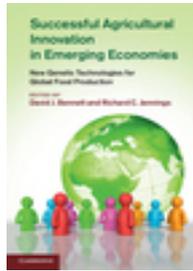


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New Genetic Technologies for Global Food Production

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Chapter

5 - Germplasm diversity and genetics to drive plant breeding for Africa

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5

Germplasm diversity and genetics to drive plant breeding for Africa

INTRODUCTION

The global food crisis of 2008 highlighted the necessity for innovation in agriculture to address food insecurity in the presence of a changing climate and a growing population. The world population is predicted to reach 9 billion within the next 40 years, requiring a 70–100% increase in food production relative to current levels (Beddington, 2010). A burgeoning world population is not the only threat to global food security. Changing lifestyles, population demographics, competition from subsidised biofuels, deterioration of natural resources and dwindling supplies of water will require considerable financial, intellectual and molecular investment in agriculture, particularly in the developing world. A Global Food Security Index (<http://foodsecurityindex.eiu.com>) has recently been created for 105 countries, with the aim of guiding the development of food security solutions. It provides a quantitative and qualitative model to identify and measure risks that drive food insecurity, based on affordability, availability and food quality. The bottom third of the table is dominated by sub-Saharan African countries. These countries include Mozambique, Ethiopia, Rwanda and Nigeria which are predicted to have the fastest growing economies over the next 2 years and are well positioned to address food security.

In these circumstances, Africa and in particular sub-Saharan Africa can lead the introduction of new agricultural technologies and in particular the deployment of the full spectrum of plant breeding technologies to address food security and sustainability of the natural resource base. Reviews outlining the deployment of new biotechnologies in plant

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breeding have been published (Lusser *et al.*, 2012) but to address the global challenges effectively will require a deeper understanding of plant breeding methods and principles together with exposure and understanding of the needs of smallholder farmers who dominate agricultural productivity in sub-Saharan Africa. We will discuss these interrelated topics through a review of the principles of plant breeding and the role of genetic diversity; a critical appraisal of crop genomics and life sciences advances and their application to plant breeding; and an analysis of the particular issues and opportunities that pertain to plant breeding in sub-Saharan Africa.

PRINCIPLES AND HISTORY OF PLANT BREEDING

During the last century genetics played a pivotal role in improving our understanding of many aspects of biology. The principles underlying heredity were first established in plants and the main practical beneficiary of these discoveries was agriculture, notably via plant breeding. The principles of plant breeding were established by Mendel who provided the first clear exposition of transmission genetics: the statistical rules governing the transmission of hereditary elements from generation to generation. Mendel introduced three fairly novel approaches to the study of inheritance: he extended observation to experimentation, he counted his plants (*Pisum sativum*), and he maintained the parent stocks of plants. At that time numerical studies were not yet part of the tradition of biology and indeed the statistical methods required to validate the observed ratios were not available. However, Mendel understood the inherent errors associated with sampling. The theory of inheritance established by Mendel is based upon the existence of hereditary particles or genes that behave in a well-defined and hence predictable manner. Arising from these principles the concepts of alleles (the alternative forms of a gene at a specific position on a specific chromosome) and the segregation and independent assortment of genes during reproduction emerged.

This we now know is a result of alleles being carried on the chromosomes, where (in general, but not always) each cell carries two paired sets of homologous chromosomes. 'Homologous' because they carry alleles for a specific characteristic at the same place on each of the chromosomes of a pair. During sexual reproduction the gametes (i.e. the sperm, pollen or eggs) each carry one or other of these homologous chromosomes. The result is that the progeny of sexual reproduction have alleles from each parent, combined, or assorted, in many different ways.

During the nineteenth century, and before the ‘rediscovery’ of Mendel’s work in 1900, plant breeders applied the Darwinian theory, i.e. that plant characters could be improved by continuous selection. Their methods involved repeated mass selection within local varieties of plants, but no great advances were made. However, in 1890 plant breeders in Sweden and France began to make single plant selections and to grow selected progeny. In essence breeding became more systematic and careful. The Mendelian rediscovery catalysed the establishment of fundamental concepts describing the particular nature of inheritance, providing a clear distinction between genotype (the genetic make-up) and phenotype (the characteristics of the plant), and a rationale for progeny testing.

