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PLANT BREEDING – BY DESIGN OR DEFAULT ?

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Over the millenium, Plant Breeding has been the lifeline for meeting the food needs of people across the world. From the days of Mendel who postulated basic laws of inheritance to the present, illustrious developments have been made in the science of plant breeding. Newer concepts evolved through continuous upgradation and modification of older ones strengthened theoretical basis and paved the way for innovative applications in practice. Population concepts came to replace single plant selection in breeding for productivity. Yield components were given due weight instead of yield alone in breeding methods. A commonality was discovered in the principles and concepts of breeding self- and cross-pollinated crops. Concepts of heterosis and hybrid breeding were more effectively applied even in self-pollinated crops like rice, for example. Synthetic and composite populations came to be bred and released for commercial cultivation in cross-pollinated crops like maize and pearl millet. Breeding for productivity targets improvement of not only yield *per se* but a number of other traits like resistance to pests and diseases, and physiological stresses in addition to those related to nutritional and seed quality. In essence, a synergistic interfacing of plant breeding with allied disciplines like plant pathology, biochemistry, agronomy, plant physiology and soil science has opened up new avenues of plant improvement.

However, such new avenues have not been greatly used by practical plant breeding. Breeders do work with limited variability and breed for varieties with high-er yield. In a way, they tend to exploit the genetic variability in early generation populations and which resulted from early cycles of selection (Cooper *et al.*, 1998). These capacities serve as major disincentives to broadening the genetic base of developed varieties and to the introgression of genes governing desired traits from germplasm or landraces.

In general, breeders attempt only established breeding procedures, mostly pedigree methods, and search for productive segregants in the generated variability. In the event of the search becoming successful, a new variety for evaluation across growing sites becomes available. If not, the process is initiated from a new cross. Techniques developing such varieties are, at the most,

tentative and rarely have a targeted edge. An attempt is made in this paper to outline an avenue of plant breeding directed by theoretical developments in the genetic basis of breeding.

The simplest equation, widely known, connecting phenotype (P) with genotype (G) is

$$P = G + E \text{ where } E \text{ is the environmental value.}$$

Being of first order, this equation connects respective mean values. The peculiarity of this equation is that both the variables, G and E are unknown and only P can be measured. Estimates of G and E values cannot therefore be obtained. It was R.A. Fisher who gave an alternative to use this relationship between P and G. Under the constraint that G and E are independent, he used the 2nd order equation, $6_P^2 = 6_G^2 + 6_E^2$ where $6_{(.)}^2$ represent variances. When the material is grown in a field design, an ANOVA (analysis of variance) would provide an estimate of 6_E^2 so that 6_G^2 can be obtained from the equation. However, it is now known, this simple model is not valid and the contribution of the genotype-environment interaction is quite substantial to modify the basic equation as $P = G + E + (G \times E)$. This complex equation does not admit of simple solutions unless, again, highly simplifying assumptions are made. In general, therefore, such a simplified model can be applied in practice only with a low confidence.

It is a tough task to define an individual genotype precisely. Even if we restrict ourselves to characterisation of an individual only by QTs, there would be a multitude of them. Each QT is known to be governed, in general, by a large number of genes. Individual effects of such genes are relatively small but the interaction effects are quite high. In other words, epistasis has a major role to play in the expression of QTs. Recent developments of the subject have clearly shown that environment too has a specific role in the expression of QTs. For example, plant genotypes that are native to a tribal area and grown continuously by tribal farmers adopting their traditional practices in a usually fragile environment express extremely valuable site-specific characteristics. For instance, tolerance to erratic rainfall, high temperature, resistance (including near immunity) to biotic stresses, nutritional quality, and medicinal properties are a few of the many such documented traits. Their expression is highly tuned to environment – both ecological and cultural, the practices under which they are grown continuously in an environment (Worde and Mekbib, 1993). In a

way, therefore, even the modified model incorporating G x E interaction cannot fit optimally some practical situations. Nevertheless, the fundamental model serves the valuable purpose of generating basic hypotheses, concepts and definitions of various parameters. It is indispensable and has been a catalyst in developing complex models to define practical situations commonly encountered in plant breeding.

