

## Crop improvement in the era of climate change: an integrated, multi-disciplinary approach for common bean (*Phaseolus vulgaris*)

Phillip E. McClean<sup>A,B,F</sup>, Jimmy Burridge<sup>C</sup>, Stephen Beebe<sup>D</sup>, Idupulapati M. Rao<sup>D</sup> and Timothy G. Porch<sup>E</sup>

<sup>A</sup>Genomics and Bioinformatics Program, North Dakota State University, Fargo, ND 58102, USA.

<sup>B</sup>Department of Plant Sciences, North Dakota State University, Fargo, ND 58102, USA.

<sup>C</sup>Department of Horticulture, Pennsylvania State University, University Park, PA 16802, USA.

<sup>D</sup>Bean Program, Centro Internacional de Agricultura Tropical (CIAT), AA 6713, Cali, Colombia.

<sup>E</sup>USDA-ARS Tropical Agriculture Research Station, 2200 PA Campos Avenue, Suite 201, Mayaguez 00680, Puerto Rico.

<sup>F</sup>Corresponding author. Email: [phillip.mcclean@ndsu.edu](mailto:phillip.mcclean@ndsu.edu)

**Abstract.** Climate change and global population increase are two converging forces that will jointly challenge researchers to design programs that ensure crop production systems meet the world's food demand. Climate change will potentially reduce productivity while a global population increase will require more food. If productivity is not improved for future climatic conditions, food insecurity may foster major economic and political uncertainty. Given the importance of grain legumes in general – common bean (*Phaseolus vulgaris* L.) in particular – a workshop entitled 'Improving Tolerance of Common Bean to Abiotic Stresses' was held with the goal of developing an interdisciplinary research agenda designed to take advantage of modern genotyping and breeding approaches that are coupled with large scale phenotyping efforts to improve common bean. Features of the program included a multinational phenotyping effort to evaluate the major common bean core germplasm collections and appropriate genetic populations. The phenotyping effort will emphasise the response of root and shoot traits to individual and combined stress conditions. These populations would also be genotyped using newly emerging high density single nucleotide polymorphism (SNP) marker arrays or next generation sequencing technology. Association analysis of the core collections aims to identify key loci associated with the response to the stress conditions. Companion bi-parental quantitative trait loci (QTL) experiments will act as confirmation experiments for the association analysis. The upcoming release of the genome sequence of common bean will be leveraged by utilising population genomic approaches to discover genomic regions that differentiate stress-responsive and non-responsive genotypes. The genome sequence will also enable global gene expression studies that will highlight specific molecular-based stress responses. This collective knowledge will inform the selection of parental lines to improve the efficiency of common bean improvement programs.

**Additional keywords:** phenotyping, genotyping, statistical genetics, biotic stress, genomics, marker assisted selection.

Received 26 April 2011, accepted 11 August 2011, published online 8 November 2011

### Introduction

By all credible estimates, climate change over the next few decades will be dramatic. Chief among these changes will be decreases in water availability and increases in ambient air temperatures in major agricultural production areas (Battisti and Naylor 2009; Lobell *et al.* 2011). From a crop improvement perspective, the physiological responses that allow plants to be most productive in these new environments must be better defined and the genetic factors that control these responses must be discovered and introgressed into modern varieties (Yadav *et al.* 2011). There is an urgent need for coordinated efforts to confront climate change through genetic improvement begin immediately because it is likely to take

10 years to introduce these genetic factors into a broad array of new plant varieties once they are discovered.

The International Center for Tropical Agriculture (CIAT; Cali, Colombia) convened a workshop entitled 'Improving Tolerance of Common Bean to Abiotic Stresses' from 2–4 November 2010. A multidisciplinary group of international plant researchers met to share perspectives and develop a research plan that addresses the need for developing abiotic stress tolerance in common bean (*Phaseolus vulgaris* L.). Common bean is a major crop worldwide and a significant protein source in countries in Central and South America, SubSaharan Africa and parts of Asia. Importantly, many areas in these regions are predicted to be negatively impacted by climate

change (Lobell *et al.* 2008). This scenario is especially true for drought. Whereas more developed countries may have the capital to invest in the agricultural infrastructure necessary to mitigate certain stressors, such as drought, through the development of extensive irrigation systems, other countries do not have that opportunity. The lack of appropriate infrastructure and other solutions to mitigate climate change may result in a serious food security risk and its associated social and political consequences.

During the workshop, the current status of research on abiotic stress in common bean was presented. Elcio P. Guimarães (CIAT) described CIAT's emphasis on developing eco-efficient agriculture systems that increases productivity and reduces poverty while maintaining food security and preserving natural resources (CIAT 2009). Central to this focus is an effort to develop breeding strategies for improving tolerance to abiotic stresses. On a global scale, Andrew Merchant (University of Sydney, Australia) provided a description of the World Universities Network Plant System Research Network, which is assisting the common bean community to use collaborative approaches to combat climate change through the international research community. The network provides an organisational framework to address climate change through the development of approaches at the plant functional level. A critical principle of the network is the development of basic and applied tools and assessment methods to measure plant responses to various stresses.

