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Baenziger, P. Stephen; Graybosch, Robert A.; Dweikat, Ismail M.; Wegulo, Stephen N.; Hein, Gary L.; and Eskridge, Kent M., "Outstanding in their field: The phenotype of the 21st century plant breeder" (2008). *Faculty Publications: Department of Entomology.* Paper 254.
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In R. Appels, R. Eastwood, E. Lagudah, P. Langridge, M. Mackay, and L. McIntyre (ed)
Proc. 11th International Wheat Genetics Symposium. August 24 -29, 2008. Brisbane, Australia.
http://ses.library.usyd.edu.au/bitstream/2123/3325/1/O51.pdf

Outstanding in their field: the phenotype of the 21st century plant breeder

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Plant breeding is a highly interdisciplinary science that requires the skills and teamwork of many scientists to be successful. In the 21st century, plant breeding will reap the benefits of the rapid advances in genomics research and understanding, as well as, advances in information and mechanical technology. The skill and success of plant breeders will be determined by their ability to use their resources efficiently, retaining those proven methodologies and augmenting them with novel approaches to meet their breeding objectives. Once the objective is determined, the plant breeder must: 1. identify and incorporate the needed genetic variability, 2. inbreed and select the useful variant, and 3. evaluate the successful variants to determine those with commercial potential. It has long been understood that plant breeders need to be ruthless with their germplasm so as to avoid wasting time and resources on lines that will never have the opportunity to be released or become useful parents. It may be that with the plethora of new tools, efficient plant breeders will have to be equally ruthless with their access to and use of technology. Though the outcomes of plant breeding are new cultivars, the importance of plant breeding remaining an experimental science will be highlighted, especially for those with the responsibility of educating the next generation of plant breeders in an increasingly privatised world. Finally, some of the great challenges facing wheat improvement that can be addressed by genetics will be discussed as we look to the future.

INTRODUCTION

Though 2008 may represent a brief moment of high food prices and food insecurity due to global shortfalls of food grains, it seems that the benefits reaped for so many years by the Green Revolution are now being consumed by a world that continues to grow in population and wealth, and is becoming increasingly urbanized. Though we have long considered population growth as the major cause of increased consumption, even if population size stabilized, there would be an increased need for wheat due to increased wealth and urbanization (Rosegrant et al., 1999; Carter, 2002). Furthermore the demands on agriculture for non-food human needs such as forage for animals, grains for biofuels, and remediation of environmentally deleterious effects of human activities, have lead to a fierce competition among crops for planting area in regions where multiple crops can be grown.

There are three ways to meet this increased demand: put more land into production (very difficult to do as only marginal lands are not being farmed today), add more irrigated land with its higher production capabilities (again very difficult to do due to limited water supplies and also the loss of previously irrigated land to salinity), or increase productivity through genetic or management improvements. Within the area of management improvements, growers have already captured many improvements (e.g. weed free fields due to herbicide use, or disease free fields due to fungicide use) and further improvements will be made by using crop inputs more efficiently (e.g. nitrogen use). Hence it would appear that the role of genetic improvement is becoming increasingly more important. This increasing importance has led to the recognition that inadequate plant breeding capacity hinders economic development (Tillman et al., 2002; Guimaraes et al., 2007) and to discussions on how to build plant breeding capacity (e.g. the Global Partnership Initiative for Plant Breeding Capacity Building, http://km.fao.org/gipb/; Global Plant Breeding, http://cuke.hort.ncsu.edu/gpb/index.html). Though there may not be adequate resources in every developing nation, in many developing and developed nations plant breeding is well supported as an expensive science and plant breeders are in high demand. Hence the question, what and who will the 21st century plant or wheat breeder be? For the purpose of this paper we will use a narrow definition of plant breeder as one whose goal is to release improved cultivars. Clearly many plant breeders also work in germplasm enhancement and this narrow definition is not intended to deprecate these highly needed efforts.