Yet this model was the first to provide a meaningful link between P and G, in broad terms. But the question remains how best one can define an individual genotype, particularly when a large number of QTs, including qualitative, biochemical and molecular descriptors among a host of such others, describe one aspect or the other of the genotype. Further, each trait is almost invariably governed by many genes each with multiple alleles. It may not also be possible *apriori* to easily guestimate the number of genes. In addition, individual gene effects on a trait cannot be measured but can be hypothesized at the most. Likewise environmental effects (means) cannot be measured, though statistical designs and analysis can estimate variances and effects on a set of assumptions. These imbedded implications, not easily perceived or accounted for, bring to focus the complexities involved in defining an individual.

Most often, individuals are differentiated by the phenotypic values of single traits, though complex. Seed, fodder or oil yield, resistance to a single disease or a more proliferous pest, and nutritional quality traits like protein content are a few examples of such a characterisation. In addition, it is being increasingly realised that an individual is defined better by simple components than by a complex trait *per se*. For example, yield components are reinforcing indicators of yield than the single trait, yield. This would suggest, as is now known, that characterisation of individuals would be more efficient on multiple traits than on a single trait. Such traits would preferably be QTs or be transformable as QTs for enabling a quantitative analysis and evaluation. An associated problem, however, is the choice of an optimal set of multi-traits out of a large number available. As continuous variables, QTs are supposed to be governed by an underlying Normal distribution and it serves as a base for statistical inferences and practical decision making.

The subject of genetic characterisation was dealt with in an instructive way by Langham (1961). He classified individuals into two broad groups – High (H) and Low (L), though the logic stands the possibilities of classification into

as many groups as desired. H, Medium (M) and L are three groups. The M group can further be partitioned into M1 and M2 to provide four groups. For demonstrating the utility of this principle, however, we would consider only two groups, H and L as considered by Langham. According to him, High genotypes possess genes capable of expressing high phenotypic effects but are prevented from doing so by the 'retarding' effect of residual genetic background (RGB) (Fig.1). Low genotypes possess similarly low genes capable of expressing extremely low phenotypic effects but are again prevented from doing so by the 'enhancing' effect of RGB.
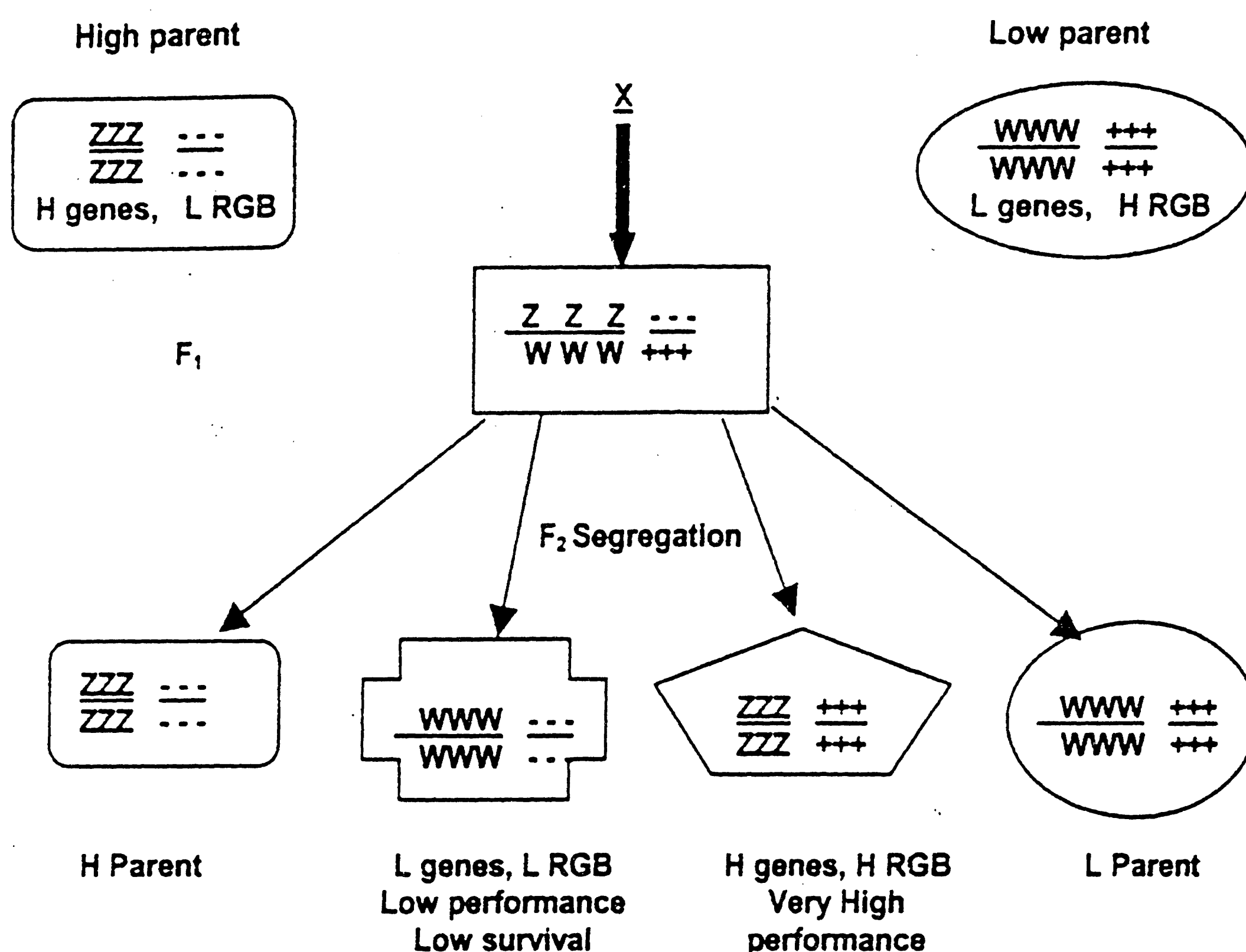

