African Journal of Biotechnology Vol. 3 (10), pp. 489-496, October 2004
Available online at http://www.academicjournals.org/AJB
ISSN 1684–5315 © 2004 Academic Journals

Review

Applied genomics in the improvement of crops grown in Africa

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Accepted 15 September, 2004

Crop biotechnology seems to be in its infancy in Africa, some national researchers are well trained in this area but lack of funding from their national governments does not allow them take advantage of their knowledge and professional skills. Among the agro-biotechnology tools, tissue culture ranks first in the micro-propagated and tree crops. DNA marker-aided breeding for a range of traits (particularly to overcome diseases and pests or low input environments) should become the second most important application of agro-biotechnology in the mid-term. Molecular markers are being used worldwide to tag specific chromosome segments bearing the desired gene(s) to be transferred (or incorporated) into breeding lines (or populations). In this way, indirect selection with co-dominant molecular markers tightly linked to the gene(s) controlling the characteristic(s) of interest improves response to selection, because heritability for co-dominant markers equals to 1. Molecular markers are therefore descriptors that offer reproducible results for characterizing genotypes. Similarly, applied plant genomics also improves the understanding of crop gene pools, which are being enlarged by including transgenes and "native" gene pools. Furthermore, finding new genes adds value to traditional agricultural products. There are many on-going applications of DNA markers in research-for-development and crop improvement for crops grown by African farmers. Marker-assisted selection and –aided introgression are being employed by private and public plant breeders mostly to locate and select genes for controlling important quality and disease or pest resistant traits.

Key words: Genomics, crops, biotechnology, breeding, Africa.

INTRODUCTION

Food production in the tropical developing world must rise dramatically to keep pace with the expected increase in population. Many of the staple foods of the developing world feed tens of millions of poor people daily yet receive relative little attention from the biotechnology industry, because they are not major cash crop commodities (they are mostly consumed in the home or village). Although many types of intervention will be important, much of the increase will need to come from advances in crop productivity. The successful augmentation of traditional approaches to plant breeding based on advances in applied biotechnology will be a critical component in this endeavor (Dodds et al. 2001).

The primary resource of plant breeding programs is the genetic variability available within germplasm closely related to the crop of interest. However, the success of crop improvement programs is highly reliant on the power and efficiency with which this genetic variability can be manipulated. Genetic markers offer plant breeders the potential of making genetic progress more precisely and more rapidly than through phenotypic selection. DNA markers also offer the possibility of addressing previously unattainable goals such as pyramiding disease resistance genes. The potential impact of molecular breeding is equal for crops in both temperate and tropical regions. In particular, progress in model systems offers

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the possibility of supporting both substantial and rapid developments in tropical crop improvement that would not be conceivable through traditional methods.

The centers of the Consultative Group on International Agricultural Research (CGIAR) are committed to the application of biotechnology techniques to assist the investigation, genetic improvement and phyto-sanitation of their mandated crops. During the past two decades the international institutes and their collaborators have effectively established routine *in vitro* techniques to support these activities and have subsequently transferred these tools to a range of national programs across the region. On this basis, it is now appropriate for the research centers of the CGIAR to follow a similar scenario with the application and transfer of DNA marker technologies. In this regard, the CGIAR Generation Challenge Program aims to bridge that gap by using advances in molecular biology and harnessing the rich global stocks of crop genetic resources to create and provide a new generation of plants that meet these farmers' needs. Generation is one of three pilot challenge programs of the CGIAR, and involves an international, multi-institute, cross-disciplinary collaboration designed to ensure that the advances of crop science and technology are applied to the specific problems and needs of resource-poor people who rely on agriculture for subsistence and their livelihoods (http://www.generationcp.org/).

DNA marker technology offers to dramatically enhance the efficiency of plant breeding just as molecular biology has revolutionized research in the life sciences. The theoretical advantages of marker-assisted selection have long been recognized but the facilitating technology has been too expensive and too slow. However, more recently, advances in automated technology have finally presented the possibility of efficiently applying these techniques at the scale of modern plant breeding programs. At the same time, the large-scale exploration of plant genomes that is now possible will rapidly narrow the gap in knowledge between the model systems and lesser-studied crops.

