Population plant breeding: making a big picture from all the little pieces

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INTRODUCTION

Breeding, both animal and plant, is an extension of the natural evolutionary process with the influence of humans and occurs mainly in domesticated populations. While evolution brings about cumulative changes in the genetic structure of populations by means of natural selection over time among the phenotypes that occur in the population in a climatic and biotic environment, humans can manipulate populations through selective mating and selection of phenotypes with desired characteristics other than fitness to the environment in which they occur. Plant breeding can improve populations in a much shorter time than natural selection and can be used to produce phenotypes expressing traits that may not be desirable in a natural population. Allard (1965) notes that many successful colonizing species have developed genetic systems that have 'appropriate compromises' between the high recombination potential of out crossers and the fixation and stability of inbreeders. This balance between the ability to produce new genetic combinations and the preservation of existing successful genotypes is the key to rapid, long term evolutionary success. By taking a population approach to breeding, it is possible to apply cross-pollinated techniques to normally self-pollinated crops, such as wheat and barley, and make greater progress in specific traits, and to maintain this progress over a greater period of time. While a population breeding perspective is somewhat different from the traditional approach, the general techniques are nearly the same. By improving the genetic architecture of the overall population through recurrent cycles of selection and recombination, it is possible to accumulate a greater number of alleles with positive effects on a trait(s) than in more traditional, single cycle, restricted population approaches (Comstock, 1996).

POPULATION PLANT BREEDING

A population approach to breeding means treating a group of crosses as a single population, with the objective of maximizing overall genetic improvement through a series of cycles of recombination and selection. Most self-pollinated crops are managed as individual, isolated biparental populations with the objective being to select the best homozygous line(s) from the best cross(es) to become a new, improved cultivar(s). Most economic traits are quantitative in nature so it is virtually impossible to produce the ideal genotype with all of the desirable alleles in a reasonable sized population in a single cycle (Falconer, 1981). It is more feasible to derive such a superior genotype using several cycles of selection and recombination among the most desirable phenotypes in a series of intermediate populations (ie. recurrent selection; Comstock, 1996). By accelerating the generation advance from crossing to a level of homozygosity that makes selection for a quantitative trait such as yield possible, cycle time can be reduced and more cycles can be conducted in a given time period. Crosses among the selected progeny in each cycle maintains a larger effective breeding population size to give an opportunity to accumulate a high proportion of the desirable alleles in individual plants produced in the advanced cycles (Falconer, 1981). This leads to a higher probability of producing a genotype with a high proportion of the total potential desirable alleles in the population.

After making a biparental cross, the traditional approach is to self-pollinate a number of plants in each generation, with or without selection, to reach a level of homozygosity with will give a reasonably homogeneous progeny line, and then increase the line in bulk to obtain the necessary quantity of seed to conduct replicated yield trials. During the selfing process, the genetic variation of the parents is randomly re-distributed from within the heterozygous F1 plant to among the advanced generation lines (see diagram Falconer 1981, pg 243). The total genetic variation increases, the variation within lines decreases, the variation among lines increases; the heritability also increases as the progeny become more genetically similar to the parental types. If a population is carried in bulk (or SSD), this ultimately leads to a 'pseudo' land race which consists of a heterogeneous group of homozygous individuals in which selection of individual plants can be used to develop true-breeding pure lines for evaluation. The challenge in breeding is to identify the earliest generation with an adequate level of homozygosity (and subsequent progeny homogeneity) to conduct yield trials, and then to multiply the progeny in bulk to obtain the required amount of seed in the shortest possible time. Traditionally, the best line(s) will be selected from within each cross and the best lines from among all the crosses will be released as cultivars and [eventually] used as parents in a further round of biparenetal crosses after a number of years of further evaluation. With a population approach, several of the best lines would be selected from many of the original crosses in the population and intercrossed with several other selected lines in each cycle. Further line evaluation will be subsequently used to identify those to become cultivars. Although the genetic variation within each line becomes [nearly] fixed during the selfing process and there is a consequent loss of diversity within each line, if a sufficient number of lines are produced from each biparental cross and an appropriate number of crosses were made in the initial population, there is a minimal loss of total diversity in the overall population and nearly all the original diversity can be 'recovered' in the next round of crossing. If the selection process is effective, the majority of the original genetic diversity 'lost' is that resulting from the expression of unfavourable alleles. Thus, in a properly designed population structure, a large amount of <u>desirable</u> diversity for the traits under selection [as well as those not currently being subjected to selection] can be maintained, while at the same time significant progress in performance for those traits under selection can be made in the population as a whole. The population will accumulate desirable alleles through the selection and recombination process and will continue to generate new variation through recombination among independently assorting loci as well as by breaking repulsion linkages among desired alleles. As the population accumulates a greater frequency of desirable alleles (and allele combinations), the probability of producing a line with a high proportion of the desired alleles becomes a reasonable probability (Comstock, 1996).A successful genotype produces the desirable phenotypic 'picture' from the combined expression of many favourable alleles with small effects.

