

The Theory of Pre-Breeding

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ABSTRACT

Population changes and their dependent gene frequencies are affected by mutation, selection, random fluctuations, meiotic drive, and migration. The effects of selection pressure on relatively small populations can have dramatic effects on gene frequency and hence on breeding progress. This selection, driven by necessity, has resulted in "narrow base" sugarbeet populations. This paper presents examples of population changes which can occur (have occurred in sugarbeet) in populations subject to intense selection. The utility of gene frequency analysis and its use as a predictive tool is outlined. Sugarbeet breeders, geneticists, and agronomists now attempting to collect and introgress wild germplasm into breeding populations will be aided by attention to principles presented in this paper.

Additional Key Words: gene frequency, germplasm, breeding, selection

A definition of 'pre-breeding' is certainly not manifested in the literature. However, R. W. Allard has loosely defined the word 'domestication' as "the bringing of a wild species under the management of man. It is a method of plant breeding in the sense that, when successful, it provides domestic types that are superior to ones previously available" (Allard, 1966). Allard further amplified the definition by adding, "When a plant breeder transfers one or a few desirable genes from a wild relative to a cultivated type, he is, in a sense domesticating the wild species in part." To the current author, a definition of 'pre-breeding' encompasses the salient features of Allard's definition of 'domestication' as presented above. Hence, I present the following as a definition of pre-breeding: "Any manipulation of germplasm leading to domestication."

Status of Current 'Typical' Base Population. Nearly all sugarbeet breeders would agree that the genetic base of our current sugarbeet populations is narrow. It is the intent of this paper to examine why this is so from a population genetics standpoint.

Our original sugarbeet population can be compared to a large fish pond as pictured in Figure 1. When our breeding programs were in their infancy, we were interested in only a few essential characters such as disease resistance. As time passed, other characters were added to our want list. For illustrative purposes, an abbreviated list in ascending order of need might have been as follows:

- Disease resistance, e.g., curly top virus resistance
- Disease resistance plus cytoplasmic male sterility (CMS)
- Disease resistance, CMS, plus increased yield
- Disease resistance, CMS, yield, plus monogerm seed
- Disease resistance, CMS, sugar yield, monogerm, plus quality
- Disease resistance, CMS, sugar yield, monogerm, quality, plus seed production

Each time a character was added to the plant breeder's list, the fewer fish that were caught and the more that had to be thrown away — breeders did not throw them back. Driven by necessity, plant breeding efforts resulted in new fish ponds with fewer fish having the desired attributes (Figure 2). In short, genetic variation was significantly reduced.

In order to facilitate our discussion, a review of the Hardy-Weinberg law is in order (Stern, 1943). If p = the gene frequency of A and q = frequency of its a allele and $p + q = 1$, then following random mating, the distribution of genotypes in the population occur in the following ratios: $p^2AA : 2pqAa : q^2aa$. If we know, for example, that the frequency of, say, green hypocotyl plants (q^2) is

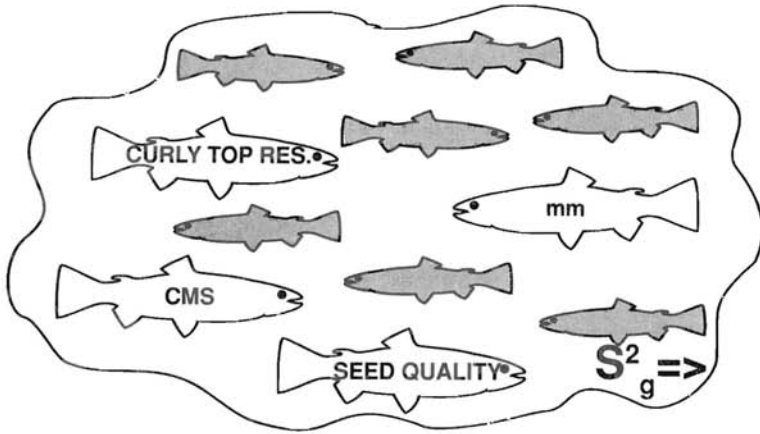


Figure 1. Fish pond illustrating beginning sugarbeet populations. Population is characterized by high genetic variance (S^2_g) for needed traits.