In many instances, genomics data will be a vital link in the development of knowledge-led breeding schemes. Advances in genomics will greatly accelerate the acquisition of knowledge leading to the development of new tools for screening and manipulating genomes based on first principles. For example, more information will be available on the mechanistic basis of hybrid vigour that will allow more directed approaches to design or manipulate this phenomenon. Similarly, a better understanding of epistasis and genotype-by-environment interaction in the expression of complex agronomic characters will facilitate the development of rational approaches for the precise manipulation of quantitative trait loci (QTL). Meanwhile, DNA markers and gene sequencing will provide quantitative means to determine the extent of genetic diversity and the need for broadening the genetic base of breeding populations with exotic or wild genetic resources. Furthermore, with information obtained using molecular markers, patterns of crop evolution and adaptation can be investigated and this new knowledge should be used to develop evolutionary breeding schemes.

USE OF GENETIC MARKERS IN PLANT BREEDING

Choice of technology

The theoretical advantages of indirect selection using genetic markers were first reported nearly eighty years ago. However, it was not until the development of DNA marker technology, that a large enough number of genetic markers could be generated to accommodate the needs of modern plant breeding programs (Table 1). Now there is a profusion of DNA markers, each having a different set of advantages in particular application (For further information http://www.nal.usda.gov/pgdic/tutorial/lesson4.htm).

Random amplified polymorphic DNA (RAPD) and amplified fragment length polymorphism (AFLP) markers are highly effective for germplasm evaluation and certain molecular breeding approaches (such as the introgression of a novel trait from exotic germplasm). Both can be used without prior knowledge of the genome to rapidly and efficiently screen the genome. However, RAPD analysis suffers from problems of repeatability in many systems, especially when transferring between populations or laboratories as is frequently necessary with marker assisted selection programs. Conversely, ALFP analysis has significant practical limitations for routine screening of large breeding populations in marker assisted selection systems.

Markers based on known genomic sequence information, e.g. SSR, EST, SNP are extremely effective and appropriate tools for molecular breeding as they are based on simply protocols yet readily provide reliable high quality data. However, they are all expensive and time consuming to develop as they require extensive cloning and sequencing efforts.

Choice of trait and strategy

The decision of which traits in a plant breeding warrant the application of DNA markers requires intensive discussion between molecular biologists and plant breeders. Factors affecting this decision will include ease, cost and stage of traditional selection for that character as compared to the cost, time saving and enhanced precision of indirect selection based on molecular markers.

The cost-benefit analysis must identify that indirect selection has a real advantage over traditional

Table 1. Major classes of genetic markers.

Morphological traits	Such as seed or flower color are seriously limited in number and their expression can be differentially affected by the environment.
Proteins	Seed storage proteins, structural proteins and isozymes provide very cost effective markers but their number may be limiting and their expression is not neutral.
Restriction fragment length polymorphism (RFLP)	Requires hybridization of probe DNA with sampled plant DNA and although provides high quality data has a severely restricted throughput potential.
Random amplified polymorphic DNA (RAPD)	The first of a new generation of markers based on the polymerase chain reaction (PCR). This technique uses arbitrary primers for initiating amplification of random pieces of the sampled plant DNA. This technique requires no knowledge of the genome to be screened but suffers from problems of inconsistency when transferred between populations and laboratories.
Simple sequence repeat length polymorphism (SSR)	This technique provides high quality, highly consistent results but the markers are expensive to develop as they require extensive sequence data from the species of interest. However, once developed this type of marker is easily transferred between populations or laboratories and is amenable to high throughput screening.
Amplified fragment length polymorphism (AFLP)	In this approach the sample DNA is enzymatically cut up into small fragments (as with RFLP analysis) but only a fraction of fragments are studied following selective PCR amplification. Although this assay provides a great quantity of marker information, it is not particularly well suited to high throughput marker assisted selection.
Expressed sequence tag (EST)	The development of EST markers is dependent on extensive sequence data of regions of the genome that are expressed. However, once developed they provide high quality, highly consistent results and because they are limited to expressed regions of the genome, markers themselves are directly associated with functional genes. As with SSR markers, EST markers are amenable to high throughput screening
Single nucleotide polymorphism	The majority of differences between individuals are point mutations due to single nucleotide polymorphisms. As such, there are a vast number of potential SNP markers in all species. Massive amounts of sequence data are required to develop SNP markers, particularly as many may be population specific. However, their great advantage lies in the potential to screen them through simply yes/no tests that can be readily automated to facilitate mega-throughput screening through the use of technologies such as micro arrays.

