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Concept of Heterotic Group and its Exploitation in Hybrid Breeding

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A B S T R A C T

Narrow genetic base is one of the most important limiting factors for yield improvement and is a bottleneck in any of the breeding programs. Information on genetic diversity and heterotic groups is very useful in inbred line development and help breeders to utilize their germplasm in a more efficient and consistent manner through exploitation of complementary lines for maximizing the outcomes of a hybrid breeding program. Development of hybrid oriented heterotic populations and application of schemes for improving combining ability is an integral part of hybrid breeding in maize and other cross pollinated crops. Broadening the genetic base of heterotic pools is a key to ensure continued genetic gain in hybrid breeding. The selection of parents and breeding strategies for the successful hybrid production will be facilitated by heterotic grouping of parental lines and determination of combining abilities of them. Assigning germplasms into different heterotic groups and patterns is fundamental for exploitation of heterosis for hybrid development. If once heterotic groups and their pattern are identified then large number of hybrid combination can be developed, within short period of time because grouping of lines in different clusters would avoid the development and evaluation of unnecessary hybrids from these heterotic patterns. Our objectives of this review are (i) Review various methods used to assign germplasm into heterotic groups and identify their heterotic pattern in different crops on the basis of experimental evidence supporting them. (ii) Listing out various heterotic groups and heterotic patterns in different crops and (iii) Examine advantages and disadvantages of the concept of heterotic groups and patterns.

Introduction

The application of heterosis in crop breeding and production is the most important contribution of plant genetics to the development of agricultural technology in the last century (Zhang *et al.,* 1998).The phenomenon of heterosis was defined by Shull (1952) as "the interpretation of increased vigor, size, fruitfulness, speed of development, resistance to disease and to insect pests, or to climatic rigors of any kind manifested by crossbred organisms as compared with corresponding inbreds, as the specific results of unlikeness in the constitution of the uniting parental gametes". For our purposes, we will define heterosis as the difference between the hybrid and the mean of its two parents (Schnell, 1961).

Information on heterotic groupings of germplasm is essential for hybrid breeding program. Assigning germplasms into different heterotic groups is fundamental for the maximum exploitation of heterosis for hybrid cultivar development. Similarly, information on genetic diversity is also very important for hybrid breeding and population improvement programs for assessing the level of genetic diversity, characterizing the germplasm and assigning them into different heterotic groups (Reif *et al.,* 2003). For an efficient hybrid breeding program, it is desirable to organize the germplasm into heterotic groups (Reif *et al.,* 2007).

The classification of elite germplasm and inbred lines into different heterotic groups is an important task in any of the breeding program (Hallauer *et al.*, 1998). Introgression of exotic germplasm is often suggested for increasing the genetic differences between opposite heterotic populations with an expected increase in heterotic response (Beck *et al.*, 1991; Vasal *et al.*, 1992a, b; Ron Parra and Hallauer, 1997).

Melchinger and Gumber (1998) defined a heterotic group "as a group of related or unrelated genotypes from the same or different populations, which display similar combining ability and heterotic response when crossed with genotypes from other genetically distinct germplasm groups. By comparison, the term heterotic pattern refers to a specific pair of two heterotic groups, which express high heterosis and consequently high hybrid performance in their cross." The concept of heterotic patterns includes the subdivision of the germplasm available in a hybrid breeding program in at least two divergent populations, which are improved with inter-population selection methods. Heterotic patterns have a strong impact in crop improvement because they predetermine to a large extent the type of germplasm used in a hybrid breeding program over a long period of time (Melchinger and Gumber, 1998). Heterotic pattern is a key factor for utilizing germplasm to maximize performance of the population crosses and derived hybrids (Eberhart *et al.*, 1995). The development of successful maize (*Zea mays* L.) hybrids requires establishment of heterotic patterns, defined as the cross between known genotypes that expresses a high level of heterosis (Carena and Hallauer, 2001).