Given the importance of plant breeding to improve stress tolerance, several presentations discussed current crop improvement principles and practices. Steve Beebe (CIAT) hypothesised that current cultivars inherited from their wild progenitors a response to mid-season intermittent drought that suppresses reproduction and shuttles carbon resources to the root (Beebe *et al.* 2008). The result is that the full yield potential of the crop is disrupted under intermittent drought. The analysis of pod harvest index under irrigated and rain fed conditions and the selection of lines that translocate carbon more effectively to the developing seed under tropical intermittent rain conditions has led to improved yield and seed quality under drought. A cooperative shuttle breeding program, similar to the one applied during the early days of the Green Revolution by Norman Borlaug, is being coordinated by Tim Porch (USDA, Puerto Rico, USA) and Carlos Urrea (University of Nebraska, USA). That program is capturing drought tolerance alleles that confer broad adaptation and drought tolerance in multiple stress locations by selecting lines in early generations derived from crosses between elite drought tolerant germplasm of tropical origin with modern cultivars and breeding lines of temperate origin. The program focuses on stress occurring during reproductive development, which can cause excessive abortion of buds, flowers and pods, resulting in dramatic yield reduction because the physiological effects of abiotic stress tend to be more pronounced during reproductive versus vegetative development. Breeding lines are selected in both locations in early generations and the selected lines are then advanced and tested in yield trials through sequential testing in both locations. The goal of identifying lines with adaptation to multiple drought environments across climatic zones is beginning to be realised. The genetics and breeding for heat tolerance have been pursued

through screening under high temperature field conditions in Puerto Rico and Africa and under controlled high temperature greenhouse conditions in New York (Cornell University), leading to the improvement of dry and snap beans for heat tolerance through selection for yield components under high temperature stress during reproductive development (Porch *et al.* 2010; Wasonga *et al.* 2010).

From a physiological perspective, Elizabeth Van Volkenburgh (University of Washington, USA) described the role of cell expansion and photomorphogenesis as important contributors to higher yield. It was proposed that specific photoreceptors and red and blue light provide stimuli for H<sup>+</sup> efflux across the plasma membrane which in turn affects cell expansion via cell wall acidification, loosening and turgor regulation. The important role of roots in combating the effects of stress was a major focus of physiologists participating in the workshop. Early investigations at CIAT have shown that root architecture (deeper roots) is an inherited response that differs among common bean genotypes exposed to drought stress under different soil conditions (Sponchiado *et al.* 1989). Genotypic differences in root traits under multiple stress conditions were further emphasised by Jimmy Burrige (Pennsylvania State University, USA). Phosphorus (P) efficient genotypes of common bean develop more adventitious roots, shallower basal roots and longer, denser root hairs. Root hair length, adventitious rooting and basal root growth angle under P stress were shown to be under the control of multiple quantitative trait loci (QTL) (Miguel 2004; Yan 2004; Ochoa *et al.* 2006). Furthermore, deeper basal roots were also shown to be an advantage under water stress conditions although at the cost of reduced P acquisition (Ho *et al.* 2005). Those root architecture traits that increase biomass production under drought and low P conditions have been identified and simple screening protocols for these traits have been established (for examples, see [www.psu.edu](http://www.psu.edu), accessed 15 February 2011). Research continues to focus on identifying other traits involved in combined drought and low P stress.

Idupulapati Rao (CIAT) described recent research at CIAT on water stress. Confronted with a mandate to provide adapted genotypes to many areas of the world, of which 60% is affected by drought, CIAT has incorporated abiotic stress tolerance as a breeding objective. Supporting this objective is a research program that aims to (1) understand those physiological mechanisms of stress tolerance and (2) develop markers associated with the stress response. These tools will assist the selection of genetic materials that exhibit both yield improvement and stability. Although deep rooting offers access to more moisture, as evidenced by higher values of stomatal conductance and canopy temperature depression, it does not result in greater yield for many genotypes. However, photosynthate partitioning to grain does play a major role in drought tolerance (Beebe *et al.* 2009). Partitioning has been quantified as pod partitioning index (pod biomass at harvest as a percent of total biomass at mid-pod fill) and pod harvest index (grain weight as percent of total pod biomass) (Beebe *et al.* 2010). Both parameters showed significant correlations with yield under stress. Pod harvest index measured under drought stress also correlated with yield in an acid, aluminum toxic soil, suggesting that this is an effective variable for measuring

tolerance to different abiotic stresses. Since the movement of photosynthate during stress is necessary to support yield, it follows that pod harvest index is correlated with yield under different stress factors. Other traits of importance were maturity and root vigour and depth. Matthew Blair (CIAT) described blocks of yield QTL under drought that are located on chromosomes Pv8 and Pv10 that were discovered in a Mesoamerican  $\times$  Mesoamerican cross (Blair *et al.* 2011).

