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THE UTILIZATION OF COLLECTIONS IN PLANT BREEDING AND PRODUCTION

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INTRODUCTION

Although plant collecting is extremely useful in elucidating the taxonomic and evolutionary relationships between different species and varieties, its principal justification is to obtain natural variability that can be useful in broadening germ plasm pools for plant improvement. Others have presented suggestions for improving the thoroughness, efficiency and utility of collections as well as proposals for their multiplication, storage and subsequent distribution to interested parties. If these commendable efforts are to have an impact on crop yields, the genetic variability must also be effectively incorporated into improved types.

NECESSITY OF A CLEARLY DEFINED GOAL

The key to successful utilization of variability from broad gene pools requires that the crop breeder have a clear concept of what he is trying to introduce, and why. Knowing this, he can search for the trait and in turn incorporate it genetically into a usable variety, (i.e., cultivar), hybrid or synthetic.

After crossing, the breeder must rigorously select among the progeny for the desired trait combined with good agronomic type, and accept only a minimum of undesirable characteristics that are introduced from the wild type. Some workers seem to have an almost mystic respect for any type of variability coming to them from a wild source. There are many desirable genes in the world collections, but most of the variability is detrimental. Most wild types have very low yield potential. The task and art is to incorporate the desirable characteristics into a cultivar without becoming drowned in undesirable material. This can only be done by having a clear concept concerning the characteristic being introduced and its potential value. Moreover, the breeder must have a sound grasp of the relative effectiveness of different breeding methods for incorporating valuable genes into cultivars.

To define the goal and the methods is fairly straightforward in the case of a search for genetic resistance to a new pest or disease, such as a new virulent race of a cereal rust. The scientist develops an effective test to identify resistance to the pathogen or insect. He then screens all available material until he encounters adequate resistance. This resistance must then be incorporated into a suitable background. While the principle of finding and utilizing resistance genes is quite simple and has been widely used in plant breeding for the past 50 years, the actual breeding procedure can be both long and difficult. The pathogen must often be separated into races and the screening done on an individual race basis. The pest or pathogen generally must be cultivated artificially under laboratory conditions. Efficient screening must often be done with seedlings or only portions of a plant and this must be related to field attack on the whole plant. Host-pathogen relationships, the effect of environment, the stability of the reaction under different ecological conditions and many other aspects must be established; nevertheless in such specific cases the breeder usually has a clear idea of the type of character being introduced.

The search for truly revolutionary traits for use in the overall improvement of crops plant is more complicated. It involves recognizing the potential of a given characteristic and visualizing its value when incorporated into a commercial variety or hybrid. Unfortunately, there does not seem to be any substitute for the ingenuity and vision of the individual scientist in recognizing a valuable new trait in a wild background and appreciating its potential usefulness for crop production. As with the more specific cases of resistance to insects or disease, there still remains the more difficult task of actually incorporating the desirable trait into an appropriate background while minimizing the effects of related problems including undesirable linkages, the unsuitable performance of the trait in a new background, negative relationship with other desirable agronomic and disease factors, etc.

THE NORIN WHEAT EXAMPLE

An example of such a trait and its impact will illustrate several principles. Following the second world war, Dr. S.C. Salmon of the USDA, visited Japan in order to study the agricultural research that had been done in that country. Among the materials that attracted his attention was a group of short statured, high tillering wheats. Dr. Salmon envisaged the value of this dwarf trait in areas where weak straw is a limiting factor in increasing fertilizer use in wheat, and he sent samples to some scientists including Dr. O.E. Vogel, USDA wheat breeder at Washington State. Dr. Vogel crossed some of these with the variety Brevor and subsequently sent some F_2 and F_3 seeds to many interested workers.

In addition to excellent straw strength and high tillering the Japanese Norin dwarf wheats were found to have a large number of seeds per head (largely due to more fertile florets per spikelet). However, they were very poorly adapted to Washington and extremely susceptible to disease. An even greater problem was the fact that the dwarf complex was soon found to be tightly linked to a shrunken, poor quality grain type. Many workers tried to break this linkage and failed. Dr. Vogel, however, had the vision and perseverance to break this linkage and produce dwarf selections with acceptable grain type. The resultant variety, Gaines, is the most significant winter wheat variety in several decades and has shattered yield records throughout its area of adaptation. Yields of 10 tons per hectare (i.e., 150 bu./acre) are not uncommon among the better farmers, and verified yields of more than 14 tons have been obtained.