Fig. 1. Genetic Basis of Improvement through High X Low crosses

Further, High genes express extremely high phenotypes when they, as well as the RGB, are homozygous and nearly equal phenotypes result when they and the RGB are heterozygous. But Low genes can express their potential only in a 'retarding' homozygous RGB. H x H and L x L crosses result in situations resembling essentially their parents and hence in a low frequency of heterotic crosses, if at all. But H x L crosses produce heterozygous progeny genotypes in heterozygous RGB. Their phenotypes express high effects and can be better than their superior parent for some traits. More potential transgressive

segregants homozygous for High genes expressed in homozygous and enhancing RGB can be selected in the segregating F_2 and higher generations.

High – Low method of characterisation provides one way of identifying genetically divergent parents. The underlying logic is deductive. The efficiency of identification should hypothetically improve when characters providing independent identity information are included. Methods are now available to aggregate information provided by a set of dependent characters (Arunachalam and Bandyopadhyay, 1984; Arunachalam, 1993). Based on general combining ability effects, parents were classified as H and L and used further in hybridisation and breeding programmes (Arunachalam and Bandyopadhyay, 1979; Bandyopadhyay and Arunachalam, 1980). Such characterisation can also be done on trait means and various other criteria; but a strong logic, need and application potential for such characterisation are to be in place *apriori*.

In the process of multi-trait characterisation, equal weight is given to every component character used in characterising an entry as High or Low. In the absence of a logical and repeatable method of assessing the weights to be attached to the component characters, the characterisation cannot undoubtedly be improved by the use of weights. Since the methods of characterisation are flexible enough to admit of more component characters, the problem of weighing can partially be overcome if we use a large number of component characters spanning the entire growth phase, from seedling to maturity of the plant. This, in a way, is also an attempt to take into account the phenotypic expression of a large sample of genes that define the genotype.

Vast literature supports the results on the utility of High x Low crosses in practical plant breeding. High x Low multiple-top crosses were found useful in corn improvement as far back as 1939 (Mangelsdorf, 1939). Dwarf x Tall crosses were frequently successful in rice, wheat, triticale, sorghum and in plantation crops like coconut (Bavappa and Sukumaran, 1976). Exotic x Indian and Temperate x Tropical crosses were the base for the development of pure lines and hybrids of sorghum in India (Rao and Rana, 1978). Winter x Spring combinations are commonly tried in wheat to transgress current yield levels. Even by subjecting winter varieties to summer adaptation and *vice-versa*, it was possible to step up the yields of soybean (Tsai, Lu and Oka, 1967). High x Low combinations were found to rank first in yield potential in barley (Fejer and Jui, 1979). Our work and those reported in literature thus points to the need for

incorporating genetical, geographical and combining ability divergence in the choice of fruitful parents for hybridisation.

