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CONVERGENCE–DIVERGENCE IMPROVEMENT IN PLANT BREEDING

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Abstract: *There are set of terms used to support convergence–Divergence in plant breeding viz., convergence, divergence, convergent–divergent evolution, convergent–divergent selection and convergent–divergent improvement (breeding). Convergence (convergent evolution) means the evolution of unrelated species getting into similar adaptive areas, resulting in structures bearing a nearly similar resemblance, where divergence (divergent evolution) is adifferent combinations or a setat an angle to one another in a herring-bone fashion e.g. lateralspikelets of the two-row barley spike. Convergence breeding (convergent improvement) is a breeding method involving the reciprocal addition to each of two inbred lines of the dominant favorable genes lacking in one inbred and present in the other; backcrossing and selection are performed in parallel, each of the original lines serving as the recurrent parent in one series. Convergence-divergence selection isa breeding scheme in which selection of promising genotypes is made in a bulk population at different locations followed by bulking of selection and allowing mating among them in a pollination field; the harvested bulk seeds constitute the basis for the next propagation cycle. This study is done in many crops especially many cereals and forage crops which not only helped in pooling the desirable trait into a single genotype but also emerging the better breeding lines.*

Key words*: Convergence, divergence, evolution, lineage, selection.*

Introduction: The process of convergent-divergent selection was first used successfully in maize (*Zea mays* L.) to improve yield when exercised over several production environments [1]. This kind of selection applied to a base population can be useful in investigating the genetic control of quantitative traits [2], the correlated response of other characters [3] and developing genotypes for physiological studies [4].

Convergent–divergent selection (Fig. 1) is a modification to ear to row method in corn. In Lonquist's experiment he collected equal amount of seeds from C_0 bulk (base) were sown at five locations or environments and promising genotypes were mass selected naturally/ artificially in different environment. Random mating in them was arranged by constructing a central pollinating field with equal part of seeds from each location. Bulk seeds were harvested from the population field represents an improved C_1 bulk which is likely to be adopted over all the five environments. The next cycle repeated using the C_1 bulk, here greater phenotypic stability can be expected and ecological tolerance can be enhanced by mass selection carried out over diverse ecological zones. This ensures high genetic variability by natural selection, thus increased population tolerance to environment. This is because of the exploitation of both stabilized and diverse selection. Here intercrossing from diverse group forms maximum heterotic population which helps to evolve heterotic population with considerable ecological tolerance [1]. This technique is a method which is an improved version over convergent and divergent breeding (crossing) schemes which has been practiced over the centuries knowingly or unknowingly in crop improvement.

Convergent Crossing: The principle of convergent improvement is necessarily concerned only with favorable factors which are completely or partly dominant, and which therefore can be recognized in the heterozygous condition. Back pollinating may be utilized of course to transfer a desired recessive factor from one selfed line of corn to another. Occasional selfing will be necessary in such cases to bring the factor into expression. The procedure of back cross breeding has given [5] for producing a smooth-awned barley, i.e., use of back crossing in small-grain breeding. It is possible that convergent improvement may result in increased yields of the crosses as well as of the parental lines. Convergent method as a tool of improving the productiveness of selfed lines of corn without interfering with their behavior in hybrid combination [6]. Convergent crossing involves conservative methods of crossing plants. The primary goal of convergent crossing is to incorporate a specific trait into an existing cultivar without losing any of the existing desirable traits [7]. Hence, one (or several) parent(s) serves as a donor of specific genes and is usually involved in the cross only once. Subsequent crosses entail crossing the desirable parent (recurrent parent) repeatedly to the F_1, in order to retrieve all the desirable traits.