Modern, industrial-level screening techniques are now available. These high-throughput methods are useful for rapid field and greenhouse screening, once a phenotype has been determined to be correlated with a trait. Arnd Kuhn (Jülich Research Center, DEU) described approaches that are now available. Root traits are now becoming a major focus for stress tolerance in this research effort. Nuclear magnetic resonance can effectively determine root structure of plants grown in the soil and root function can be assessed using positron emission tomography. Rhizotrons are now available that can describe root growth patterns under various conditions. A major challenge is making these approaches cost effective for programs with limited resources.

### Research plan

Water and heat stresses are major limitations to crop productivity. Given the short time frame available to alter the baseline genetic makeup of germplasm for crop improvement under the present climate change predictions, concerted efforts must begin to further understand the physiological mechanisms of tolerance to these two important stress conditions, identify genetic factors that control the physiological responses, pyramid those factors into new germplasm and select those combinations that lead to the maximisation of yield under individual and combined drought and heat stress. To truly address international food security needs, the effort must be global because a single genotype will not be adapted to all current common bean production systems. The benefit of a coordinated global effort is that the genetic factors can be tested in a multitude of drought and heat stress environments allowing geneticists and breeders to discover the best combination of factors that provide local or regional adaptation to the stress.

The measurement of above ground biomass, such as yield and yield components, is important for determining genotypic response to heat and drought stress and will be a key breeding objective. Common beans are particularly sensitive to high night-time temperatures during reproductive development, thus, higher minimum temperatures due to global warming are of special concern. Carefully selected screening locations will provide relatively consistent drought and heat stress during reproductive development from year to year. Excessive drought stress in dry climates can be controlled through drip, furrow or overhead irrigation, although year-to-year variation in ambient temperature is expected. Owing to location and year variability, phenotypic plasticity and genotype  $\times$  environment interactions in the abiotic stress response (Ramírez-Vallejo and Kelly 1998), replicated and multi-location trials, possible through such an international effort, will allow for better estimation of the genetic and physiological components involved in the complex abiotic stress response.

Although roots are an essential component to combating stress, they have received little attention in bean breeding efforts. Roots are the chemical, physical and anatomical interface between many of the essential components necessary for the plant to succeed in stress environments by acquiring the essential minerals required for physiological processes and, most importantly, tapping the water resources necessary for plant survival. From that perspective, a central research question that should inform stress research is: what functions that define root plasticity, architecture and resource use efficiency alleviate stress while providing yield stability in multiple agro-ecosystems? The recent research by Beebe *et al.* (2008) identified genotypes of common bean that outperformed commercial checks under terminal drought conditions while maintaining strong yield competitiveness in favourable environments. Additionally, on soils deficient in P, these lines yielded as well as genotypes selected specifically for tolerance to low P conditions. These lines clearly demonstrate phenotypic plasticity. It is important to understand what physiological and anatomical functions underlie this plasticity. From a genetic perspective, defining the genomic regions that are critical for these two successful stress responses would facilitate the incorporation of these genes into other genetic backgrounds. Greatest success will be realised by a cooperative research effort that builds on past knowledge and expertise. Therefore, it is necessary to define the components of a coordinated bean improvement program targeting those particular conditions that will become larger constraints to the crop as the global climate changes.

Legumes utilise their symbiotic relationship with Rhizobia to fix nitrogen. This is an important contribution to soil fertility and is likely to increase as the price of nitrogen fertilisers continues to rise steadily. Therefore, understanding the effect of climate change on N fixation should be an important consideration of an effective research plan. Water stress reduces N fixation in common bean. For example, Ramos *et al.* (1999) observed a 50% reduction in nodule weight and number when a water-stress tolerant bean cultivar was grown in soil at 30% of soil field capacity of water. Additionally, nitrogenase activity was drastically reduced under these conditions. Importantly, genetic variation exists for nodule number and for the ability to fix nitrogen for bean plants grown under water stress-induced conditions (Aydi *et al.* 2008).

### Phenotyping

Without accurate and reproducible phenotyping of plants under multiple stress conditions, it is impossible to make significant advances in crop improvement. Although the greenhouse has some benefits for selection of breeding lines for abiotic stress tolerance (convenient location, relatively well controlled growing conditions), the most rapid improvement will be achieved by screening and selecting breeding materials in the target environments in which they will be produced. These environments should be selected to represent the meteorological and geographic range in which a particular stress or a combination of stresses, occur under common bean production conditions. As an example, terminal and intermittent drought stress can occur in both arid and subhumid environments since rainfall during

different seasons of the year can vary dramatically in tropical and subtropical environments. Once appropriate environments are identified, it will become necessary to carefully catalogue the different conditions under which a stress is expressed and select screening locations that best represent these conditions. Since the goal of the program should be to improve yield in as many production regions as possible, the testing sites should represent key international production regions.