approaches - i.e., it is cheaper or easier than phenotypic selection because it allows a substantially smaller population to be evaluated in the field, and reduces the number of breeding cycles necessary to reach a set goal. Likewise, it frees important labor at a crucial stage of the season, thereby substantially increasing the precision of selection. Characters that typically fall into these groups include those traits difficult or expensive to score in the field such as certain types of disease resistance, root development and male sterility/fertility restoration loci, or traits that are expressed late in the growing season such many quality characters. There are also other situations warranting the application of DNA markers, including new breeding strategies made possible through the application of molecular markers - i.e. screening resistance to quarantined diseases, or pyramiding genes from diverse sources. DNA markers can be employed to assist a wide range of components of modern breeding programs (Table 2).

Costs and benefits of using DNA markers in plant breeding

Until recently the cost and throughput potential of DNA marker analysis has restricted the use of this technology to the research and development programs of public research institutes and multinational breeding companies. However, the global focus on sequencing entire genomes of microbes, model animal species and now plant species, has driven rapid developments in automated, high throughput sequencing machines. Fortunately for plant breeders, these machines are also highly appropriate tools for high throughput screening of DNA markers. This increasing demand for high throughput systems for genomic analysis is also driving a simultaneous reduction in the unit costs associated with such screening. Consequently, not only is it now practical to screen DNA markers on the scale of modern plant breeding programs but the costs of doing so are

Table 2. DNA markers application in plant breedind.

DNA Markers	Applications
Improved access and utilization of germplasm resources	DNA marker analysis for defining the genetic structure of plant populations, species, genera and families in order to optimize the acquisition, management and utilization of germplasm collections
Genetic analysis of breeding populations	For many crops, particularly tropical vegetatively propagated crops, the current genetic and cytogenetic knowledge restricts crop improvement efforts. Molecular markers are contributing to a substantial resurgence of progress in these areas.
Parental selection and predicting progeny performance	Based on genetic diversity estimated by DNA marker analysis.
Marker assisted selection	When introgressing traits from exotic germplasm, DNA markers can be used for indirect selection of that trait plus simultaneous selection of offspring with the least amount of other genomic material from the exotic parent
Marker enhanced backcross breeding	When introgressing traits from exotic germplasm, DNA markers can be used for indirect selection of that trait plus simultaneous selection of offspring with the least amount of other genomic material from the exotic parent.
Pyramiding genes from diverse sources	It may not be possible to identify different sources of resistance to the same disease through field evaluation. However, it is useful to combine different sources of resistance in the same cultivar in order to reduce the chance that the pathogen will evolve mechanisms to breakdown this resistance. Similarly, many genes may contribute to important agronomic characters such as yield but it may not be easy to identify the presence of individual genes through field evaluation.
Fingerprinting for impact assessment and protection of plant breeders' rights	By identifying unique DNA marker fingerprints, elite lines can be identified in farmers' fields and in the pedigree of new cultivars.
Comparative mapping	Recent studies on both cereal and legume crops have shown a high level of similarity of certain genes and the position of those genes in the genome across members of this diverse group. These developments will allow the considerable progress in model systems to be increasingly utilized in related and unrelated species and genera.
Gene isolation, function and manipulation	Based on dense DNA marker maps, scientists can move onto the isolation and characterization of single genes and whole genomic regions. From this point, rapid progress can be made in determining gene function or transferring important genes across species barriers.
Fingerprinting pests	DNA marker analysis for phytosanitation screening or monitoring changes in pest populations in order to predict the breakdown of current sources of resistance to viruses, bacteria, fungi, nematodes, arthropods and insects).

becoming increasingly plausible alternatives to the costs associated with glasshouse, nursery and field evaluation. Most recently, the development of micro-array technology offers the future opportunity of simultaneously screening the entire genome of a plant. This massive reduction in size and simultaneous increase in scale of throughput will revolutionize genetic mapping and marker-assisted selection.

MARKER-ASSISTED BREEDING IN SUB-SAHARAN AFRICA

The development of many classes of DNA marker

remains technically demanding and, therefore, beyond the scope of typical plant breeding stations, whether they be commercial companies in industrialized countries or national programs in sub-Saharan Africa (Crouch and Tenkouano 1999). For commercial companies, the simple and cost effective solution is to contract such developmental work to nearby specialist genomics companies or research institutes. In contrast, with the development of DNA markers based on the polymerase chain reaction (PCR), the actual routine screening of breeding populations has become a realistic activity for any breeding station already capable of low tech. tissue culture operations such as micro-propagation and production of double haploid populations.

