**White Paper**

**Application of Genomics to the Production of Climate Resilient Crops: Challenges and opportunities**

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# 1 Agro-biodiversity, Climate Change Challenges and Potential Genomics-Led Plant Breeding Solutions

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**The context**

Intensive cultivation of a limited number of crops over the last 10,000 years has drastically narrowed the number of plant species humans rely on for their various needs including; food, feed, feedstock, fibre, fuel, shelter and other applications ([Gepts 2004](#_ENREF_182); [Harlan 1992](#_ENREF_208)). Domestication has often been a haphazard affair with some regions (such as Europe) domesticating few species, while other regions have been responsible for many of the major crops now grown ([Meyer et al. 2012](#_ENREF_328)). In pre-colonial times, many crops species were introduced by Europeans into Africa and other ‘trading’ countries, potentially displacing indigenous crops (and also laying the foundation of many of the current crops grown, in Africa in particular). A number of these were species were then further enforced, through their development as commodity cash crops, serving often distant markets ([Alpern 1992](#_ENREF_12), [2008](#_ENREF_13)). Scientific breeding and the intensification of agriculture have been the most significant developments over the past hundred years. The Green Revolution introduced dwarfing genes, coupled with increased use of artificial nitrogen fertilizer, further genetic improvement to utilize the increased resources and highly tailored management of biotic and abiotic stresses ([Khush 2001](#_ENREF_261); [Pingali 2012](#_ENREF_359)).

These three key steps in agricultural history - domestication, displacement of native crops by major commercial crops together with genetically limited introductions of non-native species and the intensification of agricultural production during and since the Green Revolution - each represent potential bottlenecks, which may have reduced the genetic and trait diversity within major crop species available for further improvements in agricultural production or may even have influenced whether a crop species is still used today in agriculture.

Despite this series of decreases in crop diversity (or even, because of), food production, of the major staples has increased significantly in the last century in most of the world ([Fischer et al. 2009](#_ENREF_156)). This on-going process has led to consistent improvements in both the yield and quality of many important crops, with subsequent improvements in human nutrition and health. For example in wheat, a four-fold increase in grain yield in the United Kingdom (and a number of other countries) over the last 100 years was driven equally by genetic enhancement and by improved agronomy or crop husbandry. Similar yield improvements have been seen in oil production in Malaysian oil palm over the same time period, despite these being very different crops ([Calderini and Slafer 1998](#_ENREF_80); [Corley and Lee 1992](#_ENREF_105)) although oil palm remains only a partially domesticated crop. These remarkable improvements have been driven primarily by conventional plant breeding coupled to intensification and simplification of production systems. For wheat, this included a major step change resulting from the Green Revolution reduced height genes derived from the Japanese Norin 10 wheat variety which contained both Rht1 and Rht2 short alleles ([Borojevic 2005](#_ENREF_58); [Reitz and Salmon 1968](#_ENREF_384)). In oil palm, the major yield step change was the recognition that the shell-thickness gene of the fruit was under monogenic control and the heterozygous combination of contrasting alleles led to fruit with a 30% oil yield advantage over the homozygous, thick shell genotypes ([Beirxaert and Vanderweyen 1941](#_ENREF_34); [Singh et al. 2013](#_ENREF_450)).

Such increases in food production have been largely driven by selection for yield and adaptation (and against yield-reducing factors, such as susceptibility to pathogens and pests) and optimization of crop husbandry practices (through high inputs such as the use of fertilizers, herbicides, pesticides, and mechanization) to minimize the impact of environmental flux. However, selection under such ‘ideal’, high-input, environments in many countries and species is likely to have led to the loss of some of the genes for efficiency or adaptation to stress(es); particularly if such genes have minor deleterious effects when present in non-stressed or high-input environments (e.g. as postulated for some disease resistance genes; Brown ([2003](#_ENREF_66))).

This situation presents three potential challenges: to modify our selection criteria to focus on efficiency or adaptation/tolerance to stress(es) rather than total yield, to determine whether such efficiency/stress-tolerance genes are still present and exploitable in our elite material and wider breeding germplasm and also to develop new and to expand the use of minor crops, particularly where they offer better nutrition, environmental sustainability and/or resilience and require lower inputs than current major crop species. While a number of studies have suggested that there has not been a significant decrease in genetic variability within major crop germplasm in recent years (more of a reorganization), this has so far been an assessment of ‘anonymous’ or ‘neutral’ genetic diversity and may hide the loss of alleles for traits that may not have been selectively neutral. Furthermore, recent genomic studies suggest that the major reduction in genetic diversity occurred during the initial domestication step and much less during subsequent steps (reviewed in Gepts ([2014](#_ENREF_183))). The altered agricultural paradigm away from high inputs or at least towards stability and environmental resilience of yields alongside decreasing inputs is a significant challenge. Agricultural will also need to tackle (or perhaps return to) more complex production systems. The drive for high yields has led to simple agricultural systems at large scales; monocrop, monogenotype, uniformity and intensive management. In some regions of the world, this process can be taken further, particularly where crops produce the highest yields. For other regions, a more environment/location specific and complex agriculture may be needed, which maximizes the production of the system but uses complexity to introduce greater resilience into the system. However, the changing demographics of the world population, particularly increasing urbanization and an aging farming population, mean that dealing with complexity may not be simple.

Crop production is now facing the ‘perfect storm’ of climate change and high population levels, combined with increasing costs (both monetary and environmental) of phosphate and nitrate fertilizer representing a significant challenge to increasing the intensity of food production further, using a single agricultural paradigm ([Fischer et al. 2009](#_ENREF_156)). This challenge may become overwhelming in the face of climate instability. The failure to address global food production is starting to be evidenced by increasing food prices and greater global food insecurity ([FAO 2014](#_ENREF_147)). Continued failure to maintain increases in food production will lead to further increases in food prices in developed countries and social unrest and famine in developing countries.

Climate change will impact food supply unless actions are taken to increase the resilience of crops. There is predicted to be a deficit of 9% for maize, 11% for rice and 14% for wheat because of global climate change by 2020 ([Hisas 2011](#_ENREF_219)). The main causes of yield loss include: global warming (especially due to night temperature increasing plant respiration and higher day temperatures leading to more frequent high temperature events triggering decreased fertility); changes of rainfall pattern, which lead to droughts and floods; and other extreme weather events, the frequency of which may increase due to the changing climate. Crop pathogens and pests may also change their geographical distribution, with predicted increases in severity due to changes in rainfall, increasing temperatures and CO2 concentrations. Furthermore, elevated CO2 levels will also reduce the nutritional quality of many crops, while some crops may even become more toxic due to changes in the chemical composition of their tissues ([Dwivedi et al. 2013](#_ENREF_134)) and references therein.

There is clearly a requirement to accelerate advances in crop production; however options to facilitate this are limited. Increasing oil prices and diminishing phosphate supplies will lead to reduced fertilizer applications in a number of regions of the world, with a negative impact on food production. The potential to increase food production by increasing pesticide use is limited due to health and environmental concerns. However, there remains great potential to improve the germplasm of many crops through crop breeding and the introduction of novel alleles from wild relatives into major crops or even through the development of new crops through directed breeding and domestication of the best candidates and these are considered to offer the greatest potential for crop production to meet human needs in the future. While genetic modification remains controversial in a number of countries, in practice it will be an invaluable tool alongside enhanced breeding approaches. Most approaches so far have focused on pest tolerance and management enhancement, but in the last decade both experimental and commercial materials are beginning to address quality and subtler agricultural phenotypes. By understanding more about how crop systems work, we should be able to tailor modifications to produce gene alleles and phenotypes beyond the range available through exploitation of existing genetic variation.

Conventional breeding has supported the expansion of the human population of the world. Even where major step changes have occurred, such as the development of reduced-height cultivars during the Green Revolution or herbicide-/insect-resistant transgenic crops, these step-changes have occurred against a background of continuous adaptation and improvement through classical breeding approaches. Adapting existing crop breeding pools to biotic and abiotic stresses brought by climate change will indeed be the main task to ensure affordable food supply – especially for the resource-poor, who today face food insecurity and associated health risks. Moreover, plant breeding for host-plant resistance, which leads to fewer pesticide sprays and reduced fuel use, and improved input-use efficiency, especially for nitrogen, will lower greenhouse gas emissions (GGE), thereby potentially mitigating further climate change.

The field of genomics offers tools to help address the challenge of increasing food yield, quality and stability of production through advanced breeding techniques. Genomics can provide breeders with the knowledge they need to make more rapid selections and apply advanced breeding strategies to produce climate resilient crops. The application of (often) anonymous DNA markers to facilitate marker-assisted selection (MAS) procedures still fundamentally works within the confines of conventional breeding systems. Advances in plant genomics offer further means to improve our understanding of crop diversity at the species and gene levels, and will provide DNA markers to accelerate the pace of genetic improvement. The ensuing knowledge and tools could lead to a sound use of such genetic endowments for breeding new cultivars. A genomics-led breeding strategy for new cultivars should start by defining the stress(s) that will likely affect crop production and productivity under a certain climate change scenario. Data from multi-environment testing provide an opportunity for modeling “stress-impacts” on crops and target populations of environments: They can be used for choosing areas where climate change scenarios already occur or to be mimicked by choice of suitable screening sites for further selecting promising germplasm. Plant breeders and genebank curators will search for morphological and physiological traits in available germplasm that could enhance crop adaptation under such climate variability. In this regard, crop physiology may help define the ideotypes to be pursued for enhancing such adaptation. Moreover, the use of geographic information systems and passport data can allow identification of accessions for stress-prone environments, whereas the available characterization, including DNA fingerprinting, and evaluation data plus mapping of desired genes or quantitative trait loci (QTL) will assist in selecting promising accessions for further screening against specific stress(es). Likewise, precise phenotypic assessments and appropriate biometrical analysis will help find unique responses of a set of genotypes in a given phenological stage influenced by variation of weather patterns. This information will be further used in marker-aided breeding approaches such as genome-wide selection of promising germplasm for further use in crop breeding aiming at both population improvement and cultivar releases.