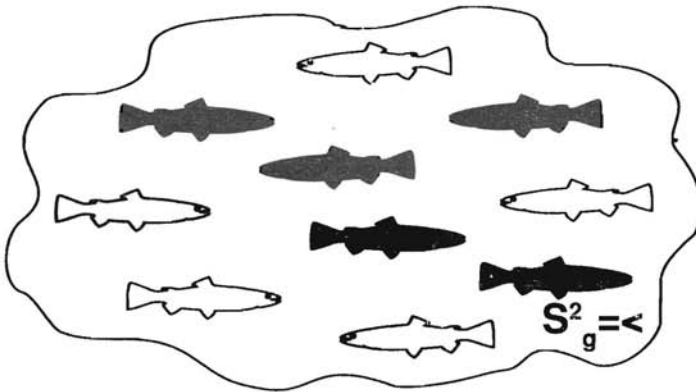


Figure 2. Fish pond more typical of current sugarbeet populations. Population is characterized by low genetic variance for many traits.

0.3, then $q = \sqrt{0.3} = 0.55$ (the gene frequency of a), and $p = 0.45$ (the gene frequency of A). The probable distribution of genotypes in the population can now be computed as follows:

$$p^2RR : 2 pqRr : q^2rr = (0.45)^2 : 2 (0.45) (0.55) : (0.55)^2 = \\ 0.2 RR : 0.5 Rr : 0.3 rr$$

Usefulness of Gene Frequency Analysis. It might be asked, what is the utility of gene frequency analysis? Without gene-frequency analysis, we could only suspect that some of the red hypocotyl plants would likely be heterozygous, and know that whenever two such heterozygotes were crossed, a quarter of the progeny on the average would be green hypocotyl. But we could not know which of the red hypocotyl plants were heterozygous. Knowing, however, that the homozygotes (RR) and heterozygotes (Rr) should occur in the population in a ratio of 2:5, it is easy to predict the results of crosses between red hypocotyl plants. The probability of parent plant A being heterozygous = $5/7$; the probability of parent plant B being heterozygous = $5/7$; and the probability of both parents being heterozygous = $5/7 \times 5/7 = 25/49$. Therefore, approximately half of the crosses between red hypocotyl plants will be between heterozygotes. Other crosses between red hypocotyl plants, RR X RR and RR X Rr will have no green hypocotyl progeny. The matings between heterozygous red plants will be expected to have progeny with hypocotyls in the ratio of 3/4 red : 1/4 green. The probability of a green hypocotyl progeny from a red X red cross is, therefore, as follows:

$$\text{Probability that a given cross is between two heterozygotes} \\ = 25/49$$

$$\text{Probability of green progeny plants from this cross} = 1/4$$

$$\text{Probability of green progeny plants from red X red cross} = \\ 25/49 \times 1/4 = 25/196$$

Therefore:

Red hypocotyl X red hypocotyl crosses in our population should produce approximately 7/8 red : 1/8 green hypocotyl plants.

Population Changes. When we speak of changes in a population, from a genetic viewpoint, we are speaking of changes in gene frequencies (gene q). These changes are affected by mutation, selection, random fluctuations, meiotic drive, and migration. Although all of these factors may have affected sugarbeet populations to some extent, selection has had the greatest impact. This selection, driven by necessity, has resulted in "narrow base" populations with which we must now deal.

Selection and Gene Frequency. Selection is dependent on gene frequencies and, consequently, breeding progress also is indirectly dependent on gene frequency. For example, when 'a' is frequent relative to A, say $q = 0.9$, there are about five times as many homozygous recessives as there are heterozygotes in the population. But when 'A' and 'a' are equally frequent, there are only half as many homozygous recessives as there are heterozygotes. Further, when the frequency of 'a' is reduced to 0.01, there are only about 198 plants in the population that will carry it hidden in the heterozygous condition for every plant that shows the recessive trait. When we are dealing with populations of finite size, the risk of loss from the population is very great for alleles at very low frequency. The significance of chance fluctuation is related to the number of representatives of an allele being sampled, as well as to the frequency of the allele. If an allele has a frequency of 0.01 in a population of 5,000 plants, there are actually 100 representatives of this allele in the population, almost all of them in heterozygotes. An allele with a frequency of 0.01 in a population of 50 individuals is in a much more precarious position. There is only one representative of this allele in the population, and it exists in a single plant. Failure of this plant or its progeny to survive would allow the allele to be lost.