The Norin × Brevor crosses were also the basis of a revolution in the yields of Mexican spring wheats. The same problem of a close association between short stature and shrivelled grain was encountered and also finally broken by means of a vigorous program of hybridization and selection. The results have been very rewarding. Within three years of the introduction in 1962 of the two first semi-dwarf commercial varieties, the Mexican national yield rose one ton per hectare (i.e., 15 bu./acre), and yields have continued to increase. The national average yield now stands at three tons per hectare (45 bushels per acre). Many farmers harvest five ton yields on large acreages and a few of the best achieve yields of seven to eight tons per hectare.

Of even greater world wide importance is the fact that the Mexican wheats have shown high yield in almost all spring wheat regions of the world. They have had the highest overall yield in the Inter-American Spring Wheat Yield Nursery, the Near East American Spring Wheat Yield Nursery and the subsequent International Spring Wheat Yield Nursery every year in which they have been entered. This includes ten sets of international yield trials (Borlaug, Ortega, and Garcia, 1964; Borlaug, Ortega and Rodriguez, 1964a, b, c, d; Krull *et al.*, 1966).

Additionally, these wheats are providing the basis for a sharp change in the production patterns and yields of wheat in several Near Eastern countries. Pakistan and India have both moved vigorously in buying, multiplying and distributing these high yielding, fertilizer responsive varieties. During 1967 alone, more than 60,000 tons of seed of these varieties were purchased from Mexico for planting in other countries, the largest amounts going to Pakistan and Turkey. There will be between 10 to 13 million acres of Mexican semi-dwarfs grown in Pakistan, India, Turkey and Afghanistan in 1967–68 crop season. The results of collecting a few grains of Japanese wheat are indeed impressive.

There are several lessons that can be drawn from this example that are rather generally applicable to the identification and utilization of variability from collections:

Principle 1. The person who made the collection had the vision to see its possible application. A collecting team should consist of people with a wide range of competence and training. This should include fields ranging from basic cytogenetics and genetics to a broad agronomic background in soil fertility, water management and commercial crop production practices. A person with only a narrow interest in cytology and evolution would probably not have appreciated the production potential of these dwarf wheats and might have thought of them at most as an interesting genetic marker. By the same token a person only concerned with soil fertility would be unlikely to appreciate the significance of a taxonomically important 'missing link'.

For this reason we maintain that collection teams should include a scientist with broad agronomic background as well as a taxonomist, a cytogeneticist and a pathologist. Thus, the likelihood of recognizing and collecting new types of both academic and practical importance would be enhanced. The inefficiency in utilizing genetic variability of the present collections is often due to the fact that the person making the collection did not appreciate the potential of the new type and never brought it to the attention of the appropriate scientists.

It might, of course, be argued that the collector has no such responsibilities and that collections should be evaluated by specialists and the information distributed to interested scientists. This kind of evaluation is also important. Nevertheless, the incorporation of an important new characteristic and the reorientation of a breeding program can usually be dated from a casual remark from one scientist to another, rather than from the massive exchange of data. It would be desirable if the collectors could appreciate some of the significance of a new type and try to interest the appropriate scientist at an early stage.

While most of the emphasis here is on new traits within the presently cultivated crops, the broadly oriented collector would also be more likely to visualize the agronomic value of a new race or species. This is particularly applicable to forage plants and other species that could possibly be used directly or with little genetic improvement.

Principle 2. *Additional desirable characteristics other than the ones actually apparent and being incorporated will frequently appear.* The primary reason for using the Norin wheats was to incorporate short, strong straw and thereby avoid lodging. However, an exceptionally high tillering capacity and a consistently higher number of fertile florets per spikelet were simultaneously obtained from these wheats. These additional features have played a significant role in markedly raising the yield potential of wheat in addition to the increase provided by superior lodging resistance. Indeed the Washington State winter wheats and the Mexican spring wheats are being widely used for crossing in order to increase the yield potential in areas of the world where lodging is not a problem.

