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The Art and Science of Plant Breeding

By J. S. Gladstones, Senior Plant Breeder

The first part of this article described the evolution of crop varieties and their improvement by simple selection. This part discusses cross-breeding and the other techniques which underly most modern plant breeding programmes.

The purpose of crossing is to generate new combinations of varietal characteristics. It does not create anything basically new. All the genetic "ingredients" of a new variety must be present in one or other of the parents.

All varieties have their relative strengths and weaknesses, and the theory is that when two are crossed it should be possible to select, from among the progeny, lines combining the strengths of the parents while discarding those combining their weaknesses. Picking the right parents is critically important.

The technique of crossing is quite simple, with some variation depending on the type of flower. The pollen-bearing bodies (anthers) of a flower are removed, using small tweezers or sometimes air suction or other methods, before they have had a chance to burst and scatter pollen which could bring about self-pollination. After this the flower is usually covered with a bag or netting to keep out insects or air-borne pollen until it is ripe for fertilization. Pollen from the other parent is then introduced and brushed or blown on to the stigma of the flower.

There are limits to which crosses are possible. Normally they can be made only among members of the same species, in plants as in animals. Occasionally wider crosses can be made, but problems of weakness or genetic instability and sterility often arise in the progeny. The horse can cross with the ass, but the resulting mule is sterile.

Even within a species there may be genetic incompatibilities which make crossing between particular varietal types difficult. How widely crossing can be safely extended...
must be discovered by trial and error for each crop.

Once a cross has been made and the resulting seed collected, the subsequent handling of breeding material depends on the plant’s normal mode of propagation.

Plants normally propagated vegetatively
(fruit trees, vines, many ornamental shrubs)

A few vegetatively propagated plants cannot produce seed at all; obviously these cannot be crossed. Assuming a cross to have been made, however, the progeny are handled in the same way as seedlings derived from uncontrolled open pollination. Promising crossbrids are multiplied by vegetative propagation (budding, grafting, etc.) for further testing. A crossbred which is better than existing varieties can be further propagated vegetatively and thus become a new variety.

The progeny of a given cross are still extremely variable. In vegetatively propagated plants, the parents themselves are often of very mixed origin and genetic makeup. The chance of any of the progeny being better than their already carefully selected parents is fairly small, but it should be better than where pollination was random, if the parents have been well chosen.

The great American breeder Luther Burbank, working in the late 19th and early 20th centuries, was one of the first to use cross-breeding extensively to develop new fruit and ornamental varieties. He is particularly remembered for his plum varieties and for the Burbank potato. Burbank introduced and tested varieties from many parts of the world, crossed varieties showing desirable characteristics, carefully selected amongst the seedling types produced, and sometimes intercrossed the best of them through several generations until he got improved types suitable for commercial propagation.

Burbank and other early breeders worked without our modern knowledge of genetics. However, their methods were, and still are, appropriate for vegetatively propagated plants, whose complexity of inheritance and long interval between generations usually defy genetic analysis.

Cross-breeding of self-pollinating seed-propagated plants

Self-pollinating seed-propagated crops such as wheat, oats and barley normally consist of genetically pure varieties which breed true from one generation to the next. Cross-breeding consists essentially of throwing selected parents into a genetic melting pot, out of which true-breeding lines with new combinations of the parental characteristics can ultimately be recovered.

If contrasting varieties are crossed, the first generation F1 is uniform. This is because each parent (unlike those in cross-pollinating and most vegetatively propagated plants) is itself true-breeding and therefore makes the same genetic contribution to each of its immediate offspring. Thereafter, however, the cross throws a wide array of types ranging more or less from one parental genotype to the other, with most combinations of parental genetic characteristics in between.

The plant breeder’s job, once he has chosen suitable parents and crossed them, is to select from among the succeeding generations those lines which combine in greatest degree the desirable genetic characteristics of the parents.