An Example of the Effect of Selection on Gene Frequencies. We can use an extreme example to demonstrate how selection affects the genetic character of a population. For illustrative purposes, suppose that we begin with a population in which just half the individuals in the population show a recessive trait (say genetic male sterility). Also suppose that this population would be at equilibrium under random mating. The distribution of genotypes and phenotypes would be as presented in Table 1.

Table 1. Plant population consisting of half recessive male sterile phenotype plants.

	Male Fertile		Male Sterile
Phenotypic frequencies	0.5		0.5
Genotypes	AA	Aa	aa
Genotypic frequencies	.09	.42	0.49
Gene frequencies	A = 0.3		a = 0.7

Now suppose that all genotype aa plants will not produce seed in a particular environment or that we rogued out all the male-sterile plants. Admittedly, this is an extreme example of complete selection against a recessive phenotype. We now have a breeding population that is reduced to two genotypes, AA and Aa. They occur in the ratio 0.09 AA : 0.42 Aa. In terms of the entire breeding population they represent 18% AA [$.09/ (.09 + .42)$] and 82% Aa [$.42/ (.09 + .42)$]. Assuming random mating of these genotypes, the next generation will be 84% fertile and 16% sterile, with 35% AA, 49% Aa, and 16% aa. We can see that a fundamental change has occurred in this population. The frequency of allele 'a' has decreased from its value of 0.7 in the previous generation to 0.4 in this generation, and there has been a corresponding increase in the frequency of 'A'. A more dramatic change has occurred in phenotypic frequencies. The recessive phenotype has declined from a frequency of 0.5 to 0.16 in only a single generation of complete selection against this trait (Table 2).

Table 2. Results of random matings after elimination of the recessive male sterile phenotype.

Type of cross	Frequency	Plant progeny frequencies		
		AA	Aa	aa
AA X AA	$(0.18)^2 = 0.03$	0.03		
AA X Aa	$2(0.18)(0.82) = 0.30$	0.15	0.15	
Aa X Aa	$(0.82)^2 = 0.67$	0.17	0.34	0.16
Total	1.00	0.35	0.49	0.16
Original gene frequencies	A = 0.3	a = 0.7		
Final gene frequencies	A = 0.6	a = 0.4		

Selection against a dominant allele can be even more effective. In the extreme case, if all plants with the dominant allele are eliminated, the allele is completely eliminated from the population in a single generation. It can return to the population only through mutation or introduction. This example, based on a simply inherited trait, illustrates what has happened to many genes in many sugarbeet populations with which we have worked.

Small Population Inbreeding Effects. Systematic inbreeding in controlled populations is contrasted with random mating in small populations; in the former, homozygosity is increased because of non-random mating, while in the latter, the zygotes are present in Hardy-Weinberg proportions. In plant breeding programs, we often use the most extreme example of inbreeding to maintain lines by self-fertilization. Although inbreeding in itself does not change gene frequencies for the population as a whole, it only results in an increase in homozygous genotypes as compared with heterozygotes. With a population of 1 and self-fertilization, a heterozygous gene pair has a 50-50 chance of being fixed as either homozygote in each generation. This is going on for all the heterozygous loci in the population at once. About half of the heterozygosity is automatically lost each generation, and fixation and loss of alleles occurs very rapidly. Under this system, a sugarbeet breeder typically would produce a large number of inbred lines, and choose from among survivors of several generations of self-fertilization, those that through chance have arrived at homozygosity for alleles that will be useful in further breeding operations.

SUMMARY

The information and examples presented in this paper are really a characterization of how our plant breeding efforts have affected the gene pool with which we have worked. Many of the changes in these pools have occurred subtly and no doubt some genes may have been lost. There is also validity in the argument that the original populations did not represent all genetic variation available in *Beta vulgaris*.

The organized efforts of the World *Beta* Network and the GRIN data base system has facilitated the collection, characterization, and storage of wild species germplasm. The concerted efforts of those employing these systems is showing the potential of reversing the trend of ever-narrowing *Beta* germplasm bases. Ideally, introduction and enhancement of wild or exotic germplasm will not only impede further narrowing of the germplasm base but actually increase genetic variation and hence widen the population base. Certainly, this must continue to be the goal.

LITERATURE CITED

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