A number of examples are now available in published literature where High x Low crosses have provided a high frequency and magnitude of F_1 heterosis. (Table 1). The early segregating F_2 generation has also provided a high frequency of desirable recombinants amenable for further breeding.

Table 1. Efficiency@ of High x Low crosses in producing F_1 heterosis

Crop	System	Group		
		H x H	H x L	L x L
Brassica campestris	[1]Single crosses	29	57	14
	[1]3-way crosses	33	58	9
	[2]Multiple cross-multiple pollen hybrids	26	52	22
Pennisetum americanum	[3]Single crosses	35	47	18
	[4]Triallel crosses	26	57	17
	Flowering time	23	51	26
	Grain yield	34	43	23
	100 – seed weight	20	50	30
	Ear length	35	43	22
Triticale	[5]Single crosses	53	37	10
	100 – seed weight	30	56	14
	Number of tillers	31	69	0

@ measured as the percentage (p) of heterotic crosses falling in various groups out of the total number of heterotic crosses; Figures in the table are the p values.

Source : 1. Katiya,R.K. and Arunachalam,V. (1981); 2. Bandyopadhyay, A. and Arunachalam, V. (1980); 3. Reddy, B.B. and Arunachalam, V. (1981); 4. Arunachalam, V. and Reddy, B.B. (1979); 5. Srivastava, P.S.L. and Arunachalam, V. (1977)

Experimental evidence in groundnut further suggests that F_3 populations descending from heterotic F_1s provide a higher frequency of desirable selections compared to those from non-heterotic F_1s (Table 2). This
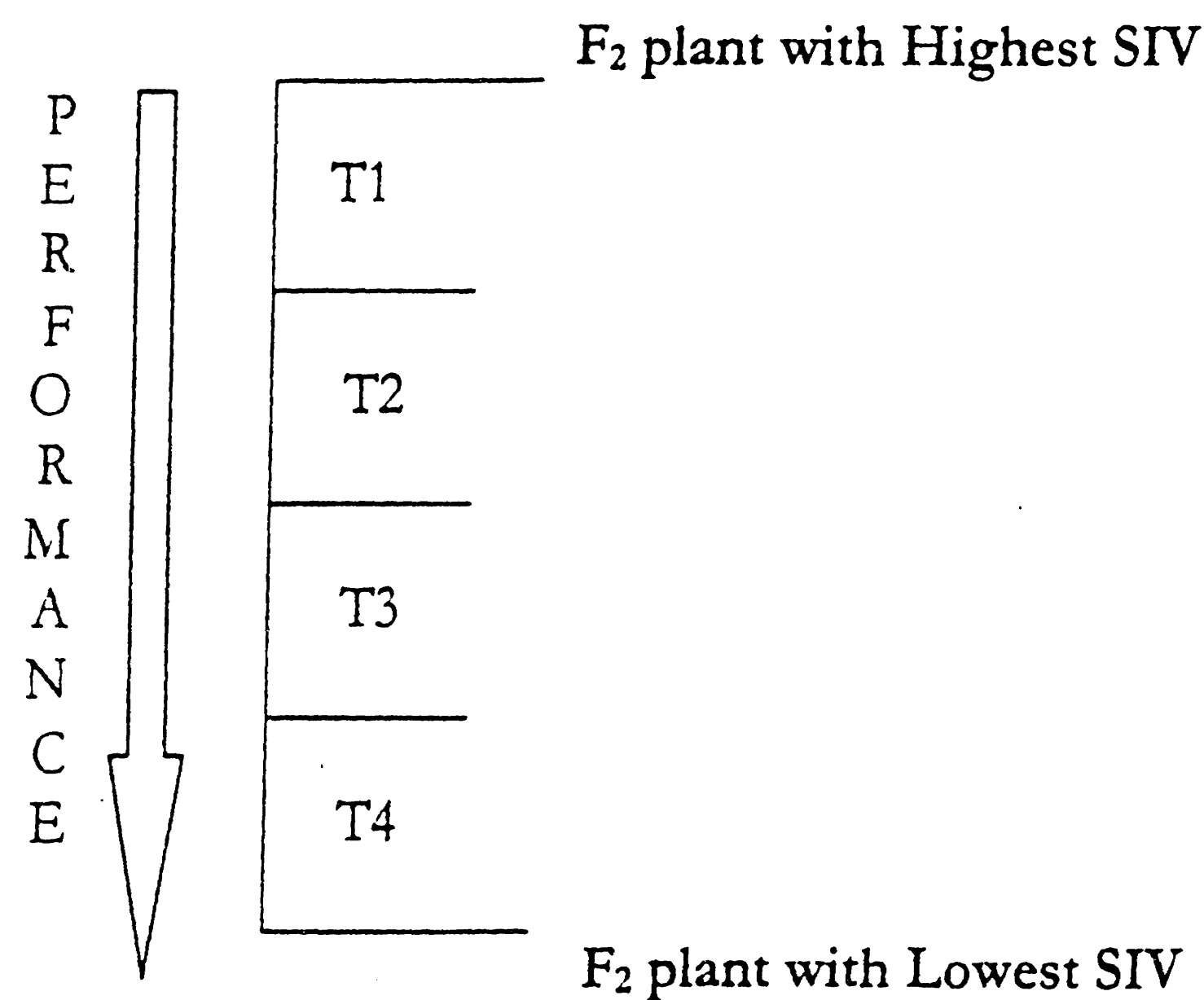
result would re-emphasise the need to target for increased frequency of heterotic F_1s in plant breeding.

