DRAFT FOR DISCUSSION

White paper on GCP research components: Informative molecular markers

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Acronyms, short names and abbreviations – Informative molecular markers

AarhusU	Aarhus University, Denmark
ABA	abscisic acid
ACPFG	Australian Centre for Plant Functional Genomics, Pty Ltd
ADOC	Allelic Diversity of Orthologous Candidate Genes project (of GCP)
AfricaRice	Africa Rice Center
Agropolis	Agropolis International, France
Agropolis–CIRAD	Centre de coopération internationale en recherche agronomique pour le développement, France
Agropolis–INRA	Institut national de la recherche agronomique, France
Agropolis–IRD	Institut de recherche pour le développement, France
Al	aluminium
Alt_{SB}	major Al tolerance gene in sorghum cross BR007 × SC283
ARI–Naliendele	Naliendele Research Station, Tanzania (of the Agricultural Research Institute)
ARS–Durgapura	Agricultural Research Station–Durgapura, India (of the Swami Keshwanand Rajasthan Agricultural University)
Barwale	Barwale Foundation, India
BF (see Barwale)	
BirsaAU	Birsa Agricultural University, India
BRRI	Bangladesh Rice Research Institute
CAAS	Chinese Academy of Agricultural Sciences
CERAAS	Centre d'étude régional pour l'amélioration de l'adaptation à la sécheresse, Senegal (*Regional Centre for Studies on the Improvement of Plant Adaptation to Drought*)
CGIAR	No longer an acronym (*formerly* Consultative Group on International Agricultural Research)
CIAT	Centro Internacional de Agricultura Tropical (*International Center for Tropical Agriculture*)
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo (*International Maize and Wheat Improvement Center*)
CIP	Centro Internacional de la Papa (*International Potato Center*)
CIRAD (see Agropolis–CIRAD)	
CMD	cassava mosaic disease
CNG	Centre National de Génotypage, France
ColoradoSU	Colorado State University, USA
CoPs	communities of practice
CornellU	Cornell University, USA
CRI–CSIR	Crops Research Institute (of the Council for Scientific and Industrial Research), Ghana
CRPs	CGIAR Research Programmes
CRRI	Central Rice Research Institute, India (of the Indian Council of Agricultural

	Research)
CRURRS	Central Rainfed Upland Rice Research Station, India (of CRRI)
CSIRO	Commonwealth Scientific and Industrial Research Organisation, Australia
DNA	deoxyribonucleic acid
DU	University of Dhaka, Bangladesh (also Dhaka University)
DWR	Directorate of Wheat Research, India
EMBRAPA	Empresa Brasileira de Pesquisa Agropecuária (*Brazilian Agricultural Research Corporation*)
ETH	Eidgenössische Technische Hochschule Zürich (*Swiss Federal Institute of Technology Zürich*)
GCP	Generation Challenge Programme (of the CGIAR)
GDMS	Genotyping Data Management System (of GCP)
HZAU	Huazhong Agricultural University, China
IARI	Indian Agricultural Research Institute (of the Indian Council of Agricultural Research)
IBONE	Instituto de Botánica del Nordeste, Argentina
IBP	Integrated Breeding Platform (of GCP)
ICABIOGRD	Indonesian Center for Agricultural Biotechnology and Genetic Resource Research and Development
ICARDA	International Center for Agricultural Research in the Dry Areas
ICRISAT	International Crops Research Institute for the Semi-Arid Tropics
IER	Institut d'Economie Rurale du Mali
IGD	Institute for Genomic Diversity, USA (of CornellU)
IIAM	Instituto de Investigação Agrária de Moçambique (*Institute of Agricultural Research of Mozambique*)
IITA	International Institute of Tropical Agriculture
INIA–Chile	Instituto de Investigaciones Agropecuarias, Chile
INRA (see Agropolis–INRA)	
INRAN	Institut National de la Recherche Agronomique du Niger
IPB	Bogor Agricultural University, Indonesia
IRD (see Agropolis–IRD)	
IRRI	International Rice Research Institute
ISRA	Institut sénégalais de recherches agricoles (*Senegalese Institute for Agricultural Research*)
JIRCAS	Japan International Research Center for Agricultural Sciences
JNKV	Jawaharlal Nehru Krishi Vishwavidyalaya, India
KARI	Kenya Agricultural Research Institute
KU	Kasetsart University, Thailand

MABC	marker-assisted backcrossing
MARS	marker-assisted recurrent selection
MAS	marker-assisted selection
MDR	multiple disease resistance
MoiU	Moi University, Kenya
NAARI (see NaCRRI)	
NaCRRI	National Crops Resources Research Institute, Uganda (of the National Agricultural Research Organisation or NARO)
NAU	Nanjing Agricultural University, China
NCSU	North Carolina State University, USA
NDAUT	Narendra Dev University of Agriculture and Technology, India
NIAS	National Institute of Agrobiological Sciences, Japan
NRCRI	National Root Crops Research Institute, Nigeria
NSFCRC	Nakhon Sawan Field Crops Research Center, Thailand
OregonSU	Oregon State University, USA
PI	Principal Investigator (for GCP)
PSNRU	United States Plant, Soil and Nutrition Research Unit, USA (of USDA–ARS)
PSU	The Pennsylvania State University, USA
Pup1	phosphorus uptake 1 (gene)
QTLs	quantitative trait loci
RAKCA	Rafi Ahmad Kidwai College of Agriculture–Sehore, India
RARS–Nandyal	Regional Agricultural Research Station–Nandyal, India (of the Acharya N G Ranga Agricultural University)
RI	Research Initiative (of GCP), *formerly* Challenge Initiative (CI)
RIL	recombinant inbred line
SABRN	Southern Africa Bean Research Network
SARI–CSIR	Savanna Agricultural Research Institute, Ghana (of the Council for Scientific and Industrial Research)
SAU	South Asian University, India
SCAR	**sequence characterized amplified region**
SCRI	Scottish Crop Research Institute, UK (*now* The James Hutton Institute)
SIRDC	Scientific and Industrial Research and Development Centre, Zimbabwe
SNP	single-nucleotide polymorphism
SSR	simple sequence repeat
TAMU	Texas A&M University, USA
TNAU	Tamil Nadu Agricultural University, India
UAlberta	University of Alberta, Canada
UAS	University of Agricultural Sciences (Bangalore), India

