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ON THE CONCEPT OF POPULATIONS

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A mendelian population (or population, for short) is defined as a "reproductive community of sexual and cross-fertilising individuals that share a common gene pool" (6). This implies that members of a population should share a common ancestry, however remote it may be. In this paper, we confine our attention to plant populations.

Two important requirements are basic to populations. One is the inherent capability of admitting high cross-pollination to ensure complete random mating. The other relates to commercial seed production fulfilling seed certification standards.

While populations are usually advocated in cross-pollinated crops, they are also relevant to often cross-pollinated systems and crops endowed with useful genetic mechanisms like self-incompatibility and genetic male sterility. Despite the known fact that populations can rarely compete with hybrids in producing attractive yields, they are preferred for several reasons.

- (a) Populations possess better buffering capacity against biotic and abiotic stresses by virtue of their genetic heterogeneity.
- (b) When a population shows yield decline over time, it can easily be replaced.
- (c) When populations of various crops and varied genetic structure permeate into the crop growing regions over time, an automatic genetic barrier is constructed checking the quick spread of virulent races of pathogen. Such an in-built mechanism is absent in hybrids even when they occupy sizeable area.
- (d) Compared to the high cost of hybrid seed production, seeds of populations can be produced at a low cost. With proper information extension, farmers can be encouraged to save seeds for the next sowing.

The concept of populations has been viewed and projected from various angles. Most often discussion has centred on one type of populations, namely synthetics (1, 10). Allard (1) has observed that a "synthetic variety has come to be used to designate a variety that is maintained from open-pollinated seed following its synthesis by hybridisation in all combinations among a number of selected genotypes.

The genotypes that are hybridised to produce a synthetic variety can be inbred lines, clones, mass-selected populations, or various other materials." He also noted the deficiencies of this definition. Singh (10) has pointed out that the Syn 1 generation derived from Syn 0, is designated as the synthetic variety in some crops like sugarbeet. He has further observed that the next generation Syn 2 obtained by open-pollination of Syn 1 would show depression in its performance due to decrease in heterozygosity by random mating, a statement that is difficult to defend scientifically, as would be seen later. Simmonds (9) on the other hand, is of the opinion that "the term 'synthetic' applies to experimental (rather than commercial) populations compounded from inbred lines randomly mated; they may be transient (when the nomenclature Syn 1, Syn 2, Syn 3 etc., is usual) or long-continued, when they become, in effect, specialised open pollinated populations." The properties of a population are better described by this definition than the earlier ones.

In order to understand and appreciate the concept of populations, it is first essential to know the theoretical basis of constructing populations and sustaining them over time. For simplicity we consider a population governed by a single diallelic gene, K and the dynamics of changes that occur due to natural selection. The results will then be extended to situations relevant to plant populations that concern us. Let the three possible genotypes KK, Kk and kk occur under complete random mating with frequencies conforming to Hardy-Weinberg equilibrium; if not, as we know, one generation of random mating will restore Hardy-Weinberg frequencies. Under natural selection let the three genotypes have fitnesses given below :

Genotype	KK	Kk	kk
Frequency	p^2	$2pq$	q^2
Fitness	$1-s_1$	1	$1-s_2$

where p = frequency of gene K, $q = 1-p$

s_1 and s_2 are coefficients of selection and in this situation, there is heterozygote superiority as is still true in many practical situations. This selection model has been discussed in many text books (7, 8). If the size of the population is sufficiently large and there is complete random mating, the population will settle down to a stable equilibrium after a few generations (depending on the coefficient of selection). At this

equilibrium, the gene frequency of K will be $p_e = \frac{s_2}{s_1 + s_2}$ and all the three genotypes

KK, Kk and kk will exist with frequencies p_e^2 , $2p_e q_e$, q_e^2 . Unless some other forces like small population size, non-random mating or selective elimination, are imposed on this population, it will remain stable with all the possible genotypes present. This equilibrium population is a balanced polymorphism.

The mean fitness at this equilibrium is given by $W = 1 - \frac{s_1 s_2}{s_1 + s_2}$ and it is lower than the fitness (= 1) of the fittest heterozygote. The quantity, $\frac{s_1 s_2}{s_1 + s_2}$ by which the mean fitness is depressed at this polymorphic equilibrium is designated as a genetic load (to be more precise, segregational load) to the population. If any force (enumerated earlier) drifts the population away from equilibrium, the population, in due course of time will end up in either of the terminal states or simple equilibria, $p_e = 0$, or $q_e = 0$. When $p_e = 0$, the population will consist only of recessive homozygotes, kk and when $q_e = 0$, it will entirely consist of dominant homozygotes, KK .

We illustrate that the above theoretical basis holds good for populations, in particular, synthetic and composite populations. Populations consist of homo- and heterozygotes in equilibrium. In the case where homozygotes only are superior in yield, pure lines would yield better than populations. Alternately when pure heterozygotes are superior in yield, hybrids would perform better than populations. In situations other than these two, populations can be relevant. The cardinal feature of a population is its homeostatic properties, namely, its capacity to resist sudden environmental changes including biotic and abiotic stresses. This capacity is conferred on a population by heterozygotes which have superior buffering ability. In general, therefore, a population is known to have lesser yielding ability than a hybrid but is preferred when yield stability in the presence of stresses (like disease, pests, water stress and erratic monsoon) is one of the major concerns.