The possibility of such fringe benefits is usually well appreciated. Indeed, this is often the reason given for indiscriminately saving progeny of crosses involving wild types. One must, as suggested earlier, have a definite concept of the primary goal but should always be cognizant of possible additional desirable traits that can be obtained.

One of the basic defects of long backcrossing usually used for the incorporation of new rust resistance genes is that genes with additional fringe benefits are eliminated and have no opportunity to express themselves. If doublecrosses or only one or two backcrosses are used, most of the parental type can be recovered but there is still some opportunity for other new desirable genes to be introduced assuming very large F_2 populations are grown. The often cited advantage of the strict backcross method of plant breeding is that the parental type is fully recovered with the exception of the one gene being added. This is also its chief disadvantage. The insistence of five or more backcrosses has limited many cereal breeding programs to only the incorporation of new resistance genes with almost no possibility of improving the yield base. Unfortunately, these short-sighted methods still prevail in many areas of the world, including the developed countries.

Principle 3. *The desirable character(s) which are incorporated may be genetically associated with objectionable traits.* Such linkages caused a great many difficulties both in Washington and Mexico in using the Norin wheats, and the tightness of the linkage completely discouraged many other workers. High grain yield in Norin derivatives was strongly linked to such undesirable characteristics as shrivelled grain (low test weight), weak gluten, partial pollen sterility, especially in late tillers, and extreme susceptibility to all three of the rusts. Persistence with the use of large populations at both Washington State and in Mexico, however, prevailed with the aforementioned results. A high negative correlation between two desirable traits does not mean it is impossible to get the desired combination but simply indicates that more work and larger segregating populations are necessary.

GENERAL CONSIDERATIONS

It is difficult to generalize about how to utilize gene resources or even where valuable new genes are likely to be found. Plant scientists must be constantly on the watch for indications of characteristics that might allow major breakthroughs in production. The manner of utilizing these characteristics often depends on the manner of inheritance (whether simply inherited or multigenic), relationship with other traits, ease with which the trait can be identified., etc.

However, some general considerations relating to choice of methods are worth mentioning. Plant collections should be evaluated under a wide range of environmental conditions. Some characteristics are easily identified under certain environments but indistinguishable under others. Indeed almost any trait will vary its expression with differing environments, the exceptions being traits such as awned vs. awnless. Both maturity and plant height vary considerably with soil fertility, water availability, temperature and day length. Not only do the actual values differ but the relationship between varieties may vary. In wheat, for example, Penjamo 62 and C-271 are similar in height under low fertility and/or drought conditions, but C-271 grows very tall under more optimum conditions while Penjamo 62, possessing a Norin gene, stays relatively short and therefore is more lodging resistant. Thatcher and Sonora 64 will head within one day of one another at 50° N latitude at Winnipeg, Manitoba, but Thatcher may head 80 days later than Sonora 64 at the 28° latitude of Ciudad Obregon, Sonora, in Mexico. The effect of date of planting—as it influences whether days are increasing or decreasing in length—also strongly influences Thatcher's behaviour in both maturity and grain yield, while it has little effect on Sonora 64. This day length response has great significance. Sonora 64 is well adapted and high yielding over a wide range of latitudes whereas Thatcher cannot be grown successfully with good yields at latitudes of less than 38° to 40°.

Disease reaction may vary widely between locations due to differences in race complexes as well as the effect of climatic factors. Testing with purified races of a pathogen under controlled conditions is helpful in establishing the relative effects of these factors. However, such tests are not always completely applicable to field conditions and are more costly than testing with a severe field epiphytotic.

Collections of wild relatives of crop plants are often tested under a wide range of environments. It is important that data from such plantings be conveyed to other interested scientists. There is considerable interest today in developing a system by which data can be stored and distributed to interested parties. Unfortunately, the data available on even the best collections have usually been taken rather haphazardly. There is often little appreciation of the effect of environment in the expression of nearly all characters of interest to plant breeders, in establishing the relative effects of these factors (see Chapter 39 by Finlay and Konzak).