Table 2. F_2, F_3 Performance in relation to F_1 heterosis in 3-way crosses in groundnut

		h+	h-	t
No. of crosses giving selection in F_3		20	32	52
	f	17	22	39
	p	85	69	75
Crosses showing high range of selection in F_3	f	14	19	33
	p	70	59	63
Crosses that had more than 50% of F_2 plants in top half of F_2 ranked distribution and gave selections in F_3	f	10	10	20
	p	59	45	51

h+ = heterotic; h- = non-heterotic; t = total; f = frequency; p = percentage

As earlier indicated, selecting the best diagnostic set of characters out of a large number is a complex problem. But such a diagnostic set is expected to define an individual (genotype) with high efficiency. One method that was tried in many experiments and found to be effective in identifying the diagnostic set is the stepwise multiple regression analysis (see, for example, Prabhu, Arunachalam and Bandyopadhyay, 1990; Arunachalam, Koteswara Rao and Bandyopadhyay, 1992). Selection indices can be very efficient when constructed on the set of diagnostic traits. F_2 plants can be assayed for those traits and a selection index value (SIV) can be computed for each F_2 plant. Based on SIVs, F_2 plants can be arranged in descending order of performance to provide an F_2 ranked distribution (FRD). FRD can be dissected into four equal segments, T_1, T_2, T_3 and T_4; T_1, T_2 constituting the top 50 per cent of FRD (Fig. 2; also Table 3). Experimental evidence has clearly shown that a high frequency of productive segregants are located in T_1 and T_2, and a breeder need not look beyond them, in general (Koteswara Rao, 1984; Prabhu, 1986).

```
                                    _____ F₂ plant with Highest SIV
    P    ┌─┐     ┌────────
    E    │ │     │  T1
    R    │ │     │
         │ │     ├────────
    F    │ │     │
    O    │ │     │  T2
    R    │ │     │
    M    │ │     ├────────
    A    │ │     │  T3
    N    │ │     │
    C    │ │     ├────────
    E    │ │     │  T4
         └┐│     │
          ▼      └────────
          V               F₂ plant with Lowest SIV
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Each segment T_1, T_2, T_3, T_4 represent 25% of F_2 plants in descending order of performance measured by SIVs; T1 = top and T4 = bottom stratum

Fig. 2. F_2 ranked distribution on the basis of SIVs

Table 3. Striking differences between simple and multivariate (D^2) distance

	Simple distance	Multivariate distance
Genotype defined on	Single traits one at a time	Many traits simultaneously
Information on traits	i. Empirical scoring on single trait distance differences (+1, 0 or −1) ii. Added over each trait	Is a single multivariate measure
Trait dependence	Ignored	Given specific emphasis
Gene interaction	Irrelevant	Taken into account
Environmental contribution	Zero weightage	Phenotypic expression is the base
QTs as continuous variates with small major and large interaction effects	Not recognised	Given due weightage

High-Low method is one of the simple methods to separate divergent genotypes. This would efficiently work in the case of a small number, say about 10, of potential varieties available with the breeder using which further