THE WORK OF PLANT BREEDERS

As has often been discussed previously, the first goal of any wheat breeding program is to carefully select the breeding objective or outcome, in this case the characteristics desired in a cultivar. Once this is done, wheat breeders will need to: 1. introduce genetic variation, 2. inbreed and select among the variants, and 3. evaluated the selected lines in the diverse and varied environments where the lines may eventually be grown as a released cultivar (Baenziger and Peterson, 1992; Baenziger et al., 2005, 2006; Baenziger and DePauw, 2009). These topics have been reviewed in detail elsewhere, so here we will only present a few key points. Resource management is critical in each of these aspects, and while breeders have long known they will have to be ruthless in culling their germplasm, they will also have to be ruthless in selecting which techniques or methodologies they use.

First, though the introduction of variation has historically been done by sexual crosses to make hybrids (usually single, three-way, double, or back crosses), mutation breeding has been highly successful for some traits (e.g. herbicide resistance; Newhouse et al., 1992) and is becoming more important with the targeting induced local lesions in genomes (TILLING) mechanism (McCallum et al., 2000). Similarly, though there is currently no commercial transgenic wheat, the technology is so powerful and necessary that it must be used. It is a matter of when, not if, transgenic wheat will be commercially deployed.

Probably the most common question wheat breeders need to consider in this phase is how many crosses do they need to make? Historically, many programs made relatively few crosses, often 60 or less. However, most wheat breeders would consider 250 crosses as the minimum and many programs make 1,000 or more crosses. The total number of crosses made will depend upon the number of parent lines available, the percentage used for cultivar development versus those made for parent development, as well as, how the resultant populations will be used (discussed below with selection). The total number of F_1 seed from a cross will depend upon the cross type and the size of the population needed in the next generation to adequately represent the genotypic array. Though rarely stated, the number of crosses is also dependent upon whether or not the resultant populations are exchanged with other breeding programs. For example, if there where 4 wheat breeding programs and each program made 400 crosses and shared them (total 1600 crosses available for the 4 programs), effectively they would have more populations to work with than if each program made 1000 crosses and did not share. Alternatively, consider the progress that could be made if there were 1600 crosses for cultivar development and 2400 crosses for germplasm enhancement, if all the crosses were available for sharing.

Once the variation has been introduced, the wheat breeder must decide how best to select and inbreed. As selection can begin with the F_1 progeny of a three-way or double cross and is always used in backcrossing, selection will be discussed before inbreeding. The breeder can use marker assisted selection or phenotypic selection and in every selection protocol there is a hierarchy in which the breeder must choose in what order the traits will be selected. Also, the numbers can definitely work against the wheat breeder unless some traits are fixed by carefully selecting the parents. In early generations, such as in three-way crosses, marker assisted selection for allele enrichment is commonly done. Depending upon how the cross is made and using a three cross as an example [(A x B) x C], for each segregating QTL or allele, one fourth (QTL or allele only from A or B), one half (QTL or allele from A and B, or only from C), three fourths (QTL or allele only from A or B and from C), or all (QTL or allele only from A, B, and C) of the three-way cross seed will have the desired QTL or allele. Of course, marker assisted selection is not needed in the last case other than to prove the parents were as expected. Assuming the QTL or allele is in one half of the F_1 progeny seed and 20 F_1 seed were created, at most 4 QTL or alleles can be selected [$(1/2)^4 = 1/16$] which means in a perfect world, 1 F_1 seed would have all the desired QTLs or alleles. Most breeders would want more than 1 F_1 seed to represent the gametic array of the selected population; so many additional three-way cross F_1 seed will need to be created. As more F_1 seed is needed, the total number of unique crosses may decrease to accommodate the larger F_1 population size that is needed. Hence allele enrichment in the F_1 generation should be used on as few critical traits as possible. Considering later generation selection, seed is less limited and again the hierarchy of selection is important. For example, whenever simple selection techniques can be used to eliminate undesirable phenotypes from the F_2 population they should be used. Some examples of simple selection techniques include spraying segregating populations for herbicide tolerance (Pozniak and Hucl, 2004), planting populations so the winter or spring growth habit segregants will be winterkilled or not vernalized, inoculating with disease so resistant types can be selected, or optically sorting for kernel colour or hardness (Dowell et al., 2006). These selection protocols can quickly eliminate obvious undesirable types at relatively low cost and with high efficiency. The resulting population is smaller but contains valuable traits at a higher frequency than would the unselected population. The needed population size becomes more manageable. Finally as selection assays vary in cost, whenever possible it is best to eliminate early generation lines where there are thousands of possibilities using the least expensive assays and use the more time consuming and expensive assays only after the number of lines has been reduced.