UC–Davis	University of California–Davis, USA
UCB	Universidade Católica de Brasília, Brazil
UCR	University of California–Riverside, USA
USA	United States of America
USD	United States dollar
USDA–ARS	Agricultural Research Service, USA (of the United States Department of Agriculture,)
USPSNL (see PSNRU)	
UTalca	Universidad de Talca, Chile
UVa	University of Virginia, USA
VT	Virginia Polytechnic Institute and State University, USA (also Virginia Tech)
WARDA (see AfricaRice)	
YAAS	Yunnan Academy of Agricultural Sciences, China

Background and process

A series of white papers are being drafted by the Generation Challenge Programme (GCP) team in collaboration with external experts. The goals are to communicate the outputs and deliverables from each research component during 2004–2014 and to explore options for enabling and ensuring that the potential benefits of these components will be fully realised in the future. At this stage, the white papers are really a first analysis for internal use.[1] They are expected to evolve over time, shaped by progress made during GCP's remaining time and by the evolution of international agricultural research for development, particularly in terms of the 'moving landscape' of socio-economic, political and environmental issues in which operate the research portfolios of the CGIAR Consortium of International Agricultural Research Centers and related CGIAR Research Programmes (CRPs). Each white paper is designed to contribute to GCP's orderly closure in 2014 by considering the following three questions:

1. What research assets will be completed by the end of GCP's lifetime in December 2014?

2. What research assets can best continue as integral components of the new CGIAR Research Programmes (CRPs) or elsewhere?

3. What research assets may not fit within existing institutions or programmes and may require alternative implementation mechanisms?

This paper focuses on the outputs and options for GCP's informative molecular marker component. Outputs have been achieved through (a) collaborative work among three sets of actors: a broad network of partners in regional and country research programmes, the CGIAR and academia; and (b) through capacity enhancement to assist developing-world researchers to tap into new genetic diversity and access modern breeding tools and services. GCP research activities have produced the research products described below[2].

Introduction and rationale

Recent developments in plant molecular genetics have provided plant breeders with powerful tools to identify and select Mendelian components underlying both simple and complex agronomic traits. DNA markers enable identification of genes and genomic regions (quantitative trait loci or QTLs) associated with the expression of numerous qualitative and quantitative traits important for crop breeding. Today, scientists are able to genetically dissect pathways that

[1] This GCP white paper, like the others in this series, is not a conclusive, static document. Instead, it will continue to grow and evolve as the processes of evaluation and deliberation advance toward GCP's end in 2014.

[2] GCP is supported by generous funding from an array of donor organisations listed at http://www.generationcp.org/network/funders. See also descriptions of products at http://www.generationcp.org/impact/product-catalogue and of the institutions that generated them at http://www.generationcp.org/research/research-projects.

control important biochemical and physiological parameters, and thus better understand how they are regulated. As a natural extension of the 'discovery phase', molecular markers permit the pyramiding of favourable alleles in targeted genetic backgrounds through molecular breeding. The genetic dissection of a target trait starts with positioning neutral polymorphic markers along the crop genome to construct a genetic map to identify QTLs or to define haplotypes for association studies. Once a marker is identified as linked to a region of interest and explains a significant percentage of the phenotypic variance of the target trait, it is designated as an informative marker.

For simply inherited traits (ie, those that have high heritability and are regulated by only a few genes) or to manipulate a genomic region expressing a large percentage (more than 20%) of phenotypic variance, informative molecular markers linked to those target genomic regions can generally be used in a predictive way. That is, those markers can be used to identify favourable alleles at target loci in new germplasm and to trace the introgression of those alleles into new crosses between a donor line possessing those favourable alleles with elite or popular germplasm presenting poor performance for that target trait. The two most popular molecular breeding approaches based on predictive markers are: (1) marker-assisted selection (MAS), which is the selection of specific alleles for traits conditioned by a few loci; and (2) marker-assisted backcrossing (MABC), which facilitates the transfer of a limited number of loci from one genetic background to another.

For polygenic traits, the use of informative molecular markers is more challenging because the predictability of genetic effects across genetic backgrounds is considerably reduced. This is a result of the genetic complexity of the trait, including factors such as epistasis, gene networking and interactions that generally interfere with significant genotype-by-environment interaction. In other words, a marker can be associated with the expression of a trait of interest in one cross but not necessarily in others. For complex traits, such as grain yield, drought tolerance or low nitrogen soil efficiency, informative molecular markers are identified in a given segregating population by the allelic effects at those loci, allowing identification of the best performing offspring in the same segregating population.

