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Role of Chromosome Blocks in Heterosis and Estimates of Dominance and Overdominance[1]

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ABSTRACT

Chromosome blocks are the genomic units of genetic transmission in sexual reproduction. We work with chromosome blocks, not individual genes in our conventional breeding and genetic research. Thus, chromosome blocks underpin heterosis and estimates of gene action. Chromosome blocks vary in size according to intensity of linkage (frequency of recombination) and the number of sexual generations (the approach to linkage equilibrium); however, all we usually know is the number of sexual generations. Even in the transfer of *single gene traits* by backcrossing, we usually do not know how much genetic material is linked to the gene of interest. The latter is sometimes referred to as *linkage drag*. D.F. Jones clearly recognized the role of chromosome blocks in 1917 when he proposed dominance of linked factors as a means of accounting for heterosis. The proposition is elegant because it acknowledges the cumulative effect of linked dominant genes as transmission units. In the years to follow there was much debate about gene action, and heterosis was sometimes interpreted as true overdominance—single loci at which the heterozygous phenotype exceeds that of either homozygote. Maize (*Zea mays* L.) researchers were careful to point out that estimates of dominance variance exceeding that for straight dominance could be due to either overdominance or linkage disequilibrium of linked loci with favorable alleles in repulsion phase (pseudo-overdominance). Maize researchers went on to compare degrees of dominance in F_2 populations in linkage disequilibrium with populations in F_8 through F_{16} in linkage equilibrium. Estimates for degree of dominance were reduced with the approach to linkage equilibrium indicating that the initial heterosis was more likely due to Jones' dominance of linked factors in linkage disequilibrium, than due to true overdominance. In autotetraploid alfalfa, we reached the same conclusion from results indicating dominant linked factors in chromosome blocks, and not multiple allelic interactions, explained improvement and maximum heterosis. Currently, molecular-marker-facilitated investigations of quantitative trait loci in maize report often finding higher yield in the heterozygote than in either homozygote. Based on past research and the fact that chromosome blocks are the units of sexual transmission, it seems likely that the bulk of these heterozygote effects are due to dominance of linked factors as proposed by Jones. Dominant alleles at different loci complement each other by masking recessive alleles at

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respective loci. The gene action is nonallelic gene interaction or epistasis. Finally, the cumulative action of genes in chromosome blocks not only explains the breeding behavior of cross-pollinated crops, but also explains the fixation of transgressive traits in self-pollinated crops, and the ability of auto- and allopolyploids to conceal deleterious recessive traits.

Plants have three genomes: nuclear, plastid, and mitochondrial; however, most of the DNA among the three genomes is organized on chromosomes in the nucleus. This discussion of heterosis will concern genes on chromosomes and the trait of interest will be yield. Probably all will agree that yield usually is a complex trait controlled by many genes. The effects of some genes will be large enough to identify as quantitative trait loci (QTL) that cosegregate with molecular markers. The effects of other genes will be small, but have a cumulative effect on yield. In any case, once it is agreed that many genes are involved, genetic linkages are bound to exist. Linkages define the chromosome blocks in this discussion. Our knowledge of genetics and sexual reproduction indicates that the chromosome blocks are the units of genetic transmission that underpin heterosis, and estimates of dominance and overdominance.

The book *Heterosis* edited by Gowen (1952) contains chapters by the pioneers in heterosis, and was very useful in preparing this review. The book is based on presentations at the benchmark conference on Heterosis held at Iowa State in the summer of 1950. More recently, the genetic basis of heterosis has been reviewed by Brewbaker (1964), Jinks (1983), Sprague (1983), and Stuber (1994). A review of the biochemical and physiological basis of heterosis can be found in an excellent article by Rhoades et al. (1992).

REALITY OF CHROMOSOME BLOCKS

The number of chromosome blocks is a function of the chromosome number and the number of crossovers per chromosome arm during meiosis. Both factors vary among crop species, but in all species there is a relatively small number of chromosome blocks or units of genetic transmission relative to the amount of nuclear DNA and presumed number of genes. In general, there is only one to two crossovers per chromosome arm per meiocyte. The positions of crossing over will differ in each meiocyte; hence the linkages also will differ, but the number of chromosome blocks will be relatively similar among the gametes produced by each meiocyte. In homozygous inbred lines the position of crossing over has no effect on linkages or the genotype of the gamete. On the other hand, in heterozygous materials both the linkage order and genotype of the gamete are affected by the position of crossing over. Thus, F_1 hybrid plants with the same genotype will produce an array of different gametes in linkage disequilibrium based on different positions of crossing over in different meiocytes.

How many chromosome blocks do we work in heterozygous or segregating parents in our breeding programs? In maize, if we assume about three crossovers per chromosome pair, there would be 3 blocks × 10 haploid chromosomes, or about 30 units of genetic transmission per gamete. In alfalfa (*Medicago sativa* L.)

if we assume about 2 crossovers per chromosome pair there would be about 2 blocks × 16 haploid chromosomes, or about 32 transmission units. The exact number is not important because the number of units of genetic transmission will be small compared with the number of genes in the genome in any species.

DEFINITIONS

Additive, dominant and overdominant gene action are essentially defined in Fig. 6–1. An important consideration in discussing gene action is that an allele with complete dominance also has an additive effect. Moreover, these additive effects are cumulative, thus giving rise to the often used expression: heterosis is due to the cumulative effects of favorable alleles with partial to complete dominance (Hallauer & Miranda, 1988).

Genetic equilibrium (the Hardy-Weinberg Law) is when the relative frequencies of each allele tend to remain constant from generation to generation in the absence of mutation, selection, random drift, and migration. In diploids, genetic equilibrium is reached after one generation of random mating, e.g., in the F_2 or Syn-1 generation. Linkage equilibrium on the other hand, approaches a practical state about F_8 and approaches the real state at about F_{16}, as we will see in the case of maize discussed later. The difference between genetic equilibrium and linkage equilibrium is central to this discussion of chromosome blocks.