A rather systematic scheme of testing under environments that are known to reveal easily distinguishable differences would be very helpful in gathering more useful data from the plant breeding viewpoint. For example, wheat stripe rust data from Damascus, Syria, where the disease is seldom damaging, are not as useful in choosing parental material as are data from Quito, Ecuador, or Njoro, Kenya, where the disease is severe and where very virulent races prevail. Race changes make it necessary to periodically re-evaluate lines in critical zones. Unfortunately, there is no known way to evaluate the resistance to races that have not yet appeared.

The same principle of re-evaluation applies to a whole range of agronomic traits as production practices are constantly being up-graded around the world. For example, lodging resistance is much more important today than it was in the days before inexpensive nitrogen fertilizers became available. Today, Mexican farmers are clamouring for double dwarf and triple dwarf wheat varieties to replace the semi-dwarf varieties which now lodge under their intensive programs of fertilization.

Even with the limitations they possess, the present available world collections of the major crop plants contain a tremendous range of variability. The major hurdle to unlocking their secrets and utilizing the valuable characters has been our inability to satisfactorily classify this variability. Classification studies have been frowned upon as routine, while at the same time mutation research to induce variability has been glamorized. The natural variability in collections has been ignored. Mutation research has clearly shown that genetic variability can be produced by various mutagenic agents. However, up to now this induced variability has made little impact in agricultural production.

Progress in varietal improvement in the past has seldom, if ever, been restricted because of the lack of available variability in wild and primitive populations, as well as in the world's cultivars. Progress has been slow rather because of the lack of imagination, vision and efficiency in identifying and incorporating the existing variability into improved varieties.

Induced mutations simply contribute some additional variability to that already available, and there is little evidence that this additional variability is radically different in type or amount from that already available in even fairly rudimentary crop collections. It should be clearly understood that mutation research is seldom a substitute for plant breeding but simply a means of extending genetic diversity when limited. Developing countries frequently divert their limited funds and trained personnel from the urgent task of feeding people to the more academic work in mutations. The trend is confounded further by the glamor generally associated with this type of work.

This is not to say that useful mutants cannot be created. When talented mutation geneticists work side by side with outstanding plant breeders their programs are likely to be better oriented and more likely to produce significant results. A case in point is the recent development of Sharbati Sonora, a white grain mutant from red grained Sonora 64 by Drs. Swaminathan and Varughese. Because white grain is preferred in India for chappatis, Sharbati Sonora will likely replace Sonora 64 as a commercial variety.

There is a need to emphasize the urgency of increasing the completeness of the collections of the major crop plants. After untold centuries of traditional agriculture, many of the countries that contain the primary and secondary centers of origin of these genera are rapidily changing their production pattern by introducing varieties or hybrids of high yield potential with the fertilizer and other management factors to realize this yield potential. The native types and older varieties can not compete under these new conditions and are being rapidly replaced. This applies particularly to wheat in the Near East as well as to sorghum, rice, millet, and maize in Africa, Asia and the Americas. During the past two years, Afghanistan, one of the richest countries in diversity of native wheats, has begun to move aggressively in changing its traditional patterns of wheat production. The same is happening in Turkey.

NEW TYPES OF VARIABILITY NEEDED

Finally, it might be worthwhile to consider some of the types of agronomically important variability that are particularly worth searching for and could make a strong impact on production.

1. *New disease resistance sources.* Probably the most valuable contribution of the present collections of wheat, oats and barley has been to provide resistance to new diseases and new races of diseases. The incorporation of this resistance has allowed high stable yields while minimizing the hazards of disease attack. The best manner of continuing this sucess is to have large, diverse collections of these important cereals available so that resistant types can be found to any new race or disease.

It is also important that different and broader types of resistance be found. There are indications that certain wheat varieties have an adult broad-spectrum of field resistance to many races and that this resistance is much more stable to race changes than seedling, hyper-sensitive resistance genes. Increased stability and breadth of resistance would allow the breeder to spend a higher percentage of his efforts on yield and agronomic factors rather than disease resistance.