The most exploited heterotic pattern is the cross between Iowa Stiff Stalk Synthetic (BSSS) and Lancaster Sure Crop heterotic groups. Crosses among inbred lines that derive from unrelated heterotic groups are known to have better grain yield performance than those crosses among lines belonging to the same group (Moll *et al.*, 1965; Hallauer *et al.*, 1988; Melchinger, 1999).

Molecular markers have shown to be useful classifying unrelated inbred lines into heterotic groups (Smith *et al.,* 1997; Pejic *et al.*, 1998; Senior *et al.*, 1998; Lu and Bernardo, 2001; Li *et al.,* 2002). Based on this information, the integration of molecular markers in maize-breeding programs can increase their efficiency. Simple sequence repeats (SSR) have been extensively used as genetic markers in eukaryotic genomes (Tautz, 1989). Such markers have large number of advantages over the amplified fragment length polymorphism (AFLP), random amplified polymorphic DNA (RAPD), and restriction fragment length polymorphism (RFLP) markers (Pejic *et al.*, 1998; Senior *et al.*, 1998; Gethi *et al.*, 2002).

Some authors have demonstrated the efficiency of the identification of heterotic groups of maize lines by using molecular procedures such as restriction fragment length polymorphisms (RFLPs) (Ajmone-Marsan *et al.*, 1998; Benchimol *et al.*, 2000; Pinto *et al.*, 2003; Warburton *et al.,* 2005), amplified fragment length polymorphisms (AFLPs)

(Oliveira *et al.,* 2004; Legesse *et al.,* 2007) and simple sequence repeat (SSR) markers (Reif *et al.*, 2003; Barata and Carena, 2006). An advantage over conventional methods is that few divergent lines are not discriminated, and consequently, heterotic groups are formed that contain genotypes, which unequivocally represent the differences in the allele frequency of the populations. This necessitated a study of heterotic relationships among Iranian maize germplasm. Choukan *et al.,* (2006), using cluster analysis from genetic distance based on SSR makers to evaluate Iranian maize inbred lines reported that the lines could be classified into four preliminary heterotic groups.

Concept of heterotic groups and pattern

The phenomenon of heterosis was first detected in maize. Shull defined heterosis in 1952 as, "The increased vigour, speed of development, resistance to disease and insect pests, or to climatic rigours of any kind, manifested by crossbred organisms as compared with corresponding inbreds as the specific result of unlikeness in the constitutions of the uniting parental gametes." The term heterotic group refers to "a group of related or unrelated genotypes from the same or different populations, which display similar combining ability and heterotic response when crossed with genotypes from other genetically distinct germplasm groups" (Melchinger and Gumber, 1998). 'Heterotic pattern' refers to a specific pair of 2 heterotic groups that express high heterosis and high hybrid performance in their cross.

Criteria for the identification of new heterotic groups and patterns

Several criteria have been suggested to choose promising heterotic groups: high mean performance and large genetic variance in the hybrid population in the target region(s), high per se performance and good adaptation of the parent populations, and a higher ratio of the variance due to general ($\sigma2$ GCA) versus specifi c combining ability ($\sigma2$ SCA) (Melchinger and Gumber, 1998; Reif *et al.*, 2005a). Low inbreeding depression in the source materials for the development of inbreds; and a stable CMS system without deleterious side effects, as well as effective restorers and maintainers, if hybrid breeding is based on cytoplasmic male sterility.

Various methods to develop Heterotic groups

Pedigree analysis

The heterotic pattern increases the efficiency of hybrid development, inbred recycling and population improvement. The Reid and Lancaster groups were identified based upon pedigree and geography analysis of inbred lines used in the Corn Belt. Wu (1983) attempted to classify inbred lines into 4 or 5 groups based on pedigree analysis and to predict heterotic patterns used in China.