In autotetraploids such as alfalfa and potato (*Solanum tuberosum* L.), genetic equilibrium is approached asymptotically in about the F_{12} generation. Linkage equilibrium then becomes a theoretical state that would require more generations than possible in most breeding programs. Historically, chromosome blocks have been termed effective factors by Mather and Jinks (1973), and linkats by Demarly (1979). The term effective factors is generally used in the literature where researchers have estimated the number of effective factors controlling certain traits (Dudley et al., 1974). In alfalfa we have used linkats when discussing chromosome blocks (Bingham et al., 1994).

Repulsion phase linkage, linkage disequilibrium, linkage bias, and pseudo-overdominance are used interchangeably in the literature. The terms all describe the model of a chromosome block with dominance and recessive linked loci in

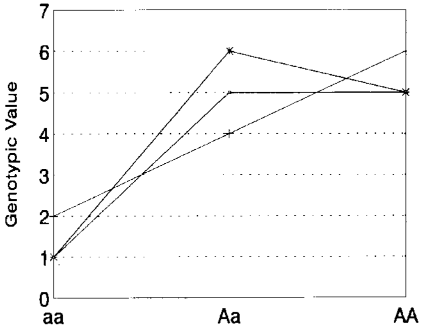

Fig. 6–1. Genotypic values at a theoretical locus with alleles A and a with additive (+), dominant (☐). and overdominant (*) gene action.

A	a	A	a
b	B	B	b
C	c	c	C
d	D	d	D
Repulsion Phase Linkage		Coupling Phase Linkage	

Fig. 6–2. Theoretical models of chromosome blocks in repulsion and coupling phase linkage, respectively.

Fig. 6–2. Similarly, coupling phase linkage (Fig. 6–2) also can contribute to linkage disequilibrium, linkage bias and pseudo-overdominance. Coupling phase linkage is often discussed in self-pollinated crops and in the case of improved inbreds of cross-pollinated crops. In either coupling or repulsion phase linkage, the dominant alleles at different loci complement each other by masking recessive alleles at respective loci. This complementary gene interaction is nonallelic gene interaction or epistasis.

HISTORICAL PERSPECTIVE

Heterosis was first used by Shull, as a synonym for hybrid vigor, and was not intended to suggest any mechanism (Shull, 1952). Heterosis is perhaps the greatest genetic phenomenon in nature that can be exploited without understanding it. Thus, a great seed industry is based on it, while we are continuing to do research to understand the genetic mechanisms of heterosis.

There have been two explanations of heterosis beginning with East (1908), Shull (1908, 1911), and East and Hayes (1912), all of whom believed that different germplasms produce a developmental stimulus that increases with the diversity (heterozygosity) of the uniting gametes. This is now called the overdominance hypothesis. Under this interpretation, the heterozygote has an advantage (Hull, 1952). Alternatively, heterosis can be produced by the masking of deleterious recessive alleles in each strain by dominant, or nearly dominant alleles from the other strain. This is the dominance hypothesis. Davenport (1908) was the first to emphasize that the effects of deleterious recessive genes tend to be concealed in heterozygotes by dominance. Bruce (1910) and Keeble and Pellew (1910) appear to be the first to explicitly state the dominance hypothesis.

Objections to the dominance hypothesis between 1910 and 1917 were that selection in maize failed to produce inbred lines as good as hybrids (Shull, 1911; East & Hayes, 1912), and that there was an absence of a skewed F_2 distribution expected from the expansion of 3/4 dominants + 1/4 recessives (Emerson & East, 1913). These objections were largely dispelled when Jones (1917) pointed out that with close linkage, and Collins (1921) found that with a large number of factors even without linkage, the two hypotheses became indistinguishable. Thus,

INBRED PARENT 1

CHROMOSOME

I		II		III	
A	A	m	m	W	W
b	b	N	N	x	x
C	C	o	o	Y	Y
d	d	P	P	z	z

6 loci with dominant alleles

INBRED PARENT 2

CHROMOSOME

I		II		III	
a	a	M	M	w	w
B	B	n	n	X	X
c	c	O	O	y	y
D	D	p	p	Z	Z

6 loci with dominant alleles

F_1 HYBRID

A	a	m	M	W	w
b	B	N	n	x	X
C	c	o	O	Y	y
d	D	P	p	z	Z

12 loci with dominant alleles

Fig. 6–3. Models of linked genes on chromosome blocks patterned after the model by Jones (1917). An inbred with six loci with dominant alleles linked in repulsion, when crossed with an inbred with six different loci with dominant alleles, produces an F_1 hybrid with 12 loci with dominant alleles.

what appeared to be overdominance could be explained by linked dominant factors.

The proposition of D.F. Jones (1917) that dominance of linked factors could account for heterosis is a benchmark. Jones' model is presented in Fig. 6–3, using inbred parents and three hypothetical chromosomes. Each chromosome has two dominant and two recessive loci linked in repulsion, it is assumed that one inbred has one set of dominant alleles and the other inbred has a different set in a complementary repulsion-phase linkage. In total, one inbred has six loci with dominant alleles for yield, as an example, and the other inbred has a different set of six. In the F_1, there is a dominant at each locus for a complementary set of 12 loci with a dominant allele, and a hypothetical F_1 yield double that of either inbred. Inbreds of maize that were only one-half as productive as the hybrid were common at the time.

Jones went on to discuss how with relatively tight linkage of dominant and recessive alleles it would be difficult to recombine in any one individual in later generations any greater number of dominants in the homozygous condition than were present in the parents. This disarmed the criticism about not being able to produce pure breeding maize lines as high in yield as the F_1. Following the hypothetical case into the F_2 generation by selfing or sib-mating, he demonstrated that linkage of the dominant factors in repulsion produced a normal distribution of hypothetical yield based on the number of loci with a dominant allele. This disarmed the second main criticism of the dominant hypothesis in that no skewedness was expected with linkage. The final point in Jones' paper anticipated the eventual population improvement in maize. He pointed out that recombination in this dominant linked factor model provided a means of understanding how certain homozygous individuals (and varieties) may possess a greater number of desirable characters than others.

