Origin of the Concept of Maximum Heterozygosity in Autotetraploids

by Yves Demarly

Please note: This contribution from Professor Demarly describes the origins of the concept of maximizing heterozygosity in alfalfa. It is reproduced in its original elegance to preserve his thoughts in his hand. The information was used in a paper given at The Alfalfa Genome Conference, 1999 at Madison, Wisconsin: "Maximizing Heterozygosity and Progressive Heterosis in Alfalfa" by Robin Groose, Yves Demarly, and Michael Dunbier. A forthcoming MGR will contain a literature review of the subject.

78000 . Versailles
14 Allée des Gardes Royales

April 9th

Dear Prof. Bingham,

I am pleased to send a copy of some data that I transmit to Robin groose with the hope that they could help him when writing his paper -

Sincerely

Y. D

Yves Demarly.

- 1 - As I was in charge of alfalfa improvement, in the fifties, the general model for allogamous plants was the successful hybrid corn production in the USA. At that time the particular behavior of autotetraploids was unknown. Accordingly I produced a large number of inbred progenies (until 5, even 6 and 7 generations of selfing)

- 2 - Two experiments involving these inbred progenies convinced me that heterosis for autotetraploids did not fit with diploid model.

- 3 - The first experiment (1954) consisted in submitting different levels of selfing to a kind of top-cross with the natural population from which they were extracted:

I_0 (natural population)
↓ gives by selfing (without selection)

			green matter yields of the progenies
I_1	used as females	× pollinated by I_0 →	91%
I_2		× " " →	77%
I_3		× " " →	71%
I_4		× " " →	68%

I_0 = 100%.
L.S.D = 6%

From these results I concluded that:
" the more the female parent was inbred, the more it was difficult to restore hybrid vigour in one crossed generation "

-4- The second experiments (1958; 1960; 1961) complemented these results : They consisted in four comparisons (several years, several locations) between single hybrids, three ways hybrids and double hybrids. These comparisons involved approximately 50 hybrids of each kind -
All the results were consistant showing that single hybrids were inferior (less producing) than three ways hybrids which themselves were inferior to double hybrids : The mean figures were

105 for single hybrids
109 for three ways hybrids
112 for double hybrids

} all differences are significant

Consequently it became clear for me that in autotetraploid plant it was not the heterozygosity which was important for heterosis but the richness in allelic diversity

tetragenic > trigenic > digenic .

Then the number of interactions between homologous alleles would influence the level of heterosis's.
From these findings I published a synthetic paper in 1963 : Génétique des Tétraploïdes et Amélioration des plantes (Annales Amél. Pl., 1963, 13 (4) 307-400)
Though written in french, I was called in 1964 to present this at Ames (iowa). Dudley and his colleagues were stimulated with the results -

-5- It appeared later that the behaviour of inbred lines and of hybrids during their multiplications could not be fully explained by the allelic population models -

Then I developped in the seventies the concept of linkat which opened to structural heterosis.

The idea of linkat can be summarized as follows:

- The genes locations along chromosomes have been shaped during the evolution of species -
- Consequently alleles of genes interacting for the best selective values were clustered into protected segments of chromosomes called linkats.
- Having a good selective value these segments concentrated inhibitors of recombination. On the other hand they are bounded by recombinogen areas Hence genetic factors controlling crossing over are associated with locus clusters of linkats -
- In normal conditions the protected blocks of linkats behave as segregational units; but when bad conditions (environment, change in breeding regime, in vitro culture...) arise, the structural cohesion of linkats can be altered -

In conclusion we can say that

1°/ linkats are functionnal, segregationnal and selective clusters of alleles

2°/ a cohesive strength is associated to each structure of linkats. This cohesion is controlled by genetic factors acting in cis or trans.

-6- Consequently we must think of heterozygotes not only in terms of point alleles, but also in terms of linkats ; that is to say that two different compositions of homologous linkats may induce a global heterotic effect even if some alleles inside the linkats are identical.

for instance :

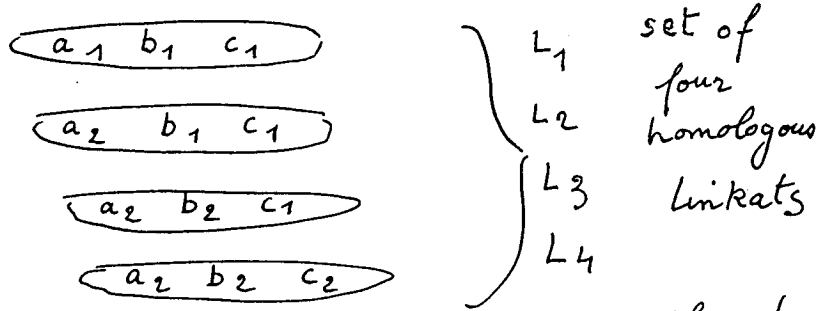
homozygote pair of linkats { $a_1\ b_1\ c_1\ d_1\ e_1$ / $a_1\ b_1\ c_1\ d_1\ e_1$

heterozygote pair of linkats { $a_1\ b_1\ c_1\ d_1\ e_1$ / $a_2\ b_1\ c_1\ d_2\ e_1$

The unit being here linkat and not allele this is called structural heterozygotes which induce a structural global heterosis

-7-

For autotetraploid plants this structural heterosis is of some importance.



This is a structural tetragenic genotype though every allelic locus is digenic. Consequently even if molecular analysis reveals digenic alleles composition we may have a maximum heterosis as if tetragenic. In fact the homologous functional units have a diversity of four

- 8 - In the seventies such considerations may sound as merely speculative.
In fact most of present results, as well from the field as from molecular analysis (functional clusters, recombinogen areas, genetic control of C.O) show that it could be a valuable model to understand heterosis in autotetraploid crops.

References:

1963 Demarly. Y. - Genetique des Tetraploïdes et Amelioration des plantes. Ann Amel. Plantes, 1963, 13 (4), 307-400.

1979 Demarly. Y - The concept of linkat. Proc. Conf. Broadening Genetic Base Crops. Wageningen 1978 Pudoc Wageningen, 1979.