It takes several generations after a cross before the true-breeding state is again reached. The progeny of individual plants selected out of the second (F2) generation after crossing still vary considerably, but with each succeeding generation half the basic genetic factors (genes) by which the two parents differed again become true-breeding. By about the sixth generation, any plant selected cut will breed substantially true and can be multiplied for plot-testing. Once a crossbred line breeds true it is described as being “fixed”.

![Pure seed production plots of an improved strain of Spearwood Brown Globe onion developed at the Department of Agriculture's Vegetable Research Station.](image-url)
The process by which genes from the two parents sort themselves out among the progeny during these early generations is termed genetic segregation. Their inheritance and behaviour in segregation is the classic field of study of genetics.

William Farrer, working in New South Wales in the late 19th century, was the first deliberately to use this method of breeding. It differs fundamentally from that described above for vegetatively propagated plants and used by breeders such as Burbank, in which the first generation after crossing (F1) is genetically variable because it is derived from genetically heterogeneous parents, and itself provides the immediate basis for new varieties.

Clearly anticipating Mendel's genetic laws (which were not re-discovered until after the turn of the century), Farrer crossed traditional tall-growing, late-maturing wheat varieties, of English origin, with early-maturing, short-growing Indian lines. From the segregating progenies he selected pure-breeding lines combining the desirable field and quality characteristics of each, giving us varieties such as Federation, with short straw to allow mechanical stripping, high quality and relatively early maturity. The new varieties allowed expansion of wheat growing from high rainfall districts into the present wheatbelt.

Greater knowledge of genetics and of the physiological bases of yield in different crops has made our techniques surer than in Farrer's day. Basically, however, our methods of breeding self-pollinating seed crops remain very much the same as he developed them nearly 100 years ago.

Cross-breeding of open-pollinating seed-propagated plants

Cross-pollinating seed crops, such as rye and maize, present quite different breeding problems.

Varieties are not genetically pure. They consist of freely interbreeding populations which, although uniform enough in appearance, are usually genetically diverse. The traditional breeding method is that of simple mass selection of the most desirable-looking plants in each generation to form the base population of the next generation, taking care to select enough plants to avoid loss of vigour through in-breeding.

Cross-breeding, in its simplest form, is merely an extension of this method. Parent varieties carrying between them the characteristics re-
quired in a new variety are grown together and allowed to cross-pollinate freely. Mass selection towards the required combination of characteristics is then applied through subsequent generations of the combined population.

"Hybrid" and "synthetic" varieties

The development of so-called "hybrid" varieties has become a prominent feature of breeding in a number of wholly or partly cross-pollinated crops, notably in maize. It depends on the phenomenon of heterosis or hybrid vigour, which is the unusual vigour and yielding ability often shown by the first generation after a cross. This is, of course, the inverse of inbreeding depression. (The term "hybrid" used in this way is somewhat misleading, because nearly all varieties derive ultimately from planned or spontaneous crosses and are therefore hybrids. In practice, "hybrid" refers to cases where the commercial crop consists of first, or at the most, second generation hybrid plants from a set combination of parents.)

Particular combinations of parents give different degrees of hybrid vigour, so breeding consists largely of selecting parent lines based on their ability to "click" to produce superior hybrid offspring.

It is a long-term process, involving the testing of hybrids from large numbers of potential parents in all combinations, then selecting within the best parent lines for still further improvement in "combining ability". This leads to some inbreeding depression. (The term "hybrid" used in this way is somewhat misleading, because nearly all varieties derive ultimately from planned or spontaneous crosses and are therefore hybrids. In practice, "hybrid" refers to cases where the commercial crop consists of first, or at the most, second generation hybrid plants from a set combination of parents.)

The development of "male sterile", or otherwise self-incompatible lines which can only produce seed when pollinated by a fertile sister line or by another variety, has greatly facilitated both testing and the production of hybrid seed at a cost which makes the enterprise commercially worthwhile. It has made it feasible to develop hybrid varieties in a few crops which normally are predominantly self-pollinating, such as sorghum.