Crow (1993) noted that Sewall Wright published a series of three papers in the 1920s on the effects of inbreeding and crossing in guinea pigs that are important in the history of heterosis. Wright noted the decline in vigor with inbreeding; the fixation of different traits in different lines; the immediate recovery of vigor when inbred lines are crossed; and the predictable decline when hybrids are inbred. He stated that although these results are all direct consequences of Mendelian inheritance and dominance, they are equally consistent with partial dominance or overdominance.

In the late 1940s there was a resurgence of interest in idea that heterozygosity as such was important in heterosis. In plants, this was largely because of maize studies by Hull (see Hull, 1952). He introduced the word overdominance to describe the situation. Hull (1952) notes that Fisher (1918, 1931) used the term *super-dominance*, but that the term had never caught on. At the conference on heterosis, Hull (1952) listed eight factors as evidence of overdominance in the genetics of grain yield of maize. The list appears very dated now because of successful population improvement in maize, and because of significant inbred and hybrid improvement since 1950. Nevertheless, Hull's list is historically important and presented here in its entirety.

Evidence of overdominance in the genetics of grain yield of maize consists of:

1. Failure of mass selection and ear-to-row selection beyond the level of the adapted variety.
2. Crossbreeding recombinations of parent lines of elite hybrids yield little more than the original varieties.
3. Hybrids of second-cycle and third-cycle lines yield little more than those of the first cycle.
4. Homozygous maize yields 30% as much as heterozygous maize.
5. No evidence of epistasis in maize yield.
6. Regression analyses of yields of F_1s and inbred parents indicate a zone of nearly level regression near the upper end of the range of present data, where it might be predicted with the kind of artificial selection which has been practiced, and in the event of overdominance.
7. There is some evidence that selection for general combining ability alone with respect to yield is effective and this too is consistent with the expectation of overdominance theory.
8. The fact of hybrid maize is hardly to be explained as other than a result of selection for specific combinability, which in turn is manifestly dependent on heterozygosity of maize yield genes.

In the same period of the late 1940s through the 1950s, overdominance was championed by some fruit fly geneticists. Crow (1993) presents an engrossing chronology of the geneticist personalities and their views. Crow's article provides a thorough treatment of the evolution of thought patterns about heterosis by Crow and others, and he relates heterosis to mutation, mean fitness, and genetic load. At the time of the heterosis conference in 1950, Crow (1952), Dobzhansky (1952), and others believed that although overdominant loci might be exceptional, they were of disproportionate influence in maintaining a stable equilibrium with intermediate allele frequencies. By 1955, according to Crow, Dobzhansky changed from the view that overdominant loci were exceptional, though important, to the view that they were ubiquitous.

Muller disagreed with Dobzhansky, and the details are best obtained from Crow's article (1993). Evidently, Muller's emphasis on partial dominance and appropriate additivity between loci led him to believe that selection is an efficient process. He noted the success of breeding programs in plants and animals, and believed that a positive eugenics program would be effective. Dobzhansky, believing in overdominance, contended that selection would be complicated and unpredictable. Crow (1993) points out that indeed selection under an overdominance model would be complicated, because, Haldane had shown that at equilibrium with overdominance, the parent offspring correlation in fitness is zero.

Crow (1993) noted that the arguments that he presented in 1948 for overdominance in maize yield had not held up with newer data. He cites the articles from Nebraska and North Carolina on the decrease in dominance over generations with the approach to equilibrium. These articles are reviewed in the following section of this chapter. Crow further notes that relatively high yielding maize inbreds have now been developed. They are not yet as good as the best hybrids but they are better than would be expected if there were a large contribution from overdominance. Thus, in maize, Crow agrees with the interpretation of pseudo-overdominance due to linkage disequilibrium.

DECLINE IN EVIDENCE FOR OVERDOMINANCE IN MAIZE

There was a scholarly ferment about heterosis around 1950 judging from the literature and the articles delivered at the heterosis conference (Gowen, 1952). It was a most timely conference because the pioneers in the concept and terminology were able to record their thoughts and conclusions in person. From this ferment came several important articles on mating systems and procedures to estimate the degree of dominance controlling quantitative characters (Comstock & Robinson, 1952; Robinson et al., 1949; Gardner et al., 1953). Estimates of the degree of dominance in open-pollinated populations were in the range of partial dominance (Robinson et al., 1955). On the other hand, estimates based on the F_2 generation of a single cross of two inbreds were in the range of overdominance (Robinson et al., 1949; Gardner et al., 1953).

The authors were careful to point out that it was theoretically possible to obtain estimates of overdominance due to repulsion phase linkages in their material even though the individual genes may have no more than partial dominance. Moreover, they noted that advanced generations of hybrid populations obtained by random mating and approaching linkage equilibrium could be used to determine whether linkage was in fact an important source of bias in the estimates. This set the stage for definitive experiments to follow at North Carolina State University and the University of Nebraska.

The strategy was to advance the generations by random mating toward linkage equilibrium with an opportunity for free recombination between successive generations. This should allow linkages between loci to break up. Linked chromosome blocks containing loci with dominant and recessive alleles would mimic overdominance because of the cumulative effect of the dominants, and their break up would reduce the overdominant effect on the average.

In Nebraska, results comparing F_2 and F_8 populations of maize in linkage disequilibrium and approaching equilibrium respectively, involved a cross of inbreds M14 and 187-2 (Gardner & Lonnquist, 1959). The inbreds were considered typical of lines used in the Corn Belt at the time. The strategy, used the North Carolina Design III, which produced the F_2 by selfing the F_1, and the F_8 by allowing random pollination in large isolated blocks each generation. Then, randomly chosen F_2 and F_8 plants were used as male parents and each was crossed to each inbred parent to produce pairs of backcross progenies from respective male parents. One hundred such pairs were tested at two locations. Results from the two locations differed somewhat but still allowed the following general conclusions. The degree of dominance and the dominance variance were lower for every quantitative trait studied in the F_8 generation compared with the F_2. This indicated that estimates of overdominance in the F_2 were biased upward as a result of repulsion phase linkages many of which were broken by the F_8 generation. In the F_8 generation, estimates of dominance were no more than partially or completely dominant. Interestingly, there were consistently high additive genetic variances in the F_8 generation compared with the F_2 generation.