Incorporating MAS techniques within breeding programs has had an impact on the development of new genotypes of crops. Genetic mapping and QTL analysis, association genetics (AG) studies and (more recently, but still largely unproven in crop plants) genomic selection (GS) approaches have accelerated a dissection of the genetic control of agricultural traits, potentially allowing MAS, QTL and AG studies or direct calculation and selection of high value genotypes (GS) to be made in the context of breeding programs. Until recently, AG and GS were hampered by the need for very high marker density coverage of the genome. The development of next-generation sequencing (NGS) methods has made the development of very large number of markers even in relatively research-neglected crop species possible, either through development of Single Nucleotide Polymorphism (SNP) chips after large scale SNP discovery or Genotyping-by-Sequence (GBS) approaches to sequence genomic representations. Even so, many of the current application of NGS-based marker sets are still largely using essentially ‘anonymous’ markers to generate associations between marker and trait or genome-wide breeding values for a trait.

Recent advances in DNA sequencing technology are revealing the genetic blueprint for many of our important crop species. Understanding genetic diversity in a species at the DNA sequence level permits the identification of agronomically valuable gene variants as well as a means to select for these genes in breeding programs. Genomics and the associated ‘omic’ technologies also offer the potential to de-anonymize the markers that are used for marker-assisted breeding. Where this has been done for a limited number of genes and applied widely in breeding programmes – e.g. the development of so-called ‘perfect markers’ for photoperiod and vernalization requirement that are very important for the optimal adaptation of crops such as wheat to different environments – these markers reflect directly the sequence-level variation responsible for the agricultural trait variation. Eagles ([2010](#_ENREF_136)) used the diagnostic markers for photoperiod sensitivity gene (*Ppd-D1*) and vernalization genes (*Vrn-A1*, *Vrn-B1* and *Vrn-D1*) to investigate the optimal adaptation of wheat in Australia. The copy number of a specific gene or gene family has also been associated with variation for traits that underpin adaptation, such as winter hardiness in barley ([Knox et al. 2010](#_ENREF_267)), plant height and flowering time in wheat ([Diaz et al. 2012](#_ENREF_125); [Pearce et al. 2011](#_ENREF_358)). An understanding of such gene networks and the identification of the sequence-level (or epigenetic) variation that underlies agricultural traits conferring environmental resilience, such as heat-tolerance, would revolutionize our ability to truly breed for new ideotypes. These could be suited to particular environments and include the appropriate combination of stress-tolerance genes for desirable traits, even for performance under environmental volatility itself. This would apply to major staple crops, but as importantly also for minor and underutilized crops, where there is an appropriate niche or an outstanding trait is present. There may be some environments where the continued growth of major crops, even with the use of enhanced genomics to introduce new variation and traits, is simply no longer viable and alternative crops may hold the answer to sustainable agriculture in such situations. As an example, results from a number of QTL mapping studies in wheat suggest the identification of QTL that are consistently associated with heat tolerance traits on chromosomes 2B, 7B and 7D ([Paliwal et al. 2012b](#_ENREF_352); [Pinto et al. 2010](#_ENREF_360)). These are promising results that could be used now as indirect selection criteria for accumulating desirable traits for improved yield under increasing heat stress. Dissecting and identification of the basis of these desirable traits through genomics would allow selection of the best existing alleles directly and the conscious design of new ones.

Over millions of years, nature has evolved new genes, and shuffled and selected these genes in a wide range of environments to produce the diversity we see in wild species. In contrast, the selection and domestication of crops by humans is relatively recent, having occurred over the last 10,000 years. During the domestication and breeding process, there has been a significant reduction of genetic diversity in our major crops, alongside a selection for yield under highly managed agricultural environments. Currently breeders are shuffling the combinations of relatively few alleles to produce enhanced combinations that provide increased yield and other attractive agronomic characteristics. In many large genome crop species, even this reshuffling process is limited by restricted recombination patterns within the species, leading to the consistent inheritance of blocks of genes, raising issues of linkage drag and also fixed linkage blocks which may not contain the best possible combination of alleles. Breaking down these linkage constraints will allow breeders to access novel combinations from within their current elite parents. The need to evaluate the genetics of the very processes that allow genes to be recombined between parental genotypes in crops is needed. Genomics offers the potential to greatly increase further the diversity of alleles available to breeders through the mining of allied genepools and the genomes of crop wild relatives (CWRs). Genomics tools also enable the rapid identification and selection of the rare novel beneficial genes and their controlled incorporation into novel germplasm. As we enter the age of genomics, this technology will be used to help safeguard our future through increased food security. The application of genomics for crop germplasm enhancement offers, therefore, the greatest potential to increase food production in the coming decades, in what is likely to be a more locally adapted and diversified agriculture. The application of genomics for crop improvement varies between crops and also between the major breeding companies and smaller domestic or specialist crop breeders. With the continued rapid advances in genome technologies, the application of genomics to identify and transfer valuable agronomic genes from allied genepools and crop relatives to elite crops will increase in pace and assist in meeting the challenge of continued global food production.

Diversification of agriculture could significantly improve agricultural resilience, but the application of genomics to a far broader range of crops is also required, to allow the full potential of many of these species to be achieved, as well as for the staple crops which will continue to represent the main focus of breeding research. Knowledge-intensive crop breeding approaches will contribute to develop climate-proof, genetically-enhanced seed-embedded technology – which together with sustainable agro-ecosystem management, eco-efficient crop husbandry and sound postharvest handling – will assist feeding the world in this century affected by climate change. This White Paper provides an overview on the state-of-the-art of genomics-led breeding for the most important staples that feed the world and how to use and adapt such genomics tools for developing crops (major, minor or niche) with desired traits that enhance adaptation to, or mitigate climate change.

# 2 Genomics of Climate Resilience in Major Crops

*Andrew H. Paterson*

## 2.1 Introduction

In the face of “the ‘perfect storm’ of climate change combined with increasing costs of phosphate and nitrate fertilizer” (Chapter 1), this raises the question: how will we ensure the food security of a still-expanding population, among which 15% are already food-insecure, ([Diop et al. 2002](#_ENREF_126); [Rosegrant et al. 2002](#_ENREF_404); [Serageldin 2004](#_ENREF_430)) while requiring agriculture to use less water than in the past?

The sharp 21st century rise in food and energy prices may be a harbinger of the need anticipated by many leading agricultural scientists for a new Green Revolution ([Tuberosa et al. 2005](#_ENREF_495)), of broader scope than its predecessor. A central element of the first ‘Green Revolution’ was the widespread adoption of high yielding semidwarf (SD) rice varieties with improved harvest index, lodging resistance and “responsiveness” to high inputs (primarily nitrogen and water) ([Matson et al. 1997](#_ENREF_323); [Tilman 1998](#_ENREF_488); [Vitousek et al. 1997](#_ENREF_521)), contributing to their adoption in irrigated areas that occupy 57% of world rice lands.

The second Green Revolution will need to be driven much more heavily than the first by input constraints, for example focusing more greatly on how to maximize productivity in rainfed areas ([Cantrell and Hettel 2004](#_ENREF_85); [Conway 1998](#_ENREF_103)), but sharing with the first a central role of genetics as a delivery system for improvements. An unparalleled era of discovery in plant biology was ushered in with the sequencing of the entire genome of the botanical model Arabidopsis thaliana ([Bevan et al. 2001](#_ENREF_41)), and has been quickly followed with genome sequences for most major crops and leading botanical models ([Lee et al. 2012](#_ENREF_291); [Paterson et al. 2010](#_ENREF_357)). More recently, massively parallel ‘re-sequencing’ technologies ([Shendure and Aiden 2012](#_ENREF_443)) have permitted science to move beyond single ‘reference genomes’ to begin to catalog the diversity that permit some cultivars, or more frequently their wild relatives, to survive and flourish in the face of often harsh and always fluctuating conditions.

In this section, expert practitioners briefly summarize the states of knowledge of the genetic blueprints of many leading crops, together with information about breeding needs and priorities related to climate resilience. Genomic tools and resources are widely available and being employed in most of these plants and will soon be ubiquitous, aiding ‘marker assisted selection’ strategies that can be successful even based only on phenotypic information. Knowledge of gene functions is less consistent, leveraging to varying degrees the accumulated information from botanical models. But even in models, the exact functions of most genes remain unknown, and exploring the many variations conferred during angiosperm diversification represent an opportunity to identify a host of solutions to agricultural challenges.

One recurring theme among these chapters might be generalized as “advancing the productivity frontier”, continuing and strengthening efforts to improve crop productivity and quality under generally favorable conditions, as well as intrinsic defenses against pests, maximizing the amount and quality of food that can be produced from the most arable land. Particularly large incremental returns on investment may be realized in crops that have received relatively limited prior attention, but which may be of great importance in parts of the world where development challenges are the greatest and market failure is most acute. In widely grown crops with long histories of improvement, large investments may be required to realize small incremental gains, but such gains will be leveraged quickly across large production areas.

Perhaps a more distinguishing element of a second Green Revolution may be “transforming production systems.” In many crops, for example vegetables, a prior focus has been almost exclusively on quality and productivity, as the high crop value justifies investments to provide optimal inputs (water, fertilizer). Constraints on the cost and supply of inputs are already motivating shifts to breeding strategies more analogous to those of lower unit value crops, where abiotic stresses have long been an important dimension of crop improvement. More radical transformations may be attractive in many crops. Consideration of how to expand agriculture to provide plant biomass for production of fuels or chemical feedstocks ([Tilman et al. 2009](#_ENREF_489)), highlights many advantages of perennial crops that are equally pertinent to food production with input constraints ([Glover et al. 2010](#_ENREF_190)). Breeding ratooning or even perennial forms of some crops ([Cox et al. 2002](#_ENREF_112)) may be a logical extension of practices such as the use of ‘winter’ or ‘spring’ forms to maximize productivity in response to large seasonal climatic variations.

In summary, a second Green Revolution driven largely by input constraints, may integrate activities toward “advancing the productivity frontier” and “transforming production systems.” Genomic tools provide an infrastructure to lay bare the secrets of the genetic potential of plants to respond to a range of environments. Much foundational work remains to be done – and translating this information into climate resilient crops will require additional large investments, as detailed in the following sections for many major crops. In that agricultural initiatives can take 15-30 years to yield maximal returns ([Alston 2000](#_ENREF_14)), the required investments need to be made now.

## 2.2 Cereals and Millets

*Roberto Tuberosa*

Cereal and millets account for the largest portion of the human diet and are a staple to billions. Their production is increasingly threatened by the recent changes in weather patterns brought about by global warming, particularly in less-developed countries where the consequences of a changing climate have a devastating socio-economic impact. Reaching a level of cereal production sufficient to sustain an adequate level of global food security will require the effective integration of conventional plant breeding with the novel ‘omics’ approaches that allow us to dissect and more effectively manipulate the genetic make-up of resistance to abiotic stresses ([Langridge and Fleury 2011](#_ENREF_286)).