Crop improvement depends on the mobilisation of new allele combinations into an improved genotype. The first step is to assess the available genotypic variation for a particular trait. Currently, the two largest collections of common bean are managed by CIAT (~36 000 accessions) and the United States Department of Agriculture National Plant Germplasm System (USDA NPGS; ~17 000 accessions). Both of these organisations maintain core collections that were established to represent the variation within the cultivated form of the species. Although these collections have been successfully mined for genes for disease resistance, large scale screening for traits that are inherently quantitative in nature have been performed only to a limited extent (e.g. Urrea and Porch 2010). As a first step to assess variation, seed stocks of these collections should be increased to sufficient numbers for screening in replicated trials at multiple locations. In addition, new cultivars are consistently being released from modern breeding programs that aim to support production in a specific location and often these are not broadly tested. To better understand the phenotypic variation in these materials and their potential for broad usage, a population of modern cultivars from throughout the world should also be established and evaluated in the same environments.

The breadth of these trials should be considered as of utmost importance. It is envisioned that the entire domesticated core collections from CIAT (~1400) and the USDA NPGS (~425) should be evaluated. Related species that possess specific traits of interest would also be included in select trials. As a companion trial, ~500 modern cultivars/advanced lines would also be considered. Because of the extensive populations structure within common bean (Kwak and Gepts 2009; McClean *et al.* 2011), careful stratification will be necessary. First, there is a range of photoperiod responses (White and Laing 1989). Therefore, trials consisting of subsets of these entire collections should be grown only in environments where they can produce seed and show a typical yield response. The broad testing envisioned here will require an initial screening of the material for photoperiod response in a selected subset of environments that cover day length (latitude) and temperature (altitude) variation.

What specific traits should be measured? The obvious first choice is yield. Yet, phenotypic data should be collected using appropriate experimental designs in which carefully selected checks provide reliable estimates of performance of the lines under consideration. For indirect selection purposes, establishing correlations of certain traits with yield is also necessary. Traditional agronomic traits such as phenology, shoot biomass, days to flowering, days to maturity and yield components are relatively easy to assess and have in the past been associated with tolerance to drought and heat. Abiotic stress indices, such as the geometric mean and percent yield reduction, will also be important in assessing genotypic response to stress

versus non-stress conditions (Ramírez-Vallejo and Kelly 1998; Porch *et al.* 2009) in order to ensure broad adaptation and yield stability. Incorporating measurements of canopy temperature depression and stomatal traits such as the number, size and conductance of stomata (Hetherington and Woodward 2003; Beebe *et al.* 2010), along with general phenology, would be useful to link the underlying physiological responses to abiotic stress and to the plasticity necessary for adaptation to a changing environment (Nicotra *et al.* 2010).

Since remobilisation of photosynthate from shoot to reproductive tissues appears to be a drought-tolerance response (Beebe *et al.* 2009), pod and seed measurements should also be included (Beebe *et al.* 2010). Root traits such as number of basal and adventitious roots, depth, length and thickness of basal roots and dispersion of lateral roots have been associated with low P tolerance (St Clair and Lynch 2010). Since it was noted that tolerance to drought and low soil P levels are associated (Beebe *et al.* 2008), these would be logical traits to measure. The 'shovelomics' techniques, developed by the Lynch laboratory (Pennsylvania State University, USA), will be adopted. This technique enables the rapid assessment of 10 root crown traits and would accelerate data collection and provides an inexpensive tool that has broad application for many research settings (Trachsel *et al.* 2011). In addition to the crown characteristics, cultivar and strain variation for nodulation and N<sub>2</sub> fixation exists (Rosas *et al.* 1998) and improved biological nitrogen fixation (BNF) can be achieved through selection. Nodulation will be evaluated during the 'shovelomics' assessment by observing quantity, size and colour of nodules. Making multiple observations at once allows for efficient selection of superior accessions.

To exploit the data more systematically, the research team will standardise the manner in which each phenotypic trait is measured. The systematisation of data collection will provide continuity among the phenotypic data even as populations of different genetic composition are evaluated at multiple worldwide locations.

#### *Marker-assisted selection in common bean*

Common bean breeders are major adopters of molecular marker technology. In the United States, >90% of new germplasm and cultivars released in the past decade were developed with the aid of the technology. The current marker suite used by breeders is the outcome of concerted worldwide efforts to develop PCR-based markers associated with important disease resistance loci. These markers are publicly available markers and address diseases important to bean production throughout the world. Recently funded programs, such as the Common Bean Coordinated Agricultural Project supported through the USDA, are posed to significantly increase the number of molecular markers available for the discovery of new marker-trait associations. The project recently released the first of 1536 single nucleotide polymorphism markers designed for the Illumina genotyping platforms (Golden Gate and Infinium). The final goal of the marker development portion of the project is to increase the overall number of markers, identify a subset of market class specific markers and to develop associated indel-based markers designed for inexpensive gel-based assays.