In 1960, estimates of dominance in F_2 versus F_8 generations derived from two North Carolina hybrids were published (Robinson et al., 1960). Once again estimates of dominance decreased with the approach to linkage equilibrium in the F_8 in both populations. As in the Nebraska study, this indicated that estimates of overdominance in the F_2 were biased upward as a result of linkage bias. The authors noted that dominance variance if biased by linkage is expected to be reduced following recombination regardless of the type of linkage. Moll and Robinson (1967) published four more estimates of dominance on North Carolina materials taken to F_8, F_{12}, and F_{13}. Average level of dominance was decreased in the advanced generation in all cases. In the North Carolina materials, additive variance also decreased over generations of recombination, although the decreases were less than those for dominance. This permitted some interesting interpretations. The authors indicated that there might be no change in additive genetic variance following recombination if the repulsion and coupling linkages tended to balance each other. An increase in additive variance could occur with predominantly repulsion phase linkages in the parent lines. Recall that this is what happened in the Nebraska material (Garnder & Lonnquist, 1959).

With initial coupling-phase linkages, the additive genetic variance would be expected to decrease, the rate of decrease being dependent upon the predominance of the coupling linkages. Hence, the North Carolina materials must have contained a preponderance of coupling phase linkages. Coupling phase linkages are thought to be indicative of improvement and are commonly referred to in self-pollinated crops with pure line varieties.

The capstone on the estimates of dominance in the Nebraska population is at generation F_{16} (Fig. 6–4). The values represent an average of those from Lonnquist (1980), and from Gardner (1992, personal communication) in a similar figure (Crow, 1993). Tests at different locations gave slightly different values,

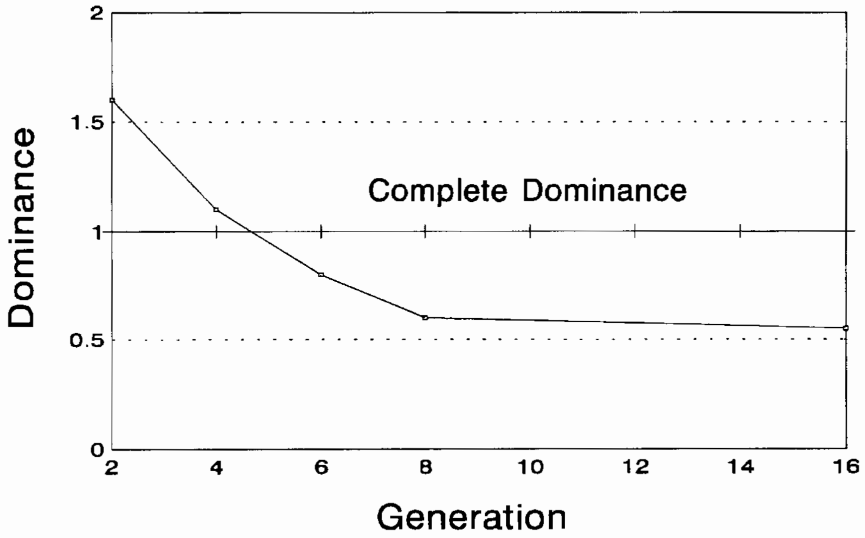

Fig. 6–4. Summary of results showing a decrease in estimates of dominance in maize with the approach to linkage equilibrium (Gardner & Lonnquist, 1959; Lonnquist, 1980; Gardner, 1992, personal communication).

but the trends in the estimates of dominance and the conclusions are the same. The estimates of dominance decreased with the approach to linkage equilibrium. The decrease between F_8 and F_{16} was small, indicating that F_8 estimates are practical and realistic. Both F_8 and F_{16} estimates of dominance are in the range of partial dominance.

SHIFT FROM OVERDOMINANCE TO CHROMOSOME BLOCKS IN ALFALFA

Alfalfa behaves as an autotetraploid and heterosis progresses to a maximum one or two generations after a single cross (Bingham et al., 1994). Progressive heterosis is due to complex tetrasomic segregations. Researchers studying progressive heterosis always noted that they could not distinguish between linked chromosome blocks and multiple alleles at a locus producing overdominance in the progressive heterosis phenomenon (Demarly 1963; Dunbier & Bingham, 1975; Groose et al., 1989); however, between 1965 and 1975 heterosis in alfalfa was often discussed in terms of overdominance. About 1975 researchers began long-term research to separate the effects of chromosome blocks from multiple alleles. In this research, cultivated autotetraploid alfalfa was haploidized to produce cultivated diploids, and diploid hybrids were chromosomally doubled to produce two-allele autotetraploids that could not contain more than one interaction of two alleles. Multiple allelic interactions of three or four alleles at a locus were eliminated. Two allele populations were produced from single plants by first selfing, and then sib-mating. Sib-mating and selection were

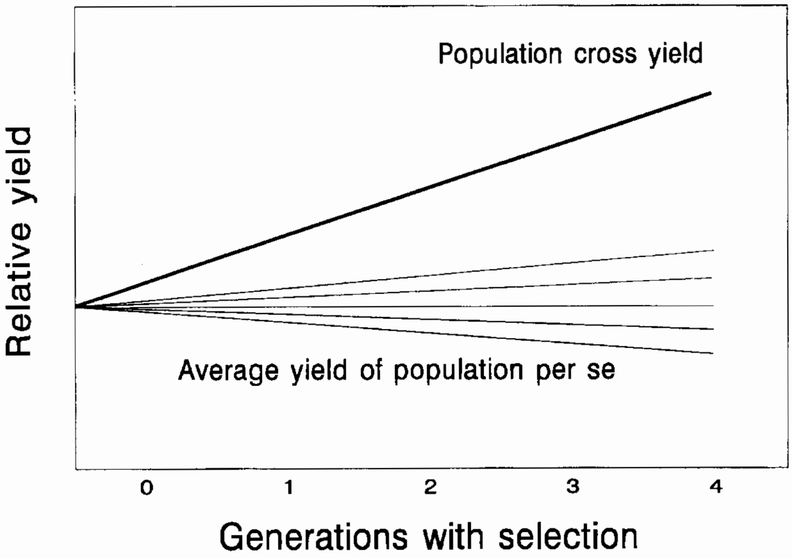

Fig. 6–5. Yield improvement in population crosses of alfalfa following generations of inbreeding and selection in individual populations.

