Potato Genome Sequencing Consortium: Final Report for GB

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1. PREFACE

The multinational Potato Genome Sequencing Consortium (PGSC) was initiated by the Plant Breeding Department of Wageningen University & Research in the Netherlands in 2004 with the aim of generating a genome resource for potato. Initially, although GB researchers had expertise to contribute to the project, funding was not available for them to do so. During 2008 Potato Council, Scottish Government, Defra and BBSRC agreed a mechanism to provide support for GB participation in the project. Details of the final consortium, comprising researchers from 14 countries, is available at: http://www.potatogenome.net/index.php/Main_Page

Although the work is much more strategic than the projects that Potato Council would normally support, our involvement was essential in ensuring British participation in the consortium. Consequently, there hasn't been a time lag between the completion and publication of the genome sequence and the utilisation of the new information in GB R&D projects. The availability of the genome sequence will continue to be of benefit and will underpin all future genetic analysis and breeding in potato.

Potato Council, 2012

2. SUMMARY

In July 2011 an international team of scientists from 14 countries, including GB, published the full potato genome sequence in the highly prestigious journal Nature. This achievement holds tremendous promise for accelerating the traditionally time-consuming process of developing new potato varieties. It is vitally important that new varieties are bred and released more rapidly to keep ahead of the biotic and abiotic challenges to the global potato industry and also to help ensure global future food security. Potato breeding is compromised by the genetic complexities of the crop – its inability to be inbred and having four sets of chromosomes (tetraploidy) instead of the usual two.

The Potato Genome Sequencing Consortium (PGSC) was formed in 2004, but did not really start in earnest until 2008, due to delays in securing funding. The genome of the potato, in common with other organisms, is comprised of a series of 'bases' often referred to by the letters A, C, T and G that are linked together in 'strings' called chromosomes. One copy of the potato genome is 850 million bases spread over 12 chromosomes and which encode approximately 39,000 genes. Each potato variety has four, often highly distinct copies of each of these genes. An important aspect of the PGSC's work was the use of a 'doubled monoploid' (DM) clone of the Phureja group of potatoes which has two identical copies of each gene. This clone was made some time ago in the USA by making a 'monoploid' with only one set of chromosomes then doubling it using tissue culture techniques. Phureja types are virtually identical to conventional potatoes in their genome sequence and the use of DM made the task of sequencing the genome much simpler.

The genome sequencing process itself is quite simple nowadays, thanks to the recent development of 'massively parallel' next generation sequencing (NGS) methods which have revolutionised genome analysis. Basically potato DNA is isolated by a simple procedure used for all plants, and then it is physically 'sheared' into small pieces using a sonication process. The small DNA fragments are then sequenced using NGS technology which can sequence about 1 million small fragments of DNA at one time. The major task is in 'assembling' the genome which involves matching millions of short sequences to find the overlaps between them to build larger and larger sequence 'contigs', a highly computationally intensive task only possible with sophisticated software and massive computing power. Another major step in the genome analysis is known as 'annotation', the process by which the genes are identified and if possible ascribed a putative function based on the sequence similarity to genes from other species and certain other sequence features.

Prior to sequencing the genome, the PGSC had developed a very dense 'genetic and physical' map of potato whereby the genetic position of a large number of markers was known in relation to 'physical' locations of genome features. However this effort did not tell us about the specific genes contained in a potato variety, and it is the genes that are responsible for all potato traits. Nor did it tell us where the genes reside in relation to the locations of previously analysed traits such as tuber quality and disease resistance. A full genome sequence provides the exact location of the genes in relation to genetic maps and the markers they contain. Once we know the location of a trait gene, say tuber shape, we can use the locations of markers near the trait 'locus' to see directly into the genome and identify the genes that may be responsible for the trait.

