

Recent advances in understanding genetic basis of heterosis in rice (*Oriza sativa* L.)

Avances recientes en el conocimiento de la base genética de la heterosis en arroz (*Oriza sativa* L.)

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ABSTRACT

Heterosis is perhaps one of the greatest practical achievements of the science of plant breeding and has been extensively used in crop improvement. Therefore, an understanding of its potential genetic basis is imperative. Extensive studies in crop plants including rice have been made to elucidate the genetic factors underlying heterosis. Various research groups have proposed dominance, overdominance and epistasis as major genetic basis of heterosis and recent advances in molecular biology have helped to validate these findings in various crop species. Despite, tremendous advances in molecular marker techniques, QTL analysis and genomics, conclusive evidence in support of either of these theories is still elusive, as all of these factors seem to be mutually non-exclusive. Nowadays, focus is increasingly shifting to study heterosis at genomic level to identify the genomic regions that evoke heterotic effect and introgress such regions into elite rice lines to develop high yielding hybrids. Advances have also been made in expression profiling and relate differences in transposon and repeat content in parental lines to heterotic effect.

Key words: Rice, heterosis, genetic basis, molecular markers

RESUMEN

Heterosis es quizás uno de los mayores logros prácticos de la ciencia del mejoramiento de plantas y ha sido extensivamente usada en el mejoramiento de los cultivos. Por lo tanto, un conocimiento de su base genética potencial es imperativo. Se han realizado extensivos estudios en plantas cultivadas incluyendo el arroz para elucidar los factores genéticos que causan la heterosis. Varios grupos de investigación han propuesto la dominancia, la sobredominancia y la epistasis como principales bases genéticas de la heterosis y avances recientes en biología molecular han ayudado a validar estos descubrimientos en varias especies cultivadas. A pesar de los avances tremendos en las técnicas de marcadores moleculares, análisis de QTLs y análisis genómico, una evidencia conclusiva en soportar una de estas teorías todavía no se ha definido, como todos estos factores parecen ser mutuamente no exclusivos. En la actualidad, el enfoque está moviéndose rápidamente hacia el estudio de la heterosis a nivel genómico para identificar las regiones genómicas que induzcan el efecto heterótico e introducir tales regiones dentro de líneas élites de arroz para desarrollar híbridos con altos rendimientos. Se han realizado también avances en el perfil de expresión y relacionar diferencias en el contenido repetitivo y del transposon en líneas parentales para efecto heterótico.

Palabras clave: Arroz, heterosis, bases genéticas, marcadores moleculares

INTRODUCTION

The phenomenon of superiority of F_1 over its parents is heterosis (Syn. hybrid vigour). The term heterosis was coined by Shull (1908) for quantitative measure of superiority of F_1 over its parents. The phenomenon of heterosis has been a powerful force in the evolution of plants and has been exploited extensively in crop production (Birchler *et al.* 2003). The successful development of hybrid maize in 1930 gave great impetus to breeders of other crops including rice to utilize the principle of hybrid production by exploiting heterosis. In fact the

exploitation of heterosis has been the greatest practical achievement of the science of genetics and plant breeding (Alam *et al.* 2004). The impact of this phenomenon can be judged by the fact that rice in its wild state produces only a few hundred spikelets whereas, the improved inbred varieties produce about 40,000 filled spikelets and rice hybrids about 52,000 filled spikelets per square meter (Mir, 2002).

Heterosis is a widely documented phenomenon in diploid organisms that undergo sexual reproduction. Although rice is a naturally self pollinated crop, strong heterosis is observed in their

F₁ hybrids. Though heterosis has been observed for various morphological, physiological and biochemical characters, in an applied breeding programme, the concern primarily with the economic yield potential (Ahmad, 1996). In practical breeding programmes, usually the standard heterosis is considered, which is defined as superiority of F₁ hybrid as compared to highest yielding check, and is estimated as:

$$\text{Heterosis (\%)} = \frac{\text{F}_1 - \text{Standard Check}}{\text{Standard Check}} \times 100$$

In rice, heterosis was first reported by Jones (1926) who observed that some F₁ hybrids had more culms and yield than their parents. Between 1962 and 1967 a number of suggestions came from different corners of the world regarding commercial exploitation of heterosis as a major component of rice improvement programmes at national and international level. There was, however lack of enthusiasm regarding such applications by most of the rice breeders because of rice being a strictly self-pollinated crop.