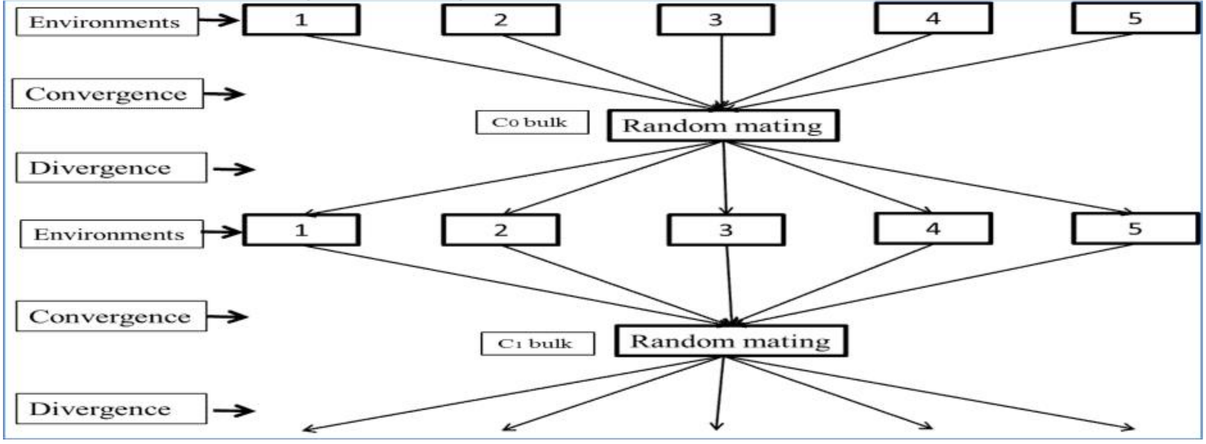

Fig.1 Convergent–Divergent Selection Scheme

Divergent Crossing: In divergent crossing genetically divergent parents are crossed for recombination of their desirable genes. To optimize the results, parents should be carefully selected to have the maximum number of positive traits and a minimum number of negative traits (i.e., elite × elite cross). This way, recombinants that possess both sets of desirable traits will occur in significant numbers in the F_2. The F_1 contains the maximum number of desirable genes from both parents. There are several ways to make divergent crosses (Fig.2a) i.e. 1) single cross [8], where two elite lines are available that together possess adequate traits, a single cross [single cross (A × B)] may leads to incorporation of desired traits, all that is needed in the breeding program. In 2) Three-way cross, [9] desirable traits occur in several cultivars or elite germplasm. In this case, three crosses may be required in order to have the opportunity of obtaining recombinants that consist of all the desirable traits. If a three-way cross [(A × B) × C] product will be the cultivar, it is important that the third parent (C) be adapted to the region of intended use. 3) In Double cross [10] two single crosses [(A × B) × (C × D)] are made. The method of successive crosses is time-consuming. Further, complex crosses such as double crosses have a low frequency of yielding recombinants in the F_2 that possess a significant number of desirable parental genes. When this method is selected, the targeted desirable traits should be small (about 10). The double-cross hybrid is more genetically broad-based than the single-cross hybrid but is more time-consuming to make. 4) Diallel cross [11] is one in which each parent is crossed with every other parent in the set (complete diallel), yielding $n - (n - 1)/2$ different combinations (where n is the number of entries). This method entails making a large number of crosses. Sometimes, a partial diallel is used in which only certain parent combinations are made. The method is tedious to apply to self-pollinated species. Generally, it is a crossing method for genetic studies.

Convergent Divergent-Evolution to Breeding: Evolution is the change in heritable traits of populations over successive generations. It gives diversity at every level of organization i.e. Species, organisms, and even molecules. This process aid the plant breeding for better selection practice. Convergent evolution is the evolution of two or more different lineages towards similar morphology due to similar adaptive pressures which is due to forced similar evolutionary pressure. In this case animals or organism's different organs are adopted to do a specific function. Eg. Wing of bird and insects looks different but functions same, for flying. In plants the aerial roots and leaf both function in air exchange between environment and plant body. whereas, divergent evolution means a kind of evolutionary change that results in increasing morphological difference between initially more similar lineages due to habituating in different environmental conditions. Divergent evolution is just opposite of convergence where a similar organ can be used for different functions. It is popularly termed as adoptive hypothesis, where the same organ present in different organisms function differently. Eg. The legs of cheetah and monkey are utilized for different functions, whereas the roots of some plants utilized to absorb nutrients, where the roots of banyan trees are utilized for establishing a new plant or to expand the tree coverage across the area. The similar principle i.e. convergent divergent selection, which is a crop improvement technique, makes combination of different species/family/genera or spreading an adoptive breeding line to a new area. This kind of breeding makes new combinations as well as brings desirable traits into a single platform and makes selection of improved lines.