practiced in subsequent generations of the two allele populations. Population improvement for yield was realized in a set of experiments (Pfeiffer & Bingham, 1983) and another set a decade later (Woodfield & Bingham, 1995; Fig. 6–5). Improvement in crosses was explained by accumulation of favorable alleles with additive to completely dominant effects. Improvement took place over generations of recombination between the chromosome blocks brought together in the original diploid hybrid. Allelic interactions or overdominance could not increase in this breeding strategy, thus implicating the theory that the accumulation of favorable alleles on chromosome blocks and not overdominance in alfalfa was responsible for the yield gains.

HETEROSIS IN SINGLE CHROMOSOME BLOCKS

At the 1950 Heterosis Conference, Jones (1952) described his backcrossing experiments involving single chromosome blocks. Several deep inbred lines of maize, one of which was in the 41st generation of continuous self-fertilization, were crossed to unrelated inbred lines carrying dominant marker genes. The markers were red cob, yellow endosperm, and non-glossy seedlings. They were chosen because they had little or no effect on plant growth. The strategy was to backcross the markers into the inbreds, which at BC6 essentially restores the original inbred condition, except for the chromosome block containing the dominant marker and its linked genes. Segregates in BC6 with the dominant marker are heterozygous for the chromosome block, while normal segregates are homozygous for the inbred condition. Thus, any heterotic effects of that single chromosome block can be studied. Jones measured the effect of each block on height. Differences were small, but nearly all indicated a heterotic effect on height. He considered the three marked chromosome blocks as samples of typical chromosome blocks, and concluded that there are genes in all parts of the maize chromosomes that contribute to normal growth and development.

The same concept of studying the effects of chromosome blocks from teosinte in an inbred of maize was discussed by Mangelsdorf (1952). He carried out four generations of backcrossing teosinte into an inbred of maize, and measured the effects of the added chromosome blocks on the inbreds traits and performance. Introgressed segments involved blocks of genes because the segments had multiple effects. In recent research on the origin of maize Doebley et al. (1995) have transferred teosinte blocks into maize and maize blocks into teosinte using reciprocal backcrossing. The strategy of studying single chromosome blocks has provided insight on the evolution of epistasis and dominance in maize.

Lamkey et al. (1988) discussed the importance of chromosome blocks in a study of the contribution of the long arm of maize chromosome 10 to heterosis. They used the ingenious method of B-A translocations to transfer intact chromosome segments from one inbred line of maize to another, and then study the heterotic effect of the segment in an otherwise inbred background (Robertson, 1964; Peterson & Wernsman, 1964). In the study by Lamkey et al. (1988) the long arm of chromosome 10 is only about 3% of the genome, but accounted for 9.4 to 20.8% of total heterosis.

Burton (1986) identified chromosome blocks in the heterozygous condition in isogenic populations of pearl millet [*Pennisetum glaucum* (L.) R.Br.] in several creative ways. He demonstrated the existence of heterosis due to single heterozygous chromosome blocks and suggested how they could be used to increase the forage yield of a top yielding hybrid. For example, Burton and Werner (1991) backcrossed conventional genetic markers into inbreds of pearl millet and found significant heterotic effects of single blocks. Burton and Wilson (1995) described a modification of the method to screen for heterozygous chromosome blocks in tropical land races of pearl millet, that can replace the block in the male parent of a top producing F_1 hybrid and increase forage yield. The method works with chromosome blocks in which a single visibly selectable marker is located. Thus, only a small amount of the genome is evaluated for new chromosome blocks in that region, yet measurable heterosis is found in the single chromosome blocks of some land races. Currently, molecular markers can be used in marker assisted selection, and the transfer of single blocks for plant improvement is expected to increase.

HETEROSIS ASSOCIATED WITH QUANTITATIVE TRAIT LOCI

The benchmark hybrid of maize inbreds B73 × Mo17 has been used to identify QTL contributing to heterosis (Stuber, 1992; Stuber et al., 1992). A modified Design III and molecular markers were used to identify QTL in the F_2–F_3 when the hybrid population was still in linkage disequilibrium. Whenever a QTL for grain yield was detected, the heterozygote had a higher phenotype than the respective homozygote, with only one exception. It seems likely, based on the previous results in maize where the level of dominance decreased with the approach to linkage equilibrium, that pseudo-overdominance due to linkage disequilibrium is involved in the heterozygotes in early generations.

Cockerham and Zeng (1996) extended Design III to include linkage, two locus epistasis, and the use of F_3 data, and applied it to Stuber's maize data. Their analysis strongly suggested that there are multiple linked QTL in many chromosomes. They pointed out that when several QTL are linked, with an aggregation of dominance effects, pseudo-overdominance can be created and observed in the single marker analysis. The interesting test will be to random mate the population to at least F_8, and compare the levels of dominance in the two populations. Even after separation of as many linked loci as possible by recombination there still may be clustering of some genes contributing to a QTL effect.

Khavkin and Coe (1995a,b) found evidence of clustering of genes for growth and development in maize. They surveyed data from naked-eye polymorphisms and published molecular marker data, and found functional clusters of genes distributed nonrandomly along all 10 chromosomes. They presume that clusters are functional units of genes expressed in concert and affecting plant development. Major QTL for plant height, earliness, and grain yield are visible manifestations of developmental clusters. It will not be surprising if such clusters turn out to be tightly or completely linked on chromosome blocks. Thus, it may be necessary to clone and sequence QTL in order to identify the numbers of genes involved and their direct effects.