The availability of this large number of markers distributed throughout the genome makes possible detailed association analysis. Association studies utilise the collective recombination history of a defined genetic population to discover new marker/trait associations. In practice, the geneticist creates a population of many genotypes that is subsequently grown in replicated field trials under conditions that represent various stresses. The extensive field evaluation trials consisting of many genotypes, as described above, is an ideal dataset for these experiments. Each of the lines is also genotyped with a collection of genome-wide markers. A SNP platform is ideal for this step because of the ease of use this high-throughput marker system. The phenotypic and genotypic data is then analysed using techniques that control for population structure and relatedness and for multiple marker testing (Mamidi *et al.* 2011). The result of this analysis is the discovery of markers associated with the particular trait of interest.

From a genetic factor discovery perspective, careful preplanning and shared phenotyping approaches will enable the international research program to maximise the discovery of important genetic factors associated with a stress using association genetics approaches. For example, as long as the phenotyping is consistent, results from multiple trials, even if using a different marker set, can be combined to generate larger and more robust datasets. In this regard, the development of effective imputation techniques that enable researchers to predict the marker genotype at each missing locus greatly expands the sizes of populations that researchers can effectively manage (Marchini and Howie 2010). This is a significant development in that different populations and markers can be used at different loci as long as the phenotype is collected using the same protocol. For example, imputation techniques are enabling human researchers to pool genotypic data from multiple worldwide trials to discover loci associated with multiple human diseases. Most recently, this approach was used to discover new loci associated with Alzheimer's disease (Naj *et al.* 2011).

Association mapping (AM) experiments identify loci that are associated with specific phenotypes. Two recent experiments in barley (Cockram *et al.* 2010) and *Arabidopsis* (Atwell *et al.* 2010) are worth noting. Each used a large population of genotypes to evaluate many phenotypes, 32 with barley (*Hordeum vulgare* L.) and 107 for *Arabidopsis*. Strong associations were detected using statistical techniques that account for population structure and relatedness. Importantly, many markers were discovered that mapped within or near genes previously discovered to be factors controlling a specific trait.

These genes were discovered previously using data from QTL experiments based on bi-parental populations that capture only a subset of the variation within a species. Therefore bi-parental QTL experiments to confirm AM marker trait associations should continue to be a priority. The large exhaustive phenotyping results described above will inform the selection of relevant parents for bi-parental population development. Ideally, several populations will be produced. These new populations can then be genotyped using the emerging high density marker sets and QTL can be identified using an approach such as composite interval mapping.

#### *Applications of the common bean genome sequence to climate change research*

In the near future, the common bean genome sequence will be released. This sequencing project, funded by the USDA and the US Department of Energy, will provide a major resource for abiotic stress and other common bean genetic research areas. A first application is to capture a transcriptome profile of gene expression during stress and non-stress conditions using RNA-seq technology. Here, RNA is collected from tissues that experience some level of a stress, converted to a DNA template and sequenced using modern high-throughput sequencing techniques (Ozsolak and Milos 2011). The sequence reads represent the genes expressed under the stress (or the normal) condition and the number of reads for each gene are proportional to the level of gene expression. The assembled and annotated genome is critical because it serves as a reference to determine which genes are affected by the stress. Severin *et al.* (2010b) describe the development and application of RNA-seq to the study of global gene expression in soybean. Similar patterns of expression can be coupled with genetic experiments to determine if any genes located at major QTL are cycling under various stress conditions.

The availability of a whole-genome reference sequence can also be used to discover regions of a genome associated with a specific phenotype by using either genetic or natural populations. As an example, near isogenic lines of soybean differing for a protein QTL (Bolon *et al.* 2010) were screened with SNPs that were discovered by comparing sequences from an RNA-seq analysis. The polymorphisms were used along with the reference genome sequence to define a QTL interval on chromosome 20 (Severin *et al.* 2010a). This technique could be applied for any stress once appropriate genetic stocks are developed representing differing QTL genotypes associated with a specific stress phenotype.

A novel population genomics approach was described by Turner *et al.* (2010) to discover candidate genes associated with adaptation to specific soil types. They created samples by pooling DNA from *Arabidopsis lyrata* individuals collected from geographically distinct sites containing granitic or turpentine soils. DNA sequence data were collected from the pooled samples using next generation sequencing techniques. Polymorphic loci were discovered and population differentiation statistics were used to identify genes that were highly fixed in one population or the other. The candidate genes included metal transporters and metal detoxification genes. A similar approach could use pools of landrace DNA derived from individuals found in well designed field trials to express contrasting phenotypes for a trait(s) associated with a specific stress. This approach will create a catalogue of genes that can be used as a query with the data generated from the RNA-seq experiments to determine if the gene expression pattern of any of the genes is cycling with regards to changing environmental conditions.