In the past decade, genomics-based approaches have been extensively deployed to dissect the genetic make-up of abiotic stress tolerance in cereals, particularly for drought, by far the most important stress in terms of yield reduction. Importantly, genomics-based approaches have contributed to broaden our understanding of the molecular and functional basis of abiotic stress tolerance in cereals, facilitating the adoption of novel strategies for more effectively tailoring crop genomes. Given the quantitative nature of abiotic stress tolerance, quantitative trait loci (QTLs) have been the main target of studies to identify the loci regulating the adaptive response of cereal crops to unfavorable environmental conditions, particularly for drought-adaptive traits ([Serraj et al. 2009a](#_ENREF_431); [Serraj et al. 2009b](#_ENREF_432); [Tuberosa 2012](#_ENREF_494); [Wassmann et al. 2009a](#_ENREF_527)). The most notable examples of traits targeted by QTL analysis include root architecture ([Hammer et al. 2009](#_ENREF_206); [Landi et al. 2010](#_ENREF_282); [Landi et al. 2002](#_ENREF_283); [Landi et al. 2007](#_ENREF_284); [Lynch 2013](#_ENREF_306); [Lynch et al. 2014](#_ENREF_307); [Sanguineti et al. 2007](#_ENREF_414); [Steele et al. 2013](#_ENREF_466); [Steele et al. 2007](#_ENREF_467); [Uga et al. 2013](#_ENREF_505); [Wasson et al. 2012](#_ENREF_529)), the accumulation of water-soluble carbohydrates and their partitioning to storage organs ([Rebetzke et al. 2008b](#_ENREF_380); [Salem et al. 2007](#_ENREF_408); [Snape et al. 2007](#_ENREF_457)), abscisic acid concentration ([Kholova et al. 2010](#_ENREF_260); [Landi et al. 2005](#_ENREF_285); [Rehman et al. 2011](#_ENREF_382)), stay-green ([Borrell et al. 2014](#_ENREF_59); [Yadav et al. 1997](#_ENREF_541); [Yang et al. 2007](#_ENREF_545)), canopy temperature ([Lopes et al. 2014](#_ENREF_300); [Lu 2005](#_ENREF_304)) and carbon isotope discrimination (Δ13C) ([Rebetzke et al. 2008b](#_ENREF_380))

As the unpredictability of weather patterns increases with global climate change, the identification and selection of QTLs with a consistent additive effect on yield *per se* (i.e. independently from flowering time), across a broad range of soil moisture regimes, becomes increasingly important if we are to raise yield potential. Although these QTLs are the exception rather than the rule, a few notable cases have been reported in rice ([Bernier et al. 2007](#_ENREF_40); [Sandhu et al. 2014](#_ENREF_412); [Venuprasad et al. 2012](#_ENREF_520)), bread wheat ([Bonneau et al. 2013](#_ENREF_54); [Quarrie et al. 2005](#_ENREF_369); [Snape et al. 2007](#_ENREF_457)), durum wheat ([Maccaferri et al. 2008](#_ENREF_309)), sorghum ([Ejeta and Knoll 2007](#_ENREF_143)) and maize ([Prasanna et al. 2009](#_ENREF_365)).

Global warming is intimately associated with an increase in temperature that accelerates leaf senescence, disrupts starch accumulation and curtails yield, particularly when combined with drought. In wheat, a major QTL located on chromosome 4A explained 27 and 17% of reduction in yield under drought and heat stress, respectively ([Pinto et al. 2010](#_ENREF_360)). The same study also identified common QTLs for drought and heat stress traits on chromosomes 1B, 2B, 3B, 4B, and 7A. Yield QTLs were shown to be associated with components of other traits, supporting the prospects for dissecting crop performance under abiotic stress conditions into physiological and genetic components in order to facilitate a more strategic approach to breeding ([Reynolds and Tuberosa 2008](#_ENREF_393)). Additional QTLs with concurrent effects under both heat and drought conditions have been described by ([Wang et al. 2012](#_ENREF_522)).

In rice, the result of a study based on 227 intensively managed irrigated farms ([Welch et al. 2010](#_ENREF_530)) forecast a net negative impact on yield from the warming expected in the coming decades, and clearly show that diurnal temperature variation must be considered when investigating the impact of climate change. Higher temperatures are thought to reduce rice yields through two main pathways: (i) high maximum temperatures, that in combination with high humidity cause spikelet sterility, and (ii) increased night time temperatures that may reduce assimilate accumulation ([Wassmann et al. 2009b](#_ENREF_528))

Under certain conditions, global climate change will further curtail crop yield due to increased soil salinity. As an example, irrigation aimed to counteract drought also increases soil salinity when crops are irrigated with even slightly saline water. Salinity already affects over 20% of the world's agricultural soils. In durum wheat (genome AABB), two major QTLs have been shown to control shoot Na+ accumulation via Na+ exclusion ([James et al. 2006](#_ENREF_246)). Both exclusion genes represent introgressions from an accession of *Triticum monococcum* (genome AA). Remarkably, under standard conditions, durum wheat containing the salinity tolerant allele at TmHKT1;5-A - one of the two salt-tolerance loci - performed the same in the field as durum wheat that lacked the beneficial allele at this locus. But under saline conditions, it outperformed its durum wheat parent, with increased yields of up to 25% ([Munns et al. 2012](#_ENREF_341)). The Na+ exclusion gene has also been introgressed into five cultivars of bread wheat (genome AABBDD) by using durum × bread wheat interspecific crosses and marker-assisted backcrossing (MABC); the resulting backcrossed lines are under field evaluation in Australia (R. James and R. Munns, personal communication).

In barley, the evaluation of a mapping population derived from a cross between a wild barley (*Hordeum vulgare* ssp. *spontaneum*) accession and cultivated barley (*Hordeum vulgare*) allowed for the identification of a major QTL capable of limiting Na+ accumulation in the shoots under saline conditions ([Shavrukov et al. 2010](#_ENREF_441)). In rice, several QTLs for salinity tolerance have been identified ([Wang et al. 2012](#_ENREF_522)) indicating that pyramiding by marker-assisted selection (MAS) of QTLs can be applied to enhance rice salt tolerance.

Flooding is one of the abiotic stresses that has a frequency and intensity that is increasing due to global warming and associated changes in rainfall patterns. Hence, the importance of having cereal crops able to withstand the anoxic conditions associated with waterlogging and/or extended submergence. Among cereals, rice is the crop most heavily damaged by submergence stress which periodically affects approximately 15 million hectares of rain-fed lowland areas in Asia where it has been estimated to cause annual losses in excess of US $1 billion ([Mackill et al. 2012](#_ENREF_311)) In rice, the *Sub1* QTL accounts for a major portion of variability for survival under prolonged submergence. Positional cloning of *Sub1* has revealed a cluster of three putative ethylene response factor genes, namely *Sub1A*, *Sub1B,* and *Sub1C*. Further work unequivocally assigned the functional polymorphism to *Sub1A* ([Xu et al. 2006](#_ENREF_539)) Additional QTLs for submergence tolerance have recently been identified ([Septiningsih et al. 2013](#_ENREF_429)).

Following the identification of *Sub1A*, MABC was used to efficiently convert submergence-susceptible rice varieties into tolerant ones in only three backcross generations. Accordingly, markers were developed for introgressing *Sub1* into six popular varieties to meet the needs of farmers in flood-prone regions ([Bailey-Serres et al. 2010](#_ENREF_31)). The cultivation of these new varieties across over 1 million hectares has significantly increased yield and food security for the local farmers. These results clearly demonstrate the effectiveness of MAS for introgressing agronomically beneficial QTL alleles into elite material. The success of this work is largely due to the major effect of the *Sub1* QTL and the stability of its effect in different genetic backgrounds under submergence conditions.

In maize, Mano ([2005a](#_ENREF_314)) identified QTLs for adventitious root formation at the soil surface, one of the most important adaptations to soil waterlogging which can severely impair root growth at an early stage, thus reducing the capacity of the plant to extract soil moisture at a later stage when water shortage is more likely to occur. Several QTLs for adventitious root formation have been mapped, and a major QTL was mapped on chromosome 8 ([Mano et al. 2005b](#_ENREF_315)).

Several factors limit the ability to obtain reliable QTL data, and most importantly, their deployment in breeding programs through MAS. Among such factors, the environment dependence of QTL expression is of primary importance in order to obtain reproducible data and effectively assess the true value of a particular QTL ([Collins et al. 2008](#_ENREF_100)). This aspect is particularly relevant for stress tolerance traits, since as compared to other traits, their phenotypic variance and the direction of the additive effect are greatly influenced by environmental factors and the intensity of the stress. Improving crop performance under water-limiting conditions via MAS may also require the consideration of QTLs for tolerance to other factors that impair root growth and functions, such as nematodes in bread wheat, high boron in barley and bread wheat, and aluminum toxicity in maize and sorghum.

From a breeding standpoint, a noteworthy story in the public domain for the outcome of MAS to improve drought tolerance has unfolded in rice, where MABC allowed for the introgression of the alleles for greater root length at four QTLs from variety Azucena into Kalinga III, an upland variety characterized by a rather shallow root system ([Sterk et al. 2007](#_ENREF_468)). These efforts have resulted in the release of the first MAS-derived drought-tolerant rice variety - Birsa Vikas Dhan 111 (PY 84) - in the Indian state of Jharkhand ([Steele et al. 2013](#_ENREF_466)).

Equally compelling is the release of maize hybrids by Syngenta based on the adoption of Agrisure Artesian™ Technology, a proprietary molecular approach able to optimize selection procedures of corn under drought conditions1,2. Similarly interesting results have been reported by Pioneer-DuPont for the AQUA[[1]](#footnote-1)max™ hybrids obtained through the Accelerated Yield Technology™ AYT platform ([Cooper et al. 2014](#_ENREF_104)). The validity of these recently released maize hybrids under dry conditions is shown by their superior performance in the severe summer drought that has stricken the US corn belt in 2012 (for further details, see 1,2).