In the short-term at least, the international institutes of the CGIAR together with their collaborators in the Generation Challenge Program or contractors in industrialized countries, and NEPAD BioSciences East and Central Africa (BECA) aim to provide a convenient yet catalytic bridge for national programs in the region who wish to enter into these new fields. In this way, it is hoped that human resources and functional facilities within the national programs can be developed through participation as an active partner in appropriate projects. In this way the international centers will also act as a conduit for ready access to knowledge and technologies in this rapidly advancing field.

Many commercial companies in industrialized countries find it cost effective to also contract out the routine screening of breeding populations (up to a threshold of around 500,000 samples per year). However, in Sub-Saharan Africa the international organizations are committed to developing national infra-structural capacity in this discipline to both increase the efficiency of national breeding programs and to stimulate the development of entrepreneurial enterprises. Moreover, we consider that routine screening of simple PCR-based markers is an appropriate entry point into genomics for many national programs in the region. Some critics claim that with the infra-structural limitations across much of Africa, that the region is not ready for full-scale entry into this field. However, we would warn that the future development of African agriculture desperately needs the intensive attention of biotechnologists focusing on those crops and constraints unique to this region (Table 3). In acknowledgment of this need and following their tremendous success in supporting biotechnology research for rice in Asia, the Rockefeller Foundation has recently made a major commitment to supporting research to apply biotechnology to African crops for the development of tolerance or resistance to drought and the parasitic weed *Striga* (Haussmann et al. 1999). Similarly, the United States Agency for International Development (USAID) provides significant funding to regional and national undertakings in crop biotechnology throughout the continent. In 2003 NEPAD, mostly with funds from Canada's International Development Agency (CIDA) launched BioSciences East and Central Africa. These examples show some of the resources that are available for building the needed capacity for molecular breeding in the continent.

At the International Institute of Tropical Agriculture (IITA), plantain improvement was nominated as the model system for developing molecular breeding systems within this institute (Ortiz, in press). This reflects the unique problems and opportunities in *Musa* breeding, including the long generation time and high space requirement of the crop, and the nascent development of plantain breeding. For plantain breeders in West Africa, parthenocarpy (the ability to develop fruit in the absence of seed development) is an ideal character for the initiation of a marker assisted selection program. Parthenocarpy seems to be controlled by just a few genes yet a high proportion of current breeding populations are non- parthenocarpic but can not be identified as such until close to harvest. As such, marker assisted selection for parthenocarpy at the seedling stage would have a dramatic influence on breeding efficiency. The identification of relatively simple pilot projects that can demonstrate substantial improvements in breeding efficiency is a key element for the subsequent widespread acceptance and adoption of these techniques. In contrast, for millet breeders in Africa working together with the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), the application of markers for downy mildew resistance or cytoplasmic male sterility may offer a similarly important starting point.

Vegetatively propagated crops

The first generation of DNA marker analysis of the vegetatively propagated crops at IITA has focused on germplasm characterization, construction of preliminary linkage maps and development of disease diagnostics in plantain/banana, cassava and yam (Ortiz, in press). In this diverse group of crops that are only associated through their reliance on clonal propagation during field production, there is no clearly allied model crop system.

Legumes

Preliminary DNA marker work at IITA in this family concentrated on genetic analysis and germplasm diversity studies in cowpea. More recently, comparative genome mapping of cowpea and mung bean has been achieved. Similar progress has been made in diversity analysis and mapping studies of ICRISAT mandated legume crops (groundnut, chickpea and pigeon-pea) (Dwivedi et al., in press). Ultimately this should be extended to comparisons with soybean (also an IITA mandated crop) and temperate peas. In this way it is hoped that comparative mapping to these intensively

Table 3. Future prospect in the breeding of tropical food crops with DNA markers in sub Saharan Africa.