The common methods of inbreeding are single seed descent, doubled haploid (especially with the advent of the wheat by maize system [Laurie and Reymondie, 1991] and the improved microspore culture [Liu et al., 2002]), backcrossing, and selfing in the field, plus in some cases the use of off-season nurseries. Often the process is determined by the objective, the selection protocol, and the resources needed to inbreed and select a line. In single seed descent and doubled haploidy, the key question is at which generation should the process begin and how homozygous (homogeneous) do the resulting lines need to be (Baenziger et al., 2006). While the most time can be saved by using F_1 or F_2 plants, often at least one generation of selection is needed to remove obvious unwanted segregants and thus reduce the number of lines that need to be screened or evaluated. It should be noted that the above selection protocols often require populations to be grown in environments that are representative of the target population of environments, hence precluding the use of off-season nurseries or greenhouses. The importance of this point is that as more time is devoted to selection and in countries where genetic heterogeneity in cultivars is

tolerated, some inbreeding methods lose some of their time sensitive value, e.g. the double haploid and single seed descent methods. For example, single seed descent for one or two generations may make sense in the United States where heterogeneity is accepted, but with F_3-derived F_4 families forming the basis of many of our cultivars, it is difficult to see how doubled haploids can fit into our breeding protocols except in those cases where extremely rapid responses are needed. Finally, rapid inbreeding may be detrimental or unnecessary if you have episodic selection events. Simply, if relatively important traits can be screened infrequently or have a high genotype by environment interaction (GEI), the question becomes, is it necessary to rapidly inbreed only to have to wait while you collect important data on the homogeneous lines to determine if they are worthy of cultivar release. If the selection can occur while the line is inbreeding, it may reduce the need for rapid inbreeding. The contrary argument would be that if better evaluations can be made on homozygous or homogeneous lines, then perhaps it is still worth rapidly developing the inbred lines.

The final stage before cultivar release is the extensive evaluation phase. At this stage, there is often little that one can do, other than extensively test, to build a database that ensures that accurate information is given to producers to enable informed decisions (Cullis et al., 2000; Baenziger et al., 2006: Roozeboom et al., 2008). This must be done over time and locations and should target environments where the cultivar will most likely be recommended to be grown, but also surrounding environments that will test its robustness. However, these trials still need to be undertaken in the most efficient manner (generally considered to be using incomplete block designs or nearest neighbour analyses; Stroup et al., 1994), grown in the most representative locations, and correctly interpreted (Roozeboom et al., 2008). As the lines continue to be advanced, the complexity and expense of the selections assays will also increase. While considerable information is available on how to analyse GEI, there are two aspects that need developing in detail. The first is ensuring that the locations are representative of critical regions within the target population of environments. For example, historically Nebraska has three major ecogeographic zones previously determined by years of data (Peterson, 1992). These zones also represent three major prairie grassland zones, again indicating their differences. Of our six main testing locations, two are in the western zone, one to two are in the central zone, and two to three are in the eastern zone. Ideally, in each zone, one location can be lost to hail, drought, winterkilling, etc. and we will still have representative data for the zone. While these three zones are representative of the diverse growing conditions in Nebraska, they also represent the diverse growing conditions in the northern Great Plains. Basically, the western NE zone represents the higher elevation wheat growing region of the northern Great Plains, the central region represents central Nebraska and South Dakota, and western Kansas, and the eastern zone represents eastern Nebraska, South Dakota, and Kansas. Hence, historically when lines have done well in all three zones, they tend to be widely adapted and grown in the northern Great Plains. The second aspect is that with the right testing locations, it is important to learn from those locations how to interpret the data. In this case, every testing site in every year tells a story if you are perceptive. The breeder that is most successful will be able to understand why one line did well or poorly at a site based upon the line's and site's history. Basically, there are many ways to get to the same or similar phenotype; but learning how that phenotype occurred is critical. It is for this reason, that many breeders plant, take their notes, and harvest their plots. We are looking for those subtle signals that help us understand our lines and how they will perform, especially as the differences among the very best lines are small.

