**Breeding hybrid cultivars**

**What is a hybrid cultivar?**

A **hybrid cultivar**, by definition, is the F1 offspring of a planned cross between inbred lines, cultivars, clones, or populations. Depending on the breeding approach, the hybrid may comprise two or more parents. A critical requirement of hybrid production is that the parents be unidentical. As will be discussed next, it is this divergence that gives hybrids their superior performance. The outstanding yields of certain modern crops, notably corn, owe their success to the exploitation of the phenomenon of **heterosis** (hybrid vigor), which is high when parents are divergent. Much of what we know about hybrid breeding came from the discoveries and experiences of scientists engaged in corn hybrid cultivar development. However, commercial hybrids are now available for many crops, including self-pollinating species.

**Brief historical perspective**

One of the earliest records on hybridization dates back to 1716 when American Cotton Mather observed the effects of cross-fertilization in maize, attributing the multicolored kernels to wind-borne intermixture of different colored cultivars. However, it was the German T. G. Koelreuter who conducted the first systematic studies on plant hybridization in 1766. Even though previous observations had been made to the effect that offspring of crosses tended to exhibit superior performance over the parents, it was G. H. Shull who in 1909 first made clear scientific-based proposals for exploiting heterosis to produce uniform and high-yielding cultivars. Unfortunately, the idea was at that time impractical and potentially expensive to commercially exploit. In 1918, D. F. Jones proposed a more practical and costeffective approach to producing hybrid cultivars by the method of the double cross. Double-cross hybrids produced significantly more economic yield than the singlecross hybrids originally proposed by Shull. Single-cross hybrid seed was then produced on weak and unproductive inbred parents, whereas double-cross seed was produced on vigorous and productive single-cross plants. The corn production industry was transformed by hybrids, starting in the 1930s Other notable advances in the breeding of hybrids were made by researchers including M. I. Jenkins in 1934 who devised a method (topcross performance) to evaluate the effectiveness of parents in a cross (i.e., combining ability). Through this screening process, breeders were able to select a few lines that were good combiners (productive in a cross) for use in hybrid breeding.

The next significant impact on hybrid production also came in the area of techniques of crossing. Because corn is outcrossed and bisexual, it is necessary to emasculate one of the parents (i.e., make one female) as part of the breeding process. In the early years of corn hybrid breeding, emasculation was accomplished by the laborintensive method of mechanical detasseling (removal of the tassel). The discovery and application of **cytoplasmic male sterility** (**CMS**) to corn hybrid programs eliminated the need for emasculation by the late 1960s. Unfortunately, the success of CMS was derailed when the **Texas cytoplasm** (**T-cytoplasm**), which was discovered in 1938 and was at that time the dominant form of male sterility used in corn breeding, succumbed to the southern leaf blight epidemic of 1970 and devastated the corn industry. It should be mentioned that mechanized detasselers (rather than CMS) are used by some major seed companies in hybrid seed production of corn today.

Realizing that the limited number of inbred lines used in hybrid programs did not embody the complete genetic potential of the source population, and with the need to develop new inbred lines, scientists embarked on cyclical recombination (by recurrent selection) to generate new variability and to improve parental lines. Breeders were able to develop outstanding inbred lines to make single-cross hybrids economical enough to replace double-cross hybrids by the 1960s. By this time, corn hybrid production programs had developed a set of standard practices consisting of the following, as observed by N. W. Simmonds:

1. Maintenance and improvement of source population by open-pollinated methods (recurrent selection).
2. Isolation of new inbreds and improvement of old ones (by backcrossing).
3. Successive improvement of single-cross hybrids by parental improvement.
4. CMS-based seed production.

The application of hybrid methodology in breeding has socioeconomic implications. The commercial seed industry has rights to its inventions, which generate royalties. More importantly, because heterosis is maximized in the F1, farmers are generally prohibited from saving seed from the current season’s crop to plant the next year’s crop. They must purchase seed from the seed suppliers each season. Unfortunately, poor producers in developing countries cannot afford annual seed purchase. Consequently, local and international (e.g., international agricultural research centers such as the Centro Internationale de Mejoramiento de Maiz y Trigo (CIMMYT) in Mexico) efforts continue to be largely devoted to producing propagable improved openpollinated cultivars for developing countries.

The idea of commercializing hybrid seed production is traced to Henry A. Wallace, an Iowa farmer, who studied self-pollination and selfing of corn in 1913. His industry led to the founding of the Pioneer Hi-Bred Corn Company in Iowa, in 1925. In 1933, only about 0.1% of US corn production was devoted to hybrid seed. Today, hybrid seed is planted on almost all corn fields. Hybrids are also gradually being embraced by developing countries (see Chapter 26).

**Concepts of hybrid vigor and inbreeding depression**

As previously stated, the hybrid production industry thrives on the phenomenon of hybrid vigor.

**Hybrid vigor**

**Hybrid vigor** may be defined as the increase in size, vigor, fertility, and overall productivity of a hybrid plant, over the midparent value (average performance of the two parents). It is calculated as the difference between the crossbred and inbred means.

**Hybrid vigor = {[F1 − (P1 + P2)/2] / [(P1 + P2)/2]}**

The estimate is usually calculated as a percentage (i.e., × 100).

The synonymous term, **heterosis**, was coined by G. H. Shull. It should be pointed out immediately that, as it stands, heterosis is of no value to the breeder (and hence farmer) if a hybrid will only exceed the midparent in performance. Such advantageous hybrid vigor is observed more frequently when breeders cross parents that are genetically diverse. The *practical* definition of heterosis is hybrid vigor that greatly exceeds the better or higher parent in a cross. Heterosis occurs when two inbred lines of outbred species are crossed, as much as when crosses are made between pure lines of inbreeders.