Vegetatively Propagated Crops	
Plantain and banana	Current priorities for the molecular breeding of *Musa* crops focus on the development of appropriate marker-assisted selection schemes for parthenocarpy, apical dominance/regulated suckering and short cropping cycle. Thereafter, the focus will turn to markers for post-harvest characters and for favorable alleles contributing to heterosis in components of yield.
Cassava	The development of markers for post-harvest characters and virus resistance appears to warrant the greatest emphasis for cassava breeders. In the longer-term, it is proposed that attention should focus on the development of DNA markers for tolerance to abiotic stresses and for storage characteristics.
Yam	Many of the important agronomic characters in yam breeding are difficult or expensive to score. On this basis, marker assisted selection could be warranted in this crop for resistance to nematodes and viruses, tuber dormancy, and post-harvest characters (texture, taste and oxidation). For yam, progress in the molecular breeding of potato might provide good orientation but cannot promise any direct benefits.
Legumes	
Cowpea	As in most legumes grown in the semi-arid tropics, insect pests present the overwhelming constraint. Thus, in cowpea, the development of markers for resistance to thrips, bruchids, *Maruca* and pod borer is considered of greatest priority. In the longer term, markers for resistance to the parasitic weed *Striga* and markers for genes contributing to drought resistance are considered a high priority intervention
Groundnut (or peanut)	Drought, fungi, viruses, bacteria and insect pests are among the major constraints in groundnut production. The identification of genome regions bearing the genes controlling tolerance or resistance to these constraints may be the main target, as a first step, for marker-assisted selection aiming to pyramid resistance within the cultivated gene pool or for germplasm enhancement with wild species, which possess the resistance genes for most biotic constraints. In addition, DNA markers should be used to identify diverse germplasm that can be used to broaden the genetic base in groundnut breeding.
Chickpea	*Ascochyta* blight, *Fusarium* wilt, root rots, *Botrytis* gray mold and pod borer are among the most important diseases and pests of chickpeas. A preliminary genetic map has been developed in this species but considerable work remains to identify markers, particularly for tolerance and resistance to biotic stresses.
Soybean	Tremendous advances in all aspects of the molecular breeding of soybean are being made in advanced laboratories particularly in the USA. Although, these may provide substantial background understanding and perspective, many of the constraints to soybean cropping in sub-Saharan Africa are very different. A high priority, for example, could be the use of marker-assisted breeding for selecting lines with the ability to cause germination of *Striga hermonthica*, a parasitic weed affecting maize but not soybean. In the longer term, increased nodulation and resistance to pod shattering would be highly important candidates for marker-assisted selection systems.
Pigeon pea	*Fusarium* wilt, sterility mosaic virus, *Phytophthora* blight and pod borer substantially reduce crop productivity of pigeonpeas. Resistance breeding to achieve both stability and productivity are top priority in the genetic enhancement of this pulse. Thus, DNA markers for pest and disease resistance will also be of utmost importance. The development of F_1 hybrid cultivars of pigeon pea was the first amongst the legume crops. For this reason, the development of marker-assisted selection for new sources of fertility restoration will also have high priority in this crop.
Cereals	
Sorghum	The major stresses affecting sorghum are drought, *Striga*, grain mold fungal diseases, anthracnose, foliar fungal diseases and insect pests such as stem borer, shoot fly, midge and head bugs. The use of microsatellite markers to assess genetic diversity has been helpful in defining new breeding strategies in this crop. Now the development of DNA markers for resistance to pests and diseases is receiving greatest priority, e.g. in breeding new populations for *Striga*-prone environments.

Table 3. Contd.

Pearl millet	The most important constraints are drought, high soil temperature, downy mildew, panicle diseases and insect pests. Markers for downy mildew resistance have already been developed and successfully used to aid the backcross breeding of a parental inbred line for an F_1 hybrid cultivar which is now grown on more than one million hectares across India. However, in the long-term marker-assisted selection should be used to generate new cultivars combining this source of resistance with horizontal polygenic background resistance in order to lengthen the probable life span of new cultivars
Maize	The development of biometrical techniques and their association with DNA marker data is probably more advanced in maize than any other crop. Based on comparative mapping, it is likely that sorghum in particular will greatly benefit from general advances in the molecular breeding of maize. However, in common with soybean, many of the specific constraints to maize production in sub-Saharan Africa are very different from those in the USA. Again of greatest importance is the identification of markers for resistance to the parasitic weed *Striga* and insect pests such as *Sesamia*. The development of *Striga* resistant maize cultivars is crucial for the future success of maize production in sub-Saharan Africa, but it is sometimes extremely difficult or expensive to screen for this trait.
Rice	Due to the great importance of this crop combined with its relatively small genome size, rice is probably the most intensively studied crop in terms of traditional and molecular genetics. In addition, when the genomes of the various cereal crops are aligned, rice can be placed at the very core, and thus rice has become known as the nodal species for the cereal crops. This finding has intensified molecular genetic research on rice, as progress in sequence-based research can be made mostly quickly in the crop with the smallest genome and then findings can be extrapolating to other cereal crops.

researched crops will facilitate rapid progress in the lesser-studied crops. In particular, all the major legume crops of the semi-arid tropics are greatly troubled by insect pests. As the main sources of resistance to such pests tend to be found in exotic germplasm, the development of marker-aided backcross schemes is a high priority in these crops.