A high quality, well-annotated genome sequence of potato provides an invaluable foundation which can be combined with existing knowledge of potato genetics to develop the tools for improved breeding strategies. For example it has already led to the development of more than 10,000 new genetic markers which are helping to analyse important potato traits, such as disease resistance and tuber dormancy. In some cases it will be possible to use small sets of these and related markers to select within potato breeding programmes. Now that the sequences of the ~39,000 genes in potato are known, this information can be used to design strategies to utilise in breeding the tremendous sequence diversity present in potato varieties and more primitive germplasm. Another goal is to use the genome sequence to identify the actual genes responsible for certain traits, opening up the possibility of deployment through both conventional and transgenic routes. For example recent work involving the James Hutton Institute (JHI) has been focussed on genes affecting tuber dormancy and the response to ethylene treatment – we know where some of the genes are from genetic analysis of populations which vary for these traits. The current goal is to use the knowledge about where the genes are to identify the actual genes responsible for dormancy and ethylene response in the genome. This would allow us to manipulate the trait more easily and to develop markers for use in potato breeding programmes.

3. TECHNICAL SUMMARY

The aim of the UK component of the PGSC project was: Sequencing the 'gene space' of potato chromosome IV, comparative analysis with tomato and development of a gene-based mapping platform.

The corresponding objectives were to:

- Contribute to the production of a high quality draft of the genome of potato, to include at least 95 % of the genes.
- Develop an integrated genetic and physical reference map based on the sequenced potato clone.
- Develop a high quality sequence (with minimum gaps) for chromosome IV
- Compare potato and tomato Chromosome IV structure and organization.

The genotype used is a doubled monoploid *Solanum tuberosum* group Phureja DM1-3 516 R44 clone (hereafter referred to as DM) and it was sequenced using a whole genome shotgun (WGS) approach. Over 90% of the genome is represented by ~600 of the largest genome fragments (hereafter referred to as superscaffolds). For anchoring and orientating assembled super scaffolds along the 12 potato chromosomes, a *de novo* genetic map was also developed using a range of different marker types. A total of 4,836 markers were deployed on a diploid backcross potato population (DM/DI//DI) comprising 180 plants. This approach supported by other available mapping resources resulted in anchoring of 917 superscaffolds to their approximate closest genomic positions on the integrated genetic and physical map of potato covering a length of 651 Mb. The 651 Mb that could be mapped represents ~90% of the 727Mb genome assembly and includes ~90% of the 39,031 predicted genes. Furthermore, the anchored 651 superscaffolds have been ordered and assembled into pseudomolecules corresponding to the 12 potato chromosomes. Like any other genome sequencing project, there are still gaps in the genome i.e. between the superscaffolds. As the UK effort was originally focussed on chromosome 4, we selectively chose (using BAC-end hits) and sequenced 82 DM BACs spanning gaps

between chromosome 4 superscaffolds. This has further improved the overall coverage of chromosome 4 and, hence, reduced the number of sequence gaps.

The mapping part of the project has led to development of a highly-dense potato map linked to the genome assembly. This includes the development of over 4000 new sequence-based genetic markers, the vast majority of which are linked directly to the genome assembly. The population of plants used for the mapping work is available from CIP (Lima, Peru) but it is unlikely it will be used in the UK due to quarantine issues with its importation.

The main scientific highlight is the completion of potato genome sequence, assembled and ordered into an integrated and highly dense genetic and physical map. Other highlights include the identification of 39,000 genes in potato, the high level of haplotype diversity and the observation that the potato genome contains many ancient and recent 'segmental duplications'.

The main conclusions are that the potato genome is a moderately repetitive genome, containing ~39,000 coding genes, although there is evidence for alternative transcripts for as many as 60% of these genes. The genome is highly duplicated and contains many short segments showing conserved synteny with other plants such as rice and grape.

The DM WholeGenome Shotgun sequencing project has been deposited at DDBJ/EMBL/GenBank under the accession AEWC00000000. Genome sequence and annotation can be obtained and viewed at http://potatogenome.net.