In pearl millet, three major QTLs for grain yield with low QTL × environment interactions were identified across a range of post-flowering moisture environments ([Bidinger et al. 2007](#_ENREF_43)). One of these major QTLs accounted for up to 32% of the phenotypic variation of grain yield under drought conditions. The effects of this QTL have been validated in two independent MABC programs in which the 30% improvement in grain yield general combining ability expected of this QTL under terminal drought stress conditions was recovered in introgression lines, based on the information provided by the markers flanking the QTL ([Yadav et al. 2011](#_ENREF_542)).

Major efforts to improve salinity tolerance in rice via MAS are underway for introgressing *Saltol*, a major QTL regulating rice growth under saline conditions. The initial MABC lines for *Saltol* were developed using variety FL478 as the donor for high level of tolerance. Several MABC lines have now been developed with the beneficial FL478 *Saltol* allele combined with the background of several popular cultivars susceptible to submergence ([Thomson et al. 2010](#_ENREF_484)) Further work is in progress to determine the relative tolerance effect of different *Saltol* alleles as well as the ultimate effect that this seedling-stage tolerance will have on crop establishment and grain yield under field conditions, particularly in areas where salinity is high at the beginning of the season such as in coastal areas during the monsoon season.

With only few exceptions as listed above, the vast majority of loci that affect crop yield *per se* under environmentally constrained conditions have a rather small effect. Therefore, combining the beneficial alleles by MAS at QTLs of minor effects quickly becomes impractical and would constrain the potential for achieving yield gain due to the action of other loci. In this case, it is preferable to adopt genome-wide selection (GS) based breeding methods, rather than attempting to manipulate the trait by MAS at multiple loci ([Bernardo and Yu 2007](#_ENREF_39); [Ziyomo and Bernardo 2013](#_ENREF_563)). The implementation of GS in cereals is now facilitated by the availability of abundant Single Nucleotide Polymorphisms (SNPs) that are amenable to high-throughput profiling at relatively low cost ([Ganal et al. 2014](#_ENREF_172); [Romay et al. 2013](#_ENREF_402); [Trebbi et al. 2011](#_ENREF_491)).

Genomics-based approaches and next generation DNA sequencing (NGS) have ushered in sequence-based breeding strategies that will increasingly expedite the dissection and cloning of the loci controlling abiotic stress tolerance while providing unparalleled opportunities to tap into wild relatives of crops, hence expanding the reservoir of genetic diversity available to breeders ([Edwards and Batley 2010](#_ENREF_139); [Edwards et al. 2013](#_ENREF_140); [Feuillet et al. 2008](#_ENREF_154); [Tuberosa et al. 2011](#_ENREF_498)). In view of the complexity and low heritability of yield, particularly under drought and other abiotically constrained conditions, GS will likely provide the most powerful approach to raise the yield potential to the levels required to meet the fast-increasing global demand in cereal grain. This notwithstanding, MAS will remain a valid option for major loci (genes and/or QTLs) while QTL cloning will become a more routine activity thanks to a more widespread utilization of high-throughput, accurate phenotyping ([Araus and Cairns 2014](#_ENREF_23); [Tuberosa 2012](#_ENREF_494)), sequencing ([Edwards and Wang 2012](#_ENREF_141); [Imelfort et al. 2009](#_ENREF_229); [Varshney et al. 2009a](#_ENREF_512)) and the identification of suitable candidate genes through ‘omics’ profiling ([Gupta et al. 2013](#_ENREF_197)). Cloned QTLs will provide novel opportunities for genetically engineering abiotic stress tolerance and for a more targeted search for novel alleles in wild germplasm ([Salvi et al. 2007](#_ENREF_409)). Even with the application of advanced genomics technologies, mitigating the negative effects of climate change on cereal productivity will remain a daunting undertaking, one that will require a multidisciplinary and integrated approach that will eventually allow breeders to more effectively select cereals that are more reliant to climate change and ensure a sufficient level of food security for the decades to come.

## 2.3 Oilseeds and Pulses

*Henry T. Nguyen, Rajeev Varshney, Babu Valliyodan and Paul Gepts*

Oilseeds and pulses are major food crops, due to their unique protein and oil-rich characteristics. Being a major class of cash crops, increase of global production and yield of oilseeds and pulses with improved protein, carbohydrate, and oil for food, feed, and industrial applications are needed. This can be achieved through improved agronomy and the development of cultivars suited to diverse growing conditions. Major biotic and abiotic stresses are the most serious production constraint for global oilseed and pulse production, and are predicted to worsen with anticipated climate change. Advances in genomic technologies including next generation DNA sequencing helps to provide genome sequence information for these crops. Gene discovery has been expedited through functional genomics tools, and comparative analysis of genomes is now feasible. In addition, the development of abundant DNA marker systems helps to accelerate trait introgression and breeding programs for oil seed and pulses crop improvement.

### Soybean:

Soybeans are native to the Far East and were domesticated and grown as early as 5,000 years ago by farmers in China. They were first brought to North America in 1804 and late in the century US farmers began to grow soybeans as forage for cattle. The unique seed composition of soybean makes this crop the world’s most valuable legume, with numerous food, feed, health and industrial uses. Among legumes and cereals it has the highest protein content (40%) and the second highest oil content (20%). Other valuable components include vitamins, minerals, and isoflavones that are important to human and animal health ([Liu 1999](#_ENREF_297)). From the onset of the 20th century, more soybean accessions were collected and several of these germplasm accessions laid the foundation for the development of more productive varieties and the rapid development of the US and South America as world leaders in soybean production (www.soystats.com). Now, more than 80% of the world’s soybeans are grown by the US (33%), Brazil (28%), and Argentina (21%). In 2010, soybeans represented 58 percent of world oilseed production, and the U.S., soybean and soy product exports exceeded $38.9 billion ([The American Soybean Association 2011](#_ENREF_480)). As the production and the potential use for soybeans increased, the need for greater genetic diversity in them was recognized. With increasing world demand for soy-based food for humans and high protein meal for livestock feed, there is increased economic potential for productive, high protein soybean varieties.

High-throughput DNA sequencing, and all “omics” platforms have increased the amount of plant genome information from which we can infer proteins and often major biochemical and regulatory networks. Various high throughput genomics methods have been used to catalogue the gene expression, protein changes and the dissection of biochemical regulatory networks associated with plant responses to stress and plant development. Since the newly sequenced *G. max* genome became available in 2010 ([Schmutz et al. 2010](#_ENREF_423)), the focus of soybean research has shifted towards performing genome-scale experiments, leading to a massive output of biological information. The soybean genome encodes 46,430 protein-coding genes and approximately 5,700 transcription factors and signaling related transcripts ([Wang et al. 2010](#_ENREF_526)). This information has opened new avenues to apply molecular genetics, plant breeding and genetic engineering approaches to design and develop soybean cultivars with improved stress tolerance and enhanced yield.

### Common bean

*Phaseolus* beans are an essential part of the diet of millions of people in Latin America and Eastern Africa, and are a source of proteins, vitamins, and minerals ([Broughton et al. 2003](#_ENREF_65); [Gepts et al. 2008](#_ENREF_184)). There are two main uses of beans: as dry grain and green pod. Of the five domesticated *Phaseolus* species, common bean (*P. vulgaris* L.) is the most important economically. The main producing and consumption countries are located in Latin America and Eastern Africa (www.faostat.org). Around 60% of the growing area is subject to drought and heat ([Thung and Rao 1999](#_ENREF_487)), and yield losses can reach up to 80% when drought affects the crop early in its development ([Rao 2001](#_ENREF_374)). Both drought and heat stress are most damaging during the reproductive phase of bean development. Drought stress is broadly divided into terminal and intermittent types. The former is the most frequent because bean are often planted in residual soil moisture ([Rosales et al. 2012](#_ENREF_403)). Heat stress occurs above the optimum temperature range of 18°C/28°C (average of 23-24°C), and yields decline to zero at 37°C ([Laing et al. 1984](#_ENREF_278); [Prasad et al. 2002](#_ENREF_364)). Simulations show that global climate change – affecting principally temperature, rainfall, and CO2 levels, will impact bean production ([Thornton et al. 2009](#_ENREF_485)). Genetic studies and cultivar breeding have shown that heat and drought tolerance are under complex genetic control, although a single instance of a major gene has also been observed ([Asfaw et al. 2012](#_ENREF_28); [Schneider et al. 1997](#_ENREF_425); [Shonnard and Gepts 1994](#_ENREF_445)). The selection of lines with improved drought tolerance has been successful ([Beebe et al. 2008](#_ENREF_33); [Singh 2007](#_ENREF_453); [Urrea et al. 2009](#_ENREF_507)). The development of MAS methodology for drought tolerance has been initiated (e.g., ([Asfaw et al. 2012](#_ENREF_28); [Schneider et al. 1997](#_ENREF_425))). MAS will be aided by genomic resources being developed in common bean, including whole-genome sequences of the Andean (accession G19833: phytozome.jgi.doe.gov/pz/portal.html#!info?alias=Org\_Pvulgaris ([Schmutz et al. 2014](#_ENREF_424))) and Mesoamerican (accession BAT93: www.genoma-cyted.org; accession OAC Rex: www.beangenomics.ca/) bean genomes) and a bean breeder’s genome toolbox and database (phaseolusgenes.bioinformatics.ucdavis.edu/).