Marker-assisted recurrent selection (MARS) is the most efficient approach, based on linkage disequilibrium, to improve complex traits. It allows the identification of several genomic regions involved in the expression of complex traits and through successive recurrent selection cycles the best-performing genotype within a single population or across related populations can then be 'assembled'. Although MARS is routinely used in private-sector breeding programmes, few reports are available on its use in public-sector breeding programmes. An exception is its use as the breeding method of choice for GCP's Research Initiative (RI) projects.

To understand the genetic basis of target traits and identify linked or gene-based markers at QTLs involved in the expression of those target traits is a must to to successfully improve germplasm through molecular breeding. Consequently, the discovery, development and use of these markers are cornerstone activities within GCP.

The objectives of GCP's informative marker component are to:

1. Identify informative markers for polygenic traits to test (a) their effectiveness in breeding programmes led by scientists in developing countries, and (b) their ability to accelerate understanding of the genetic basis of key traits such as drought tolerance.

2. Develop informative molecular markers that can be used in a predictive mode to conduct integrated breeding for crucial, simply inherited traits for target crops in developing countries

3. Identify new 'secondary traits', associated with key target traits, and test their applicability in breeding programmes.

To achieve these objectives, GCP has supported about 25 projects, mainly competitive. In Phase I (2004–2009), the focus was first to understand the genetic basis of simple and complex traits and to identify new traits with potential application in breeding. In Phase II (2010–2014), the discovered informative markers were used to increase the efficiency of crop breeding as conducted through commissioned projects embedded in GCP's seven Research Institutes RIs (http://www.generationcp.org/research/research-initiatives).

Overall, GCP has invested about USD 18 million in developing informative markers. This sum represents about 12% of the Programme's total budget of USD 150 million spread over 11 years.

Project activities and outputs

Informative molecular marker development in Phase I resulted from competitive discovery projects that explored, in several crops, the genetic basis of tolerance or resistance to selected biotic and abiotic constraints, including drought. As a result, many projects yielded useful and important information on QTLs associated with traits, thus allowing better understanding of their genetic regulation. Some predictive markers for traits, addressing several crop productivity constraints (mainly biotic stresses), were developed from the discovery phase. Most of them have already been used in successful molecular breeding projects. However, for highly polygenic traits the predictive value of most informative markers was generally reduced but their use has been successful through the MARS approach (Research Initiatives, Phase II).

The following examples of projects will indicate GCP's overall contributions to the development of informative markers. Products of these projects and others may be viewed in Annex 1.

Drought tolerance

The genetic basis for drought tolerance is complex, being regulated by many genes. Drought tolerance may be better described as a set of traits although, most often, certain of these are more important, as directly correlated with yield components, or more dominant than others.

QTL discovery across genomes

Despite this complexity, the strategies of plant species to tolerate drought often present clear similarities (eg, reduced transpiration, floral synchrony and long roots). It was thus felt that a common genetic basis may also exist for drought tolerance (or, conversely, sensitivity to drought) across species. To explore this, several projects were conducted in various ways with variable results.

For example, a collaborative project among CIMMYT, IRRI and Agropolis–INRA (France) looked for QTLs and genes controlling tissue growth rate under water stress, sampling leaves across three cereals (maize, rice and wheat) and across three organs in maize (roots, leaves and silks or female reproductive organs). The project combined new approaches of phenotyping (controlled conditions and field), modelling, quantitative genetics and comparative genomics. QTLs for similar drought-tolerance characteristics were discovered across species, several co-located across genomes, but all expressed a limited amount of phenotypic variance, which is expected in maize.

Starting from a different angle, IRRI's scientists attempted to identify common genes in rice and wheat that resulted in grain failure in rice and wheat under water-stressed conditions. QTLs were found in both crops and interesting information was generated, leading to better understanding of the genetic nature of the target traits.

The Allelic Diversity of Orthologous Candidate Genes (ADOC) project took the hypothesis even further, aiming to characterise allelic diversity at orthologous loci of candidate genes for drought tolerance in seven GCP crops (barley, common beans, cassava, chickpeas, potato, rice and sorghum). Work was conducted on reference collections of about 300 accessions for each crop and generated an extensive list of potential candidate genes for drought tolerance regulation.

QTL discovery in a single genome

Rather than using the comparative approach, several projects focused on single crops when targeting drought QTL discovery. Drought-tolerance QTLs were found in wild barley for a large set of morphological traits and yield components. A study in common beans dissected the genetic basis of root architecture, and discovered that plants with longer roots and root hairs having a curling lateral growth habit were more drought tolerant. In rice, loci associated with delayed senescence also conferred increased drought tolerance. Drought tolerance in cassava was extensively studied: traits evaluated included those related to root production, leaf conductance, leaf retention, shoot fresh weight, abscisic acid (ABA) and sugar and starch accumulation in leaves and stems. They were quantified in segregating populations under

different water regimes in Brazil and Colombia and several physiological parameters were correlated with root biomass. These studies generated considerable information and allowed the identification of new traits for drought tolerance screening in cassava.

A genetic study, conducted on a broad and diverse panel of drought-tolerant rice varieties, identified common QTLs across different genetic backgrounds. These informative markers were successfully used to pyramid QTLs from selected genotypes to develop even more highly tolerant breeding lines. Another rice study used bi-parental populations to identify a series of predictive markers for drought tolerance, leading to the development of highly tolerant rice lines for India. The lines are currently undergoing national multilocational trials, prior to release.

In spring wheat, informative QTLs were also found for several physiological traits associated with drought. These findings facilitated the development of a panel of drought-tolerant genotypes from the composite collection in the genebank held at CIMMYT. The informative markers are now used to introgress favourable alleles from the 'stable' QTLs into new crosses in China and India.