Hybrid varieties have become particularly important in some vegetable crops, where the small cost of the seed relative to total returns justifies substantial cost in hybrid seed production if this improves yield, quality and uniformity in the final marketed product.

Hybrid varieties are attractive to commercial breeders because a fresh supply of seed is needed for each crop. If a farmer saves his own seed, both hybrid vigour and the uniformity of the particular cross are lost.

Because hybrid vigour depends on particular combinations of genetic factors, it should be possible, in the long run at least, to approach the same result by genetic upgrading of normal open-pollinating populations. Ways have been devised to accelerate this process by using some of the methods of hybrid breeding to produce so-called "synthetic varieties". Potential hybrid parents are crossed in all possible combinations. Those giving the best results over all crosses, that is, the ones with the best "general combining ability", are then grown together to intercross amongst themselves.

Synthetic maize varieties produced in the U.S.A., Mexico and elsewhere are now closely approaching the best hybrids in yield. This is obviously advantageous to growers, because the cost of seed is considerably reduced compared with hybrids, and they are again able to keep their own seed.

Synthetic varieties have particular application in isolated regions and with economically less important plants such as cross-pollinating pasture grasses, which cannot support a specialist hybrid seed industry. For isolated or ecologically variable areas they have the added advantage over conventional hybrids that they usually contain within them a broad range of genetic variability, upon which natural or artificially imposed mass selection can act to produce and maintain an enhanced degree of local adaptation.

Creation of new genetic variability: mutation breeding

Sometimes the genes for a required plant characteristic are not available, or are available only in varieties which are otherwise so undesirable that to use them for crossing would create major breeding problems. In this situation a breeder may look for natural mutants of the desired type within existing adapted varieties. Failing that, he may try to induce mutation artificially.

The mutagenic effect of X-rays was discovered in 1928. It is now known that many physical radiations, such as atomic radiation, are mutagenic. Many chemicals—often cancer producing—can also produce mutations, and we rightly fear their effects. Mutagens play random havoc with the genetic materials of plant and animal cells, and the effects are nearly always deleterious and often lethal.

For plant breeding, however, it does not matter greatly that 99 per cent. or more of the mutations are useless. What is important is the occasional "mild" mutation of a desired type, which can be used to breed from. Mutagens are particularly efficient at destroying unwanted plant functions such as production of oestrogens in clover, or alkaloids in lupins. They also quite readily bring about changes in flowering time.

An advantage is that specific required changes can sometimes be induced in varieties which are already well adapted and suitable in other respects. Against this is that even if the required change is achieved, it may be accompanied by other, undesirable genetic effects, which can be hard or even impossible to breed out.

Breeding of the oestrogen-free subclover variety Uniwager, as an artificially induced mutant of Geraldton, illustrates both the weaknesses and, potentially, the strengths of the method.

Uniserra serradella is another variety bred by artificial mutagenesis. It was chosen as the best of a large number of early-flowering mutants induced in the Pitman cultivar, and rigorously selected through several generations for vigour and seed yield before bulking for release. Hopefully, the disabilities suffered by Uniwager appear to have been largely avoided in this case, but the final success of the variety has yet to be proved.
Opinion is still divided about the ultimate place of artificial mutagenesis in plant breeding. From present indications it would seem to be a useful adjunct to conventional methods, particularly where natural sources of genetic variations are not readily available.