### Chickpeas

Chickpea (*Cicer arietinum* L.), a self-pollinated diploid crop with a basic chromosome number of eight (2*n* = 2*x* = 16) and 740 Mb genome size ([Arumuganathan and Earle 1991](#_ENREF_27)), is grown on receding soil moisture following the rain season in arid and semi-arid regions of the world. Several abiotic and biotic stresses pose a threat to high and stable yields of chickpea. Among abiotic stresses, terminal drought is the major problem, and in addition lower temperatures (<10°C) and salinity (NaCl), mainly during reproductive period and podding stages ([Vadez et al. 2012](#_ENREF_508)), lead to considerable yield losses. In addition to *Helicoverpa armigera* (pod-borer), Fusarium wilt (FW) and Ascochyta blight (AB) are the most important biotic stresses that challenge chickpea production ([Sharma et al. 2008](#_ENREF_437)). To overcome these production constraints and meet the growing demand for chickpea, efforts at national and international levels have led to the development of large-scale genetic and genomic resources. These include more than 2000 simple sequence repeat (SSR markers) ([Gaur et al. 2011](#_ENREF_178); [Lichtenzveig et al. 2005](#_ENREF_294); [Nayak et al. 2010](#_ENREF_345); [Sethy et al. 2006](#_ENREF_435); [Winter et al. 1999](#_ENREF_536)), ESTs ([Buhariwalla et al. 2005](#_ENREF_68); [Varshney et al. 2009c](#_ENREF_516)), 454/FLX expressed gene transcript reads ([Garg et al. 2011](#_ENREF_175); [Hiremath et al. 2011](#_ENREF_217); [Jhanwar et al. 2012](#_ENREF_250)), BAC-end sequences ([Thudi et al. 2011](#_ENREF_486)), DArT genotyping arrays with 15,360 features ([Thudi et al. 2011](#_ENREF_486)), SNPs ([Hiremath et al. 2012](#_ENREF_218)), and functional markers ([Choudhary et al. 2012](#_ENREF_94)). Genomic resources have been used to understand the existing genetic diversity and exploit it in breeding programs ([Choudhary 2012](#_ENREF_93); [Upadhyaya et al. 2008](#_ENREF_506)). Several intra- and inter-specific genetic maps have been developed ([Gaur et al. 2011](#_ENREF_178); [Gujaria et al. 2011](#_ENREF_196); [Hiremath et al. 2012](#_ENREF_218); [Millan et al. 2010](#_ENREF_329); [Nayak et al. 2010](#_ENREF_345); [Radhika et al. 2007](#_ENREF_370); [Thudi et al. 2011](#_ENREF_486)) and genomic regions have been reported to be responsible for different biotic stresses ([Anbessa et al. 2009](#_ENREF_19); [Anuradha et al. 2011](#_ENREF_22); [Cobos et al. 2005](#_ENREF_98); [Iruela et al. 2007](#_ENREF_232); [Kottapalli et al. 2009](#_ENREF_272); [Sharma et al. 2004](#_ENREF_439); [Udupa and Baum 2003](#_ENREF_503)), abiotic stress ([Rehman et al. 2011](#_ENREF_382); [Vadez et al. 2012](#_ENREF_508)) and agronomic traits ([Cobos et al. 2009](#_ENREF_99); [Rehman et al. 2011](#_ENREF_382)). Attempts have also been made to assess genetic variability among the pathogens and understand their pathogenicity on different chickpea cultivars ([Sharma et al. 2005](#_ENREF_438); [Sharma et al. 2010](#_ENREF_440)). The development of early flowering limits the impact of terminal drought. In this context efforts were made to understand the genes related to flowering time ([Hegde 2010](#_ENREF_212); [Kumar and van Rheenen 2000](#_ENREF_275); [Rajesh et al. 2002](#_ENREF_371)). Attempts have also been made to exploit genetic variation present in wild species of chickpea by making wide crosses ([Jaiswal et al. 1986](#_ENREF_245); [Singh and Ocampo 1997](#_ENREF_449)), and advanced backcross QTL (AB-QTL)-breeding has been initiated at ICRISAT. Recent advances in next-generation sequencing and high-throughput genotyping technologies, has promoted genomics assisted breeding in chickpea, and two major marker-assisted breeding programs are underway to enhance race-specific resistance to FW in elite cultivars and AB through an accelerated crop improvement program (ACIP) sponsored by the Department of Biotechnology, Government of India, and to enhance drought tolerance in elite cultivars in India and sub-Saharan Africa (SSA) as a part of Tropical Legume – I (TL-I) of the CGIAR Generation Challenge Programme in collaboration with the Bill and Melinda Gates Foundation. Other modern breeding approaches, including marker-assisted recurrent selection (MARS) and genomic selection (GS) are also underway at ICRISAT. Two physical maps based on BAC/BIBAC ([Zhang et al. 2010](#_ENREF_558)) and BAC libraries have been developed (<http://probes.pw.usda.gov:8080/chickpea/>). The genome sequence of both Kabuli (<http://www.icrisat.org/gt-bt/ICGGC/GenomeSequencing.htm>) and Desi (<http://www.nipgr.res.in/home/home.php>) chickpeas have recently been published ([Jain et al. 2013](#_ENREF_243); [Varshney et al. 2013](#_ENREF_517)) and will lead to an acceleration of genomics based chickpea improvement.

### Pigeonpeas

Pigeonpea (*Cajanus cajan* L*.*) has a diploid genome (2n = 2x = 22) of 833.07 Mb (see ([Varshney et al. 2012](#_ENREF_514))). It is cultivated on an area of 4.92 million hectare yielding 3.65 million tones with an average productivity of 800 kg/ha ([FAO 2010](#_ENREF_146)). In spite of continued breeding efforts and its immense importance in sustainable agriculture, the production per hectare remained static over the last three decades ([Varshney et al. 2010](#_ENREF_515)). Several abiotic and biotic factors in pigeonpea growing areas account for this yield gap ([Varshney et al. 2012](#_ENREF_514)). Among biotic stresses, Fusarium wilt ([Saxena 2008](#_ENREF_420)) and sterility mosaic disease (SMD) may lead to 95 to 100% yield losses. In addition, phytophthora blight is of economic concern, and insect pests including *Helicoverpa armigera* and *Maruca vitrata* Geyer, *Clavigralla horrida* Germar and *Melanagromyza chalcosoma* Spencer also pose a major threat to pigeonpea production. Among the abiotic constraints, salinity and water logging severely affect pigeonpea production ([Saxena 2008](#_ENREF_420)). Until recently, pigeonpea was considered as “orphan crop” in the genomics era owing to the limited availability of genomic resources ([Burns et al. 2001](#_ENREF_72)). However, there are now more than 3000 SSR markers available in the public domain ([Bohra et al. 2011](#_ENREF_52); [Dutta et al. 2011](#_ENREF_132); [Saxena et al. 2010](#_ENREF_421)), with the majority of these markers developed as a part of International Initiative on Pigeonpea Genomics (IIPG, http://www.icrisat.org/gt-bt/iipg/Home.html). Large numbers of ESTs from FW and SMD challenged plants have been generated ([Raju et al. 2010](#_ENREF_372)), supported by 454/FLX transcript reads ([Dubey et al. 2011](#_ENREF_131); [Dutta et al. 2011](#_ENREF_132)) and transcriptome assemblies ([Dubey et al. 2011](#_ENREF_131); [Kudapa et al. 2012](#_ENREF_274)). Recently, KASPar assays have been developed for 1,616 SNPs in pigeonpea (Saxena et al. 2012). The availability of the 3,000 SSR markers facilitated development of inter- as well as intra-specific genetic maps using several F2 mapping populations ([Bohra et al. 2012](#_ENREF_53)). Furthermore, DArT based paternal and maternal-specific genetic maps were also developed ([Yang et al. 2011](#_ENREF_546)). In addition to these inter-specific genetic maps, further SSR-based genetic maps with low to moderate marker density were developed for cultivated pigeonpea ([Hong et al. 2010b](#_ENREF_222)). Efforts are underway to integrate SNP markers onto these genetic linkage maps. Anonymous markers were applied initially for trait mapping, for example, a bulked segregant analysis (BSA) approach was used to map *Fusarium* wilt resistance with RAPD markers([Kotresh et al. 2006](#_ENREF_271)), SMD resistance was mapped with AFLP markers ([Ganapathy et al. 2011](#_ENREF_173)), and plant morphology with RAPD markers ([Dhanasekar et al. 2010](#_ENREF_124)). The SSR based genetic maps for F2 populations were coupled with extensive phenotyping data for the identification of QTLs for various traits of economic concern ([Bohra et al. 2012](#_ENREF_53); [Gnanesh et al. 2011](#_ENREF_191)). Diagnostic SSR markers have also been developed to facilitate hybrid breeding and adoption, and for purity assessment of two hybrids ([Bohra et al. 2011](#_ENREF_52); [Saxena et al. 2010](#_ENREF_421)). Initiatives have been taken at ICRISAT to develop two backcross populations for AB-QTL analysis and their subsequent use in AB-breeding, realizing the scope for AB-breeding in improvement of pigeonpea.

### Groundnuts

The cultivated groundnut (*Arachis hypogaea* L.), is the fourth largest oilseed crop in the world. Globally it is cultivated in more than 100 countries ([FAO 2010](#_ENREF_146)), with annual production of 35.5 million tons. The largest producers of groundnut include China, India, Sub-Saharan African countries and Central and South America. Developing countries account for over 97.6% of the world groundnut production area with average yields of 1522 kg ha-1. Asian and African continents accounts for 56% and 40% of global groundnut area, where the crop is grown mostly by smallholder farmers under rain-fed conditions with limited inputs. Groundnut is largely grown under rain-fed conditions in the semi-arid tropics. In these conditions, drought is a major production constraint as rainfall is generally erratic and insufficient ([Reddy et al. 2003](#_ENREF_381)). Groundnut is a self- pollinated crop with a tetraploid (2n = 4x = 40) genome of 2891 Mbp. Production is greatly challenged by several biotic/abiotic stress factors. Among biotic factors, early leaf spot (ELS; caused by *Cercospora arachidicola*), late leaf spot (LLS; caused by *Cercosporidium personatum*), rust (caused by *Puccinia arachidis*) and groundnut rosette disease (GRD) cause up to 50% yield losses. In addition, groundnut bud necrosis, bacterial wilt and nematode diseases have also been found to be prevalent in some regions, and fungal aflatoxin contamination deteriorates product quality. Terminal drought is the most important abiotic stress, reducing crop productivity significantly. The overall timing and intensity of drought stress has a very important impact on peanut productivity. Water deficit during the seed filling phase (50–80 DAP) results in the greatest reduction in yield, whereas pod yield can be increased by water deficit during the pre-flowering phase ([Nautiyal et al. 1999](#_ENREF_344)). In comparison to irrigated conditions, groundnut under rainfed conditions reduces yield by about 520 lb/acre (Virginia Coopertaive Extension, 2012).