2. *Resistance to pests.* Almost all important economic plants from forage grasses to forest trees are occasionally menaced by a new pest or plague. Large collections of diverse germ plasm are the only means of confronting such threats. Once the problem becomes apparent, the collection can be screened and the resistant types introduced into commercial production either directly or in crosses.

A recent example of this is the increasing importance of the cereal leaf beetle in the northern United States. The collections are being intensively tested to find resistance to this insect. A considerable number of the pubescent leaf types of wheat from India, Afghanistan and Pakistan show resistance.

3. *Dwarfness.* Dwarf varieties were responsible for the success of grain sorghum in the southwestern United States. These dwarf varieties and subsequent hybrids contain at least two dwarfing genes and allow intensive management and high yields without lodging. Short statured types have been very successful in rice, wheat and millet, and considerable effort is being devoted to developing them in maize, oats, barley

and many other crops. Dwarf fruit trees are becoming popular because of the ease in harvesting from shorter trees.

There is a great need for new types of dwarfing in all of the major crop plants. For example, with the discovery of the cytoplasmic sterility restorer mechanism for hybrid wheat, it has become quite important to find dominant dwarf genes. The Norin dwarf genes behave as recessives, and the F_1 of a cross between a normal and semi-dwarf variety is almost as tall as the taller plant. Such an F_1 hybrid could not be grown in Mexico at the present time since the presently grown varieties are all dwarf and strong strawed. A dominant dwarf gene would, however, allow the use of a tall parent in the cross. It appears that the variety Tom Thumb, originating from a collection made in the 1930's in Tibet may carry such a dominant dwarf factor, but additional sources would be of interest (CIMMYT, 1967).

4. *Cytoplasmic sterility—fertility restorer mechanisms for hybrids.* Systems involving cytoplasmic male sterility and the corresponding fertility restorers have allowed scientists to develop hybrid onions, sorghums, millets, maizes, etc. which commercially utilize the yield advantage of heterosis. A similar mechanism for wheat is being intensively studied in several countries. There is also a need for such a mechanism in most of our agricultural and horticultural plants. Collections, particularly those involving wild species, have generally been the source of these mechanisms.

Even for the crops presently using hybrids, there is a need for improved sterility–fertility mechanisms. In wheat, for example, pollen fertility restoration depends on at least two major genes plus a number of important modifying factors. Large populations must be handled to get the required recombinations and it is, therefore, very difficult to produce lines that will fully restore fertility in the F_1 hybrid. A one-gene restorer mechanism would save endless hours of work and millions of dollars of research money (CIMMYT, 1967; Rodriguez *et al*, 1967).

5. *Earliness.* Improved varieties and hybrids of crop plants are almost always earlier in maturity than native types, and there is a need for new earliness genes in almost all crop plants. As fertilizer use increases, a given variety tends to have a longer life cycle. The plant breeder must produce still earlier varieties since fertilizer use is increasing rapidly in all countries. Earlier commercial varieties also allow double cropping in many areas of the world.

6. *Quality factors.* The Opaque-2 factor in maize has also been shown to be associated with high lysine content and consequently with

increased nutritional value. The protein in these lines is, in fact, nearly as nutritious as that in milk. Several institutions including the Rockefeller Foundation are beginning large programs to identify and utilize genes controlling the amino acid content of several of the basic food crops. Recently, certain ryes and Triticales have been found to be as high in lysine content as the Opaque-2 maize (Mertz, Bates and Nelson, 1964; Villegas, unpublished thesis).

Currently genes are being sought that will increase the quantity as well as the quality of protein. Until recently there was very little evidence in wheat of important genetic differences in protein percentage at the same yield level. However, within the past few years, the variety Frondozo and its derivative Atlas 66 have been shown to carry a factor that contributes a 2–3 per cent higher protein content at the same yield level. These types of genes undoubtedly occur in many species and could represent a significant improvement in nutrition for many countries (Johnson, Schmidt, Mattern and Haunold 1963).