4. INTRODUCTION

Potato is the world's most important vegetable crop and the 3rd largest global food crop. Despite its importance as a food crop throughout the world, the genetics of many potato traits is poorly understood and is complicated by its highly heterozygous polyploid genome. Unlike diploid crops, most potato varieties have four copies of each of the 12 chromosomes. This makes it very difficult to follow inheritance patterns, especially in relation to the many complex traits with which breeders are compelled to work. Many important agronomic traits are poorly understood; genes affecting these traits remain largely undiscovered and their locations on the 12 chromosomes are often imprecise. The potential of modern genomics tools and a genome sequence in particular in alleviating such negative aspects of the potato as a genetic system have long since been realised. The intention of the Potato Genome Sequencing Consortium to move in this direction was indicated in 2004. The PGSC has also foreseen the requirement for and benefits accruing from an integrated sequence and genetic reference map to fully exploit and achieve the goals and objectives of the genome sequencing initiative. Consequently, in parallel to the genome sequencing, other synergistic efforts were initiated to genetically order and anchor the sequenced potato genome. The sequencing and anchoring of the potato genome will provide a major boost to gaining a better understanding of potato trait biology and will underpin all future breeding efforts.

In the first phase of the sequencing activity, involving 'chromosome by chromosome, BAC by BAC' strategy on a highly heterozygous potato clone RH (full name RH89-039-16), the overall progress of the project was slow and uneven among participating member countries. Moreover, each participating country had its own strategy for

sequencing the relevant chromosome, which would have resulted in a very 'uneven' coverage of the genome. Considering these shortcomings and with the simultaneous availability of affordable high throughput 'next generation sequencing' (NGS) technologies, the consortium as a group decided (at a meeting in Carlow, Ireland in June 2009) to modify its strategy to facilitate more efficient sequencing of the entire potato genome. The revised strategy aimed to achieve high genome coverage using *de novo* NGS based whole genome shotgun sequencing strategy coupled to moderate usage of Sanger based sequencing. To overcome the genome assembly issues rendered by genome heterozygosity, the heterozygous RH clone was replaced by a fully homozygous doubled monohaploid clone (DM). Following significant revisions to the strategy of the PGSC in June 2009, the milestones and timetable for their delivery were re-defined as follows:

Production of Solexa data: August-September 2009
Release of the Solexa-basedgenome assembly: Late 2009
Production of 454 data: June-September 2009
Production of Fosmid-end sequences: April-June 2009
Production of BAC-end sequences: July-August 2009
Generation of a transcriptome resource: June 2010
Development of genetic map: August-October 2009
Building of the first draft sequence of the Potato DM genome: early 2010
Publication of the first draft of the potato DM genome sequence: mid 2010

5. METHODS AND RESULTS

5.1. DM whole-genome shotgun sequencing using Illumina Solexa platform

Libraries were constructed from DM genomic DNA, 125x coverage of the potato genome was achieved using Solexa sequencing. This include (a) 70.6 Gb of 37-73bp paired-end reads using the Illumina GA2 from 16libraries with insert lengths of 200-811bp and (b) 18.7 Gb ofIllumina mate-pair libraries (2, 5 and 10 kb insert size).

5.2. DM whole-genome shotgun sequencing using Roche 454 platform

Roche 454 GS FLX Titanium platform was used to generate longer sequence reads. Intotal, 7.2 Gb, 0.7 Gb and 1.0 Gb of 454 single-end, 8 kb paired-end (PE) and 20 kb PE reads were generated and applied for gap filling to improve the assembly.

5.3. Production of Fosmid-end sequences

Fosmid (~35kb insert size) libraries from the DM genome were made and clones were end-sequenced using Sanger technology.

5.4. Production of BAC-end sequences

BAC (>100kb insert size) libraries from the DM genome were made and clones were end-sequenced using Sanger technology. As a part of quality assessment of the assembled genome, 10 DM BAC clones were Sanger sequenced.

5.5. Generation of a transcriptome resource

Both Roche 454 GS FLX Titanium and Solexa/Illumina whole transcriptome sequencing was performed to improve the quality of genome annotation. Greenhouse grown plants were used for tissue sampling from wounded and normal leaves, roots, shoots, stolons, tubers, flowers and petioles while *in vitro* material was used for tissue sampling from control plants, roots, shoots, leaves, callus, and various biotic and abiotic treatments such as salt, osmoticum, salicylic acid, plant growth regulators, heat, cold, *Pectobacterium* and Late blight infection.

45 libraries (16 RH, 29 DM) subjected to Illumina RNA-Seq analysis. 743M reads were obtained (RH: 140M; DM 603M).This amounted to 31.5Gb ofRNA-Seq data representing all major tissue types, developmental stages, and responses to abiotic and biotic stresses. For annotation purposes the reads were mapped against the DM genome sequence (90.2% of 824,621,408 DM reads and 88.6% of 140,375,647 RH reads). Using these data in combination with *ab initio* gene prediction, protein and EST alignments, we annotated 39,031 protein-coding genes with comparable functional annotation as other angiosperms.