FIXING HIGH PARENT HETEROSIS IN SELF POLLINATED CROPS

Heterosis in self-pollinated crops also was discussed at the Heterosis Conference in 1952. Smith (1952) referred to high parent heterosis as transgressive vigor and showed that by using inbreeding and selection it was possible to develop improved lines of tobacco (*Nicotiana tabacum* L.) which exceeded the high parent and sometimes even the F_1 in most characteristics. This strategy is perhaps the mainstay of the pedigree method in breeding self-pollinated crops.

Powers (1952) reinforced the recovery of inbred lines in tomato [*Lycopersicon lycopersicum* (L.) Karsten] and barley (*Hordeum vulgare* L.) that retained the advantages attributed to heterosis. He used marker genes and was very explicit about the importance of blocks of linked genes in the process. In fact, Powers used the markers in tomato to provide proof of recombination of genes to produce segregates with greater weight per locule in F_2 and backcross segregates than in the F_1. He noted that if heterosis associated with several markers were due solely to an interaction of the marker genes as in the overdominance hypothesis, then it would not be possible to obtain homozygous lines possessing the increases. Thus, linked genes in complementing chromosome blocks provide an explanation of heterosis and associated gene action in breeding systems in both cross- and self-pollinated crops.

CHROMOSOME BLOCKS ARE A UNIFYING CONCEPT FOR HETEROSIS IN ALLO- AND AUTOPOLYPLOIDS

Allopolyploids (disomic polyploids) have fixed heterozygosity in the two or more genomes they possess {wheat (*Triticum aestivum* L.), oats (*Avena sativa* L.), soybean [*Glycine max* (L.) Merr.], cotton (*Gossypium hirsutum* L.), tobacco, and others}. Hexaploid wheat is self-pollinated and homozygous within each of its three genomes, but has potential heterozygosity and genetic complementation among its three genomes (Mac Key, 1970). Proof of this complementation is the famous nullisomic–tetrasomic compensation series in wheat (Sears 1966). Removal of a chromosome from one genome (nullisomic), can be compensated by extra homeologues (tetrasomic) in another genome. Homozygosity of an unfavorable allele in one genome may be complemented by a more favorable allele on a homeologue in another genome. Some of the nullisomic tetrasomic lines have a distinctive phenotype, but they are viable because of genomic compensation (Sears, 1966). Thus, disomic polyploids can benefit from the advantages of fixed hybridity and self-fertilization (Mac Key, 1970).

Autopolyploids (polysomic polyploids) ensure their heterozygosity through cross-pollination (potato, alfalfa, birdsfoot trefoil (*Lotus corniculatus* L.), and many forage grasses). Polysomic segregation of heterozygotes is known to protect recessive alleles from segregation in the homozygous condition. The familiar monohybrid (Aa) disomic F_2 segregation, where 1/4 homozygous recessives are revealed is reduced to a mere 1/36 in the equivalent tetrasomic segregation (AAaa). Segregations with two loci are even more extreme: the diploid is 9:3:3:1 versus the autotetraploid that is 1225:35:35:1.

The extent to which disomic and polysomic polyploids share a dependency on heterozygosity among genomes and at individual loci, respectively, was discussed previously (Mac Key, 1970; Bingham, 1980). These previous discussions focused on the polysomic locus, e.g., the tetrasomic locus with potentially four different alleles and allelic interactions (overdominance); however as noted earlier, alfalfa research has demonstrated that accumulation of favorable dominant alleles, not overdominance, explained genetic gains (Pfeiffer & Bingham 1982; Woodfield & Bingham, 1995). A genetic model involving complementary genes in repulsion phase linkage blocks explained results. As established earlier in maize, overdominance effects were due to complementary genes associated with linkage disequilibrium (Gardner & Lonnquist, 1959; Robinson et al., 1960; Moll & Robinson, 1967; Lonnquist, 1980).

A simple model involving two loci in repulsion phase linkage demonstrates the genetic similarity of allo- and autopolyploids due to chromosome blocks (Fig. 6–6a and 6–6b, repsectively). The model indicates that complete complementation (100%) in the disomic tetraploid (Fig. 6–6c), would still be 94% in the progeny of the tetrasomic tetraploid (Fig. 6–6d). The potential frequency of loci with dominants in the two types of polyploids is essentially similar. This is striking, especially considering that disomic polyploids are predominantly self-pollinated and that the polysomics are outcrossed. In spite of the different modes of reproduction, the two types of polyploids have similar genetic architecture. Thus chromosome blocks provide an explanation of the fixed heterozygosity in disomic