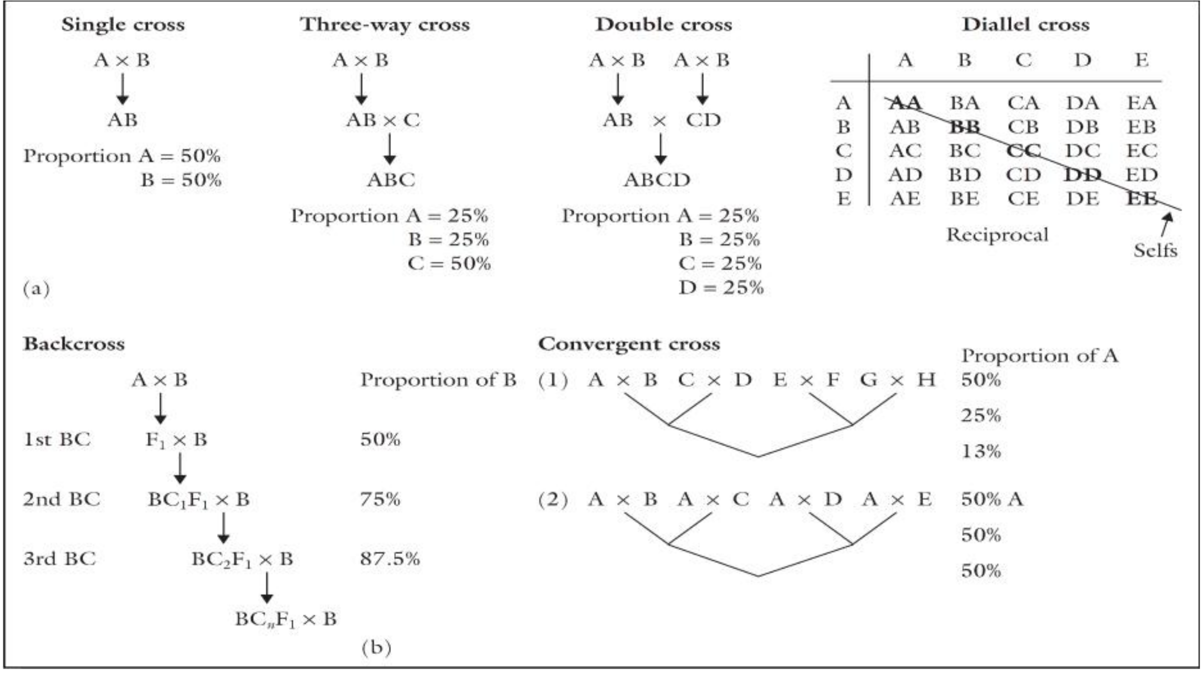

Fig.2 some convergent (b) and divergent (a) crosses in plants (George Acquaah, 2007)

Convergent-Divergent Studies through Marker Assisted Evaluation (MAS): MAS is a supplementary tool for conventional selection tool, works with the principle of linkage. The markers are located near the DNA sequence of the desired gene and are transmitted by the standard laws of inheritance from one generation to the next; there is a scope to evaluate the traits in a faster way [12]. Response to phenotypic selection can be evaluated and associated genes can be identified using molecular markers. The Illinois long-term selection experiment on maize oil and protein contents [13] and marker-assisted evaluation [14] provides such an example. The long-term divergent selection response can be attributed to the accumulative action of alleles with similar effect that had been dispersed among the individuals of the original population [15], while de novo mutations may be an alternative explanation for this divergence, as studied by selection for bristle number [16] and wing pattern in Drosophila. This selection tool offered unique opportunity to investigate the genetic basis of kernel chemical traits and have been used to produce maize populations to map the QTL responsible for the selection response [14].

Divergent selection has been done to identify the transgressive segregants in rice [17]. Transgressive segregation of tiller angle was found in two rice F_2 populations, two types of true-breeding extremes were obtained, one with broader tiller angle and the other with narrow tiller angle. Transgression of tiller angler was confirmed in the two extreme crosses [18]. For loci contributing to variation in tiller angle, the alleles of similar effect were proved to be dispersed in the original parents but pyramided in the extreme selections. By crossing two extreme strains each derived from one original cross, new transgression was found in the F_2 and then two types of extremes were obtained by the second cycle of divergent selection. By crossing the second-cycle extremes with each other and the third cycle of divergent selection for larger tiller angle, all positive alleles from the four original parents were pyramided. The transgression in each original cross can be explained by the complementary gene action, which had been dispersed between the original parents and complemented each other when they were pyramided in the extreme strains [17]. This transgression was observed due to mutation events as reported for experiments on divergent selection for bristle number in Drosophila [16].

In barley divergent selection for heading time was performed in two F_2 barley populations. Five populations were obtained from each cross: F_5 (5th filial generation), SSD (unselected control), 3E and 3L (from three cycles of selection for earliness and lateness), $2E_1L$ and $2L_1E$ (from two cycles of direct and oneof reverse selection). These populations, together with corresponding parents and F_1 generations, were evaluated over two years. The response to selection was 5.6 and 6.5 days in onedirection (earlier heading) and 7.7 and 6.7 days in the other direction (later heading) in the two crosses, respectively. 3E and 3L populations were highly transgressive as compared to their parents. It shows sizeable amount of genetic variability was still observed after two cycles of selection. Heading was probably controlled by a polygenic system with prevailing additive effects and alleles for earliness and lateness somewhat equally distributed in the parents. There were significant changes in plant height, yield, kernel weight by selecting for heading time. The early progenies were higher yielding than late ones [19].

Convergent Selection: In cereals the independent domestication of sorghum, rice and maize evolved convergent selection for large seeds, reduced domestication of the mature inflorescence and day length- insensitivity flowering. These similar phenotypes are largely determined by a small number of QTLs that correspond closely in three texa. The correspondence of these QTLs transcends 65 million of reproductive isolation. This finding supports models of quantitative inheritance that invoke relatively few genes, obviates difficulties in map based cloning of QTLs and impels the comparative mapping of complex phenotypes across large evolutionary distances, such as those that separate humans from domesticated mammals [20] and even in plants the minor differences within the species or among the species.