**Breeding for disease resistance**

Breeding for disease resistance, whether in crop or pasture plants, poses special problems. Often genetic sources of resistance to a particular disease can be found (if at all) only among primitive races. Artificial mutagenesis within existing improved varieties—a logical answer to the problem—has so far been successful in only a few cases. Sometimes it is necessary to go still further afield to undeveloped but closely related species, which can be crossed only with difficulty to our modern improved varieties. From such crosses it can be very hard to recover lines combining both the resistance and the desirable agronomic qualities of the improved parent, so resistant crossbred selections must be repeatedly crossed back to the improved parent. This is called “back-crossing.” Fortunately the genetic factors responsible for resistance are often simply inherited, and can be transferred without modification through any number of back-crosses into lines which, with increasing numbers of back-crosses, will more and more resemble the “recurrent” improved parent. Other simply inherited characteristics can be transferred from one genetic background to another in the same way, provided there is a reliable way of testing for them at each stage of the programme.

Unfortunately, the plants are not the only organisms undergoing guided evolution. Development of resistant plant varieties poses a challenge to the disease organism, with overwhelming advantage going to any strain of the organism which can evolve to overcome the resistance. Some forms of plant resistance are reasonably proof against this form of breakdown. Others, such as wheat rust resistance, break down with uncomfortable speed. Breeding then becomes a constant race between the organism and the breeder, who must use all his ingenuity to circumvent the process and stay ahead.

With the high-yielding crop varieties of the future, it may become a major undertaking merely to maintain yield levels, let alone improve them further.

**Testing**

Testing is the most tedious part of plant breeding. Early testing is limited by the amount of seed available from each selection, together with the large number of selections which must be handled. Yield testing is at best very approximate at this stage. The larger the number of lines that can be handled, and therefore the more drastic the culling possible, the greater will be the chance of success in improving yield.

With the growing importance of quality factors in crop products, it is becoming more and more necessary to select on a quality basis. Improved laboratory facilities for quality screening, e.g., for factors related to baking quality in wheat or malting quality in barley, now make it possible to include such factors quite early in the elimina-
Test rows of subterranean clover crossbreds. Pasture plant breeding and testing pose special problems because of difficulties of assessing the true value of pasture plants.

tion process. This reduces the risk of producing lines which are better yielding but which have in the end to be rejected on quality grounds. It must be recognized, however, that the more criteria are included, the less will be the chance of making rapid progress in any one of them, including yield.

Successive years of screening on the basis of yield and other relevant criteria progressively reduce the number of lines retained and increase the scope and detail of the testing to which each can be subjected. Finally, it is possible to undertake comprehensive testing of the few most promising lines over a wide range of conditions. Semi-industrial scale evaluation of quality is usually carried out at this stage to confirm or refute earlier laboratory tests, for example malting tests for barley and baking, biscuit or noodle-making tests for wheat.

Even then it is difficult to ensure that the testing is comprehensive enough. To establish fully the value of a new variety for commercial use it must be grown over many soils in many years and in many districts. As always in agricultural research, the final answer can come only from the farmer’s own paddocks.

**Special problems of pasture plants**

Pasture plant breeding and testing pose special problems. The yield of crops (normally grain) can be measured fairly readily, while quality and other criteria such as lodging and grain shedding can usually be defined and measured or observed.

With pasture plants, the ultimate return is in animal products, with important side benefits from soil improvement. Measuring these is at best a difficult and very long-term process. Even discounting soil improvement, a grazing experiment to compare returns from different pastures is expensive and can at most include only a small number of plant types. The decision as to which ones are included must already have been made on other grounds, and on these there is so far little agreement among research workers.

Nor can even the best grazing trial be conclusive. Results from a trial could easily be different depending on the location and soil type chosen; the run of seasons encountered, especially that of the establishment year; whether or not cropping phases are included; and many other factors. Duration of trials is important because plant survival is critical, and small differences become multiplied over the years.

There is a real conflict of interest between the plant, which wants to survive and reproduce, and the animal which wants to eat it. For example, should subclover burr be on the soil surface where stock can eat it in summer and autumn, or is it more important that it be buried to ensure good regeneration next season? Clearly the answer will depend on the relative values placed on short-term productivity and long-term persistence, including capacity to compete with less desirable plants in the pasture.

The final answer, even more than with crop plants, can only come from farmers’ paddocks over many years.