China was the first country to start extensive research for exploitation of heterosis for practical applications. It took China, not much time, to harness the fruits of such effort. The average yield advantage of growing commercial rice hybrids was about 20%. Presently hybrid rice area in China yield on an average 6.9t/ha compared to inbred HYV's yielding 5.4 t/ha in similar area (Virmani, 2004). The results in China have, in fact, encouraged IRRI and National rice improvement programmes of countries like India, Vietnam, Philippines, USA, Bangladesh and Indonesia to start hybrid rice breeding programmes to exploit heterosis. Hybrid rice technology has made tremendous impact on food security, rice production efficiency and employment in China and same is going to hold true outside China. The development of super rice series hybrids at IRRI based on NPT or Ideotype approach are reported to have yield potential of 12 t/ha, which means an increase of 2.25 t/ha which amounts to increase of 30 Million tones/year. Once the hybrids with 13 MT/ha are commercialized in 2005, 75 million more people can be fed annually. China has already commercialized various hybrids of super rice series such as Liang-You-Pei-Jiu (LYP 9).

Genetic basis of heterosis in rice

The genetic basis of heterosis has been a topic of contentious debate for almost a century now and is

still shrouded in mystery. The earlier workers put forth their suppositions based on quantitative genetic models but with the advancements in molecular genetics, we have been able to study this phenomenon in a more refined way. In fact, the recent studies in maize and rice to attempt an interpretation of heterosis have been greatly facilitated by molecular markers. The marker data offers an impeccable profile of genomic regions involved in trait expression and are expected to unravel the unexplained basis of heterosis (Robin, 2001).

Earlier studies put forth two possible mechanisms of heterosis: (i) Dominance hypothesis and (ii) over-dominance hypothesis. Theoretically, the two concepts are based on two different genetic phenomenon but in most of the situations, both lead to similar expectations (Mukherjee, 1995). In either case, inbreeding leads to a decline in vigour while out-breeding leads to increased vigour. In case of both dominance and over-dominance concepts, the decline in vigour is proportional to decrease in heterozygosity irrespective of the number of dominant and recessive alleles and degree of dominance. The difficulty of precise demarcation of either of two basic assumptions arises due to a number of factors.

- i) Distinction between true over-dominance and pseudo-over dominance. Linkage disequilibrium often causes bias in estimation of genetic components (non-additive), and as such heterosis may arise from repulsion phase linkage or complementary epistasis as well.
- ii) Effect of pseudo-alleles which cannot be classified as dominance or over-dominance.
- iii) Presence or absence of selection pressure may lead to heterosis due to two different genetic mechanisms.
- iv) Over-simplification of genetic models may lead to wrong interpretations.

Xu (2003) stated that as a complex character involving yield and yield components, heterosis should be genetically controlled by many genes. Although genetic study of quantitative traits has identified a limited number of QTL, each explaining a relatively large proportion of genetic variation, much more QTLs could be found when multiple populations are considered. For a specific hybrid, heterosis is more likely genetically controlled by a relatively small number of genes; for explanation of heterosis involved in all hybrids derived from a

species, a large number of QTLs will be needed. Heterozygosity and its related gene interactions are the primary genetic basis for explanation of heterosis because the hybrid is heterozygous across all genetic loci that differ between the parents. Thus, the degree of heterosis depends on which loci are heterozygous and how within locus alleles and inter-locus alleles interact with each other. Interaction of within-locus alleles results in dominance, partial dominance, or overdominance, with a theoretical range of dominance degree from zero (no dominance) to larger than 1 (overdominance). Interaction of inter-locus alleles results in epistasis. Genetic mapping results have indicated that most QTLs involved in heterosis and other quantitative traits had a dominance effect. As statistical methods that can estimate epistasis more efficiently became available, epistasis has been found more frequently and proven to be a common phenomenon in the genetic control of quantitative traits including heterosis. With so many genetic loci involved, it is unlikely that there is no interaction at all between any pair of them.