5.6. Development of genetic map

To anchor and fully orientate physical contigs along the chromosome, a genetic map wasdeveloped *de novo* using sequence-tagged-site (STS) markers comprising simple sequence repeats (SSR), singlenucleotide polymorphisms (SNP) and diversity array technology (DArT^{TM}). A total of 4,836 STS markers including 2,174 DArTs, 2,304 SNPs and 358 SSRs were analysed on 180 progeny clones from a backcross population (DM/DI//DI) between DM and DI (CIP No. 703825), a heterozygous diploid *S. tuberosum* group Stenotomum. The data was analysed using JoinMap® 4 and yielded the expected 12 potato linkage groups. The markers in the linkage groups were further anchored to the sequence superscaffolds which aided their orientating and assembling into chromosome-like pseudomolecules. Overall, linkage mapping coupled with other available map resources, anchored 917superscaffolds to their approximate closest physical positions on the integrated genetic and physical map of potato covering a length of 651 Mb. The 651 Mb (~77%of the estimated 844 Mb genome and ~90% of the assembled 747 Mb genome) anchored genome includes ~90% of the 39,031 predicted genes.

5.7. Building of the first high quality reference sequence of the Potato genome

As a result of concerted efforts of all the PGSC members, the consortium has completed a high quality reference sequence of the potato genome and released it to the public domain. First69.4 Gb of paired-end short reads was assembled into contigs, which are pieces without gaps composed of overlapping reads. Then contigs were further linked into scaffolds by paired-end relationship (300~550bp insert size), mate-pair reads (2 kb~10 kb), fosmid ends (~40 kb) and BAC-ends (~100 kb). Then the gaps were filled with the entire short read data generated through Illumina GA2. The primary contig N_{50} size was 697 bp and increased to1,318 kb after gap-filling. Further gap filling was done using single-end and PE 454 data, which increased the N_{50} contig size to 31,429 bp with 15.4% of the gaps filled.

The final assembly (v3) size is 727Mb, 93.87% of which is non-gapped sequence. Ninety percent of the assembly falls into 443 superscaffolds larger than 349 kb. However, still the potato genome assembly of 727 Mb is 117 Mb less than the estimated genome size and the remaining superscaffolds need to be specifically targeted for anchoring using bespoke markers. There are still several gaps in the assembled genome. Some parts (superscaffolds) of the ordered genome exhibit conflicts with other published data and require further investigation. Further efforts will continue to complete and overcome these issues and further improve the anchoring and the assembly of the potato genome. The sequence and other findings of the potato genome project were published in Nature (Potato Genome Sequencing Consortium, 2011). A paper on the anchoring of the genome is in preparation.

6. SUMMARY OF RESULTS

- A high-quality draft potato genome sequence has been released. A unique and homozygous doubled-monoploid potato clone (DM) was employed to overcome the problems associated with genome assembly due to high levels of heterozygosity in potato. The sequenced and assembled genome amounts to the 86% of the 844-megabase potato genome.

- The potato genome contains ~39,000 coding genes. There is also evidence for alternative transcripts for as many as 60% of these genes.

- Sequenced potato genome present evidence for at least two genome duplication events indicative of a palaeopolyploid origin.

- The genome is highly duplicated and contains many short segments showing conserved synteny with other plants such as rice and grape.

- This is the first asterid genome to be sequenced and reveals 2,642 genes specific to this large angiosperm clade.

- The mapped 90% of the genome contains ~ ~90% of the 39,031 predicted genes.

- A total of 917 superscaffolds have been anchored, ordered and assembled into pseudomolecules corresponding to the 12 potato chromosomes.

- Additional efforts have been put to improve the Chromosome 4 coverage and assembly by selectively choosing and sequencing 82 DM BACs spanning gaps between chromosome 4 superscaffolds.

- Development of a highly-dense potato map linked to the genome assembly. This includes the development of over 4000 new sequence-based genetic markers, the vast majority of which are linked directly to the genome assembly.