New genes are also needed to improve the industrial quality of several crops. This would include higher test weight and weight per seed as well as milling and baking characteristics, malting and brewing quality, and cooking quality. Not only are the genes needed to improve the industrial quality but types are needed that are simpler in inheritance. There are indications, for example, that the excellent milling and baking quality of Argentine wheats is more simply inherited (and therefore easier to incorporate) than the quality of the hard red spring wheats such as Thatcher and its derivatives in Canada and the United States. The gluten quality of Thatcher depends upon multiple recessive genes for gluten strength.

7. *Drought and cold tolerance.* Increased drought resistance would be desirable in almost any economically important plant. The range of adaptation could be increased allowing at least some production where there is none now. Of even greater importance would be the ability to resist the periods of drought that occur at least occasionally in all non-irrigated regions.

Cold tolerance is a valuable trait in the cereals and many forage crops. It is interesting to note that spring as well as winter varieties of cereals often contain valuable genes for cold tolerance. If adequate cold or frost resistance could be found to shift the winter wheat belt northward 300 miles across the prairies and steppes of northern U.S.A., Canada and U.S.S.R. it would be of enormous benefit. Since winter wheats generally utilize moisture much better than spring sown varieties this would be reflected in higher yields and a vast jump in production throughout these regions.

8. *Other specific factors.* All crops have some particular problem for which genes from collections might be important. A gene for longer coleoptile length in dwarf wheat would be valuable for many areas in the Near East where the seed is planted quite deep. Most sorghums do not set seed well in cool temperatures and genes allowing them to do so would be valuable in extending the range of adaptation of the crop to more extreme latitudes and to higher elevations in the tropics and subtropics. Certain Ethiopian collections apparently have this ability and are now being used in breeding programs with this objective in mind.

REFERENCES

Borlaug N.E., Ortega J. & Garcia A. (1964) Preliminary report of the results of the first cooperative inter-American spring wheat yield nursery grown during 1960–61. *International Center for Maize and Wheat Improvement Miscellaneous Report No.* 1. Mexico, D.F.

Borlaug N.E., Ortega J. & Rodriguez R. (1964a) Preliminary report of the second inter-American spring wheat yield nursery grown during 1961–62. *International Center for Maize and Wheat Improvement Miscellaneous Report No.* 2. Mexico, D.F.

Borlaug N.E., Ortega J. & Rodriguez R. (1964b) Preliminary report of the third inter-American spring wheat yield nursery grown during 1962–63. *International Center for Maize and Wheat Improvement Miscellaneous Report No.* 3. Mexico, D.F.

Borlaug N.E., Ortega J. & Rodriguez R. (1964c) Preliminary report of the results of the first cooperative Near East–American spring wheat yield nursery. *International Center for Maize and Wheat Improvement Miscellaneous Report No.* 4. Mexico, D.F.

Borlaug N.E., Ortega J. & Rodriguez R. (1964d) Preliminary report of the second cooperative Near East–American wheat yield nursery grown during 1962–63. *International Center for Maize and Wheat Improvement Miscellaneous Report No.* 5. Mexico, D.F.

CIMMYT (1966-67) *Report, International Maize and Wheat Improvement Center (CIMMYT)*, pp. 76–9. Mexico, D.F.

Johnson V.A., Schmidt J.W., Mattern P.J. & Haunold A. (1963) Agronomic and quality characteristics of high protein F_2 derived families from a soft red winter-hard red winter wheat cross. *Crop Science* **3**, 7–10.

Krull C.F., Narvaez I., Borlaug N.E., Ortega J., Vazquez G., Rodriguez R. & Meza C. (1966) Results of the third Near East–American spring wheat yield nursery, 1963–65. *International Maize and Wheat Improvement Center Research Bulletin No.* 5. Mexico, D.F.

Mertz E.T., Bates L.S. & Nelson O.E. (1964) Mutant gene that changes protein composition and increases lysine content of maize endosperm. *Science* **145**, 279–280.

RODRIGUEZ R., QUINONES M.A., BORLAUG N.E. & NARVAEZ I. (1967) Hybrid wheats: their development and food potential. *International Maize and Wheat Improvement Center Research Bulletin No.* 3. Mexico, D.F.

VILLEGAS E. Variability in the lysine content of wheat, rye and Triticale proteins. Unpublished Ph.D. thesis. North Dakota State University, Fargo, N.D.