Quantitative genetic analysis

Melchinger (1999) reviewed the different approaches to classify and identify heterotic groups. Diallels or factorial designs have been used when the number of populations or groups was small in tropical (Vasal *et al.*, 1999) and temperate corn (Ordas, 1991; Moreno-Gonzaler *et al.,* 1988). Development of hybrid oriented heterotic populations and application of schemes for improving combining ability is an integral part of hybrid breeding in maize and other cross pollinated crops (Hallauer and Miranda, 1981). Basis of grouping the germplasms into different heterotic groups was specific combining ability (SCA) effects for grain yield (Gurung *et al.,* 2009, Fan *et al.,* 2009). Cluster analysis based on SCA can be used to classify inbred lines into heterotic groups. Fourteen maize inbred lines, used in maize breeding programs in Iran, were crossed in a diallel mating design for investigation of combining ability of genotypes for grain yield and to determine heterotic patterns among germplasm sources, using both, the Griffing's method and the biplot approach for diallel analysis (Bidhendi *et al.*, 2012).

Geographical isolation inference

The geographical origin of the two populations contributed to the high grain yield of the cross (Moll *et al.*, 1962, 1965; Reif *et al.*, 2005b). Heterotic rice hybrids are generally derived from distant parents by geographic origin or different ecotypes (Yuan 1977; Lin and Yuan 1980). In the earlier stage of hybrid rice development in China two heterotic groups that is early season indica from southern China and midor late-season indica from Southeast Asia were identified for three-line hybrid rice based on wild abortive (WA) male sterile cytoplasm (Yuan 1977).

Use of molecular markers

Genotyping and cluster analysis of extracted genotypic DNA from the mutants and respective parents from their young leaves (1 to 2 weeks after seed germination), using the Cetyltrimethy lammonium bromide (CTAB) method (Hoisington *et al.*, 1994). These genotypes were further genotyped using twenty one Simple Sequence Repeats (SSR) markers on GenBank data base (Yu *et al.*, 2000). Genetic diversity studies determine the variation among individuals or groups of individuals using a specific method or combination of methods to analyze multivariate datasets (Mohammadi and Prasanna, 2003). Diverse datasets have been used to analyze genetic diversity in crop plants, among them which are pedigree data, morphological data (Badu-Apraku *et al.*, 2006), genetic parameter estimates (Camussi *et al.*, 1985), heterosis data (Badu-Apraku *et al.*, 2013a, b), biochemical data, and molecular marker data (Melchinger *et al.*, 1991; Betran *et al.*, 2003; Mohammadi and Prasanna 2003). Molecular marker data provide a more reliable differentiation of genotypes (Mohammadi and Prasanna 2003), since these data are less affected by environmental effects. Molecular marker data classified a set of germplasm based on genetic similarities, however Melchinger and Gumber (1998) emphasized that it has been challenging to predict heterotic relationships based on these data. Additionally, researchers agreed that field experiments are still needed to validate groupings of germplasm based on molecular marker data (Melchinger and Gumber, 1998; Barata and Carena, 2006)

We concluded that the relationships between the populations obtained by SSR analyses are in excellent agreement with pedigree information. SSR markers are a valuable complementation to field trials for identifying heterotic groups and can be used to introgress exotic germplasm systematically (Reif *et al.*, 2003; Yuan *et al.*, 2002 and Aguiar *et al.*, 2008).

Various strategy for establishment of heterotic patterns

Two well-known strategy for the establishment of heterotic pattern by Cress (1967) (Cress strategy) and another one by Melchingner and Gumber (1998) (Melchingner and Gumber Strategy).

The decision which of both strategies is superior it depends on several factors such as (i) the genetic basis of heterosis, (ii) the applied selection intensities for QTL, or (iii) the importance of favorable linkages. Further research is required incorporating recent advances on the genetic architecture of quantitative traits and on the genetic basis of heterosis to develop optimal procedures for establishing and maintaining heterotic patterns.

A very new method to develop heterotic groups is suggested by Patil (Unpublished method)

This basic formula: HF1 =Σ dy2 explains how performance (heterosis) of hybrid depends on genetic diversity and extent of dominance existing at different yield influencing loci (Falconer 1981). Development of hybrid oriented heterotic populations and application of schemes for improving combining ability is an integral part of hybrid breeding in maize and other cross pollinated crops (Hallauer and Miranda, 1981).