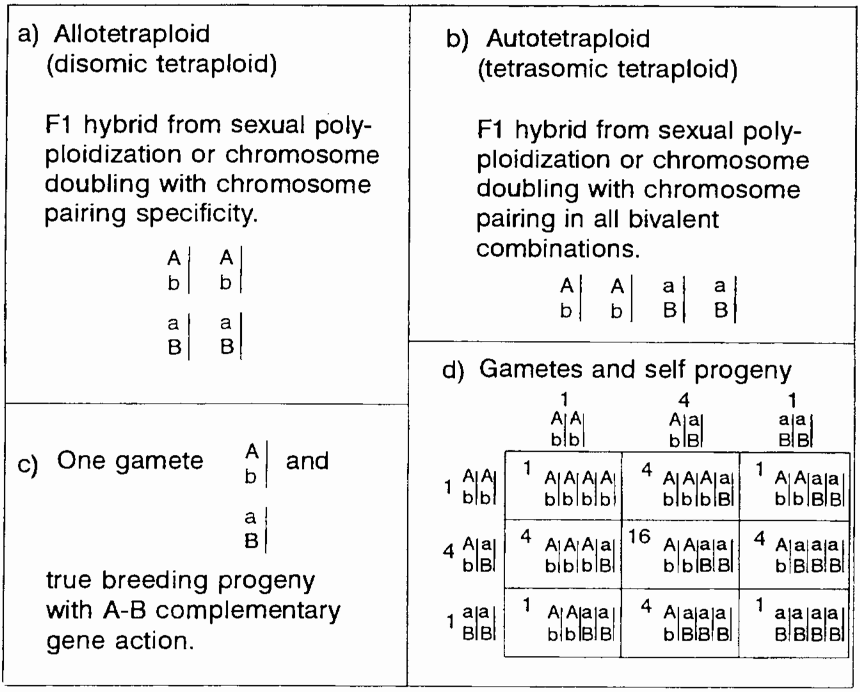

Fig. 6–6. Theoretical model of a chromosome block with two complementary loci, each with a dominant allele linked in repulsion. The consequences of using the chromosome block to produce an allotetraploid (disomic tetraploid) and an autotetraploid (tetrasomic tetraploid) are illustrated. See text for discussion.

polyploids, the high level of heterozygosity in polysomic polyploids, and the pseudo-overdominance in diploid hybrids.

SUMMARY AND CONCLUSIONS

Chromosome blocks are the unit of genetic transmission that must be considered in genetic models to explain heterosis. Individual genes are linked in chromosome blocks. Thus, estimates of gene action are due to the cumulative effect of linked blocks of genes. The genes in chromosome blocks are in linkage disequilibrium in early generations after crossing, and approach linkage equilibrium after about eight generations of random mating. Even then it is the population that is approaching linkage equilibrium; thus an individual in the population that is withdrawn and used in a cross resets the linkage disequilibrium clock.

All who have written about overdominance versus pseudo-overdominance due to linkage disequilibrium agree that the possibility of true overdominance at some loci may well occur; however, the largest component of overdominance estimates must be due to pseudo-overdominance, according to mounting evidence. Action of single genes can only be studied as changes at the locus due to new mutation, transposable elements, single gene transformations, or by kinetic data on known single gene products. This restricts the scope of potential research on true overdominance.

Improvement of inbred lines in essentially all long-term plant breeding programs must be due to accumulation of favorable genes in chromosome blocks and their associated interactions. The same can be said for population improvement of metric traits. This is the strength of plant breeding and reason for optimism about continued plant improvement.

Chromosome blocks provide an efficient way of masking several deleterious recessive alleles at once. It is concluded that linked genes on chromosome blocks provide an explanation of heterosis in diploids, the fixed heterosis in self-pollinated allopolyploids, and the relatively high levels of heterosis maintained under cross-pollination in autopolyploids. Thus, chromosome blocks provide a unifying concept for all categories of plants.

REFERENCES

Bingham, E.T. 1980. Maximizing heterozygosity in autopolyploids. p. 471–489. *In* W.H. Lewis (ed.) Polyploidy. Plenum Press, New York.

Bingham, E.T., R.W. Groose, D.R. Woodfield, and K.K. Kidwell. 1994. Complementary gene interactions in alfalfa are greater in autotetraploids than diploids. Crop Sci. 34:823–829.

Bruce, A.B. 1910. The Mendelian theory of heredity and the augmentation of vigor. Science (Washington, DC) 32:627–628.

Burton, G.W. 1986. Identifying heterotic blocks on pearl millet chromosomes with chlorophyll deficient mutants. Crop Sci. 26:537–539.

Burton, G.W., and B.K. Werner. 1991. Genetic markers to locate and transfer heterotic chromosome blocks for increased pearl millet yields. Crop Sci. 31:576–579.

Burton, G.W., and J.P. Wilson. 1995. Identification and transfer of heterotic chromosome blocks for forage yield in pearl millet land races. Crop Sci. 35:1184–1187.

Brewbaker, J.L. 1964. Agricultural genetics. Prentice-Hall, Englewood Cliffs, NJ.

Cockerham, C.C., and Z-B Zeng. 1996. Design III with marker loci. Genetics 143:1437–1456.

Collins, G.N. 1921. Dominance and the vigor of first generation hybrids. Am Nat. 55:116–133.

Comstock, R.E., and H.F. Robinson. 1952. Estimation of average dominance of genes. p. 494–517. *In* J.W. Gowen (ed) Heterosis. Iowa State College Press, Ames.

Crow, J.F. 1952. Dominance and overdominance. p. 282–297. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Crow, J.F. 1993. Mutation, mean fitness, and genetic load. Oxford Surv. Evol. Biol. 9:3–42.

Davenport, C.B. 1908. Degeneration, albinism and inbreeding. Science (Washington, DC) 28:454–455.

Demarly, Y. 1963. Genetique des tetraploids et amelioration des plantes. Ann. Amelio. Plant. 13:307–400.

Demarly, Y. 1979. The concept of linkat. p. 257–265. *In* A.C. Zeven and A.M. van Harten (ed.) Proc. Conf. Broadening Genetic Base of Crops, Wageningen, the Netherlands. 3–7 July 1978. Ctr. for Agric. Publ. and Doc., Wageningen, the Netherlands.

Dobzhansky, 1952. Nature and origin of heterosis. p. 218–224. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Doebley, J., A. Stee, and C. Gustus. 1995. Teosinte branched 1 and the origin of maize: Evidence for epistasis and the evolution of dominance. Genetics 141:333–346.

Dudley, J.W., R.J. Lambert, and D.E. Alexander. 1974. Seventy generations of selection for oil and protein concentration in the maize kernel. *In* J.W. Dudley (ed.) Seventy generations of selection in maize. ASA, Madison, WI.

Dunbier, M.W., and E.T. Bingham. 1975. Maximum heterozygosity in alfalfa: Results using haploid-derived autotetraploids. Crop Sci. 15:527–531.

East, E.M. 1908. Inbreeding in corn. Rep. Connecticut Agric. Exp. Stn. 1907:419–429.

East, E.M., and H.K. Hayes. 1912. Heterozygosis in evolution and plant breeding. USDA Bureau of Plant Industry Bull. 243. USDA, Washington, DC.