Convergent–Divergent Selection: Proposal is based on stratified mass selection in different sites within a same population previously synthesized from germplasm sources adapted to the wide area [1]. In the modifiedconvergent–divergent selection [21], the wide base and adapted population already exists and then selection based on progeny test within each site of the whole area should be more effective than phenotypic selection for its improvement and adaptive adjustments.

With a similar principle a heterogenous cucumber (*Cucumis sativa* L.) population (mostly *gynoecious*) was evaluated at five locations for single plant fruit yield at the mature fruit stage in 1981. Seeds from the highest-yielding plants were then harvested, combined and partitioned into five lots. Seeds were combined such that each location received only the superior genotypes from the other four locations. This procedure was continued for an additional four cycles using two types of selection: single plant selection for the fruit number at the mature- fruit stage (1981-82) and half sib family selection at the once over harvest stage (1983-84). In 1985, Yield improvement from selection was measured by compositing the seeds of the selected plants or families from each of the four cycles and five locations and planting them at the five locations. No progress was made for total, marketable or early yield. Percentage of culls was reduced an average of 0.7% per cycle.The yield progress might have retarded due to G X E interactions among diverse locations [22].

Worked with local maize cultivars in Brazil [23]. The genetic variability of the total carotenoid content (TCC) of kernels in a local maize population was evaluated for their economic exploitation potential as biofortified food. Two independent samples of 96 half-sib families (HSF) plus four checks were evaluated in two groups of experiments and each one was carried out in two environments. They were set out in a 10 × 10 partially balanced lattice with three replications per location; plots consisted of one row, 5.0 m long with 1.0 m between rows. TCC ranged from 11 to 23 $\mu g\ g^{-1}$, averaging ≈16 $\mu g\ g^{-1}$ in the pooled analysis over the two sets. The local composite population exhibited genetic variability in order to increase the TCC of grains in the second cycle of selection by the convergent-divergent scheme. In southern Brazil, selection in corn inbreds has done to estimate genetic statistic parameters associated with half sib selection. Here selection was directed for only two traits *viz*., grain yield, plant height and variability has present to assure substantial gain through selection [21].

Simultaneous improvement of forage traits and seed yield in orchard grass (*Dactylis glomerata* L.) has been problematic because of geographic separation of forage and seed production locations. Most attempts to simultaneously improve both forage and seed traits have relied on a single location. The objective of this study was to conduct and evaluate two cycles of convergent-divergent (C/D) and local selection for panicle seed weight (PSW) and forage traits. Phenotypic selection on a spaced-plant basis was applied at 0.25 selection intensity for forage traits, followed by 0.25 selection intensity for PSW. Both selection methods were equally effective at increasing PSW. The Realized heritabilities for PSW were highly variable among the four populations Three of the four populations had significant genetic changes of 2 to 4 days after heading, despite no direct selection pressure for heading date. There were very few significant and biologically meaningful genotype × location interactions for any trait. Therefore, selection method resulted in plants with differential adaptation when evaluated as spaced plants [24].

CIP[25] collected seeds from various regions or sources to form a base population. Seeds were planted and superior clones were selected and intercrossed. Small packages of seeds of F_1 population were returned to each site where selection continues. Clones selected at each site were intercrossed, and seeds from those populations were sent again to the coordinating site. During selection cycle and intercrossing, each region can add newly acquired elite germplasm for introgression of specific genes. Sweet potato seed families introduced from many countries as part of the modified convergent- divergent breeding scheme were first planted at Bagor for evaluation. Clones were selected for high dry matter content and reasonably high yield. Most clones had light colored flesh varying from white to yellow. They maintained about 100 clones continuously as a clonal pool to provide good material for the further selection at different sites. As new clones are selected from seedling evaluation, observational evaluation and preliminary evaluation, poorer performing clones were replaced with better ones to ensure that the clonal pool always contains the best possible clones. Some of the clones in the clonal pool were used to make crosses. Seeds provided to collaborating breeding programs as improved material. Some clones from clonal pool were made ready to distribute after meristem culture and pathogen testing.

Future Strategies: Convergent–divergent methods are the quite older techniques of crop improvement, but now along with the traditional breeding there is good scope to implicate molecular breeding approaches (like MAS, Microarray technique) in order to improve the crop's physiological, genetical and biochemical traits. The target area of research should be focused on allele mining for different traits which could be evolved from a large germplasm pool irrespective of cereal, pulse, medicinal plants or any other crops which fetch commercial value. This could be a substitute for transgenic approach to transfer the trait of interest even from other plants with the help of bridging species or genera.

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