For sustainable production, the integration of modern molecular tools, together with conventional skills will be key to controlling yield loss in groundnut. Large scale genomic resources were developed during recent years to facilitate molecular breeding in groundnut. More than 6000 SSR markers have been developed during the past decade ([Cuc et al. 2008](#_ENREF_118); [Gautami et al. 2009](#_ENREF_181); [Koilkonda et al. 2012](#_ENREF_269); [Moretzsohn et al. 2005](#_ENREF_338); [Moretzsohn Mde et al. 2004](#_ENREF_339); [Song et al. 2010](#_ENREF_458)). More recently, KASPar assays have been developed for 94 SNPs. Following the first SSR-based genetic linkage map for cultivated groundnut ([Varshney et al. 2009b](#_ENREF_513)), several genetic maps ([Gautami et al. 2012a](#_ENREF_179); [Gautami et al. 2012b](#_ENREF_180); [Hong et al. 2010a](#_ENREF_221); [Ravi et al. 2011](#_ENREF_376); [Sujay et al. 2012](#_ENREF_471)) and consensus maps ([Gautami et al. 2012b](#_ENREF_180)), were developed, and are currently available for selecting informative and uniformly distributed markers for background selection, the construction of new genetic maps and diversity analysis. In terms of trait mapping, QTLs have been identified for drought tolerance related traits ([Gautami et al. 2012a](#_ENREF_179); [Ravi et al. 2011](#_ENREF_376); [Varshney et al. 2009b](#_ENREF_513)), rust and LLS resistance respectively ([Khedikar et al. 2010](#_ENREF_259); [Sujay et al. 2012](#_ENREF_471)) andoil quality ([Sarvamangala et al. 2011](#_ENREF_418)). A MABC approach has been initiated to introgress a major QTL contributing 82.96% of the phenotypic variation for leaf rust, and recently, the MABC improved Tiftguard variety "Tifguard High O/L" has been released ([Chu et al. 2011](#_ENREF_95)). In order to diversify the primary genepool, amphiploids were developed using a range of wild AA and BB genome species ([Favero et al. 2006](#_ENREF_150); [Mallikarjuna et al. 2011](#_ENREF_312); [Simpson et al. 1993](#_ENREF_447)). Furthermore, two AB-QTL mapping populations, namely ICGV 91114 (cultivated) × ISATGR 1212 (*A. duranensis* ICG 8123 × *A. ipaensis* ICG 8206, synthetic amphidiploid) and ICGV 87846 (cultivated) × ISATGR 265-5A (*A. kempff-mercadoi* ICG 8164 × *A. hoehnei* ICG 8190, synthetic amphidiploid) have been developed ([Mallikarjuna et al. 2011](#_ENREF_312)). Recently, efforts for genome-wide segment introgressions from a synthetic amphidiploid (*A*. *duranensis* × *A*. *ipaënsis*) to a cultivated variety (Fluer 11) using molecular markers has been reported to be successful ([Fonceka et al. 2009](#_ENREF_161)).

### Canola

Canola (*Brassica napus* L.) is a valuable oilseed crop in Australia and Canada and is an important component in crop sequences to break disease cycles and reduce problem weeds. In Canada, 7.2 million ha of canola were grown in the Great Plains provinces in 2009 ([Canada 2010](#_ENREF_82)), where it is planted in late April or early May, grows rapidly in a short summer season with long, warm days and is harvested in September prior to fall frost. In southern Australia, the area sown to canola peaked at 2 million ha in 1999, declined to half that during the recent millennium drought, but recovered to 1.7 million ha in 2010 ([Statistics 2011](#_ENREF_465)). Canola is also sown in April or early May in Australia, but grows slowly through the cool late autumn and winter, flowers and sets pods in spring after the last damaging frosts, and matures with the onset of the hot, dry summer. Dual-purpose canola describes the recent use in Australia of the vegetative canola crop as forage by grazing animals in winter, after which the crop recovers and is harvested for grain ([Kirkegaard et al. 2008](#_ENREF_263)). More than 52,000 Canadian farmers grow canola, generating economic activity of $1.4 billion in Ontario and Quebec (primarily in the processing sector), and $7.5 billion in western Canada. Canola is also grown in the north central and southeastern United States. Canada is the biggest single producer of canola, with a ten-year average of 11.3 million acres harvested. Canada. However, the EU member countries combined grow more canola, and China’s rapeseed acreage exceeds Canada’s canola production. Global canola production has grown rapidly over the past 40 years, rising from the sixth largest oil crop to the second largest, and production was 10-15 percent of world oil crop production between marketing years 1999/2000 and 2008/09. Canola oil, obtained from crushing canola seed, was the third most produced vegetable oil globally in 2008/09, and between 1999/2000-2008/09, canola oil represented 13-16 percent of world vegetable oil production. Canola meal is the second largest feed meal after soybean meal. In 2008/09 (May/June), the farm gate value of U.S. canola production was $270 million. The U.S. share of world production remains small, but is of growing importance to regional economies in the Northern Plains. Almost all canola is crushed into oil and meal. Trends in the much larger Canadian canola industry have a significant impact on production and processing of canola in the United States.

Canola is particularly sensitive to water stress as evidenced by the rapid decline in production during the recent Australian millennium drought. Conversely, high rainfall and humidity promote the virulence of the major fungal pathogen of canola, *Leptosphaeria maculans*, the causal agent of blackleg disease. Hence, breeding canola for improved climate change resilience and disease resistance is a high priority.

## 2.4 Vegetables

*Philipp W. Simon*

Vegetable crop improvement is being pursued extensively and globally by seed companies, NGOs, universities, and governmental organizations, including several CGIAR research centers. Globally and regionally, many crops are identified as vegetables, and among them, breeding and genomics are well-developed and advanced for relative few. Those with whole genome sequence (WGS) published or announced are listed in Table 1.

The breeding and genomics of vegetable crops for climate resilient traits (CRTs) has received less attention than for agronomic crops. This is due to the smaller scientific effort on a per crop basis, and major emphasis on quality traits that are essential for marketable yield. This emphasis on quality has resulted in production systems that include priority access to irrigation (to minimize drought stress) and choice land (with minimal salt and nutrient stress) in climates with minimal heat stress. As global production capacity must be increased to match population growth, less prime production land is available due to salinization and desertification, and as climatic stress becomes more evident in many production regions, CRTs are receiving increased attention in vegetable crop improvement programs.

In addition to breeding vegetables for CRTs to withstand climatic stress variables directly, breeding for faster growth to attain earlier harvests has long been pursued by vegetable breeders, and this avoids exposure to some abiotic and biotic stresses. This indirect approach to avoid climatic stress is practiced by virtually all vegetable breeders.

Breeding and genomics for CRTs in tomato is the most advanced among vegetable crops. Tomato breeding and genomics for all traits, including CRTs, involve a large global effort including many breeding programs and genomics projects. Dense genetic maps and MAS projects are well-developed in tomato, and large genomic databases and tools including whole genome shotgun sequences; extensive re-sequencing; microarrays; and bacterial artificial chromosome (BAC), transcriptomic and proteomic libraries, have been developed. Several projects have focused on transcriptomic and proteomic libraries under abiotic stress conditions ([Chen et al. 2009](#_ENREF_90); [Manaa et al. 2011](#_ENREF_313); [Zhou 2011](#_ENREF_561)). These resources are being developed for not only tomato, but also allied genomic pools (AGPs) including *Solanum pimpinellifolium* and *S. chilense*. Similar efforts are in progress to develop CRT genomic tools applicable for the improvement of other vegetable crops including potato ([Aghaei et al. 2008](#_ENREF_3); [Ginzberg et al. 2009](#_ENREF_188); [Rensink et al. 2005](#_ENREF_388)), pepper ([Jung et al. 2008](#_ENREF_253)), and Brassicas ([Yu et al. 2012](#_ENREF_552)) as well as all vegetables listed in Table 1. WGS and genomic tool development projects and breeding projects for CRTs are well underway for several crops not listed in Table 1, including onion, bitter gourd, squash, pumpkin, and carrot.

Regarding use of allied gene pools (AGPs), it should be emphasized that wild species are being used to some extent in virtually all major vegetable breeding projects. Potato, however, is worth particular mention, since many wild, tuber-bearing *Solanum* species have been intercrossed to potato by breeders for decades, making an expanded genomic effort for potato AGPs particularly pertinent.

Table. 1. Status of Breeding and Genomics of Major Vegetable Crops for Climate-Resilience Traits

|  |  |  |  |
| --- | --- | --- | --- |
| **Crop** | **Breeding, genetics, marker-assisted selection** | **Molecular resources for CRTs** | **Use of allied gene pools** |
| **Solanaceaous vegetables** |  |  |  |
| Tomato | Very extensive classical genetics, breeding, and MAS | WGS published, many transcriptome/proteome libraries incl. several with CRT focus | Some WGS of AGP; use of AGP in breeding with CRT focus; some transcriptome and proteome research with CRT focus |
| Potato | Very extensive classical genetics and breeding, some MAS | WGS published, many transcriptome/proteome libraries incl. several with CRT focus | Some WGS of AGP; extensive use of AGP in breeding, some with CRT focus |
| Pepper | Extensive classical genetics and breeding, some MAS | WGS in progress, several transcriptome/proteome libraries incl. several with CRT focus | Use of AGP in breeding, some with CRT focus |
| **Cucurbitaceous vegetables** |  |  |  |
| Melon | Very extensive classical genetics, breeding and MAS | WGS published, many transcriptome/proteome libraries incl. several with CRT focus | Some use of AGP in breeding, some with CRT focus |
| Cucumber | Very extensive classical genetics, breeding and MAS | WGS published, many transcriptome/proteome libraries incl. several with CRT focus | Some use of AGP in breeding, some with CRT focus |
| Watermelon | Extensive classical genetics and breeding, some MAS | WGS in progress, several transcriptome/proteome libraries | Some use of AGP in breeding, some with CRT focus |
| **Cruciferous vegetables** |  |  |  |
| Chinese cabbage, turnip (*Brassica rapa*) | Extensive classical genetics, breeding and MAS | WGS published, several transcriptome/proteome libraries incl. several with CRT focus | Use of AGP in breeding, some with CRT focus |
| Cabbage, cauliflower broccoli, , etc. (*B. oleracea*) | Extensive classical genetics, breeding and MAS | WGS in progress, several transcriptome/proteome libraries | Use of AGP in breeding, some with CRT focus |
| **Fabaceous vegetables** |  |  |  |
| Beans | Extensive classical genetics, breeding and MAS | WGS published, several transcriptome/proteome libraries | Use of AGP in breeding, with CRT focus |
| **Compositaceous vegetables** |  |  |  |
| Lettuce | Extensive classical genetics, breeding and MAS | WGS in progress, several transcriptome/proteome libraries | Some use of AGP in breeding, some with CRT focus |

## 2.5 Perennial Fruit Crops

*Rodomiro Ortiz and Robert Henry*

The most important fruit crops worldwide are apples, bananas, citrus-oranges and grapes, while cacao and coffee are among leading commodity crops in global trade. The physiological and growth response of perennial fruit crops to climate change may be similar to that of forest trees. Temperature extremes, water stress, solar radiation and elevated CO2 will affect flowering, fruit maturity, yield and quality of temperate and tropical fruit crops. Their production cannot be easily moved across locations as may happen with annual crops when their growing areas will change due to climate change.