Emerson, R.A., and E.M. East. 1913. The inheritance of quantitative characters in maize. Nebraska Agric. Exp. Stn. Bull. 2.

Fisher, R.A. 1918. The correlation between relatives on the supposition of Mendelian inheritance. Trans. Royal Soc. Edinburgh. 52:399–433.

Fisher, R.A. 1931. The evolution of dominance. Biol. Rev. Cambridge Phil. Soc. 6:345–368.

Gardner, C.O., P.H. Harvey, R.E. Comstock, and H.F. Robinson. 1953. Dominance of genes controlling quantitative characters in maize. Agron. J. 45:186–191.

Gardner, C.O., and J.H. Lonnquist. 1959. Linkage and the degree of dominance of genes controlling quantitative characters in maize. Agron. J. 51:524–528.

Gowen, J.W. 1952. Heterosis. Iowa State College Press, Ames.

Groose, R.W., L.E. Talbert, W.P. Kojis, and E.T. Bingham. 1989. Progressive heterosis in autotetraploid alfalfa: Studies using two types of inbreds. Crop Sci. 29:1173–1177.

Hallauer, A.R., and J.B. Miranda. 1988. Quantitative genetics in maize breeding. 2nd ed. Iowa State Univ. Press, Ames.

Hull, F.H. 1952. Recurrent selection for overdominance. p. 451–474. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Jinks, J.L. 1983. Biometrical genetics of heterosis. p. 1–46. *In* R. Frankel (ed.) Heterosis: A reappraisal of theory and practice. Springer-Verlag, New York.

Jones, D.F. 1917. Dominance of linked factors as a means of accounting for heterosis. Genetics 2:466–479.

Jones, D.F. 1952. Plasmagenes and chromogenes in heterosis. p. 224–225. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Keeble, F., and Pellew, C. 1910. The mode of inheritance of stature and of time of flowering in peas (*Pisum sativum*), J. Genet. 1:47–56.

Khavkin, E.E., and E.H. Coe. 1995a. Organization of growth-regulating genes in maize: 1. The functional clusters of genes. Russ. J. Plant Phys. 42:408–420.

Khavkin, E.E., and E.H. Coe. 1995b. The organization of growth-regulating genes in maize: 2. Quantitative trait loci. Russ. J. Plant Phys. 42:558–574.

Lamkey, K.R., A.R. Hallaner, and D.S. Robertson. 1988. Contribution of the long arm of chromosome 10 to the total heterosis observed in five maize hybrids. Crop Sci. 28:896–902.

Lonnquist, J.H. 1980. Heterosis: Additivity versus dominance. An. Acad. Nac. Cienc. Ex. Fis. Nat. (Buenos Aires) 32:195–202.

Mac Key, J. 1970. Significance of mating systems for chromosomes and gametes. Hereditas 66:165–176.

Mangelsdorf, P.C. 1952. Hybridization in the evolution of maize. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Mather, K., and J.L. Jinks. 1973. Introduction to biometrical genetics. Cornell Univ. Press, Ithaca, NY.

Moll, R.H., and H.F. Robinson. 1967. Quantitative genetic investigation of yield of maize. Der Zuchter 37:192–199.

Peterson, P.A., and E. Wernsman. 1964. A monosomic-type approach to maize breeding. Crop Sci. 4:533–535.

Pfeiffer, T.W., and E.T. Bingham. 1983. Improvement of fertility and herbage yield by selection within two-allele populations of alfalfa. Crop Sci. 23:633–636.

Powers, L. 1952. Gene recombination and heterosis. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Rhoades, D., E.C. Ju, W-J Yang, and Y. Samaras. 1992. Plant metabolism and heterosis. Plant Breed. Rev. 10:54–89.

Robertson, D. 1964. Transfer of intact segments of maize chromosomes: A possible method. J. Heredity 55:107–114.

Robinson, H.F., C.C. Cockerham, and R.H. Moll. 1960. Studies on estimation of dominance variance and effects of linkage bias. p. 171–177. *In* Biometrical genetics. Int. Ser. of Monogr. on Biometry. Pergamon Press, New York.

Robinson, H.F., R.E. Comstock, and P.H. Harvey. 1949. Estimates of heritability and the degree of dominance in corn. Agron. J. 41:353–359.

Robinson, H.F., R.E. Comstock, and P.H. Harvey. 1955. Genetic variances in open pollinated varieties of corn. Genetics 40:45–60.

Sears, E.R. 1966. Nullisomic-tetrasomic combinations in hexaploid wheat. *In* R. Riley and R.R. Lewis (ed.) Chromosome manipulations in plants. Oliver & Boyd, London.

Shull, G.H. 1908. The composition of a field of maize. Rep. Am. Breed. Assoc. 4:296–301.

Shull, G.H. 1911. The genotypes of maize. Am Nat. 45:234–252.

Shull, G.H. 1952. Beginnings of the heterosis concept. p. 14–48. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Smith, H.H. 1952. Fixing transgressive vigor in *Nicotiana rustica*. p. 161–174. *In* J.W. Gowen (ed.) Heterosis. Iowa State College Press, Ames.

Sprague, G.F. 1983. Heterosis in maize; theory and practice. p. 47–70. *In* R. Frankel (ed.) Heterosis: A reappraisal of theory and practice. Springer-Verlag, New York.

Stuber, C.W. 1992. Biochemical and molecular markers in plant breeding. Plant Breed. Rev. 9:37–57.

Stuber, C.W. 1994. Heterosis in plant breeding. Plant Breed. Rev. 12:227–251.

Stuber, C.W., S.E. Lincoln, D.W. Wolff, T. Helentjaris, and E.S. Lander. 1992. Identification of genetic factors contributing to heterosis in a hybrid from two elite maize inbred lines using molecular markers. Genetics 132:823–839.

Woodfield, D.R., and E.T. Bingham. 1995. Improvement in two-allele autotetraploid populations of alfalfa explained by accumulation of favorable alleles. Crop Sci. 35:988–994.