improvement is sought. However, in many instances, plant breeders would like to classify a bigger sample of varieties (of the order of 50, for example) and arrange them in groups based on inter-varietal genetic divergence. In this context therefore, measurement of genetic divergence (GD) and choice of parents on GD to obtain heterosis have, however, been vital to plant breeding. Of the number of measures of genetic divergence proposed, Nei's distance statistic and Mahalanobis' D^2 statistic stand apart. The former was most popular earlier in human genetics applications and now in molecular techniques-driven plant breeding. The latter was widely applied in breeding for productivity in tropical and temperate crops and remains as a powerful tool in genetic classification and parental choice. A comparative evaluation of these two statistics (Table 3) focus the limitations of the former and the dendrograms used in genetic classification highlight its infirmities. Consequently, the multivariate analysis method continues to be the preferred choice, at least for plant breeding applications.

Having measured inter-varietal divergence by multivariate D^2, it is usual to group the varieties by Tocher's method and depict the groups in a two-dimensional diagram, following Rao (1952). A degree of arbitrariness in the grouping method is inherent in the choice of an allowable intra-group distance (w). Breeders, in applying this process, can theoretically obtain differing group constitution when they choose different w values. This problem was considered in depth and a non-parametric method of obtaining four divergent classes (DC) uniquely using the mean and standard deviation of the inter-varietal D^2s was devised. It was further shown that the frequency and magnitude of F_1 heterosis would remain high when parents are chosen from intermediate divergence classes, DC3 and DC2 (Arunachalam and Bandyopadhyay, 1984; Arunachalam, Prabhu and Sujata, 1998). The logic of forming divergence classes can be extended to obtain more than 4 divergence classes, if a particular situation requires.

The paradigm of four divergent classes has distinct advantages:

- Classification bias due to self-set norms is eliminated.

- Uniform number of classes enables fair comparison and contrasts across experiments, environments and crops.

- The efficiency of the methodology can be evaluated on uniform grouping based on uniform standard.

The flexibility to increase the number of groups beyond four provides an added advantage.

Based on the alignment of D^2s into various divergence classes, a method was devised to provide an alignment index for each variety (Durga Prasad, Arunachalam and Bandyopadhyay, 1985). With these methods of analysis, the concepts of optimal parental divergence for realising heterosis and the relative importance of the groups were integrated to obtain a genetic potential score for each variety on the set of traits used. Such potential scores can be computed for a set of base diagnostic traits which is agreed to be adequate for genetic characterisation; likewise it can be computed for a set of test traits. Comparison of base and test genetic potential scores would provide an efficiency index of test traits in arriving at as close a grouping as that obtained on base traits. The potential of these methods and concepts has been test verified in breeding for improvement of *brassicas*. They have also been efficiently used in evaluating the potential of isozyme markers in intra- and inter-specific genetic differentiation in *brassicas*. The methodology, and results of application value in breeding for improvement are given in elaborate detail in Arunachalam, Prabhu and Sujata (1998).