The so-called 'stay-green' effect – where tolerant genotypes retain their chlorophyll content for longer and can continue growing marginally under drought – was studied in sorghum. Four markers were used to develop improved tolerant sorghum germplasm for India.

In chickpeas, a major QTL was identified for root length in a segregating population for drought tolerance. The QTL explained a large percentage (>50%) of phenotypic variance, and informative markers linked to that QTL are now used to introgress it into elite but drought-sensitive chickpea germplasm.

Although the complex nature of drought tolerance was confirmed by all the studies reported here, five (two on rice and one each for chickpeas, sorghum and wheat) identified informative markers that have since been used in a predictive way to enable genetic gain under drought conditions in molecular breeding projects (Phase II). This was possible because all the markers identified loci that expressed a large percentage of phenotypic variance for the target traits. As well as identifying informative markers, the genetic studies led to better understanding of drought tolerance and the underlying physiological pathways. Several secondary traits were confirmed or identified as new potential traits of interest for drought screening such as carbon isotope discrimination and canopy temperature depression, root morphology, stay-green as a measurement of senescence and the elongation rate of vegetative and reproductive tissues.

Diseases and pests

Cassava mosaic virus disease (CMD)

CMD is the principal production constraint of cassava in Africa. Host-plant resistance is the most durable form of disease control. A principal source of CMD resistance in use today is *CMD2*, a dominant resistance gene that confers high levels of resistance. Molecular genetic mapping of

CMD2 identified informative markers that are tightly associated with *CMD2*. These markers are used in MAS experiments throughout West Africa to transfer CMD resistance to farmer-preferred varieties.

Striga weed

Striga is a highly damaging, parasitic, flowering plant that infests crops of many species, including legumes, maize, millet, rice, sorghum and sugarcane, throughout much of Africa. Three races of Striga (SG1, SG2, and SG3) affect cowpeas. Combining genetic resistance to all three races is difficult. Even so, SCARS MahSe 2 markers for resistance to races SG1 and SG3 were developed and are now currently in use to select Striga-resistant cowpeas in West Africa.

Downy mildew

Downy mildew of maize is a severely debilitating fungal disease. Where it does not meet with resistance or intervention, and environmental conditions are favourable, the disease can destroy an entire crop. SNP markers for downy mildew resistance in Thailand were recently developed. These are currently used for association mapping studies and introgression of resistance to elite breeding lines in Thailand.

Bacterial blight resistance and bruchids

In common beans, several markers have been identified to deploy disease and insect resistance in breeding lines. The informative marker related to bacterial blight resistance is SCAR marker SU91. A co-dominant marker with a higher linkage to the locus than SU91 has now been developed. Another informative marker, for resistance to *Zabrotes* spp (bruchid storage insects), was also developed and is being used to introgress resistance into African materials, using MABC.

A cross-species project enabled researchers to identify, characterise and use loci that conditioned quantitative resistance to the most important diseases of rice (blast and sheath blight) and maize (grey leaf spot and southern and northern leaf blights). For rice, informative markers for candidate genes that conditioned quantitative resistance in much of the diversity of the maize and rice genepools were identified. They were then used to facilitate marker-assisted selection to introgress multiple blast resistance QTLs into the important drought-resistant variety Vandana in India and IRRI. At the same time, the study also found that, for three diseases, evidence supported the hypothesis that a common genetic base may code for 'multiple disease resistance' (MDR) in maize.

Soil factors

Aluminium toxicity and low phosphorus

These major soil factors hamper cereal productivity, especially in sub-Saharan Africa and South America. Informative markers were developed for both these soil problems as part of a cloning exercise to identify major genes controlling tolerance of aluminium toxicity in sorghum (Alt_{SB}, Cornell University and Embrapa Maize & Sorghum) and phosphorus-uptake efficiency in rice (*Pup1,* IRRI*)*. The informative markers linked to these two major genes have already been used

very efficiently in breeding programmes. A more comprehensive description of these activities and related impact can be found in the white paper on *Cloned genes*.

Salt stress

Excessive salinity affects many crops globally. Salt stress is a major constraint across many rice-producing areas because of the modern rice varieties' high sensitivity to salinity. This forces farmers to continue growing their traditional landraces, which are more resistant but are low-yielding with poor grain quality. To address this issue, GCP supported the identification of a major gene involved in salt tolerance in rice, leading to the identification of *Saltol*, a major QTL for salinity tolerance. Highly linked SNP markers were developed and used to introgress tolerance into popular Bangladeshi varieties, using MABC. Varieties incorporating such tolerance have now been released.

Measuring success

The foregoing narrative indicates that notable progress was made during GCP's lifetime in activities upstream from crop breeding. These activities aimed to generate better understanding of the genetic basis of key traits, identify new traits for breeding and identify informative markers. The markers could then be used directly (predictive markers) or indirectly (historical information) in integrated breeding towards crop adaptation to an array of productivity-limiting constraints.

Published articles are good indicators of success for upstream research activities such as those conducted under this component, and GCP has exceeded expectations in this area. About 60–80 reviewed articles are published per year on GCP research and achievements (see http://www.generationcp.org/communications). About one-third are related to this research component. These papers report on the genetic dissection of target traits, informative markers identified, and validation or identification of new potential traits for breeding purposes. Most informative markers have also been reported in the respective genetic crop databases and can be consulted to evaluate achievements[3].

Success from a more applied perspective can also be measured by the number of informative markers that have been, or are going to be used in breeding programmes. Here, success is more circumscribed depending mainly on the genetic nature of the target trait. Loci identified with good predictive value have been found for major genes involved in the expression of simply inherited traits or loci expressing a significant portion of the phenotypic variance for polygenic traits.