Heterosis, though widespread in the plant kingdom, is not uniformly manifested in all species and for all traits. It is manifested at a higher intensity in traits that have fitness value, and also more frequently among cross-pollinated species than self-pollinated species. All breeding methods that are preceded by crossing make use of heterosis to some extent. However, it is only in hybrid cultivar breeding and the breeding of clones that the breeder has the opportunity to exploit the phenomenon to full advantage.

Hybrids dramatically increase yields of non-hybrid cultivars. By the early 1930s (before extensive use of hybrids), maize yield in the USA averaged 1,250 kg/ha. By the early 1970s (following the adoption of hybrids), maize yields quadrupled to 4,850 kg/ha. The contribution of hybrids (genotype) to this increase was estimated at about 60% (the remainder being attributed to production practices).

**Inbreeding depression**

Heterosis is opposite and complementary to **inbreeding depression** (reduction in fitness as a direct result of inbreeding). In theory, the heterosis observed on crossing is expected to be equal to the depression upon inbreeding, considering a large number of crosses between lines derived from a single base population. In practice, plant breeders are interested in heterosis expressed by specific crosses between selected parents, or between populations that have no known common origin.

Reduction in fitness is usually manifested as a reduction in vigor, fertility, and productivity. The effect of inbreeding is more severe in the early generations (generations 5–8). Just like heterosis, inbreeding depression is not uniformly manifested in plants. Plants including onion, sunflower, cucurbits, and rye are more tolerant of inbreeding with minimal consequences of inbreeding depression. On the other hand plants such as alfalfa and carrot are highly intolerant of inbreeding.

**Genetic basis of heterosis**

Two schools of thought have been advanced to explain the genetic basis for why fitness lost on inbreeding tends to be restored upon crossing. The two most commonly known are the **dominance theory** first proposed by C. G. Davenport in 1908 and later by I. M. Lerner, and the **overdominance theory** first proposed by Shull in 1908 and later by K. Mather and J. L. Jinks. A third theory, the mechanism of epistasis (non-allelic gene interactions) has also been proposed. A viable theory should account for both inbreeding depression in crosspollinated species upon selfing, and increased vigor in F1 organisms upon hybridization.

**Dominance theory**

The dominance theory assumes that vigor in plants is conditioned by dominant alleles, recessive alleles being deleterious or neutral in effect. It follows then that a genotype with more dominant alleles will be more vigorous than one with few dominant alleles. Consequently, crossing two parents with complementary dominant alleles will concentrate more favorable alleles in the hybrid than either parent. The dominance theory is the more favored of the two theories by most scientists, even though neither is completely satisfactory. In practice, linkage and a large number of genes prevent the breeder from developing inbred lines that contain all homozygous dominant alleles. Too many deleterious alleles would be present to make it difficult to inbreed to recover sufficient loci with homozygous dominant alleles. Inbreeding depression occurs upon selfing because the deleterious recessive alleles that are protected in the heterozygous condition (heterozygous advantage), become homozygous and are expressed. It should be pointed out that highly productive inbred lines have continued to be produced for hybrid production, the reason why single-cross hybrids have returned to dominance in corn hybrid production. To illustrate this theory, assume a quantitative trait is conditioned by four loci. Assume that each dominant genotype contributes two units to the phenotype, while a recessive genotype contributes one unit. A cross between two inbred parents could produce the following outcome:

With dominance, each locus will contribute two units to the phenotype. The result is that the F1 would be more productive than either parent.

D. L. Falconer developed a mathematical expression for the relationship between the parents in a cross that leads to heterosis as follows:



Where HF1 = deviation of the hybrid from the midparent value, *d* = degree of dominance, and *y* = difference in gene frequency in the parents of the cross. From the expression, maximum midparent heterosis (HF1) will occur when the values of the two factors (*d*, *y*) are each unity. That is, the populations to be crossed are fixed for opposite alleles (*y* = 1.0) and there is complete

dominance (*d* = 1.0).

**Types of hybrids**

As previously discussed, the commercial applications of hybrid breeding started with a cross of two inbred lines (a single cross: A × B) and later shifted to the more economic double cross [(A × B) × (C × D)] and then back to a single cross. Other parent combinations in hybrid development have been proposed, including the threeway cross [(A × B) × C] and modified versions of the single cross, in which closely related crosses showed that the single cross was superior in performance to the other two in terms of average yield. However, it was noted also that the genotype × environment interaction (hybrid × environment) mean sum of squares (from the ANOVA table; see Chapter 23) for the single cross was more than twice that for the double crosses, the mean sum of squares for the three-way cross being intermediate. This indicated that the single crosses were more sensitive or responsive to environmental conditions than the other crosses. Whereas high average yield is important to the producer, consistency in performance across years and locations (i.e., yield stability) is also important. As R. W. Allard and A. D. Bradshaw explained, there are two basic ways in which stability may be achieved in the field. Double and three-way crosses have a more genetically divergent population for achieving buffering. However, a population of single-cross genotypes that are less divergent can also achieve stability on the basis of individual buffering whereby individuals in the population are adapted to a wide range of environments. Today, commercial hybrids are predominantly single crosses. Breeders continue to develop superior inbred lines. The key to using these materials in hybrid breeding is identifying pairs of inbreds with outstanding combining ability.