The characteristics or ‘traits’ described by Mendel are discontinuous, normally related to genes (alleles) at one or a few locations on the chromosome, and their gross effect on the plant or ‘phenotypic expression’ tends to be modestly affected by the environment. Traits that vary in a more continuous fashion are frequently controlled by more than one gene and are subject to significant modifications by the environment. However, such traits are inherited in the same way as discontinuous characters, exhibiting during reproduction segregation, recombination and linkage when on the same chromosome. The genetical approach to handling continuous variation or quantitative traits is based on the theory and predictions of biometrical genetics (Mather and Jinks, 1971). Such traits are the most economically important components of plant breeding programmes, underpinning the genetic improvement of yield, and of resistance to biotic (living) and abiotic (non-living) stresses on the plant. Successful crop improvement programmes are dependent on an understanding of Mendelian and quantitative genetics principles, and the need to capture reproducible phenotypic data.

Bernardo (2002) defined plant breeding as *‘the science, art and business of improving plants for human benefit’*. Progress is dependent on: the amount and type of genetic variability available and the effectiveness of the evaluation and selection techniques employed. It is important to remember that although scientific plant breeding only began in the last century, it had its origins in the dawn of agriculture many thousands of years ago. These early efforts resulted in the domestication of our major cultivated crops. For any particular species, breeding methods are largely conditioned by the stage of evolution, development and domestication of that species. Continued selection and isolation by humans are likely to have influenced the amount of genetic variability, the life cycle, mating system, the history

of selection and type of gene action, all of which are interdependent and together determine the applicability of any breeding method.

The prime determinant of the methods practised in plant breeding is the crop's reproductive biology and breeding system. Consideration of the breeding system focuses attention on the relationship between the reproductive cells or gametes at reproduction and their control of the genetic structure of populations. Crops can be classified according to their system of propagation into:

- (1) Vegetatively propagated crops, e.g. potato, sweet potato, cassava and yam
- (2) Inbreeding (autogamous) crops, e.g. wheat, barley, rice, soya bean, cotton
- (3) Outbreeding (allogamous) crops, e.g. maize, forage grasses
- (4) A variable, intermediate group which will partly cross-pollinate and partly self-pollinate, e.g. *Brassica napus*, sorghum.

Approximately two-thirds of the world's food crops are inbreeders. For these self-pollinating crops individual genotypes (i.e. the alleles, or different forms of a gene, which an individual has with respect to a particular characteristic) are pure lines or homozygous lines, meaning that both chromosomes have the same allele for that particular characteristic. For inbreeding crops the variability which plant breeders need for selection of desired characteristics must be generated. The normal way in which breeders introduce new characteristics is by making sexual crosses, that is, by crossing the pure line with another line which has a different allele for that characteristic. The starting point for the production of a new variety of a self-pollinating species is a hybrid, called the F_1 hybrid, produced from a pair of different homozygous lines, each having identical alleles for a single characteristic. Self-pollination of the F_1 generates the F_2 progeny which is subsequently allowed to self-pollinate in the field. The result is a very diverse population which theoretically could contain all the recombinants from the parental gametes if sufficiently large numbers of plants could be grown. In the early generations the genetic variation is not fixed, so the progeny of any single plant continues to segregate, i.e. the different alleles are distributed throughout the population, leading to considerable diversity within the population. However, with each succeeding generation of selection the individual plant becomes progressively more inbred and true breeding so that a new uniform variety can usually be based on a single sixth (F_6) generation because virtually all other variation is eliminated through selection of plants with the desired characteristic or characteristics.

Traditionally, breeding methods for inbreeders have been based on variations of the pedigree system where the ancestors of the selections can be traced back to individual F_2 plants. The pedigree selection method is a long process from parents being hybridised to the release of a new variety (10–15 years). However, the most recalcitrant problem in the use of pedigree selection is the difficulty of identifying high-yielding genotypes in the early generations, where only a limited amount of seed is available and this is usually heterozygous, i.e. has both alleles. To overcome this problem breeders may delay selection until a sufficient number of plants is obtained. Once this number is achieved selection for the desired characteristic can begin until progenies are approaching homozygosity, that is, both alleles are the same and plants with the desired characteristic can be recognised. Two main approaches are used to achieve this: single-seed descent and doubled haploidy. Haploids are plants that contain a single chromosome which can be doubled to produce homozygous generations of plants in a single generation. Two methods are generally used to produce haploids. First, cultured gamete cells may be regenerated into haploid plants, and second, haploids can be induced by rare crosses between species in which the genome of one parent is eliminated after fertilisation. Doubled haploids (DH) result in an increase in selection efficiency due to the fact that homozygosity is established in a single generation. DH is now routinely used in major cereal and brassica breeding programmes and used for rapid inbred line production in maize. A new method for inducing haploids in *Arabidopsis*, a small weed long used and characterised by geneticists, has been reported based on the modifications of what is called a single centromere-specific histone protein CENH3 [5]. Both maternal and paternal haploids can be generated by crossing this *cen3* mutant having an altered CEN protein with wild-type plants. Potentially, this technique may be extended to a broad range of plants including crop species.