Cereals

Progress in the molecular breeding of cereal crops leads that of all other crop families. In particular, comparative mapping between maize, sorghum, millet and rice has shown how this approach can facilitate transfer of progress in model systems to that of lesser- studied species. The order and position of genes are highly conserved amongst the cereal crops. On this basis, the positions of useful genes in target crops may be inferred by comparing with the dense map of a related model crop (Mahalakshmi and Ortiz 2001, Mahalakshmi et al., 2002). One day the drought resistance of pearl millet may contribute to developing hardy and water-efficient sorghum, maize, rice and wheat. Conversely, based on the intensive study of genes for other important agronomic characters in rice or maize, it may be possible to make rapid developments in the improvement of these traits in sorghum and millet breeding. The breeding of F_1 hybrid varieties will be increasingly important in all cereal crops. In this respect, the development of parental selection systems based on DNA marker analysis and the identification of markers for male sterility and fertility restoration genes will be critical interventions.

OUTLOOK

The use of DNA markers for indirect selection offers greatest gains for quantitative traits with low heritability as these are the most difficult characters to work with in the field through phenotypic selection. However, this type of trait is also amongst the most difficult to develop effective marker assisted selection systems. The literature is overwhelmed with reports of DNA markers for every conceivable character across most widely grown crops. However, there is a noticeable absence of papers describing the effective use of such markers, particularly in breeding schemes all the way through to cultivar registration. Very often, this is because the markers developed in research projects lack the robustness required for effective application in plant breeding programs. In particular, the expression of these traits can be greatly affected by genotype-by-environment interaction and epistasis that can complicate the development of marker assisted selection systems to the

same extent that they confuse traditional field based selection. It can not be reiterated too often that the quality of a marker-assisted selection program can only be as good as the quality of the phenotype data on which the development of that marker was based. Consequently it will be necessary to use much larger mapping populations that are characterized in many locations across several years. The selective power of markers must then be verified in a range of populations representing the diversity of current breeding populations. Only then will it be possible to identify markers that can be effectively applied to assist the selection of complex characters.

During the next decade, traditional breeding approaches will be greatly aided by DNA marker selection enabling rapid generation of new cultivars for the small landholders in Africa and across the developing world. Innovative plant breeders are changing their *modus operandi* in order to develop objective marker-assisted introgression and selection methods that increase the efficiency of their genetic improvement programs and allow them to address new goals. To achieve success in this new endeavor, cheap, easy, decentralized and rapid marker screening procedures will be required. The international research centers of the CGIAR are committed to developing these tools in collaboration through the Generation Challenge Program with advanced research organizations in Europe, USA and across the world that can be quickly established in national plant breeding programs across Africa.

In this article we have concentrated on the current phase of structural genomics (using DNA markers for linkage mapping and marker-assisted selection). This will in turn lead to a secondary phase of functional genomics that will focus on the mining of data sets generated in the first phase. Functional genomics will link sequence data with the function of genes and lead to new insights into the behavior of biological systems. Functional genomics will offer unprecedented opportunities to readdress every question in biology and in turn will forge new frontiers in manipulating biological systems for greater production of food.

Future Prospects

Gains in crop productivity through research advances in genetic enhancement will help to achieve sustainable food security, poverty alleviation, and environmental protection in the tropics. The CGIAR has a commitment to transfer the benefits of plant biotechnology to the developing world, as genes relevant to their crops and environment become available. Therefore, genomics offers a new means for applying science to improve agriculture in areas of the world where environment and biotic stresses are the major constraints for crop productivity.

DEDICATION

The authors wish to dedicate this article in the memory of Dirk Vuylsteke (1958-2000), who tragically died in the course of his work. Dirk devoted his life to agricultural development in Africa as a biotechnologist, breeder and team leader at IITA. His innovative ideas, open-minded style, hard work and commitment to the African small landholder will always be a source of inspiration for his colleagues in the CGIAR and the new generation of scientists joining international agricultural research.

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