Syed and Chen (2005) indicated that *Arabidopsis thaliana* Col and Ler ecotypes share similar genetic backgrounds and, indeed, the performance of RILs for most of the traits examined remained within mean values of the two parents (Col and Ler) ruling out dominance complementation for the majority of traits. However, a large amount of variation was observed in the F₁ (or backcross) hybrids derived from each of the RILs and its parent, Col or Ler. These F₁ lines showed low and high performance for all of the traits studied, it is notable that high F₁ performance was observed in F₁ lines derived from RILs x Col or Ler. The reciprocal hybrids between Col and Ler did not show a comparable superiority over the two parents. Moreover, total heterozygosity is not as important as heterozygosity in individual chromosomes or segments for the observed heterosis. The data suggest that differential heterozygosity combined with epistasis may be the reason for the observed heterosis. Furthermore, the hybrid vigor occurred between two closely related ecotypes, and provides a general mechanism for novel variation generated between genetically similar materials.

Swanson-Wagner *et al.* (2006) state among other mechanisms, one attractive hypothesis for the existence of underdominant and overdominant gene action invokes the action of small interfering RNAs (siRNAs). siRNAs are typically derived from

transposons and repeats, although some genes and other sequences can generate siRNAs. siRNAs can regulate gene expression by cleaving target mRNAs and via transcriptional silencing. Maize inbreds differ radically in transposon and repeat content. Hence, inbreds are likely to differ in their complement of siRNAs. If siRNAs from one inbred do not match genes from the other inbred, the resulting hybrid could exhibit novel patterns of gene expression, including overdominance or underdominance. Overall, the results are consistent with the hypothesis that multiple molecular mechanisms contribute to heterosis.

Guo *et al.* (2004) found that the allelic expression variation occurred frequently in maize hybrids. The differential expression between the alleles could potentially result in hybrids surpassing the inbred parents in expression in different dimensions, such as (1) expression level, (2) expression timing/duration, and (3) response to developmental and environmental cues. The data suggest that the two parental alleles in maize hybrids may be regulated differentially during plant development and in response to environmental signals. Although only a small number of genes were analyzed using one each of the hybrid, distinct allelic expression patterns were found between a modern and an old hybrid. This work demonstrates that the maize hybrid is an excellent system to study allele expression variation because alleles are compared within the same genotype of a hybrid and equally affected by genetic background or environmental factors.

Auger *et al.* (2005) concluded from their data that nonadditive gene expression is quite prevalent in hybrids. The question arises as to whether and how these nonadditive expression levels contribute to heterosis. The triploid data indicate that allelic dosage affects the nonadditivity and therefore gene regulatory interactions are involved. Further work will be required to determine what spectrum of gene expression, if any, is correlated with heterosis.

Dominance as major genetic basis of heterosis

The dominance hypothesis was promulgated by Davenport (1908), Bruce (1910), Keeble and Pellew (1910) and later elaborated by Jones. This hypothesis assumes that heterosis is due to non-expression of deleterious recessive alleles in presence of beneficial dominant alleles in the resulting F₁ from

two parents. Therefore the F_1 produced from such a cross possesses superior characters because of the contribution of dominant alleles from one parent (Budak *et al.* 2002). Thus based on the dominance hypothesis, breeders should be able to fix the inbred lines with favourable alleles, and likely produce inbreds equivalent to F_1 hybrids. However, the isolation of such inbreds has been difficult likely due to a large number of loci differing between two parents. In fact the opponents of dominance hypothesis put this point as a major evidence against such an explanation of heterosis.