The whole genome sequence will move common bean into the era of genotyping-by-sequencing (GBS). This approach involves a low-pass (1×) next generation resequencing of a select number of genotypes within a population. For a bi-parental population, this might be the entire collection of lines, or for the AM panel, it could be just a subset. In these cases, tens of thousands of loci will be genotyped, creating high density maps that will enable a more

accurate mapping of causative loci. Recently, this approach has been applied to maize (*Zea mays* L., Lai *et al.* 2010), rice (*Oryza sativa* L., Huang *et al.* 2010) and soybean (*Glycine max* (L.) Merr., Lam *et al.* 2010). A streamlined GBS approach was recently described (Elshire *et al.* 2011).

### *Integrating phenotyping, genotyping and mapping results into plant improvement programs*

The ultimate goal is to improve the performance of varieties under changing climate conditions. This project is staged for that ultimate goal. The large scale screening program will initially identify parents that can be used in breeding programs. Plant breeders can begin to incorporate this variation immediately after the screening is performed. A companion effort from this introgression process will be the development of genetic populations that can be used to uncover the genetic factors associated with specific traits. Improved efficiency of line selection can be achieved through the identification of loci that are strongly associated with specific traits (high  $R^2$ ). These loci will be confirmed using the bi-parental populations and once they are confirmed they can be used for genome selection of the appropriate advanced lines. The application of genomic selection (Heffner *et al.* 2010) will ultimately be possible when the number of markers applied to improvement efforts moves from the hundreds to the thousands and ultimately, the whole genome scale. Those discoveries will be of profound importance as new crosses are made and new materials are generated in a maturing research program.

### Acknowledgements

Support for the workshop was provided by the World Universities Network and the University of Washington, Seattle, WA, USA. The work of Elizabeth Van Volkenburgh is greatly appreciated for organising and managing an effective workshop that led to this white paper.