In recent times, with the advent of molecular biology into plant breeding, it is projected that classical plant breeding based on phenotypes would give way to modern plant breeding based on (molecular) genotypes. A variety of molecular markers is now available so that every trait can be associated with a number of markers. The subject is naive and we do not attempt to discuss it in depth here. However, a few salient facts about molecular markers (MM) are presented to focus attention on the unfocused.

- MM can, at the most, mark single genes and that too codominant ones only. QTs which are controlled by many genes cannot therefore be tracked by MM.

- Because MMs mark single genes only, epistasis is irrelevant in MMs. Instead it is projected that MMs are not affected by epistasis. In particular, QTs almost always exhibit epistatic gene action.

- It is now known that there is a high contribution of environment to the phenotypic expression. This fact is a prime focus in the modern participatory plant breeding programmes. The emphasis therefore is to work in specific sites for varietal improvement instead of

testing modern varieties bred elsewhere at the sites. MMs cannot identify environmental contribution.

- MMs do not have an expression. Hence attempts establishing an association between MMs and QTs (phenotypic effects) remain incredible.

- Finally it is the phenotype that is selected for and sustained as a crop variety. Genotypic performance alone does not predict G x E interaction and therefore phenotypic performance. The importance of gene or genotypic assay using MMs is over-expressed concealing the potential of classical, time-tested methodologies.

But biochemical markers like isozymes change with environment and therefore there is a possibility to find association with QTs. Pioneer attempts at quantifying isozyme variation as QTs have shown quite encouraging results in genetic characterisation. They can efficiently be used for a first stage selection which would effectively save field evaluation of a large population. Studies on such lines with *brassica* have shown promise and are discussed with concepts, methods and inferences (Arunachalam, Prabhu and Sujata, 1998; Bharti, 1998; Aruna Kumari, 1998).

A close and critical look at the recent developments in marker-assisted breeding brings to light several areas needing incisive analysis, clear thinking and synergy with classical methods. It is quite essential to demarcate the plane of synergy and beneficial interaction. It is time to recognise that genotypic improvement (if one agrees that molecular genotypes are adequate enough) alone need not ensure phenotypic improvement unless improved genotypes are adapted to the existing environment and express their best. No longer will it always be relevant to breed improved varieties (genotypes) and fit them to receptive environments. In fact the 'green' genes available at an ecological niche like a tribal area would be a unique source which acquires special strength due to the favourable environment at the niche. While new genes from a gene bank can be introgressed into them, their integration with the environment to express a desirably good performance would remain an open question. In crops undergoing continuous improvement, the genetic gap between elite gene pools and unimproved germplasm collections is growing wider with each breeding cycle (Holley and Goodman, 1988; Martin *et al.*, 1991). Recent literature supports the idea that the effects of an allele change in relation to others