For outbreeding crop species, allele frequencies in populations need to be considered. In 1908 Hardy and Weinberg independently realised that the consequences of Mendelian inheritance in a large random mating population with no selection, mutation or migration was that there was no change in gene frequencies and genotype frequencies from generation to generation. In other words the mechanism of inheritance maintains variation. Furthermore, Hardy and Weinberg showed that there is a simple relationship between gene and genotype frequencies, which became known as the Hardy–Weinberg law.

In maize, and more recently in sorghum and pearl millet, indirect approaches are deployed based on inbreeding and cross-breeding.

Hybrid maize (*Zea mays*) is a model example of genetic theory being successfully applied to a food crop (Duvick, 2001). The classic work of inbreeding and cross-breeding was performed on maize, where the phenomena of inbreeding depression, or reduced performance, and heterosis, or hybrid vigour, were discovered. The poor vigour and seed production of the inbred strains was overcome for commercial exploitation by the use of two vigorous single crosses to be used as parents to produce double-cross hybrid seed combining the desired characteristic with the rigour of the single-cross parents. Maize yield doubled between the 1930s to 1960s with 60–80% of the gain being attributed to heterosis. Since the 1960s high-performing inbreds have been generated for use as single-cross hybrids. In addition to their use in maize, F_1 single-cross hybrids have been a significant driving force behind vegetable and tomato breeding creating uniformity, greater stability and sustainability for mechanical harvesting by using this technique of single-cross hybridisation.

Clonally propagated crops (vegetatively from parts of the plants), e.g. potato and cassava, are usually highly heterozygous and outbreeding. Breeding methods are based on intercrossing between highly heterozygous variants and selection among seed progenies. Poly-cross designs similar to that used in forage crops are also used to efficiently generate large quantities of seed. A major challenge for clonally propagated crops is the generation and maintenance of collections of genes for the crops which are free of disease. Nassar and Ortiz (2010) provide a comprehensive account of the breeding strategy for cassava that includes wide hybridisation, and introgression programmes, i.e. movement of a gene from one plant into another by the repeated backcrossing of an interspecific hybrid with one of its parent species. For example, hybridisation between cultivated cassava, *Manihot esculenta*, and *M. glaziovii* is deployed to produce disease-resistant clones, plants from parts of others, with elevated protein. For many perennial crops, breeding is challenging due to polyploidy, i.e. the plant having more than one set of paired chromosomes. This is illustrated by bananas (*Musa* spp.) that are made up of *M. acuminata* (A genome) and *M. balbisiana* (B genome) and are generally triploid (i.e. have three sets of chromosomes) and seedless (sterile). Such hybrids are widely distributed by vegetative propagation and are vulnerable to diseases such as Panama disease fungus (*Fusarium oxysporum* f. sp. *cutsense*). Recently D'Hont *et al.* (2012) published the draft genome sequence of the 523 megabase genome of a *Musa acuminata* doubled haploid genotype. This genome sequence is providing fundamental

new knowledge and insight into plant immunity genes and soluble sugar balance in ripening banana.

Bananas, plantains, cassava, potato and sweet potato as well as other indigenous African root vegetables are key to solving Africa's food and income security challenges. These vegetatively propagated crops are an excellent source of cheap energy and are a key staple food in sub-Saharan Africa. A uniquely African Green Revolution requires urgent improvement in the supply of new and improved cultivated varieties of these vegetative crops. New genome sequencing approaches of the hereditary information, coupled with new computing techniques, will enable discovery of genes controlling disease resistance in clonally propagated crops and improve our understanding of the biological mechanisms controlling post-harvest physiology.

In this section we have focused on the concepts and practices that underpin classical plant breeding. We consider that a comprehensive understanding of plant breeding methods is of critical importance to analyse how the benefits of crop genomics can best be deployed to maximise the improvement of plants to further help feed the world in a sustainable and equitable manner.