- The DM Whole Genome Shotgun sequencing project has been deposited at DDBJ/EMBL/GenBank under the accession AEWC00000000. Genome sequence and annotation can be obtained and viewed at http://potatogenome.net.

7. DISCUSSION

We sequenced and released a high-quality draft potato genome sequence that provides new insights into eudicot genome evolution. We predict 39,031 protein-coding genes and present evidence for at least two genome duplication events indicative of a palaeopolyploid origin. As the first genome sequence of an asterid, the potato genome reveals 2,642 genes specific to this large angiosperm clade. Using a combination of data from the vigorous, heterozygous diploid RH and relatively weak, doubled-monoploid DM, we could directly address the form and extent of heterozygosity in potato and provide the first view into the complexities that underlie inbreeding depression. Combined with other recent studies, the potato genome sequence helps us further in elucidating the evolution of tuberization. Given the pivotal role of potato in world food production and security, the potato genome adds to a growing set of resources for genetic and genomic analyses in the Solanaceae. These outputs will have a major impact on how research on potato is conducted and will have longer term impact on how breeding is performed.

8. CONCLUSIONS

The sequencing of the potato genome has opened up new vistas for the way potato genetics and breeding are performed making potato plant more amenable to modern genetics and genomics tools. The potato collections can now be more efficiently mined for novel alleles and beneficial traits of economical and industrial importance. The integrated genome sequence and genetic reference map will allow trait phenotype loci or QTLs defined by sequence based markers to be linked to specific genetic and physical regions of the genome. Such regions can be then used to define further markers for fine-scale mapping, or candidate genes can be sought directly from the genome sequence and associated annotation data. This step change, facilitating sequence-based genomics and aiding molecular breeding in potato, would accelerate trait-gene discovery and gene isolation. This would further shorten the time to breed new varieties and also significantly improve parental genotypic assessment.

Genome tagged molecular marker studies will be more meaningful and enable more accurate estimates of population genetic and LD parameters. The shift towards sequence based polymorphism rather than fragment based, will virtually replace centimorgan (cM) position by sequence co-ordinates and greatly increase the information output and accuracy of mapping procedures. The integrated potato genetic and physical reference map forms an important resource for linking to all current and future genetic mapping efforts by the potato community and will help to alleviate many of the complicating aspects of potato as a genetic system.

With the release of the genome of the other economically important Solanaceous plant tomato (The Tomato Genome Consortium, 2012), comparative linkage mapping and in depth sequence based synteny analysis among Solanaceae will be feasible. Given the biological and economic importance of many Solanaceous species and the diversity of their phenotypes/products (agriculturally useful parts tubers, berries etc., growth habits, wide geographical growing range, clonal propagation, regeneration), comparative Solanaceous genomics will provide a fundamental framework for tackling both applied and basic questions.

9. RECOMMENDATIONS FOR FUTURE STRATEGY

Many traits of interest to plant breeders are quantitative in nature and the genome sequence will simplify both their characterization and deployment in cultivars. Whereas much genetic research is conducted at the diploid level in potato, almost all potato cultivars are tetraploid and most breeding is conducted in tetraploid material. Hence, the development of experimental and computational methods for routine and informative high-resolution genetic characterization of polyploids remains an important goal for the realization of many of the potential benefits of the potato genome sequence. Moreover, resequencing of other heterozygous potato genomes will inform researchers on the level of diversity in breeding material and other germplasm.

10. PUBLICATIONS

Refereed publications

Visser, R.G.F., Bachem, C.W.B., de Boer, J.M., Bryan, G.J., Chakrabati, S.K., Feingold, S.,Gromadka, R., vanHam, R.C.H.J., Huang, S., Jacobs, J.M.E., Kuznetzov, B., de Melo, P.E., Milbourne, D., Orjeda, G., Sagredo, B. & Tang, X.M. 2009. Sequencing the potato genome: outline and first results to come from the elucidation of the sequence of the world's most important food crop. American Journal of Potato Research 86, 417-429

The Potato Genome Sequencing Consortium (2011) Genome sequence and analysis of the tuber crop potato. Nature 475:189-195