depending on the genetic background and wholly new or enhanced phenotypes result (Rasmusson and Phillips, 1997). It has been recognised that the interactions between quantitative trait loci (QTL) are frequent and control large effects (Lark et al., 1995). Many phenotypes are apparently conditioned by compound loci with several highly homologous genes in tandem or near-tandem array. Displaced pairing between members of such a gene family followed by crossing over can generate increased and/or decreased genomic complexity, which may influence the phenotype. In this backdrop it is logical to grant that epistasis is more important than commonly viewed in extending the phenotypic range for traits of interest (Rasmusson and Phillips, 1997). There is thus a specific need to integrate the information on genotypes gathered through "marker genotyping" with the phenotypic performance and evaluate the effects of environmental specificity on the phenotypes. Both theoretical research and practical assessment are essential to understand more on this area. But efforts in that direction would definitely add valuable clues for site-specific plant improvement.

Overall it is obvious that the current concepts of plant breeding stand on a wider logical base and have the capacity to absorb modern developments in allied disciplines like genetics and molecular biology. The broad realm of plant breeding that is now open discourages routine techniques which may bring breeding gains by chance. However, the alternative available to a breeder to bring in overall improvement is too numerous to be elaborated. Yet a few breeding steps indicated in this paper envisage realising expected improvement. To sum up, an efficient breeder would adopt concept-driven (CODE) instead of concept-independent (COIN) methods of breeding. In the former (CODE), the material genotypes are evaluated for their genetic divergence, divergence groups formed, parents chosen from intermediate divergence classes, heterotic F_1s selected, large F_2 population evaluated on a selection index based on the set of diagnostic traits and the top best (25%) or the top two (50%) strata of the FRD forwarded to identify high performers in F_3. A regular pedigree breeding program would further develop new varieties with high performance. Such sequential steps are not mandatory for the latter (COIN). The level of improvement attainable with CODE is far higher than that attainable with COIN (Figure 3).
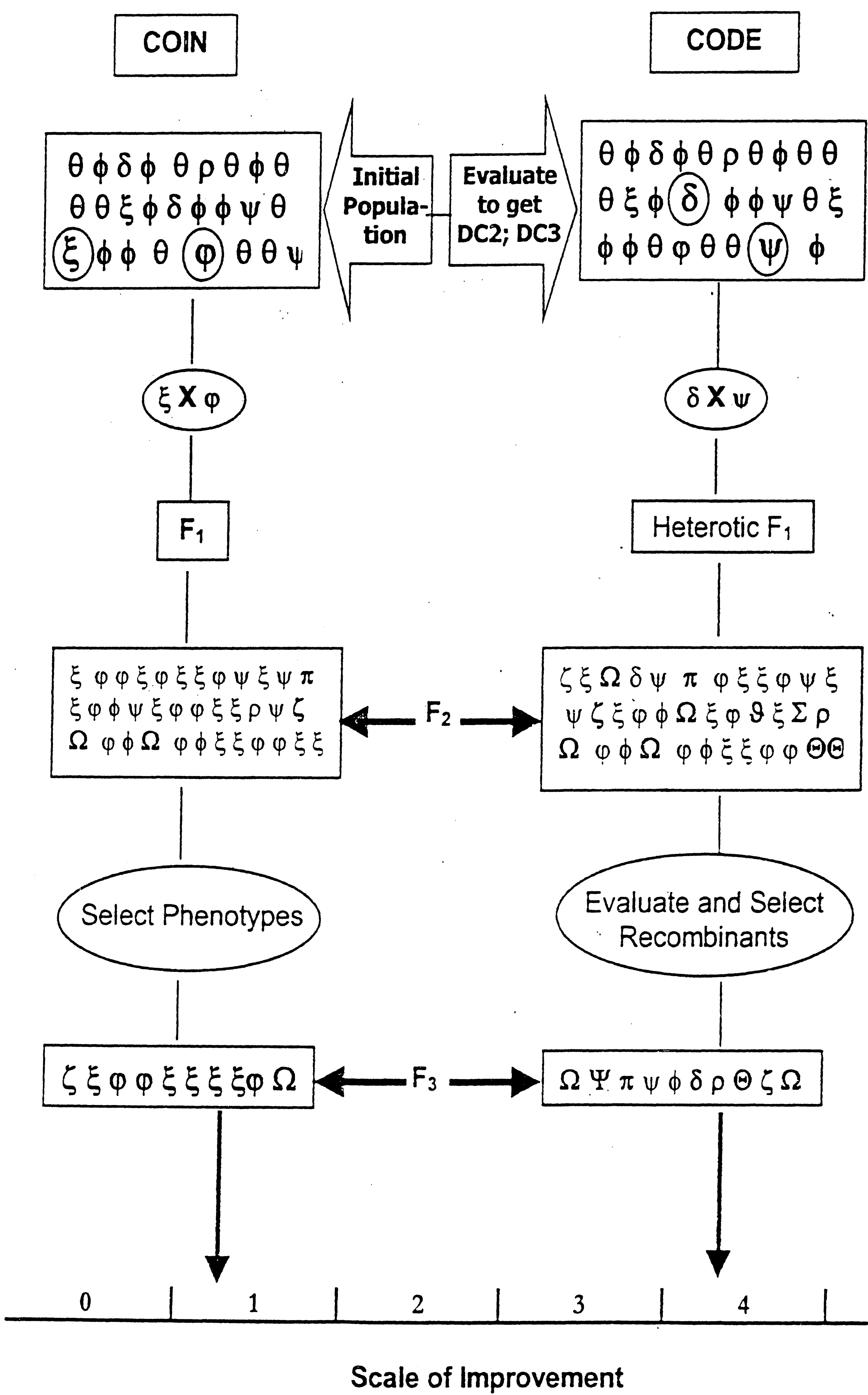
Figure 3. Concept-Independent (COIN) and Concept-Driven (CODE)
Plant Breeding

The problem therefore lies not in developing new ideas but in escaping from the old ones. In a nutshell, this is the crux of plant breeding by design in contrast to plant breeding by default.

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