Global warming will also influence the incidence and severity pathogens and pests affecting perennial fruit crops ([Dwivedi et al. 2013](#_ENREF_134)) and references therein), as they move to new areas due to changing weather. For example, scenario analyses suggest that the favorable period for the development of black Sigatoka (*Mycosphaerella fijiensis*) and other foliar plant pathogens affecting bananas may be reduced because a switch towards low relative humidity and rainfall environments, which adversely affect the pathogen. Some insects (aphids, which are virus vectors; flower thrips; and mites) may however increase their damage in bananas when grown in dry environments. Likewise, in Brazil, the distribution of root-knot nematode (*Meloidogyne* spp.) races and leaf miner (*Leucoptera coffeella*) affecting coffee may change, and their infestation will likely increase due to the production of more generations per month than before. Breeding for host plant resistance to pathogens and pests will therefore remain a very important strategy for growing healthy perennial fruit crops because rising temperatures and variation in humidity favor pathogen and pest epidemics.

Genomics-assisted breeding approaches, along with bioinformatics capability and other omics resources will be essential components of perennial fruit crop breeding, and particularly to adapt their cropping to climate change. Microsatellites (SSR) and single nucleotide polymorphisms (SNP) are being used for marker-aided breeding in some fruit crops. Genome sequencing and annotation projects include perennial fruit crops such as apple ([Velasco et al. 2010](#_ENREF_518)), banana ([D'Hont et al. 2012](#_ENREF_120)), cacao ([Argout et al. 2011](#_ENREF_26)), grape ([Velasco et al. 2007](#_ENREF_519)), peach ([Ahmad et al. 2011](#_ENREF_4)) and sweet orange ([Xu et al. 2013](#_ENREF_540)). The advances in genome sequencing, along with high-resolution genetic mapping and precise phenotyping will accelerate the discovery of functional alleles and allelic variation that are associated with traits of interest for perennial fruit crop breeding. Comparative genomics has allowed explanation of biological differences. For example, a comparison of sweet cherry and peach show the absence of ethylene production pathway genes in the non-climacteric cherry ([Koepke et al. 2013](#_ENREF_268)). Comparison of sweet and bitter almonds has identified a small set of genes that are candidates for control of bitterness in almond ([Koepke et al. 2013](#_ENREF_268)). Furthermore, progress in metabolomics, proteomics and transcriptomics will provide new knowledge for the genetic enhancement of these perennial crop species.

## 2.6 Forest Trees

*Ciro De Pace, Leland Cseke and Glenn Thomas Howe*

Forests cover 30% (about 3.8 billion ha) of Earth’s terrestrial surface. Forest tree species, the essential component of forests, are prevalently outcrossing, long-lived perennial which demonstrate a high degree of genetic diversity.

The genetic diversity within and between the biota components of forest habitats are of particular ecological relevance, not only for the biosphere, but also for the ecosystem services they provide, such as mitigation of hydrological processes, reduced erosion, increased wildlife habitat, wood and other forest products, CO2 sequestration, and support to agricultural productivity (i. e. windbreak; stabilization of hill slopes). Wild plant and animal populations can respond to ongoing disturbance and acceleration of climate change through migration and adaptation to minimize genetic drift, restriction of genetic diversity, and local extinction. Anthropogenic intervention along the natural biological path of plant adaptation to disturbance may increase forest resilience, restoration, and afforestation success. The wise use of wild forest genetic resources and genomics for selective breeding, hybridization and clonal propagation of the highly performing genotypes, are pivotal in these endeavors.

In light of the gene-pool concept developed by Harlan and de Wet ([Harlan and Wet 1971](#_ENREF_209)), the undisturbed stands and patches of native forests can be viewed as a large or scattered reservoir of genes representing the wild ‘primary gene-pool’ (GP1w) of each species composing the local tree and shrub community. The establishment of nurseries from more than one cycle of selection within the GP1w, causes the managed populations to diverge morphologically and genetically from their wild progenitors, leading to the founding of a domesticated subgene pool (GP1d) for breeding purposes. The GP1d is enriched for those target alleles underlying the adaptive performance of the extracted genotypes from the GP1w, when the selection criteria such as ‘increased fitness’, ‘tolerance to stresses’, and ‘success in the intergenotypic competition’ have been applied.

Current understanding of the genetic basis of adaptation in long-lived populations is based largely on temperate forest trees that have been evolving in response to selection pressures such as disease, drought, and cold; examples include GP1w management, domestication and breeding in genera from the northern hemisphere forests (*Populus*, *Castanea*, *Picea, Pinus, Alnus*, *Ulmus*,*)* and some from the southern hemisphere (*Eucalyptus*, *Podocarpus* pines, evergreen southern beech *Nothofagus, etc.*) ([Kole 2011](#_ENREF_270)).

There are several examples on how, during the past five hundred years, to compensate for the ever-increasing demand for wood and to reduce pressure on native forests, humans started germplasm exchange and introductions of those forest trees expressing advantageous traits such as fast growth, facile vegetative propagation, larger fruits, disease resistance, and tolerance to abiotic stresses. This activity, coupled to the wood trade, increased pathogen and parasite invasiveness episodes such as the accidental introduction from Asia in the late 1800s of the fungus *Cryphonectria parasitica*, causing chestnut blight disease in the American chestnut *Castanea dentata;* the epidemics of Dutch Elm Disease (DED) caused by the Ascomycete *Ophiostoma ulmi* in European elms; the arrival in Europe in the 1990s of the Sudden Oak Death fungal agent *Phytophthora ramorum,* causing widespread dieback and mortality of mature and juvenile Japanese larch, *Larix kaempferi* in southwest England; the recent cases in Italy of infestation of oriental chestnut gall wasp *Dryocosmus kuriphilus* in *C. sativa* fruit orchards; and of the polyfagous *Platypus mutatus* Chapuis (= *Megaplatypus mutatus* and *P. sulcatus*) (*Coleoptera Platypodidae*) in *Populus* plantations and other host-plant genera.

Invasive pathogens and insects now entering Europe could narrow the choice of plantation species for re-forestation, and undermine proposals to use tree planting as a means of mitigating climate change through carbon sequestration ([Brasier and Webber 2010](#_ENREF_62))*.* Fortunately, in most cases the forest degradation or threats posed by those events can be mitigated by using resistance genes still present in the GP1w for producing the needed resistant or tolerant GP1d for forest restoration and agroforestry based on healthy plants. Efforts are going on to: (1) restore the American chestnut to its former status by backcross breeding program designed to transfer the blight resistance genes from the GP1w of Chinese chestnuts (*Castanea mollissima*) to *C. dentata* ([Thompson 2012](#_ENREF_483)); (2) breeding programs for the development of DED resistant elms populations in the European species *Ulmus glabra* Huds., *Ulmus laevis* Pall., and *Ulmus minor* Mill., by transferring, through hybridization, genes for DED resistance from the elm species *U. parvifolia, U. pumila*, and *U. wallichiana* from Central-Eastern Asia ([Ghelardini and Santini 2009](#_ENREF_185); [Santini et al. 2010](#_ENREF_417)); (3) explore the feasibility of using the phloem content of the phenolic Tyrosol hexoside pentoside and Ellagic acid, associated with resistance to *P. ramorum* expressed by coast live oak (*Quercus agrifolia*) in stands of high infection and mortality, as biomarkers of resistance in other oak trees (<http://ucanr.org/sites/sod5/files/147556.pdf>); and (4) the introgression of the gene for resistance to *D. kuriphilus* from the Japanese chestnut *C. crenata* into the *C. sativa* genome. No significant resistance has been found for the polyphagous and extensive host range *P. mutatus* causing severe damage in commercial plantations of *Populus* spp., *Quercus* spp., *Eucalyptus* spp., and *Pinus* spp. Resistance breeding to combat local pests of native forests was also possible using the resources of GP1w expressing resistance to the defoliating fungus *Cylindrocladium quinqueseptatum* in *E. camaldulensis,* Asian longhorned beetle () in accessions of black poplar (*Populus nigra*), *Mycosphaerella Anoplophora glabripennispini* in Monterey pine (*Pinus radiata*), and white pine blister rust (*Cronartium ribicola*) in western white pine (*Pinus monticola*) ([Food and Agriculture Organization of the United Nations 2009](#_ENREF_162)).

Genetics and genomics methodologies provide the toolbox (i.e. molecular markers) for identifying the genes or DNA tags associated with the desired plant phenotype, and assist the selection from the wild forest genetic resources of the parental plants that will be intercrossed to provide the plant progenies (either full-sib or half-sib) with which to start breeding procedures for recurrent selection. Molecular markers will be extremely useful for progeny selection during the early growth stages of the seedlings possessing the putative genetic factors for trait enhancement, even when the target phenotype of the trait will be expressed years later, after the transition from the juvenile to the reproductive stage. Molecular markers will be valuable also for: *in vitro* selection of somaclones surviving stressors included in the growth medium or growing environment; fingerprinting new clones; tracing wooden artifacts; and certification of the improved nursery materials for plantations in agroforestry intervention to mitigate the effects of climate change. Molecular markers are also effective for the identification of candidate genes for elucidating the biological mechanisms of adaptation and for identifying the underlying genetic factors and interactions for forest tree domestication.

Currently, there are many approaches to discover molecular determinants of forest tree phenotypes expressed at the individual, population, community, or ecosystem level ([Stanton et al. 2010](#_ENREF_464); [Whitham et al. 2008](#_ENREF_534)). These are based on genetic analyses to discover molecular marker genotype - phenotype associations and interaction with the environment, and include: (1) Two-point linkage analysis between a marker and a qualitatively inherited trait such as a disease resistance gene; (2) Quantitative trait locus (QTL) mapping; (3) Association genetics of single nucleotide polymorphisms (SNPs) for candidate genes identified by gene expression analysis, mutation or modulation of gene function (gene silencing or promoter activation), and genome wide association; and (4) Genome selection and phenotypic evaluation. The two-point linkage approach has been used successfully a number of times to map single genes coding for resistance to biotic stressors (i.e. resistance to *Populus* leaf rust caused by *Melampsora* spp). QTLs for a number of quantitative traits including abiotic stress tolerance have also been found.