Most of the projects that had a cross-genome comparative component resulted in quite a large number of outputs but few of them had a direct application in breeding. On considering the limited predictive value of informative markers for polygenic traits, GCP decided to conduct molecular breeding based on the MARS approach during Phase II. That is, informative markers

[3] See http://www.maizegdb.org/, http://www.gramene.org/, http://www.ncgr.org/lis, http://wheat.pw.usda.gov/GG2/index.shtml and http://www.comparative-legumes.org.

are used to select the best genotypes within the segregating population of discovery, ensuring that genetic gains for highly polygenic traits like drought tolerance can be achieved. The feasibility of this approach is demonstrated by the successes reported by the private sector.

Post-GCP sustainability and projected impact

Informative molecular markers are easily stored and maintained as data in publicly accessible databases and publications. Even if particular markers fall out of use (expected after better linkages are found), the data may still serve a valuable purpose as historical data to confirm the identification of the same QTLs in different backgrounds. Importantly, stored in such institutions, most of them are or will be publically available and easily accessible through various websites. Access and sustainability for those products are therefore not issues.

The genetic studies reported under this component permitted better understanding of the genetic mechanisms of a broad and diverse set of known drought tolerance traits (objective 1), the identification of a significant number of new traits, and validation of putative traits that could be included in the selection index (objective 3). Significant progress was also achieved towards the development of highly predictive markers for aluminium tolerance in maize and sorghum and low-phosphorus and salt tolerance in rice. Predictive markers were also identified under drought conditions with some direct application for breeding from studies on chickpeas, rice, sorghum and wheat under drought (objectives 1 and 2)

With the implementation of MARS in Research Initiatives of Phase II, informative marker development work has accelerated (objective 1). Indeed, most markers needed to complete the projects have been developed and are in current use. Thus, the RIs' country partners will have the predictive marker resources to complete current projects and move forward in their future programmes.

Deployment of informative markers for both polygenic and simply inherited traits will also be significantly enhanced through virtual platforms, such as the Integrated Breeding Platform (IBP) at https://www.integratedbreeding.net/. This Platform was initiated in mid-2009 by GCP in collaboration with the Bill & Melinda Gates Foundation. The GCP Product Delivery Theme planning will also ensure the documentation, maintenance, wide availability and access to these resources through GCP's product catalogue at http://www.generationcp.org/impact/product-catalogue and by promotion through a variety of media.

On a relative scale of 1 to 5, where 5 represents the largest impact across all kinds of GCP products, regardless of activity or crop, and 0 no impact, all GCP's efforts to develop and deploy informative markers are estimated to have an impact factor of 3. Such a score indicates that the informative marker development component has a significant impact on plant breeding efficiency in developing countries.

Analysing the post-GCP placement of the informative molecular marker component

GCP has primarily a research and capacity-building function, but development investment must follow if GCP outputs are to have an impact on farmers' crop productivity in developing countries. Therefore, to have impact, the use of many of the products (eg, informative markers and screening protocols for new traits) must increase the breeding efficiency of country programmes or local private companies, thus enabling the delivery of new varieties to farmers.

What will be finished by December 2014

Our projections indicate that all activities related to the development of informative markers will be finished by December 2014. As indicated above, the impact on breeding of the outputs and products generated under that research component are variable, depending on the genetic nature of the traits studied. Even so, all research activities per se will be completed when GCP ends.

Extending activities to CRPs, Centres or other institutions

As implied above, informative marker development will be completed in a couple of years. However, the application, use and continued development of such technology need to be considered by CRPs and breeding programmes in developing countries. GCP's current molecular breeding activities are embedded in the respective crop CRPs. Hence, decisions on beginning the discovery of new informative markers or extending the use of informative markers identified by GCP is left to the CRPs and their partners as well as other breeding initiatives. Considering the nature and genetic value of the predictive markers identified with GCP support, the strong hope is that those markers will enjoy extensive use in breeding programmes of developing countries. Those informative markers will be captured in the genetic database of the IBP (GDMS) and as such will be available to the breeding community well past the end of the GCP (assuming that IBP continues its life on its own).

The use of informative markers by developing country programmes is expected to expand through emerging networks and communities of practice (CoPs) for molecular breeding, as supported and promoted by IBP. With advanced research institutes and CGIAR Centres playing a leadership and mentoring or supporting role in the use of informative markers, molecular breeding should impact significantly over the coming years on crop productivity and quality in developing countries.

Conclusion

In terms of what GCP set out to do, we believe we can rightly claim "job accomplished" for the development of informative markers, considering the objectives laid out in the original GCP

proposal. Information on informative markers and new or implemented screening protocols for target traits is well documented. The use of predictive markers and new traits should find a natural home within the CRPs and breeding programmes in developing countries (in both the public and private sectors).

However, going beyond GCP's own scope and internal assessment on meeting Programme objectives, an assessment that includes the degree of need in developing countries would most certainly indicate that the job is in fact just beginning – particularly considering the great promise and potential in the application of molecular markers to improve crop quality, resilience and productivity. In this latter respect, the work is therefore far from complete, though the foundation has been laid and significant progress has been made.

GCP remains committed to its mission and community to the last day of the Programme and will work with partners along the delivery chain to maximize successful implementation of the delivery plans developed for each Research Initiative. GCP will also closely engage with its partners until its very sunset to ensure – as far as will be possible – the integration, extension, and expansion of activities as may be required. The Programme will even help initiate related new activities that build on GCP's achievements, should there be clear added value and demand for such activities. In this way, the Programme is working to secure a broad and sustainable use of its products well beyond 2014 while mitigating against the loss of gains made this far.