Massa AN, Childs KL, Lin H, Bryan GJ, Giuliano G, Buell CR. 2011. The transcriptome of the reference potato genome Solanum tuberosum Group Phureja clone DM1-3 516R44.PLoS One. 2011;6(10):e26801. Epub 2011 Oct 28

de Boer, J.M., Borm, T.J.A., Jesse, T., Brugmans, B., Tang, X., Bryan, G.J., van Eck, H.J., Visser, R.R.F. 2011. A hybrid BAC physical map of potato: a framework for sequencing a heterozygous genome. BMC Genomics 12: 594

Popular and trade articles

G J Bryan, ‘Mapping a revolution’, Fresh Produce, 18 Nov 2011

Presentations at scientific meetings

G Bryan, The Potato Genome. Invited lecture, Universidad Nacional De Colombia, Bogota, Oct 2011

G Bryan, The Potato Genome. Invited lecture, Max Planck Institute, Koln, Germany, Sept 2011

G Bryan, The Potato Genome. Invited lecture, Canadian Plant Genomics conference (Niagara Falls), Aug 2011

G Bryan, Sequencing the Potato Genome: are we there yet? Invited lecture, Universidad Nacional De Colombia, Bogota, Nov 2010

SK Sharma (on behalf of the Potato Genome Sequencing Consortium). The Potato Genome Sequencing Initiative. The 7th Solanaceae Genome Workshop (SOL 2010), Dundee, United Kingdom, September 5-9, 2010

DM Bolser, SK Sharma, JM de Boer, T Borm, GJ Bryan, DMA Martin. In silico approaches for anchoring the potato genome. The 7th Solanaceae Genome Workshop (SOL 2010), Dundee, United Kingdom, September 5-9, 2010

DMA Martin, DM Bolser, SK Sharma, GJ Bryan. Developing informatics resources for end users of the Potato Genome Sequence project data. The 7th Solanaceae Genome Workshop (SOL 2010), Dundee, United Kingdom, September 5-9, 2010

JM de Boer, D Bolser, SK Sharma, GJ Bryan, CWB Bachem, RGF Visser. In silico integration of genetic and physical and sequence maps in potato using BAC sequence tags. The 7th Solanaceae Genome Workshop (SOL 2010), Dundee, United Kingdom, September 5-9, 2010

G Bryan (on behalf of the Potato Genome Sequencing Consortium). The Potato Genome Sequence. EAPR – EUCARPIA CONGRESS Potato Breeding after completion of the DNA Sequence of the Potato Genome, Wageningen, the Netherlands, June 27-30, 2010

SK Sharma (on behalf of the Potato Genome Sequencing Consortium). Anchoring the potato genome. EAPR – EUCARPIA CONGRESS Potato Breeding after completion of the DNA Sequence of the Potato Genome, Wageningen, the Netherlands, June 27-30, 2010

GJ Bryan (on behalf of the Potato Genome Sequencing Consortium). Progress in anchoring the Potato Genome. The 6th Solanaceae Genome Workshop (SOL 2009), New Delhi, India, November 8-13, 2009

SK Sharma (on behalf of the Potato Genome Sequencing Consortium). The Potato Genome Sequencing Initiative. The 6th Solanaceae Genome Workshop (SOL 2009), New Delhi, India, November 8-13, 2009

Other communications/outcomes

UK Press release: ‘Potato Genome Sequence released by international group of scientists’, Sept 2009

Information and data has been made available through http://potatosequence.org/. The raw data is submitted to various GenBank sequence databases and a high quality genome assembly has been released to the public under a general data access agreement typical for large scale genome projects (i.e., that the data be used to accelerate individual research and not be used to publish whole genome or whole chromosome studies. PGSC members will publish a series of joint articles describing the totality of their efforts.

Efforts are underway to use the genome sequence to develop markers for deployment in commercial breeding. One significant development is the initiation of a new ‘association mapping’ project (in partnership with a potato breeding company and funded by the TSB) which will use markers derived from the genome to detect links between important traits and individual markers, which could subsequently be used in selection of improved material. The project uses a panel of ~300 varieties and breeding clones in combination with a set of genetic markers likely to exceed 20,000 in number.

11. ACKNOWLEDGEMENTS

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