Each cycle of breeding in population is subject to the same basic evolutionary selection process as would occur in a natural environment. The most basic selection is for adaptation to the physical and climatic environment; a plant must first <u>survive</u> if it is going to contribute gametes to the production of the next generation. This step is essentially natural selection and is superimposed on every breeding program which multiplies or evaluates plants in a field environment [whether the breeder likes it or not]. The next selection step in the evolutionary (and breeding) process is tolerance to the biotic environment. Plants must have some tolerance or resistance to the pathogenic disease organisms and insects that have become evolved to parasitize them before they can produce gametes that will be used to produce the next generation of the population. They must be able to <u>thrive</u> in the 'real world' environment. Plants which can survive and thrive in the 'real world' environment must then be <u>capable of producing progeny</u>. In an evolutionary context, the number of successful progeny, relative to other members of the same population, will have a big impact on the success of a particular genotype, and the relative proportion of the progeny population that carry its specific genetic information. Although the genotypic architecture of the individual may not be passed on intact to the next generation, the relative proportion of individual alleles within the progeny population of gametes will give rise to allelic shift over generations of selection and intermating to cause the phenotypic array of the population to shift in response to the selection pressures applied to it over time. This occurs in a breeding population in nearly the same manner as it would in nature. The major difference between evolution by means of natural selection and breeding is that breeders may impose <u>additional selection criteria</u> on a population for traits that they deem desirable, and that are not related to individual survival, health, vigour, nor the number of successful progeny. Breeding is thus an extension of evolution and not a distinctly different process. Breeders can manipulate populations through selection of parents, through mating design of a population and managing population size and the environment in which a population will be grown. To be evolutionarily successful, an individual must survive, thrive and produce a large number of successful progeny. A successful cultivar must do this in an agricultural environment, as well as possess additional agronomic and quality traits.

THE RIPE SYSTEM

The RIPE system developed in barley at the University of Guelph (Falk, 2002) and utilized as the basic breeding method, seeks to maximize the evolutionary potential of a population over time by reducing cycle time through accelerated generations and offseason seed increases, combined with reliable yield, agronomic, and disease evaluations followed by intermating among the selected lines as a recurrent process. The RIPE system is an efficient, effective application of the recurrent selection concept. Efficient use of genetic male sterility, indoor growth facilities, offseason nurseries and reliable yield evaluation are all critical components of this system. It makes a big, cohesive picture of the breeding system from many small sequential, interacting steps.

The RIPE system is effective in bringing together many desirable alleles into a single, adapted, elite genotype. However, desirable alleles cannot be fixed if they are not already in the population, so it is necessary to bring in new alleles from the majority of barley genotypes in the world that are not adapted to our warm, humid, continental climate. As the climate changes, new, currently neutral or even negative alleles will become desirable and they must be introduced to the population as well. As the background gene pool changes over time in response to selection and accumulation of a constellation of alleles with epistatic interactions, new, and perhaps different, alleles will become desirable. New alleles are constantly being introduced into the Elite population from unadapted backgrounds through the introgression phase of the RIPE system. Many of these desirable alleles are currently hidden by being in background genotypes that are unadapted to the physical or the biotic target environments. They must be incorporated into an appropriate Elite background before their phenotype can be expressed and made available for selection. Any high performing genotype which is adapted to some environment in the world probably has several desirable alleles that could benefit the existing RIPE Elite population in Ontario, if they could be incorporated into it. Once the most desirable alleles are in the population, further progress may be possible by reducing any of the repulsion linkages that they bring with them and by developing positive epistatic combinations. Thus, very unadapted backgrounds may be a source of highly desirable alleles leading to further progress in performance of the Elite population. For example, significant improvement has been made in lodging resistance and in seed size in a sub-population which was synthesized using several lines of *Hordeum spontaneum* which all had small seed size and poor straw when grown in the Ontario environment. These traits have now been incorporated into the Elite population. Germplasm development is an integral part of the cultivar development process in the RIPE system.

The Elite level of the RIPE population generally has good tolerance, but not complete resistance, to powdery mildew (*Erysiphe graminis* fs *hordei*), leaf rust (*Puccinia hordei*), and barley yellow dwarf virus (BYDV) through the accumulation of minor alleles over time; no known major resistance genes are present in the population. It is typical for a line to exhibit 100% incidence and 1-2% severity to leaf rust, for example. Advanced lines and derived cultivars are generally very uniform for this type of reaction, although the severity may vary somewhat over years as the environment is more, or less, favourable for the disease development. The Elite population works very much like a cross-pollinated population in that desirable alleles are maintained in the population and new genotypes are constructed every cycle of recombination. If some of these new genotypes express a desirable phenotype, they are selected and contribute their alleles to the next generation, being combined with the desirable alleles of a number of other genotypes also selected for their desirable phenotype. If many of these phenotypically-selected genotypes carry the same alleles, or allelic combinations, those alleles will increase in the population and an increasing number of progeny will contain them, conforming to the basic Hardy-Weinberg genetic response to selection. The RIPE system is used to create new, desirable allelic combinations and then preserve and enhance them on an ongoing basis in a structured, perpetuated Elite population

The critical factor in any breeding method is that the desirable alleles must be present in the population, and must occur in a well-adapted background before they will be phenotypically expressed and become available for selection to act upon [simultaneously with the rest of the alleles in that particular genotype]. So while the allele is the unit of response to selection, the observed phenotype which results from the combination of the whole genotype (genetic environment) and the physical and biotic environment in which it is grown, is the unit of the actual process of selection. The big picture of the visible phenotype is made up of many small, interacting, genetic pieces within a specific environmental (both genetic and environmental) framework.

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