In the recent years the concept of developing heterotic populations is put to test in self-pollinated crops like cotton, segregating populations based on diverse pairs of genotypes can be the ideal base material required for implementing procedures like reciprocal selection for improving combining ability (Patil and Patil, 2003; Patil *et al.*, 2011).

Population improvement schemes have led to the development of maize lines with improved combining ability resulting in the isolation of superior hybrid combinations. The recurrent selection procedures are also suggested for often cross pollinated crops by considering cotton as an example (Miller and Rawlings, 1967) and in sorghum (Dogget and Eberhart, 1968) by utilizing male sterility system. Considering the success achieved in commercial exploitation of heterosis in cotton, sorghum, rice and such other often cross pollinated or self-pollinated crops, it is possible to visualize that such schemes of improving combining ability by following the recurrent selection schemes can be very well followed in these crops, with suitable modification in procedure in tune with the mating system of these crops (Patil and Patil, 2003).

Advantages and disadvantages of heterotic groups and heterotic patterns

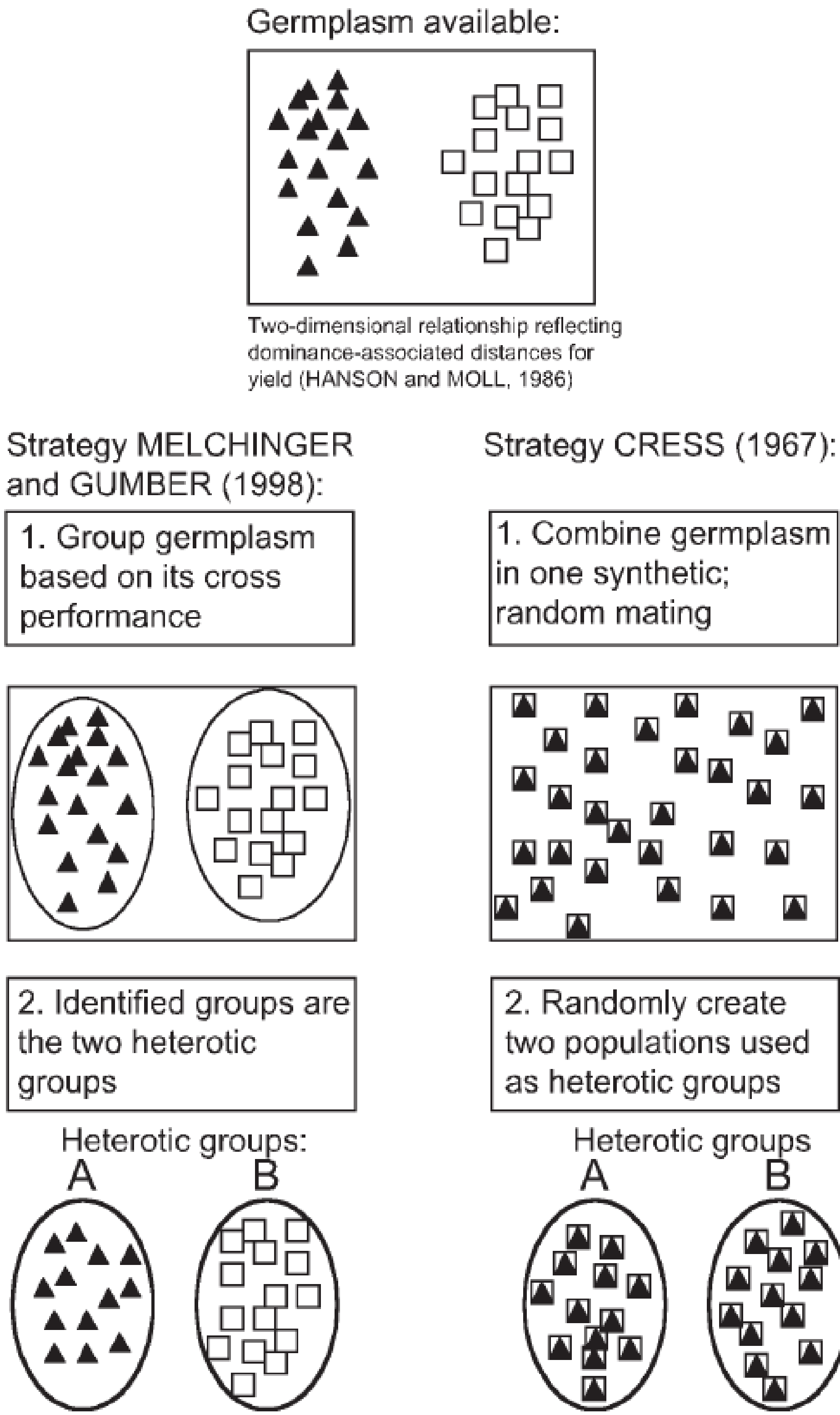
Intergroup hybrids out yielded the respective intra-group hybrids by 21% in Reid Yellow Dent × Lancaster Sure Crop crosses (Dudley *et al.*, 1991) and by 16% in Flint Dent crosses (Dhillon *et al.*, 1993). These results clearly indicate that grouping of germplasm in divergent pools is advantageous to maximize the expected heterosis. Cress (1967) evaluated in a simulation study inter- population improvement methods. He pointed out that the maximum genetic potential could not be reached in a breeding system with two strictly separated groups if the best alleles are present in only one of the two populations assuming a degree of dominance smaller than one.