Returning to the Phenotype

As perhaps can be deduced from the above paragraph, phenotypic plant breeding will always have a place. This belief is due to: 1. progressively less expensive and more molecular markers such that centralized laboratories are generally considered the most efficient way of obtaining marker data for marker assisted selection and marker assisted plant breeding. As the marker work is moved to centralized laboratories, the breeding program, which has to be site specific, can concentrate on carefully measuring the phenotype. 2. Even with the amazing marker throughput that modern marker laboratories have, breeding programs can exceed their capabilities or the resources of the plant breeding program. Visual selection for some traits remains a remarkably effective way of handling massive populations and experimental lines that are generated. 3. Plant breeding often is based upon the exception; hence the selected line may or may not have the desired markers. Many highly successful lines have the undesired marker, but due to epistasis or some other combination of QTLs or genes perform well (e.g. Scout 66 having the deleterious 2 + 12 glutenin bands (Graybosch, 1992) but was the market standard for end-use quality in the Great Plains for years; or Wesley, a highly successful irrigated and high management wheat having the deleterious yield QTL on chromosome 3A from Cheyenne; Mahmood et al., 2004). 4. Our understanding of the genome, while constantly increasing, may not fully explain the complexity of the phenotype. Recent studies have highlighted the importance of epistasis (Dudley, 2008) and QTL interactions. Complete QTL interactions will be difficult to identify and more difficult to breed for successfully. Most importantly all of the marker data, however obtained and however used, must be tied to carefully measured phenotypes to know the value of the marker(s). 5. The environment in which we grow our plants change, especially for biotic stresses. The first indication of these changes is the phenotype, hence plant breeders must always pay attention to the phenotype (e.g. the rise of Ug99 [TTKS] stem rust [*Puccinia*

graminis f. sp. *tritici* Eriks & E. Henn], Pretorious et al., 2000; and the newly discovered *Triticum* mosaic virus).

Phenotyping wheat lines for performance in diverse environments and cropping systems, disease and insect resistance, and end-use quality, as well as, adding markers to the most important lines requires the formation of a diverse wheat improvement team where the talents of geneticists, breeders, plant pathologists, entomologists, cereal chemists, agronomists, statisticians, and crop modellers work together. While few groups have all of these component parts, modern communications allow national and international efforts to work seamlessly.

Extending the Phenotype

Every wheat breeder has two concerns when it comes to recommending cultivars. The first is that despite having tested a released line in over one hundred environments, it almost assuredly will not be tested in the farm that the grower is asking for a recommendation. Hence the breeder is asked to interpolate or predict the results for an untested environment. The second concern is that while breeders expect incremental gains and recognize there is a genetic upper limit for productivity (grain yield); they do not know the grain yield response surface, specifically if it has one or numerous peaks. If it has one peak, then there is no concern, but if there are multiple peaks then every breeder would like to work on the peak which has the highest genetic limit. However, it seems more likely that there are multiple peaks, at least one for semidwarf lines and one for conventional height or tall wheat lines which remain preferred in some drought prone areas. The salient questions become: how do breeders know which peak they are working on, and if they are not working on the slopes of the highest peak, how can they get to that peak fully understanding that to go from the slopes of one peak to another you have to cross through a valley (give up grain yield)? In both cases, crop modelling may be able to help, especially if the models are able to incorporate "genetic" coefficients that truly incorporate the advances in genetic and genomic understanding (Baenziger et al., 2004; White et al., 2008). Models should predict grain yield in the farmer's environment and also provide the reasonable estimates of where the highest peak is (where grain yield is predicted to be highest).