### References

- Atwell S, Huang YS, Vilhjalmsón BJ, Willems G, Horton M, Li Y, Meng D, Platt A, Tarone AM, Hu TT, Jiang R, Mulyati NW, Zhang X, Amer MA, Baxter I, Brachi B, Chory J, Dean C, Debieu M, de Meaux J, Ecker JR, Faure N, Kniskern JM, Jones JD, Michael T, Nemri A, Roux F, Salt DE, Tang C, Todesco M, Traw MB, Weigel D, Marjoram P, Borevitz JO, Bergelson J, Nordborg M (2010) Genome-wide association study of 107 phenotypes in *Arabidopsis thaliana* inbred lines. *Nature* **465**, 627–631. doi:10.1038/nature08800
- Aydi SS, Aydi S, Gonzalez E, Abdely C (2008) Osmotic stress affects water relations, growth and nitrogen fixation in *Phaseolus vulgaris* plants. *Acta Physiologiae Plantarum* **30**, 441–449. doi:10.1007/s11738-008-0141-y
- Battisti DS, Naylor RL (2009) Historical warnings of future food insecurity with unprecedented seasonal heat. *Science* **323**, 240–244. doi:10.1126/science.1164363
- Beebe SE, Rao IM, Cajiao C, Grajales M (2008) Selection for drought resistance in common bean also improves yield in phosphorus limited and favourable environments. *Crop Science* **48**, 582–592. doi:10.2135/cropsci2007.07.0404
- Beebe S, Rao I, Blair MW, Butare L (2009) Breeding for abiotic stress tolerance in common bean: present and future challenges. Available at [http://193.43.36.176/gipbtest/images/pdf\\_files/LiteratureViews/Beebe\\_DOC\\_apb09.pdf](http://193.43.36.176/gipbtest/images/pdf_files/LiteratureViews/Beebe_DOC_apb09.pdf) [accessed 15 February 2011]
- Beebe SE, Rao IM, Blair MW, Acosta-Gallegos JA (2010) Phenotyping common beans for adaptation to drought. In 'Drought phenotyping in crops: from theory to practice. Generation Challenge Program Special Issue on Phenotyping'. (Eds JM Ribaut, P Monneveux) pp. 311–334. (General Challenge Programme: Texcoco, Mexico)
- Blair MW, Galeano CH, Tovar E, Muñoz Torres MC, Velasco A, Beebe S, Rao IM (2011) Development of a Mesoamerican intra-gene pool genetic map for QTL detection in a drought tolerant × susceptible common bean (*Phaseolus vulgaris* L.) cross. *Molecular Breeding* in press
- Bolon YT, Joseph B, Cannon SB, Graham MA, Diers BW, Farmer AD, May GD, Muehlbauer GJ, Specht JE, Tu ZJ, Weeks N, Xu WW, Shoemaker RC, Vance CP (2010) Complementary genetic and genomic approaches help characterise the linkage group I seed protein QTL in soybean. *BMC Plant Biology* **10**, 41. doi:10.1186/1471-2229-10-41
- CIAT (2009) 'Strategic directions. Eco-efficient agriculture for the poor.' (CIAT: Cali, Colombia)
- Cockram J, White J, Zuluaga DL, Smith D, Comadran J, Macaulay M, Luo Z, Kearsy MJ, Werner P, Harapp D, Tapsell C, Liu H, Hedley PE, Stein N, Schulte D, Steuernagel B, Marshall DF, Thomas WT, Ramsay L, Mackay I, Balding DJ, AGOUEB Consortium, Waugh R, O'Sullivan DM (2010) Genome-wide association mapping to candidate polymorphism resolution in the unsequenced barley genome. *Proceedings of the National Academy of Sciences of the United States of America* **107**, 21611–21616. doi:10.1073/pnas.1010179107
- Elshire RJ, Glaubitz JC, Sun Q, Poland JA, Kawamoto K, Buckler ES, Mitchell SE (2011) A rapid genotyping-by-sequencing (GBS) approach for high diversity species. *PLoS ONE* **6**, e19379. doi:10.1371/journal.pone.0019379
- Heffner E, Lorenz AJ, Jannink J-L, Sorrells ME (2010) Plant breeding with genomic selection: gain per unit time and cost. *Crop Science* **50**, 1681–1690. doi:10.2135/cropsci2009.11.0662
- Hetherington AM, Woodward FI (2003) The role of stomata in sensing and driving environmental change. *Nature* **424**, 901–908. doi:10.1038/nature01843
- Ho MD, Rosas JC, Brown KM, Lynch JP (2005) Root architectural tradeoffs for water and phosphorus acquisition. *Functional Plant Biology* **32**, 737–748. doi:10.1071/FP05043
- Huang X, Wei X, Sang T, Zhao Q, Feng Q, *et al.* (2010) Genome-wide association studies of 14 agronomic traits in rice landraces. *Nature Genetics* **42**, 961–967. doi:10.1038/ng.695
- Kwak M, Gepts P (2009) Structure of genetic diversity in the two major gene pools of common bean (*Phaseolus vulgaris* L., Fabaceae). *Theoretical and Applied Genetics* **118**, 979–992. doi:10.1007/s00122-008-0955-4
- Lai J, Li R, Xu X, Jin W, Xu M, *et al.* (2010) Genome-wide patterns of genetic variation among elite maize inbred lines. *Nature Genetics* **42**, 1027–1030. doi:10.1038/ng.684
- Lam H-M, Xu X, Liu X, Chen W, Yang G, Wong FL, Li MW, He W, Qin N, Wang B, Li J, Jian M, Wang J, Shao G, Wang J, Sun SS, Zhang G (2010) Resequencing of 31 wild and cultivated soybean genomes identifies patterns of genetic diversity and selection. *Nature Genetics* **42**, 1053–1059. doi:10.1038/ng.715
- Lobell DB, Burke MB, Tebaldi C, Mastrandrea MD, Falcon WP, Naylor RL (2008) Prioritising climate change adaptation needs for food security in 2030. *Science* **319**, 607–610. doi:10.1126/science.1152339
- Lobell DB, Bänziger M, Mogorokosho C, Vivek B (2011) Nonlinear heat effects on African maize as evidenced by historical yield trials. *Nature Climate Change* **1**, 42–45. doi:10.1038/nclimate1043
- Mamidi S, Chikara S, Goos RJ, Hyten DL, Moghaddam SM, Cregan PB, McClean PE (2011) Genome-wide association analysis identifies candidate genes associated with iron deficiency chlorosis in soybean. *Plant Genome* **4**, 154–164.
- Marchini J, Howie B (2010) Genotype imputation for genome-wide association studies. *Nature Reviews. Genetics* **11**, 499–511. doi:10.1038/nrg2796