It must be emphasized that genotypes in a population should occur in right frequencies if the population is to be stable. We know natural selection forces are universally present, however weak they may be. Superimposed over this, if the size of the population maintained over generations is not kept adequately large, some genotypes, especially lesser fit and/or recessive, run the risk of elimination which will be equivalent to artificial selection. Alternately, if there is absence of complete random mating (that may be due to pollination system, bee activity, non-uniform pollen dispersal due to wind direction, rain etc.), it will also result in genotypic selection. They would most likely disturb the equilibrium frequencies and the population would end up in genetic homogeneity (KK or kk genotypes) as explained earlier. However, one consoling feature, is that it would take a few generations for a population to reach this final homozygous state. Sufficient time would then be available for a breeder notice the consequent changes in yield level (mostly decline) in the population. That is the right time for a breeder either to replace the population or to resynthesise it.

One question of relevance is how many generations of random mating would

be needed before one can derive a population from the initial gene pool? There can be no specific answer to this important question; but from the definition of population given earlier, it is undoubtedly clear, Syn 0 or Syn 1 generations in which the progeny do not even completely attain the status of having a common ancestry, cannot be called populations. In cases where fodder is the economic product and the crop vegetatively propagated, Syn 1 can attain the status of a population, provided there is acceptable level of phenotypic uniformity needed for agronomic and cultural operations. Especially when the initial gene pool consists of genotypes with contrasting attributes, a few generations of intermating (random mating within a generation) in isolation would be needed to obtain phenotypic homogeneity retaining at the same time genetic heterogeneity. Further, random mating is a unique mating system to generate and retain heterozygosity; it can never reduce heterozygosity as has been reasoned by Singh (10). A gene pool attains the state of being called a population as soon as phenotypic homogeneity is attained. The number of generations of random mating needed for achieving phenotypic homogeneity will vary from crop to crop; usually it is estimated to be around four to six in many crops. The breeding process to generate populations is dealt in detail elsewhere (2, 4, 5). However it will be useful to delineate the salient features and differences between synthetic and composite populations most often discussed in plant breeding.

Both synthetic and composite populations are polymorphisms preferably balanced. They contain homo- and heterozygotes in stable equilibrium. Synthetics are generated from a gene pool constituted of inbreds which have good general combining ability (gca) as tested in a set of crosses. Selection for good gca is made so that any cross combination that can result under random mating will have high values for a desired trait like yield. Inbreds are insisted upon so that they can be maintained without change over time. When the performance of a synthetic population starts declining, it would mean that some desirable genotypes got eliminated in the course of maintaining the population. Then it is possible to regenerate the synthetic by constituting the base gene pool afresh from the inbreds that are maintained and repeating the breeding process. So long as the performance of inbreds maintained over time has not declined, the performance of the regenerated synthetic should match the good performance of the earlier synthetic. When one constitutes the base gene pool of a synthetic using "mass selected populations or various other materials" (1, 10), it is incumbent that the sources be maintainable genetically, or otherwise regenerating the same synthetic with earlier potential may not be feasible.

Composite populations, on the other hand, are initiated from a gene pool constituted from a variety of sources, like multiple crosses, varieties, populations and

so on. Since no restriction is placed on the source gene pool, the same composites cannot be regenerated. However since the source gene pool can be constructed with much more ease than that of a synthetic, it is possible to replace a composite by another from breeder's pipeline when needed. This is the key distinguishing feature between synthetics and composites. Thus regeneration of synthetics and replacement of composites are the general rules.

Multi-lines and varietal blends are analogous to synthetic and composite populations; the former two are relevant to self-pollinated and the latter two to cross-pollinated crops. The details of various genetic forms that would have potential for high yields would be found in Arunachalam (2, 3); the methods of breeding for populations have also been outlined (2, 4, 5). The concepts of pure lines, hybrids and populations are summarised in Table 1.

Table 1. Properties of populations and other genetic forms

Genetic form	Genetic			
	Structure	Nature	Equilibrium	Regeneration
Pure lines	Homozygote	Homogeneous	Degenerate, stable	Usually not possible
Hybrid	Heterozygote	Homogeneous	Degenerate, unstable	Possible
Composite	Homo-and Heterozygotes	Heterogeneous	Polymorphic stable	Not possible
Synthetic	-do-	-do-	-do-	Possible
Multilines	Isogenic lines	Heterogeneous	Stable	Possible
Varietal blends	Different homozygotes	Heterogeneous	Stable	Possible

In conclusion we may state that the concept of populations is a vital adjunct to that of pure lines and hybrids and it is high time due attention is paid to breeding for highly adapted productive populations as a viable alternative to stabilise yields.

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