However, it is questionable that maximum yield potential is an appropriated criterion to evaluate selection strategies. Under the assumption that a large number of QTL are underlying a complex trait such as grain yield, it is of upmost importance to increase the probability to combine at different QTL as many positive alleles as possible. Applying the concept of heterotic patterns enables breeders to simultaneously select on two inbred lines, which are combined in a single hybrid. An increased divergence between two populations of a heterotic pattern increases the probability to complementary select for favorable alleles at different loci. Melchinger *et al.*, (1987) emphasized the importance of the variances due to general (σ 2 GCA) and specific combining ability (σ 2 SCA) and their ratio for predicting hybrid performance.

Table.1 Various heterotic groups and heterotic patterns in different crops

Crop	Heterotic Group	Heteroic pattern	Country	Reference
1. Maize	U.S. dent lines, European flint lines	U.S. dent lines X European flint lines	Europe	Schnell *et al.*, 1992
	female group Stiff Stalk (SS) and the male group is designated Non-Stiff Stalk (NSS)	Stiff Stalk (SS) X Non-Stiff Stalk (NSS)	U.S. Corn Belt and Canada	Duvick *et al.*, 2004
	Tang sipingtou and Luda honggu germplasm, Lancaster Sure Crop (LSC), Reid Yellow dent (RYD)	Tang sipingtou X Luda honggu germplasm, domestic × LSC, domestic × PN, *Dom × Lan or Dom × Reid. Luda Red Cob × Lan*	USA, China	Li *et al.*, 2002, 2004.
	Suawan, Reid, Non Reid	Suawan X Reid, Suawan X Non Reid, Reid X Non Reid	China	Fan *et al.*, 2013
	Tuxpeno combines well with Cuban Flint, Coastal Tropical Flint (Caribbean Flint), Tuson, ETO, Perla and Chandelle	Tuxpeno combines well with Cuban Flint, Coastal Tropical Flint (Caribbean Flint), Tuson, and ETO Cuban Flint combines well with Tuxpeno, Tuson, Coastal Tropical Flint, and Perla. Coastal Tropical Flint combines well with Tuxpeno, Cuban Flint, and Chandelle	China	Wellhausen, 1978 Goodman, 1985 Vasal *et al.*, 1999
2. Rice	Early season *indica* from southern China and mid or late-season *indica* from Southeast Asia	Early season *indica* from southern China X mid or late-season *indica* from Southeast Asia	China	Yuan, 1977
3. Rye	The “Petkus” and “Carsten”,	The “Petkus” X “Carsten”,	Europe	Hepting, 1978
4. Faba bean	“Minor”, “Major”, and “Mediterranean”	“Minor” X “Major”, “Minor” X “Mediterranean”, “Major”, X “Mediterranean”	Europe, Germany	Link *et al.*, 2006
5. Rape seed	Asian, European winter-type and Canadian and European spring-type	Asian, European winter-type X Canadian and European spring-type	Canada and Europe	Qian *et al.*, 2009
6. Millets	Tiouma, Souna3	Tiouma × Souna3	Iran, India	Issoufou Kassari Ango, Inran, Bettina Haussmann, ICRISAT