Recent advancements in molecular genetics have made it possible to detect and individually analyze the loci underlying heterosis (Xiao *et al.* 1995). Molecular linkage maps coupled with quantitative genetic analysis help in getting a better perspective of genetic basis of heterosis. Stuber *et al.* (1992) were first to use QTL analysis for detecting genomic regions (QTL's) contributing to heterosis. In rice Xiao *et al.* (1995) used F_1 of an indica variety (9024) and a Japonica variety (LH422) and developed Recombinant Inbred Lines (RIL's) and back-cross Inbred lines ($BC_1 F_7$ and $BC_2 F_7$; Table 1). All the traits studied were subjected to QTL analysis by single point basis and interval mapping. Using QTL data from all these combined populations, they estimated the differences in phenotypic means of heterozygotes and homozygotes over all portions of genome. From the overall results of their study they found that:

- 1) Most of the QTL's (73 %) were detected in only one of two backcross generations. In 82% of these cases heterozygotes had higher phenotype (F_1 plants have a higher value of each phenotypic trait measured in comparison to either parent) as compared to the respective homozygotes.
- 2) 23 % of QTLs were detected in both backcross populations and each pair was mapped to same chromosomal location. In all these cases heterozygotes fell between two homozygotes. This finding suggested that complementation of dominant (or partially dominant) alleles at different loci in F_1 was major contributor to F_1 heterosis for different traits.

This conclusion is supported by two important findings.

The correlation coefficient between genome heterozygosity and trait values by regressing the trait value of each $BC_1 F_7$ family on its percentage of genome heterozygosity should reflect the importance of heterozygosity *per se* to the expression of a particular trait. The values of the correlation coefficient (r) for most of the traits was very low and non significant. Even some of the heterozygotes had lower phenotypes than respective homozygotes. Thus heterozygosity is not an essential feature of heterosis as proposed in over-dominance theory.

The table reveals that except for plant height and panicle length correlation coefficients for all traits are non-significant which implies that heterozygosity is not essential for heterosis. All other traits for both populations and plant height and panicle length for BC/LH422 showed no relationship between the genome heterozygosity and trait performance, indicating thereby that overall genome heterozygosity alone had little effect on trait expression.

One of the important assumption of dominance hypothesis is that we should be able to isolate, from segregating populations, a true breeding individual which is as vigorous as F_1 (because in dominance hypothesis $AA = Aa$). In their experiment Xiao *et al.* (1995) observed two recombinant inbred lines whose phenotype exceeded that of F_1 , and true breeding individuals as vigorous as F_1 were observed for all traits including grain yield.

Digenic interactions between markers associated with significant QTLs and all other markers were not significant. Thus epistasis cannot be attributed as the cause of F_1 heterosis. However, due to inherent inefficiencies and low resolution of marker based QTL studies in detecting epistasis (Tanksley. 1993), the possibility of occurrence of some level of epistasis cannot be totally excluded.

The analysis of QTL x E interactions revealed that gene action of a QTL did not change from dominance to recessiveness or partial dominance to over-dominance from one environment to other.

These lines of evidence reinforce the conclusion that dominance is the major genetic basis of heterosis in rice. Although the same results do not come out with QTL analysis in maize even though both rice and maize belong to Gramineae, share many orthologous genes and have evolved from a common ancestor. Stuber *et al.* (1992) concluded that over-

dominance is major genetic basis of heterosis in maize. The possible explanations of this contrast are:

- a) Maize possess a large number of genes for which alleles interact in a truly over-dominant manner whereas rice does not.
- b) The observed over-dominant gene action may be due to pseudo-over-dominance or occurrence of dominant and recessive alleles in coupling phase linkage (Crow, 1952).
- c) QTL mapping at present is a low resolution process.

The evidence for dominance as a major genetic basis of heterosis was also provided by Hua *et al.* (2002) who performed a QTL analysis using F_2 populations. They found that correlation between genotype heterozygosity and trait performance was very low, implying thereby that heterozygotes are not always advantageous for performance. They also concluded that dominance is a major genetic basis of heterosis in rice. Singh *et al.* (2004) studied the components of heterosis in rice and concluded that dominance is the chief cause of heterosis.