THE FUTURE OF WHEAT BREEDING

After discussing the current state of wheat breeding, a few ideas on its future are worth considering. In the authors' careers, we have witnessed globally the privatization of many previously public wheat breeding programs and the consolidation through attrition of other public programs. We have also witnessed the rapid expansion of genomic information and tools which heightened the competition for crop improvement resources, as well as, the incredible advances in computing and statistical power that allow efficiencies that were never dreamt by those of us who remember punch cards and their first scientific calculator.

Clearly wheat improvement through breeding will continue as long as consumers ask for their daily bread. Most likely wheat breeding efforts will increasingly become a private sector effort for three reasons: 1. the needed marketplace is being created to provide the economic rewards necessary to support the private sector, 2. there are obvious efficiencies with private breeding programs that cross governmental boundaries and can use diverse crops to support the needed statistical and genomic infrastructure, and 3. in many cases public breeding programs have chosen to emulate private sector breeding programs, thus blurring the lines between the two. In the last case, the public sector program can be privatized with little effect. As wheat breeding becomes increasing privatized, there are two questions that need to be answered: 1. Who will train the next generation of wheat breeders? and 2. Who will do the necessary research to advance wheat breeding methodology? It should be noted that these are not new questions and have been asked in many countries for the last 100 years.

Training the next generation of wheat breeders will continue in the public sector at universities, though new partnerships will evolve with governmental and private organizations that may have greater breadth and scope. The belief that, in the future, only the private sector can effectively phenotype lines is highly questionable and most likely will lead to undesirable outcomes. The mission of private breeding companies is to release new cultivars that generate income for their owners (shareholders). Unless the company believes they will be able to enhance their competitive edge, doing plant breeding methods research may be a low return on investment option and their commitment to phenotyping will be similarly low. To educate the next generation of plant breeders, some programs dedicated to education need to be continued, whether they be universities or public-private consortia with the necessary economic incentives to do the research.

As for who will do the needed research to advance wheat breeding methodology, it will be done in the public and private sectors and with highly flexible interactions among them. In some situations, such as marker assisted breeding (MAB), the private sector is probably already far ahead of the public sector, though epistasis may enhance the value of phenotypic breeding. While much of the MAB research remains proprietary, there is an incentive for the companies to discuss their research so as to shape plant breeding education. In other areas, such as germplasm development and research in minor crops, the public sector continues to play a vital role. In addition, the public sector has considerable resources and will need to develop mechanisms to ensure they are well used and clearly benefiting consumers and stakeholders (e.g. sharing of crosses, early generation materials, and testing sites;

supporting centralized laboratories and national efforts; constant discussions on how to increase efficiencies and education experiences). Where the public sector should consider playing a greater role would be in working with the private sector on the grand challenges affecting wheat improvement. Considering the advances in hybrid rice (*Oryza sativa* L.; Yang et al., 2007) and the current need to improve wheat production, better collaboration among public and private wheat breeding efforts on hybrid wheat may be the best hope for a more successful outcome. In the United States, the public sector entered and quickly exited hybrid wheat research, with the exception of one dedicated spring wheat program that is no longer active. Alternatively, the long-term innovation required to develop hybrid wheat may come from countries with greater nutritional needs that commit to developing solutions, rather than many of the major wheat research teams in the U.S. and Europe. The future of wheat breeding will belong, as it always has, to those willing and bold enough to embrace it.

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