Annex 1: A list of informative markers developed by GCP-supported projects

Target trait	Description	Principal Investigator (PI), institute Collaborator	Target country(s)
Aluminium toxicity tolerance in maize	Markers for *ZmMATE1*, a novel maize Al-tolerance QTL. These gene-specific markers have been used to introgress the QTL in RILs in Brazil, accelerating the improvement of elite but Al-sensitive germplasm.	**PI:** Claudia Guimarães, EMBRAPA, Brazil **Collaborating institutions:** •EMBRAPA, Brazil (Jurandir Magalhães, Sidney Parentoni, Lauro Guimarães, Andrea Carneiro, Newton Carneiro, Robert Schaffert, Sylvia Sousa, Vera Alves) •CornellU, USA (Leon Kochian, Lyza Maron, Jiping Liu, Miguel Pineros, Ed Buckler) • MoiU, Kenya (Sam Gudu)	Brazil, Burkina Faso, Cameroon, Kenya, Niger
Salt tolerance in rice	Three SSR markers identified for introgression of *Saltol*, a major and novel QTL conferring salt tolerance in rice. Highly effective markers currently in use to improve salt tolerance in rice breeding lines in Bangladesh, India, the Philippines and Southeast Asia.	**PI:** Abdelbagi Ismail, IRRI **Collaborating institutions:** • BRRI, Bangladesh (MA Salam) • DU, Bangladesh (Zeba I Seraj) • IRRI (Michael J Thomson, David J Machill, Thelma Paris)	South and Southeast Asia
Rice blast resistance	Gene-specific molecular markers for candidate defence genes associated with resistance to blast in rice. Informative for the gene but not predictive for breeding.	**PI:** Rebecca Nelson, CornellU, USA **Collaborating institutions:** • IRRI (Casiana Vera Cruz, Darshan Brar, Hei Leung)	General
Low-P tolerance in rice	Gene-specific markers for *Pup1*, a major QTL for P uptake in rice. In past and current use for improving rice lines for low-P conditions.	**PI:** Sigrid Heuer, IRRI **Collaborating institutions:** • IRRI (Abdelbagi Ismail) • JIRCAS, Japan (Matthias Wissuwa) • ICABIOGRD, Indonesia (Masdiar Bustamam, Joko Prasetiyono	Indonesia, Philippines, South Asia
Al-toxicity tolerance in sorghum	Gene-specific markers for Alt_{SB}, a major QTL for Al tolerance in sorghum. In current use for improvement of Al tolerance in elite Brazilian and African sorghum lines.	**PI:** Jurandir Magalhaes, Embrapa Maize & Sorghum, Brazil **Collaborating institutions:** • PSNRU of USDA–ARS, USA (Leon Kochian, Owen Hoekenga, Jiping Liu) •IGD, USA (Stephen Kresovich, Alexandra M Casa) • Embrapa Maize & Sorghum, Brazil (Claudia Guimarães, Robert Schaffert, Antonio Marcos Coelho, Vera Alves • INRAN, Niger (Issoufou Kaparan, Soumana Souley, Maman Nouri, Magagi Abdou, Adam Kiarí, Fatouma Beidari)	Brazil, Mali, Niger
Resistance to Striga in cowpeas	SCAR markers for Striga resistance in cowpeas. Two markers for QTL, which codes for resistance to races SG1 and SG3. Currently in use for selection of Striga-resistant cowpeas	**PI:** Satoru Muranaka, IITA **Collaborating institutions:** • IITA (Christian Fatokun, Adebola Raji, Boukar Ousmane, Dong-Jin Kim) • UVa, USA (Michael Timko)	Nigeria, Senegal