Over-dominance as major genetic basis of heterosis

The hypothesis advocating over-dominance as major genetic basis of heterosis was first proposed by Shull (1910) and East (1908). The same concept was later advocated by Gustafsson (1938), Stadler

(1939) and Hull (1945). This theory proposes heterozygosity as basic cause of heterosis by providing physiological stimulus to improved development. Over-dominance theory is also called as 'Single gene heterosis'; 'Superdominance' or 'Cumulative action of divergent alleles'. Hull (1945) strongly advocated this concept and proposed that F_1 heterosis in maize cannot be accounted for by dominant genes acting additively but can be better explained by over-dominance. But one of the biggest lacuna of this concept is that majority of evidences have been worked out in cases of single locus heterosis while as most of quantitative traits including yield is governed by a number of genes. The overdominance hypothesis for heterosis involves alleles acting in dosage adjustment manner in which neither homozygote is better than heterozygote. With this explanation, it is assumed that heterozygosity alone is the major genetic basis of heterosis. At the molecular level, the preferable level of gene product by combination effect in heterozygous state results in better catalysis of metabolic pathways that lead to increased growth and yield.

Difficulties in discriminating true over-dominance from pseudo-overdominance are major opposition to this hypothesis. Jones (1917) was first to propose that linkage causes great problems in identification of overdominance and in fact pseudo-overdominance arising out of repulsion phase linkage may often be misinterpreted as true overdominance. In such a situation the pair of linked loci would mimic a single overdominant locus thereby skewing the measure of true overdominance (Budak *et al.* 2002).

Table 1. Correlation Coefficients between Genome heterozygosity and trait value (Xiao *et al.*, 1995).

Trait	BC ₁	BC ₂
Plant height	0.204 **	0.081
Days to heading	-0.004	0.021
Days to maturity	-0.027	0.026
Panicle length	0.143*	-0.021
Panicles per plant	-0.082	-0.048
Spikelets per panicle	0.062	-0.013
Grains per panicle	0.069	-0.026
Percent seed set	0.028	-0.016
1000-grain weight	0.068	0.099
Spikeletes per plant	0.026	-0.041
Grains per plant	0.037	-0.057
Grain yield	0.091	0.017

* $p \leq 0.05$ and ** $p \leq 0.01$

Brewbaker (1964) described four theories to explain over-dominance:

1. Supplementary allelic action
2. Alternative pathways
3. Optimal amount
4. Hybrid substance

Jinks (1983) was a strong opponent of over-dominance as genetic basis of heterosis in crops like rice where according to him great improvements have been made in performance of inbred lines by alternating cycles of hybridization and reextraction (pedigree selection). However it is difficult to exclude role of overdominance in heterosis in both autogamous and allogamous crops.

Several recent studies on genetic basis of heterosis in rice have come up with strong evidences in support of over-dominance.

Li *et al.* (2001) studied the genetic basis of heterosis and inbreeding depression in rice by using five interrelated mapping populations comprising a Lemont (*japonica*)/Teqing (*indica*) RIL, two BC and two test cross populations using Zhong 413 and IR64 as testers. The non-additive gene action accounted for 62 % of trait variation while additive gene action accounted for 28.1 % of trait variation of F₁ mean values. They found that most of the QTL's (~ 90%) contributing to heterosis were over-dominant especially for grain yield, biomass, panicles per plant and grains per panicle. One of the important findings of the study was that there was no evidence of pseudo-over-dominance from repulsion phase linkage of completely or partially dominant QTL's for yield components as proposed by Crow (1952). Similar results were reported by Luo *et al.* (2001) using similar set of mapping populations. They concluded that over-dominant loci are the major genetic basis of inbreeding depression and heterosis in rice, especially for panicle per plant and grains per panicle. They stated that pronounced over-dominance resulting from epistasis by multi-locus genotypes appears to explain the longstanding dilemma of how inbreeding could arise from over-dominant genes. Hua *et al.* (2003) detected many heterotic loci in RIL's from a cross between parents of Shanyou 63 and found high degree of over-dominance in many heterotic loci. Suresh *et al.* (2004) studied molecular marker

heterozygosity and heterosis using a set of SSR and RAPD markers and found significant positive correlation between marker heterozygosity and heterosis in relation to traits such as productive tillers/plant, biomass yield and grain yield per plant.