Melchinger and Gumber (1998)	Cress (1967)
Melchinger and Gumber (1998) recommended the following criteria for the identification of new patterns: (i) high mean performance and large genetic variance in the hybrid population; (ii) high per se performance and good adaptation of the parent populations to the target environment; and (iii) low inbreeding depression, if hybrids are produced from inbreds. In practice, the choice of heterotic patterns is mainly based on the performance of the corresponding hybrid population.	Cress (1967) suggested, based on results of a simulation study, that all genetic material entered into a long-term program of inter-population selection should be combined into one synthetic population (Fig. 3). Any subsequent populations required would be obtained by sampling this synthetic. However, the results reported by Cress (1967) were based on a rather simple genetic model assuming (i) a low number of quantitative trait loci (QTL), (ii) absence of linkage between the QTL, (iii) two alleles per QTL, and (iv) no epistasis. In contrast to the suggestions of Cress (1967).


Germplasm available:
Two-dimensional relationship reflecting dominance-associated distances for yield (HANSON and MOLL, 1986)
Strategy MELCHINGER and GUMBER (1998):
1. Group germplasm based on its cross performance
2. Identified groups are the two heterotic groups
Heterotic groups:
A
B
Strategy CRESS (1967):
1. Combine germplasm in one synthetic; random mating
2. Randomly create two populations used as heterotic groups
Heterotic groups
A
B

One hypothesis is that the establishment of heterotic pools leads to a predominance of σ^2 GCA over σ^2 SCA, and thus early testing becomes more effective. Furthermore, superior hybrids can be identified and selected mainly based on their prediction from GCA effects. Experimental data of estimates of the magnitude and expected ratio σ^2 SCA: σ^2 GCA of for inter-pool compared with intra-pool crosses are limited and mostly based on few factorial combinations. First results have been presented in maize by MELCHINGER and GUMBER (1998). A lower ratio of σ^2 SCA: σ^2 GCA was found in inter- than in intra-group crosses indicating that the concept of heterotic patterns effectively supports the selection of superior hybrids. These findings are in agreement with theoretical results indicating that inter-group crosses have smaller σ^2 SCA and σ^2SCA: σ^2 GCA ratios than intra-group crosses (MELCHINGER, 1996, unpublished results).

Objectives of heterotic groups and heterotic patterns development

To get higher mean heterosis and hybrid performance.

To reduce the specific combining ability (SCA) variance and a lower ratio of SCA to general combining ability (GCA) variance.

Assigning lines to heterotic groups would avoid the development and evaluation of crosses that should be discarded, allowing maximum heterosis to be exploited by crossing inbred lines belonging to different heterotic groups.

To save the time of hybrid development.

Utilize new germplasm to broaden the genetic background of hybrid.

In conclusion, information on genetic diversity and heterotic groups is very useful in hybrid development and help breeders to utilize their germplasm in a more efficient and consistent manner. If once heterotic groups and their pattern are identified then large number of hybrid combination can be developed, within short period of time because grouping of lines in different heterotic groups would avoid the development and evaluation of unnecessary hybrids from these heterotic groups. Good heterotic group classification method can be defined as one which allow inter-heterotic group crosses to produce more superior hybrids than the within- group crosses. Heterotic patterns have a strong impact in crop improvement because they predetermine to a large extent the type of germplasm used in a hybrid breeding program over a long period of time.

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