- McClellan PE, Terpstra J, McConnell M, White C, Lee R, Mamidi S (2011) Population structure and genetic differentiation among the USDA common bean (*Phaseolus vulgaris* L.) core collection. *Genetic Resources and Crop Evolution* in press
- Miguel M (2004) Genotypic variation in root hairs and phosphorus efficiency in common bean (*Phaseolus vulgaris* L.). In 'Horticulture'. (Pennsylvania State University: University Park, PA)
- Naj AC, Jun G, Beecham GW, Wang L-S, Vardarajan BN, *et al.* (2011) Common variants at MS4A4/MS4A6E, CD2AP, CD33 and EPHA1 are associated with late-onset Alzheimer's disease. *Nature Genetics* **43**, 436–441. doi:10.1038/ng.801
- Nicotra AB, Atkin OK, Bonser SP, Davidson AM, Finnegan EJ, Mathesius U, Poot P, Purugganan MD, Richards CL, Valladares F, van Kleunen M (2010) Plant phenotypic plasticity in a changing climate. *Trends in Plant Science* **15**, 684–692. doi:10.1016/j.tplants.2010.09.008
- Ochoa IE, Blair MW, Lynch JP (2006) QTL analysis of adventitious root formation in common bean under contrasting phosphorus availability. *Crop Science* **46**, 1609–1621. doi:10.2135/cropsci2005.12-0446
- Ozsolak F, Milos PM (2011) RNA sequencing: advances, challenges and opportunities. *Nature Reviews. Genetics* **12**, 87–98. doi:10.1038/nrg2934
- Porch TG, Ramirez VH, Santana D, Harmsen EW (2009) Evaluation of common bean for drought tolerance in Juana Diaz, Puerto Rico. *Journal Agronomy & Crop Science* **195**, 328–334. doi:10.1111/j.1439-037X.2009.00375.x
- Porch TG, Smith JR, Beaver JS, Griffiths PD, Canaday CH (2010) TARS-HT1 and TARS-HT2 heat-tolerant dry bean germplasm. *HortScience* **45**, 1278–1280.
- Ramírez-Vallejo P, Kelly JD (1998) Traits related to drought stress resistance in common bean. *Euphytica* **99**, 127–136. doi:10.1023/A:1018353200015
- Ramos MLG, Gordon AJ, Minchin FR, Sprent JI, Parson R (1999) Effect of water stress on nodule physiology and biochemistry of a drought tolerant cultivar of common bean (*Phaseolus vulgaris* L.). *Annals of Botany* **83**, 57–63. doi:10.1006/anbo.1998.0792
- Rosas JC, Castro JA, Robleto EA, Handelsman J (1998) A method for screening *Phaseolus vulgaris* L. germplasm for preferential nodulation with a selected *Rhizobium etli* strain. *Plant and Soil* **203**, 71–78. doi:10.1023/A:1004346114558
- Severin AJ, Peiffer GA, Xu WW, Hyten DL, Bucciarelli B, O'Rourke JA, Bolon YT, Grant D, Farmer AD, May GD, Vance CP, Shoemaker RC, Stupar RM (2010a) An integrative approach to genomic introgression mapping. *Plant Physiology* **154**, 3–12. doi:10.1104/pp.110.158949
- Severin AJ, Woody JL, Bolon YT, Joseph B, Diers BW, Farmer AD, Muehlbauer GJ, Nelson RT, Grant D, Specht JE, Graham MA, Cannon SB, May GD, Vance CP, Shoemaker RC (2010b) RNA-seq atlas of *Glycine max*: a guide to the soybean transcriptome. *BMC Plant Biology* **10**, 160. doi:10.1186/1471-2229-10-160
- Sponchiado BN, White JW, Castillo JA, Jones PG (1989) Root growth of four common bean cultivars in relation to drought tolerance in environments with contrasting soil types. *Experimental Agriculture* **25**, 249–257. doi:10.1017/S0014479700016756
- St Clair SB, Lynch JP (2010) The opening of Pandora's box: climate change impacts on soil fertility and crop nutrition in developing countries. *Plant and Soil* **335**, 101–115. doi:10.1007/s11104-010-0328-z
- Trachsel S, Kaeppler SM, Brown KM, Lynch JP (2011) Shovelomics: high throughput phenotyping of maize (*Zea mays* L.) root architecture in the field. *Plant and Soil* **341**, 75–87. doi:10.1007/s11104-010-0623-8
- Turner TL, Bourne EC, Von Wettberg EJ, Hu TT, Nuzhdin SV (2010) Population resequencing reveals local adaptation of *Arabidopsis lyrata* to serpentine soils. *Nature Genetics* **42**, 260–263. doi:10.1038/ng.515
- Urrea CA, Porch T (2010) Phenotypic evaluation of a subset of the *Phaseolus vulgaris* core collections, the *P. acutifolius* germplasm collection and cultivars for drought tolerance in Nebraska and Puerto Rico. *Annual Report of the Bean Improvement Cooperative. Bean Improvement Cooperative* **53**, 164–165.
- Wasonga CJ, Pastor-Corrales MA, Porch TG, Griffiths PD (2010) Targeting gene combinations for broad spectrum rust resistance in heat tolerant snap beans developed for tropical environments. *Journal of the American Society for Horticultural Science* **135**, 521–532.
- White JW, Laing DR (1989) Photoperiod response of flowering in diverse genotypes of common bean (*Phaseolus vulgaris*). *Field Crops Research* **22**, 113–128. doi:10.1016/0378-4290(89)90062-2
- Yadav SS, Redden R, Hatfield JL, Lotze-Campen H, Hall A (2011) 'Crop adaptation to climate change.' (John Wiley & Sons: Hoboken, NJ)
- Yan X (2004) QTL mapping of root hair and acid exudation traits and their relationship to phosphorus uptake in common bean. *Plant and Soil* **107**, 1505–1529.