Epistasis as a major genetic basis of heterosis

Dominance and over-dominance (both proposed in 1808) remained the major genetic understandings of the cause of heterosis even though both faced contradictions. The advent of molecular marker systems such as isozymes, RFLP, AFLP and high density molecular linkage maps made it possible to dissect the loci causing heterosis, in terms of effects and dominance relationships, with more precision and reliability.

Both dominance and over-dominance concepts are based on single-locus model. But Wright (1968) proposed that most of the quantitative traits are conditioned by many loci and as such each gene replacement may have effects on many characters because genes invariably do interact with each other. He visualized a "net-like" structure of population genotypes such that the variations of most characters are affected by many loci such that each gene replacement may have effects on many characters. Based on such a perspective, epistasis should be one of the major genetic components in case of quantitative traits. Hallauer and Miranda (1988) also proposed that epistasis should contribute significantly to heterosis.

A classical study in rice by Yu *et al.* 1997 using F₃ population derived from bagged F₂ plants from a cross between Zhenshan 97 and Minghui 63 (Parents of Shanyou 63, the best hybrid in China accounting for 25 % of hybrid rice acreage) (Tables 2 and 3), the most striking finding of the study was the prevalence of epistasis in rice, with three pronounced features.

- 1) Two-locus analysis resolved larger number of loci contributing to trait expression. For grains per panicle only, counting interactions simultaneously, the significant two-locus interactions detected 25 QTL's on 9 of 12 rice chromosomes compared with 5 and 7 QTL's detected in two years for this trait.

- 2) All the three types of interactions i.e. A x A, A x D and D x D occurred among various two-locus combinations.
- 3) Multiple interaction terms were found in a considerable proportion of interacting two-locus combinations in all traits.
- Lack of correlation between genotype heterozygosity and trait expression was also observed in this study, which implies that, collectively, the effect of dominance and/or overdominance made only limited contributions to the heterosis. Dominant interactions (DD) were most relevant to F₁ data but AA was more commonly detected than AD and DA types.

Table 2. Summary of the significant ($p \leq 0.01$) interactions identified in 1994 and 1995 by searching all possible two locus interactions.

Trait	Interaction (traits)	1994	1995	Common
Yield	AA	60	91	9
	AD/DA	51	73	3
	DD	4	18	0
Tillers/plant	AA	79	105	17
	AD/DA	28	42	1
	DD	10	6	0
Grains/panicle	AA	52	80	9
	AD/DA	56	74	10
	DD	4	16	0
Grain weight	AA	84	102	27
	AD/DA	47	71	19
	DD	15	16	9
Number of Tests		7585	7681	

Source : Yu *et al.* 1997

Table 3. Two locus interactions for grain per panicle simultaneously detected by two-way analysis of variance at $P \leq 0.1$ in 1994 and 1995.

Locus 1	Locus 2	Type (1994)	Type (1995)
RG532 (1)	RM 4 (11)	AA	AA
RG173 (1)	RM203 (3)	AA	AA
C547x (1)	RG 634 (2)	AA	AA
RG236 (1)	R1440 (7)	AD	AD
		DA	DA
C112 (1)	G389a (11)	AA	AA
MX 7b (2)	Waxy (6)	DA	DA
C1447 (5)	C677 (10)	AA	AA
		DA	---
C1447 (5)	G389 a (11)	AA	AA
G1458 x (5)	G342 (6)	AA	AA
G193 x (5)	G 342 (6)	AA	AA
RG360 (5)	RG653 (6)	AD	AD
		DA	DA
RG360 (5)	G343 (6)	AD	AD
R830 (5)	RZ404 (9)	AA	AA
		DD	DD
C1023 (7)	C794 (11)	DA	DA

Numbers in parenthesis represent chromosomal locations

Source : Yu *et al.* 1997

The study also suggested possibility of higher-order interactions at least for most complex trait (grain yield). There are some lines of evidence implying existence of higher-order interactions.