OPPORTUNITIES FROM GENOMIC TECHNOLOGY

Genomics research and its application to crop breeding are at an interesting stage where two main drivers are beginning to converge. First, we have a democratisation of genomics technology where the speed (and accessibility) of sequencing is accelerating and the cost is dropping. On average we have a doubling of sequencing data output every 5 months and this has resulted in a free fall in cost per DNA base sequenced (Varshney and Dubey, 2009). In parallel, food and nutrition security is a global priority and agriculture is recognised as pivotal to generating a sustainable planet based on a viable green economy. The convergence of technological advances and the need to address global challenges has dramatically changed the perspective on the breeding of orphan crops where genomics-based approaches are no longer rate limiting (Fridman and Zamir, 2012). Future developments and applications to crop breeding are likely to be more dependent on population development, the ability to reproducibly phenotype important traits, access and utilisation of genetic variability together with the status, capacity and scale of the breeding programme. This coupled with the leadership and support of breeding programmes will be key determinants of success.

Genetic variation is the engine that drives advances in plant breeding (Morrell *et al.*, 2011). Advances in next-generation sequencing have resulted in the completion of reference genome sequences for many important crops and model plants (Ehrhardt and Frommer, 2012). For example, the draft genome sequence of pigeon pea (*Cajanus cajan*), an orphan legume crop, was published in 2011 (Varshney *et al.*, 2011), providing a platform for gene identification and for the large-scale discovery of genetic markers, particularly single-nucleotide polymorphisms (SNPs) where a single nucleotide is altered. However, further advances and application in crop breeding will require the development of genotyping by sequencing (Elshire *et al.*, 2011), resequencing of different varieties of crop plants coupled with the assembly of next-generation populations (Cavanagh *et al.*, 2008). Rapid developments in these areas are improving our understanding and knowledge of crop genomes and enabling direct translation of gene annotation to allele and haplotype (i.e. groups of genes) discovery in relation to trait and phenotype diversity. Resequencing studies and comparative population genomics of maize landraces and improved maize lines have identified regions of the maize genome influencing gene expression and the removal of *cis*-acting regulatory variation (i.e. a length of DNA which can regulate several genes and, conversely, one gene can have several such lengths) during maize domestication and improvement (Hufford *et al.*, 2012). A genome-wide analysis of 278 maize lines has also been undertaken to quantify changes occurring during the breeding process (Jiao *et al.*, 2012). This study revealed that rare alleles were accumulated during the breeding process suggesting that the relative fractions of rare alleles could be used as a selective index in breeding. The methods described for maize and rice (Xu *et al.*, 2012) illustrate the power of next-generation sequencing and genotyping by sequencing to characterise collections of germplasm as genetic resources and identify novel variant alleles for deployment in breeding. These approaches also overcome the limitation of sampling bias that has impeded the genetic evaluation of diverse germplasm collections. These studies emphasise that for many crops of relevance to Africa the bottlenecks will not be genomic resources but carefully chosen and designed populations that sample genetic variation and increase the detail of the genetic analysis of complex characters.

Community-based populations of crop plants provide great opportunities to discover, characterise and deploy alleles that have direct relevance to breeders (Hamblin *et al.*, 2011). Essentially these approaches are designed to overcome the limitations of two-parent populations

and manipulate population structure to increase genetic resolution. Although there are many potential designs, all have two components in common, the use of multiple parents to increase allelic diversity and the advancement of populations through several generations to improve genetic resolutions. One such population design is the so-called 'nested association mapping' (NAM) population first developed in maize and is based on crossing diverse strains to a reference parent B73 (Yu *et al.*, 2008) and has already been used to isolate a number of genes controlling complex traits (Kump *et al.*, 2011). Other designs involve intercrossing multiple parents to form a single large population and are often referred to as multi-parent advanced generation intercross (MAGIC) populations (Cavanagh *et al.*, 2008). This method is being deployed in wheat, rice and sorghum.

It was assumed that the dramatic drop in the cost of DNA-based assays would result in an accelerated use of marker-assisted selection (MAS) in plant breeding, in which a biochemical marker is used for selecting plants with the desired characteristic. MAS was used to introduce tolerance to submergence in water (*Sub 1*) into rice varieties grown in 15 million hectares of rain-fed lowland rice in South and Southeast Asia (Septiningsih *et al.*, 2009). While MAS has been used successfully in recurrent backcrossing (including importantly programmes to introgress transgenes from another species), its more general application has been limited (Langridge and Fleury, 2010). The reason for this is twofold: first, many of the traits of importance to breeding programmes are complex and are controlled by large numbers of genomic regions, each with relatively small genetic effect; second, the method of estimating the effect of stretches of DNA containing or linked to the genes that underlie a quantitative trait are often based on bi-parental populations that are non-representative of breeding germplasm. To overcome these deficiencies, Meuwissen *et al.* (2001) proposed a different approach known as genomic selection. In this method genome-wide panels of genetic markers are used to predict performance across the genome and has the promise to deliver more accurate predictions (Jannink *et al.*, 2010). This approach represents a paradigm change based on the ability to score large numbers of markers at low cost. The simultaneous estimate of all marker effects can be used to generate an estimated breeding value (EBV). This requires a 'training population' of individuals that have been both genotyped and phenotyped to develop a model to produce EBV (Heffner *et al.*, 2009). Such studies have been deployed in dairy cattle and are now being applied to crop plants.

