the frequency distribution of $F_2$ progeny from a cross should be skewed toward the dominant phenotype. With overdominance, a normal distribution would be expected. The $F_2$ distributions for yield and other quantitative characters generally are normal, a fact that is used as evidence against the dominance hypothesis. As a refutation of this criticism of the dominance hypothesis, it has been indicated that the amount of skewness expected is limited when the number of loci controlling a character is large (Collins, 1921).

The overdominance hypothesis proposed by Shull (1908) was supported by East (1936), Hull (1945), and others. The primary argument against the overdominance hypothesis is the extensive amount of data that demonstrate the importance of partial or complete dominance for quantitative characters and the limited amount of similar evidence for the importance of overdominance. Hallauer and Miranda (1981) reviewed the existing data for quantitative characters of maize and concluded that the evidence supports the dominance hypothesis as the genetic basis of heterosis.

The possible role of epistasis in the expression of heterosis also has been considered. Epistasis involves the interaction of alleles at two or more loci that could result in performance superior to that of independent loci. There is evidence for the presence of epistasis in the expression of quantitative characters, but epistasis seems to be considerably less important than dominance (Hallauer and Miranda, 1981).

## HETEROSIS IN DIPLOID CULTIVARS

In a diploid species with two alleles at a locus, the average heterosis of a cross is greatest for a single-cross hybrid due to the occurrence of the greatest possible number of loci with a dominant allele. For example, the mating of the inbreds *AABBccdd* × *aabbCCDD* results in single-cross individuals with a dominant allele at each locus, *AaBbCcDd*. Dominant alleles at each of the four loci for all single-cross individuals provide the highest average performance for the cross.

A three-way hybrid is produced by the mating of a single-cross hybrid to a third inbred parent. The average heterosis expressed by the three-way hybrid depends on the frequency of loci that retain a dominant allele. This is a function of the genetic relationship between the genotype of the single cross and the third parent. The frequency of loci with a dominant allele generally will be less in the three-way than in the single cross. Consider the mating of the single cross *AaBbCcDd* with the inbred *AABBccdd*. The genotypes of the hybrid progeny are *A_B_CcDd*, *A_B_Ccdd*, *A_B_ccDd*, *A_B_ccdd*. Because of the occurrence of homozygous recessive loci in some of the progeny, the frequency of loci with dominant alleles and the average heterosis in the three-way cross is less than in the single cross.

In a double-cross hybrid formed by mating two single crosses, the average frequency of loci with a dominant allele and average heterosis would be less than in a three-way hybrid. Consider the mating of two single crosses with identical genotypes, *AaBbCcDd* × *AaBbCcDd*. Homozygous recessive alleles at one or more loci in some of the progeny of this mating would reduce the average heterosis of the cross.

## HETEROSIS IN HYBRID CULTIVARS OF AUTOPOLYPLOID SPECIES

The potential use of hybrid cultivars for autopolyploid species has been evaluated, particularly for alfalfa. The expression of heterosis has been associated with the interaction of different alleles at a locus.

The number of different alleles at a locus in an autotetraploid can range from one to four. It has been proposed that maximum heterosis is expressed by a tetragenic locus (*abcd*), and declines for a trigenic (*abcc*), digenic (*aaab*), and monogenic locus (*aaaa*) (Busbice and Wilsie, 1966). Under this assumption, any mating system that enhances the frequency of loci with multiple alleles would maximize the expression of heterosis. Dunbier and Bingham (1975) tested this hypothesis by deriving populations with equivalent gene frequencies but different levels of intralocus heterozygosity. The populations with the highest expected frequency of tetragenic and trigenic loci were found to have the greatest forage yield, seed weight, and fertility.

The frequency of loci with multiple alleles in a hybrid is associated with the level of inbreeding of the parents. Double-cross hybrids have more multiallelic loci than do single-cross hybrids when parents are inbred. Consider the extreme example in which there are four homozygous autotetraploid parents, each with a different allele at a locus: *aaaa*, *bbbb*, *cccc*, and *dddd*. Single crosses between any two parents would result only in digenic loci, such as *aaaa* × *bbbb* → *aabb*.

A double cross between the four parents would result in a tetragenic locus, *abcd*. In contrast, single-cross hybrids have more multiallelic loci on the average than do double crosses when the parents are noninbred.

## IMPLICATIONS OF HETEROSIS ON CULTIVAR DEVELOPMENT

The possibility of utilizing hybrid cultivars for commercial production has been examined for virtually every crop species. The two primary motivations for the interest are increased productivity of the crop and the desire to have a seed product that must be purchased each year by the farmer.

Heterosis has been observed for seed or forage yield in essentially all crop species, but the level of heterosis is widely different among species. In general, heterosis is greatest in cross-pollinated crops and least in self-pollinated species. The commercial use of hybrids is restricted to those crops in which the amount of heterosis is sufficient to justify the extra cost required to produce hybrid seed (Chap. 35).

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