	in West Africa.	• CERAAS ,Senegal (Ndiaga Cissé) • ISRA, Senegal (Moctar Wade)	
Downy mildew resistance in maize	Markers for downy mildew resistance in maize. SNP markers for downy mildew resistance in Thailand. Currently used for association mapping studies in Thai maize lines.	**PIs:** Chalermpol Phumichai, Julapark Chunwongse, KU, Thailand **Collaborating institutions:** • KU, Thailand (Sansern Jampatong) • Department of Agriculture, Ministry of Agriculture and Cooperatives, Thailand (Pichet Grudloyma)	South and Southeast Asia
Drought tolerance for maize, rice and wheat	Markers for QTLs controlling tissue growth rate under water stress in maize, rice and wheat and across three organs in maize. Informative for QTLs only; not predictive for breeding.	**PI:** François Tardieu, Agropolis–INRA, France **Collaborating institutions:** • Agropolis–INRA, France (C Welcker) • CIMMYT (M Reynolds) • IRRI (R Serraj) • ETH, Switzerland (A Hund) • Biogemma, France (P Lessard) • ACPFG, Australia (P Langridge) • IARI, India (BM Prasanna)	General
Drought tolerance	Markers for QTL identifying genes responsible for failure of grain formation in rice and wheat under drought. Informative for QTL only; not predictive for breeding.	**PI:** R Serraj, IRRI **Collaborating institutions:** • CSIRO, Australia (Rudy Dolferus) • IRRI (Kenneth McNally, Xuemei Ji, Muthurajan Raveendran) • NIAS, Japan (Shoshi Kikuchi, Kouji Satoh) • TNAU, India (R Chandra Babu) • NAU, China (Zhengqiang Ma)	General
Drought tolerance for rice	DNA markers for drought tolerance QTL identified from diverse sources of Chinese rice cultivars. Now in use for improving drought tolerance in China and Southeast Asia	**PI:** Zhi-Kang Li, IRRI and CAAS, China **Collaborating institutions:** • Peking–Yale Joint Center for Plant Molecular Genetics and Agribiotechnology, China (Xing-Wang Deng) •IRRI (R Lafitte)	China
Drought tolerance for common beans	Markers for common bean root architectures associated with drought tolerance in greenhouse experiments. Informative only for QTL at this point. Breeding use is still being explored in the field.	**PI:** J Lynch, PSU, USA **Collaborating institutions:** • CIAT (Stephen Beebe) • PSU, USA (Kathleen Brown) • CIAT/SABRN , Malawi (Rowland Chirwa) • IIAM, Mozambique (Celestina Jochua, Magalhães Miguel) • CIAT (Idupulapati Rao)	Malawi, Mozambique
Drought tolerance for rice	Markers for QTLs for stress yield detected in genotypes Vandana/Way Rarem, IR55419-04/Way Rarem, and Apo/IR64. Excellent linked markers. Now in use for improving breeding lines in India.	**PI:** Arvind Kumar, IRRI **Collaborating institutions:** • CRRI, India (ON Singh, P Swain, LK Bose) • CRURRS, India (K Sinha, NP Mandal) • NDUAT, India (JL Dwivedi) • UAS, India (S Hittalmani; Venkatesh Gandhi) • TNAU , India (R Chandra Babu, A Senthil, S Robin) • BirsaAU, India (BN Singh, RL Mahato) • JNKV, India (P Perraju) • Barwale, India (HE Shashidhar, Abhinav	India

		Jain) • YAAS, China (D Tao) • UAlberta, Canada (Dean Spaner)	
Drought tolerance in barley	SNP markers for candidate genes for drought tolerance in barley. Informative for QTL but not predictive for breeding	**PI:** Robbie Waugh, SCRI, UK **Collaborating institutions:** • SCRI, UK (Dave Marshall, Joanne Russell) • ICARDA (Michael Baum, Stefania Grando, Maria von Korff Schmising, Salvatore Ceccarelli) • OregonSU, USA (Patrick M Hayes) • INIA–Chile (Ivan Matus) • UTalca, Chile (Alejandro del Pozo) • UCR, USA (Timothy J Close)	General
Drought tolerance in rice	Markers for QTLs conferring delayed senescence and drought tolerance in rice.	**PI:** E Blumwald, UC–Davis, USA **Collaborating institution:** •IRRI (Abdelgabi M Ismail, Rachid Serraj)	General
Disease resistance in rice and maize	Markers for disease resistance QTLs in sections of the rice and maize genomes that provide superior disease resistance to cereal diseases. These were highly informative of QTLs for traits within both species; predictability for breeding is still being established.	**PI:** R Nelson, CornellU, USA **Collaborating institutions:** •NCSU, USA (Peter Balint-Kurti) • IRRI (Darshan Brar, Hei Leung, Casiana Vera Cruz) • ICABIOGRD, Indonesia (Masdiar Bustamam) • KARI, Kenya (James Gethi, Jedidah Danson, Jane Ininda) • ColoradoSU, USA (Jan Leach) • CornellU, USA (Margaret Smith) • IPB, Indonesia (Utut Suharsono)	General
Interspecific crosses of rice	SSR markers for the chromosome 6 S1 locus, the major gene acting in the interspecific sterility barrier system. Allows elimination of infertile progeny of interspecific crosses in rice, speeding development of fertile interspecific populations. Used successfully to develop chromosome segment substitution line populations of cultivated rice with *Oryza glaberrima, O rufipogon*, and *O meridionalis*; and with *O glumaepatula* for introgression of desirable alleles into cultivated rice.	**PI:** M Lorieux, CIAT/Agropolis–IRD, France, and A Ghesquière, Agropolis–IRD, France **Collaborating institution:** • AfricaRice (M-N Ndjiondjop)	General
Drought tolerance in rice	Markers for candidate drought-responsive regulatory genes in rice mutants. Informative for the genes but no predictive value for breeding.	**PI:** A Pereira, VT, USA **Collaborating institutions:** • IRRI (Hei Leung, Rachid Serraj, Jill Cairns) • HZAU, China (Lizhong Xiong)	General
Drought tolerance in maize	SNP markers for 79 candidate genes indicating drought tolerance in maize. Candidate genes identified but no predictive value for breeding.	**PI:** Jianbing Yan, CIMMYT **Collaborating institutions:** • CornellU, USA (Tim Setter, Edward Buckler) • Agropolis–INRA, France (Alain Charcosset) • KARI, Kenya (James Gethi)	General