- 1) Fewer QTL's were detected for yield than other traits and smaller amount of phenotypic variation was accounted for by them.
- 2) At the two-locus level, the numbers of interactions detected for yield were less than component traits. This suggests involvement of genetic components not resolved by either single locus or two-locus analysis.
- 3) Significant two-locus interactions revealed "Chain-like" relationship among interacting two-locus combinations such that locus 1 interacted with locus 2, which in turn interacted with locus 3 and so on and so forth (Table 2). This implies higher-order multi-locus interactions.

Luo *et al.* (2001) also found many epistatic QTL pairs for yield and yield components. Most epistasis occurred between complementary loci, suggesting that grain yield components were associated more with multi-locus genotypes than with specific alleles at the individual loci.

More recently, Hua *et al.* (2003) studied "immortalized F₂" population produced by randomly intermitting RIL's derived from Zhenshan 97/Minghui 63 which are the parents of Shanyou 63, which is the best hybrid in China. They observed significant two-locus interactions by two-way ANOVA across entire genome, DD interaction occurred at predominantly high frequency, followed by AD/DA, with AA being the least frequent.

CONCLUSION

The understanding of the phenomenon of heterosis in terms of its genetic basis is far from adequate even after molecular dissection of the process and factors contributing to it. The majority of the earlier studies speculated dominance and over-dominance as the genetic mechanism of heterosis but the recent studies have revealed that linkage and epistasis may also have a role to play (Budak *et al.* 2002). However, one common observation in all the studies has been that no single hypothesis holds true for all the experiments and crops. It is, thus likely that the heterosis is crop dependant and population dependant. This seems to resolve the conflicting

reports from experiments designed to study the genetic basis of heterosis. Different studies which focused on understanding genetic basis of heterosis have come up with conclusions regarding different genetic elements such as dominance, over-dominance and epistasis as possible genetic mechanisms responsible for heterosis. The challenge now is how to put the pieces together to frame a comprehensive picture (Hua *et al.* 2003). In case of rice there was a strong case for dominance as depicted by Xiao *et al.* (1995) because there were many points regarding over-dominance such as pseudo over-dominance or repulsion phase linkage of dominant alleles. However, recent study of Yu *et al.* (1997) provided strong evidence for two-locus and multi-locus interactions (epistasis) especially for traits such as grain yield, which are complex in nature. They found that heterosis is not controlled by single locus alone, whether the locus behaves in dominant or over-dominant fashion, linkage and epistasis has a major role. Even net like gene interaction is prevalent for most of traits including even seemingly simple traits like days to heading.

Thus, the effects of dominance, over-dominance and epistasis of various forms are not mutually exclusive in the genetic basis of heterosis, as opposed to what was previously debated in favour of different hypothesis (Allard, 1960). All of these components have a role to play depending upon the genetic architecture of the population (Hua *et al.* 2003) i. e. single-locus heterotic effects (caused by partial, full-and over-dominance), all three forms of digenic interactions (AA/AD/DA and DD) and probably multi-locus interactions. Thus, these results may help reconcile the century long debate on the role of dominance, over-dominance and epistasis as genetic basis of heterosis.

Two different types of allele interaction, both within-locus and inter-locus, each should play an important role in the genetic control of heterosis. Contribution of a specific locus to heterosis could be due to any single type of these interactions. When multiple loci are involved that were not taken into account in the early 1900s, various combinations of within-locus and inter-locus interactions (especially dominance x dominance interaction) could contribute to the genetic control of heterosis. A full understanding of heterosis will depend on cloning and functional analysis of all genes that are related to heterosis. This process would be very similar to that for understanding disease resistance genes that

functionally appear much simpler than heterosis (Xu, 2003).

The current research on molecular breeding with heterosis aims at identification of specific genomic regions in crop plants like rice (heterotic chromosome blocks) wherein specific genomic regions conditioning heterotic expression are to be identified in diverse lines in parents which can be used for development of superior hybrids. Already in maize, the pioneer Hi-Bred International Inc. is approaching the dissection of heterosis in maize using a “Gene Calling” technology. This approach uses molecular biology and bioinformatics to dissect expressed DNA sequences responsible for hybrid vigour. Advances in rice genomics and molecular markers will help devise similar systems for dissection of heterosis at DNA level to precisely understand its genetic basis for practical application in hybrid rice development.

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