This is an exciting time for plant breeders. The basic knowledge of crop genomes has increased exponentially providing new opportunities

for crop improvement. However, there is a gap that may indeed be widening between this information and plant breeding practice. Plant breeding is resource intensive and very dependent on the accurate collection of data to support decision-making. It is also dependent on the migration of new information from the faster-moving fields of human genetics and evolutionary theory. This, coupled with new discoveries on the control of genes determining complex traits, means that plant breeding strategies and methodologies have become more advanced and dependent on new knowledge. The ever-increasing power of computer simulation (Li *et al.*, 2012) can compare different breeding strategies, include different modes of gene action and can help bridge the gap between theory and practice, but inevitably any simulation will require validation in plant breeding programmes.

In summary, plant breeding is a key technological platform that is of critical importance to feed a future 9 billion people equitably, healthily and sustainably (Beddington, 2010). The introduction of improved crop varieties has been most successful for the major crops in favourable agro-ecological areas where a combination of genetic and agronomic (fertiliser, pesticide and irrigation) factors have made approximately equal contributions. More attention needs to be focused on breeding for less favoured 'orphan crops' (Brummer *et al.*, 2011). These are of particular importance to smallholder farmers in sub-Saharan Africa and include sorghum and millets, groundnut, cowpea, common bean, chickpea and pigeon pea, cassava, yam and sweet potato. Breeding for orphan crops has lagged behind major crops but genomic technologies offer significant opportunities to reverse this trend and make a significant contribution to the key staple crops in many developing countries. To realise this goal will require the judicious application of basic plant breeding principles, coupled with appropriate experimental design to quantify phenotypic variation in a reproducible manner, to design and effect phenotypic selection regimes. There is also a need to harmonise current plant breeding practices with ecological and management practices that sustain and improve the natural resource base. In broad terms this will require plant breeders to identify and select genotypes that are climate resilient and able to maintain productivity in suboptimal conditions. In addition, creating new ideotypes (i.e. specifically designed and adapted crops with particular shoot or root architectures) that can contribute to creating and supporting ecosystems services is required (Ehrhardt and Frommer, 2012). A key objective will be to target specific environments and identify adaptive gene complexes to maximise productivity in individual landscapes.

Breeding crops that are appropriate for local conditions is vital for their widespread adaptation, and schemes to promote greater participation through the involvement of local farmers in the breeding process (participatory plant breeding) are important components of a decentralised plant breeding strategy.

WHAT DOES THIS MEAN IN THE CONTEXT OF
AFRICAN AGRICULTURE?

- This is a good time to be considering plant breeding in the context of African agriculture. A comprehensive, strategic perspective is required that will not only consider the technology but the biology of the species that are of critical importance to Africa.
- Priority should be given to clonally/vegetatively propagated crops that are well placed to benefit from developments in genomics. Identification of elite clones can form part of a participatory farming approach to facilitate uptake and dissemination of planting material. Higher-yielding, disease- and pest-tolerant new cultivars can form the basis of multiplication chains that are connected to a phytosanitary testing scheme to control plant diseases.
- Education, training and skills with a strong orientation towards species of relevance to Africa are essential. This needs to include cutting-edge research in genetics, population biology, analysis of complex traits and experimental design/statistical analysis. The goal should be to inspire a new generation of African plant breeders who can assimilate and integrate new modern concepts and approaches into practical and productive plant breeding programmes.
- New innovative partnerships between funders, breeders, policy-makers, urban planners, ecologists, educational institutions and professional communicators are needed to articulate that plant breeding is of critical importance in harmonising agricultural productivity and environmental sustainability in the developing world.
- The culture of plant breeding needs to be compatible with the goals of African agriculture to embrace species diversity and farming systems. This needs to consider the agro-ecology and socio-economic context. A bold vision for African plant breeding is needed with a focus on crops that promote not only

food security but income and productive employment. Such an holistic approach is needed to embrace the need for sustaining the natural resource base.

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