		• NSFCRC, Thailand (Pichet Grudloyma) • SIRDC, Zimbabwe (Esther Khosa) • SAU, India (Li Wanchen) • CIMMYT (José Crossa, Xu Yunbi, Magorokosho Cosmos, José Luis Araus)	
Drought tolerance across species	SNP markers for orthologous candidate genes in barley, cassava, chickpeas, common beans, potato, rice and sorghum for transcriptome regulation, cellular regulation and carbohydrate metabolism regulation of drought. Candidate gene identified but no predictive value for breeding.	**PI:** Dominique This, Agropolis, France **Collaborating institutions:** • Agropolis−CIRAD, France (Brigitte Courtois, Claire Billot, Jean-François Rami, Romain Philippe, Pierre Mournet) • CIP (Merideth Bonierbale, Roland Schaftleitner, Reinhart Simon, Percy Rojas) • ICRISAT (Rajeev Varshney, Tom Hash, Dave Hoisington, Spurthi Nayak, Hari Upadhyaya) • Agropolis−INRA/CNG, France (Dominique Brunel, Redouane El Malki) • IRRI (Ken McNally) • ICARDA (Michael Baum, Wafaa Choumane) • CIAT (Matthew Blair, Martin Fregene)	General
Disease resistance in cassava	SCAR markers for *CMD2*, a major gene conferring resistance to cassava mosaic virus disease in Africa. Now in routine use for disease-resistant variety development in East Africa and has facilitated release of resistant varieties in Nigeria and Tanzania.	**PI:** Anthony Bellotti and Martin Fregene, CIAT **Collaborating institutions:** • NRCRI, Nigeria (Emmanuel Okogbenin, Chiedozie Egesi) • EMBRAPA, Brazil (Alfredo Alves) • CRI–CSIR, Ghana (Elizabeth Okai) • NaCRRI , Uganda (Yona Baguma, Anthony Pariyo)	West Africa
Drought resistance in spring wheat	Markers for QTLs associated with yield, drought adaptation, and agronomic traits in spring wheat. Currently used for physiological and genetic studies of drought-adaptive traits. Use has led to development of drought-tolerance panel used by Wheat RI in China and India.	**PI:** Mathew Reynolds, CIMMYT **Collaborating institutions:** • CIMMYT (Daniel Mullan, Yann Manes, José Crossa) • ACPFG, Australia (Peter Langridge) • DWR, India (Jagadish Rane, B Mishra, Ravish Chatrath) • IARI, India (Satish Mishra)	General
Drought tolerance in cassava	Markers for drought tolerance in South American cassava. 187 polymorphic SSR markers identified from populations selected for drought tolerance in Colombia and Brazil. However, predictability has not been established at this point.	**PI:** Alfredo Augusto Cunha Alves, EMBRAPA, Brazil **Collaborating institutions:** • CIAT (Martin Fregene, Hernán Ceballos) • IITA (Morag Ferguson, Rosemary Mutegi) • CornellU, USA (Tim Setter, Luis Duque) • ARI–Naliendele, Tanzania (Geoffrey Mkamilo) • I ITA (Edward Kanju) • SARI–CSIR , Ghana (Joseph Adjebeng) • EMBRAPA, Brazil (Antonio Souza, Miguel Angel Dita Rodríguez, Alineaurea Silva) • KARI, Kenya (Joseph Kamau)	Brazil, Colombia, East Africa, West Africa
Drought	Markers for drought tolerance in	**PI:** Pooran M Gaur, ICRISAT	India, Kenya,

tolerance in chickpeas	chickpeas. SNP markers for a major QTL associated with a 'hotspot', harbouring several genes for root-related traits for drought tolerance. Currently used for drought tolerance improvement in chickpea breeding lines in India and East Africa in the BMGF-supported Tropical Legumes 1 project.	**Collaborating institutions:** • ICRISAT (Rajeev Varshney, L Krishnamurthy, Vincent Vadez, Shailesh Tripathi) • UAS, India (KP Viswanatha, MS Sheshashaye) • RARS–Nandyal, India (Veera Jayalakshmi) • ARS–Durgapura, India (SJ Singh) • RAKCA, India (Md Yasin)	Tanzania, other East African countries
Interspecific crosses for groundnuts	SNP markers for wild relatives of cultivated groundnuts. Diversity for desirable traits such as drought tolerance are lacking in cultivated groundnuts. Diversity may be created by introgressing desirable loci from wild relatives. These markers provide the genomic resources necessary for molecular breeding of groundnuts, and for the incorporation of wild genes into cultivated groundnuts to produce improved varieties.	**PI:** Jose Valls, EMBRAPA, Brazil **Collaborating institutions:** •UCB, Brazil (David Bertioli, Wellington Martins) • CERAAS, Senegal (Ousmane Ndoye) • ICRISAT (Vincent Vadez, Rajeev Varshney, Aruna Rupakula) • UAS, India (Udaya Kumar) • Agropolis−CIRAD, France (Angelique d'Hont) • IBONE, Argentina (Guillermo Seijo, Germán Robledo) • AarhusU, Denmark (Jens Stougaard, Lene Madsen, Niels Sandal) • TAMU, USA (Consultant: Charles Simpson)	Brazil, Africa, India
Resistance to bacterial leaf blight of rice	Markers for QTL associated with resistance to bacterial leaf blight. Informative markers for recessive resistance previously identified in Asian strain studies and found to be also resistant to African strains of bacterial leaf blight in rice (*Oryza sativa*).	**PI:** Marie-Noelle Ndjiondjop, AfricaRice **Collaborating institutions:** • Agropolis−IRD, France (Alain Ghesquière, Valerie Verdier) • Agropolis−IRD/CIAT (Mathias Lorieux) • IER, Mali (Fousseyni Cissé) • AfricaRice (Manneh Baboucarr, Dramé K Nani, Sanchez Ines, Tsunematsu Hirochi, Séré Yacouba)	West Africa
Resistance to bacterial leaf blight of rice	Gene-based SNP markers developed for bacterial blight resistance genes *xa21, xa5* and *xa13*. Now used to introgress resistance to bacterial blight in elite rice lines at IRRI.	**PI:** Susan McCouch, CornellU, USA **Collaborating institution:** • IRRI (Casiana M Vera Cruz)	Philippines, Asia