A bacterial artificial chromosome (BAC) library of the genome of a forest species may extend the genome coverage of the marker genes. The sequencing and annotation of genes in overlapping BAC clones for the target molecular marker provide information on candidate genes surrounding the marker locus associated with the trait phenotype. Genomic studies based on BAC library screening have been carried out for aspen (*Populus tremuloides*) ([Fladung et al. 2008](#_ENREF_160)), Eucalyptus (EUCAGEN, www.eucagen.org), and Pedunculate oak (*Quercus robur*) ([Rampant et al. 2011](#_ENREF_373))*.* In forestry, the search for SNPs has focused largely on “candidate genes” associated with quantitative variation, using approaches similar to the ‘case vs control’ studies in humans ([Gilchrist et al. 2006](#_ENREF_186); [Grattapaglia et al. 2009](#_ENREF_194)).

The discovery of candidate genes involved in the expression of a trait phenotype may be achieved also by the analysis of ‘gene expression’ and ‘gene function’. Gene function can be assessed by point mutations altering the encoded protein or by modulating the production of the functional protein using gene silencing or promoter activation. Mutagenic treatment with chemical agents (i. e. Ethyl methanesulfonate) producing SNP mutations which can be identified in a target gene by TILLING (Targeted Induced Local Lesions in Genomes). A variant of that methodology called Ecotilling identifies naturally occurring SNPs underlying phenotypic variation in natural populations, and it has been used as an efficient SNP discovery tool in *Populus tricocarpa* ([Gilchrist et al. 2006](#_ENREF_186)).

Gene silencing induced by RNA interference (RNAi) has been shown to provide resistance against insects (*Diabrotica*, *Helicoverpa*), bacteria (*Agrobacterium, Staphylococcus*, nematodes (*Heterodera*, *Meloidogyne*) and parasitic plants (*Orobanche, Striga, Triphysaria*), and should provide effective and durable resistance to insect parasites of tree plants such as the red palm weevil *Rhynchophorus ferrugineus* ([Niblett and Bailey 2012](#_ENREF_349)).

Genome-wide association studies (GWAS) for SNPs in candidate genes associated with wood property traits, disease resistance, drought tolerance, and metabolome has focused on loblolly pine (*Pinus taeda*) ([Eckert et al. 2012](#_ENREF_138)) and *Populus* ([Stanton et al. 2010](#_ENREF_464)). Rare functional variants, usually missed by GWAS, can be discovered by combining genome sequencing for *de novo* assembly in non-model species and restriction associated DNA (RAD)-tag genotyping of the same population ([Amores et al. 2011](#_ENREF_18)).

The sum of the effects of genome-wide markers capturing most QTLs for the target trait gives a measure of tree breeding value and is used as a predictor of performance for genomic selection (GS), which is being developed for application in Eucalyptus ([Resende et al. 2012a](#_ENREF_389); [Resende et al. 2012b](#_ENREF_390)).

Several procedures have been developed for high-throughput DNA genotyping and genome-wide marker identification in forest trees. The genome complexity reduction DArT (Diversity Arrays Technology) technology ([Alves-Freitas et al. 2011](#_ENREF_17)) and whole-exome capture using in-solution target enrichment ([Neves et al. 2011](#_ENREF_347)), have been tested successfully for genome-wide marker identification needed for GS in *P. taeda*.

A sequenced genome is an important reference for genetic markers in both GWAS and GS. On the basis of the genomic knowledge accumulated so far, species of Conifers (i.e. pines and spruce trees), Eucalyptus, Birch family (i.e., oaks and chestnuts), and Poplars have been chosen as nonclassical model eukaryotes for forest tree genome wide sequencing projects. The Conifer Genome Project (<http://www.pinegenome.org/cgp/>) aims to advance genome research in loblolly pine (*Pinus taeda*; 21,658 Mbp; n=12), and white pines (*Pinus* subgenus *strobus*), as well as *Sequoia sempervirens* (31.4 Gbp/1C; n=33), and Douglas fir (*Pseudotsuga menziesii*, 18.6 Gbp/1C; n=13). An extensive genetic resources and gene catalog was developed for *P. taeda* and *Picea glauca* (white spruce; 19.7 Gbp/1C; n=12) (<http://www.pinegenome.org/cgp/>). The GENOAK project (<http://urgi.versailles.inra.fr/Projects/GenOak>) aims to establish a high quality reference genome sequence for pedunculateoak (*Quercus robur)* (905 Mb/1C ; n=12). The *Eucalyptus grandis* (640 Mbp/1C, *n* = 11) genome has been deciphered(<http://www.phytozome.net/eucalyptus.php>) and will benefit agroforesters utilizing this fast-growing hardwood tree to support industries based on Eucalypt fibre (pulp, paper, cellulose, etc) and hardwood products (eg. poles, construction, furniture), and the production of Eucalypt feedstocks for cellulosic biofuels.

Whole genome sequencing, GWAS and GS approaches, help finding genes for important functions in forest plants, and when coupled with comparative genomics it is possible to find orthologous genes in other species, while transgenics will facilitate the verification of the hypothesis on the function of the orthologous gene in mutants or in different growth stages of the host species. A transgenic American chestnut variety expressing a wheat gene for the enzyme oxalate oxidase, which disarms the fun­gus *Cryphonectria parasitica*, has already shown resistance in the field; researchers are also developing a genetically modified (GM) version of an American chestnut accession with resistance based on genes from Asian chestnuts, and because the resulting GM plants are ‘cisgenic’, the trees containing only chestnut genes, researchers hope that the trees won’t provoke strong public objection ([Thompson 2012](#_ENREF_483)).

Examples of other genes discovered in forestry germplasm using molecular genetics approaches and transgenics are given in ([Boerjan 2005](#_ENREF_51); [Flachowsky et al. 2009](#_ENREF_159); [Gonzalez-Martinez et al. 2006](#_ENREF_193); [Harfouche et al. 2012](#_ENREF_207); [Merkle and Dean 2000](#_ENREF_327); [Neale and Kremer 2011](#_ENREF_346)). These genes may be deployed to accelerate forest tree breeding for fast response to the need of adapted populations facing environmental modification induced by climate change.

## 2.7 Industrial Crops

*Robert Henry, Joe Tohme*

Climate change will impact agriculture in areas other than just food and fiber crops. Industrial crops may be an important part of future responses to climate change, providing a sustainable alternative to the use of fossil fuels for energy and biomaterials. Energy crops may become an important contributor to reducing the cost of food production in both crop production and food distribution. The requirement is for industrial crops that minimize competition for resources with food crops, so as to allow a delivery of a net positive impact on food production costs.

Sugarcane (*Saccharum officinarum*) is probably the most important industrial crop currently. Other related grasses (e.g., *Sorghum, Micanthus* and *Erianthus*) are also likely to be used as energy crops. New dedicated energy crops such as switchgrass may also become important. Woody biomass crops may provide advantages in energy density for biomass transport and are also likely to be developed for industrial use. As such, Eucalypts may become major industrial crops ([Shepherd et al. 2011](#_ENREF_444)). Much effort needs to be devoted to the identification of the most productive and climate resilient species, and the selection of genotypes with traits that provides a biomass composition that suits industrial uses. Increased water use efficiency will be a key trait for the development of these energy crops. Nitrogen use efficiency may also be important to allow sustainable production, avoiding the high energy costs of chemical nitrogen fixation.

Genomics resources for the key crops such as sugarcane are being developed ([Bundock et al. 2009](#_ENREF_69); [Souza et al. 2011](#_ENREF_460)) and will be important tools for improving the quality of biomass for these applications and delivering climate resilient genotypes. Sugarcane genomics is challenging because of the highly polyploid nature of the genome. This makes genome assembly difficult and complicates the study of gene expression. A reference genome remains an important object for sugarcane ([Souza et al. 2011](#_ENREF_460)). Similarly, genome re-sequencing of sweet sorghum genotypes is taking place with a strong integration with breeding hybrid sorghum mainly for Brazil ([Calviño and Messing 2012](#_ENREF_81)).

The genetic improvement of biomass composition requires an understanding of the composition needed to facilitate efficient conversion to fuel or biomaterials. These traits are currently not well defined, making the identification of candidate genes difficult. They may also be complex, making them targets for discovery by whole genome analysis approaches. Other industrial crops such as rubber may also become more important as alternatives to the use of oil for many biomaterials. Genomics approaches will be important in developing these crops to cope with climate change.

## 2.8 Grasslands

*Mike Humphreys, Athole Marshall and Hongwei Cai*

Grasslands are more than “just a crop”. They occupy approximately 25% of the terrestrial Earth land-surface, an area roughly equivalent to those attributed to forestation or cultivation. However, for agriculture in many countries grasslands occupy the largest land areas contributing significantly both to national economies and to food production. For example, grasslands provide 40% overall of the European utilized agricultural area, whilst in the UK 76% of agricultural land is grassland, supporting a £6b/a industry. Grassland is predominantly used for milk and meat production. Milk production, by ruminants in particular, is a very energy efficient way to produce high quality animal proteins from cellulose rich, low quality plant forage, which is often produced on marginal land unsuitable for alternative cropping systems. Grasslands are increasingly important in bioenergy production: grassland biomass can produce heat and electricity through direct combustion, or can be converted into transportation biofuels such as bioethanol. More than this, the persistency of grasslands is essential for their impact on the environment where they have a significant role in mitigating the impact of climate change.

Amongst alternative grassland ecosystems, it is important to distinguish the climatically determined grasslands, in areas where water availability is insufficient to allow the development of forest ecosystems from the anthropogenic grasslands, these mainly located within temperate climate regions, where woody vegetation is deliberately excluded and grassland species’ communities are maintained by man for use in livestock agriculture. Amongst the latter it is also possible to distinguish long-term naturalized grasslands from cultivated grasslands, which have a wide range of variation in degree of intensification. With the exception of those instances when employed as components in arable systems as one year break-crops, grasslands generally persist over many years, and include many perennial plant species of agronomic importance. Their persistency provides continuity to complex, bio diverse interacting plant, animal and microbial ecosystems. As a consequence, and unlike most alternative crops, grasslands make a major contribution in the dynamics of atmosphere, hydrosphere, and continental surface interactions that influence changes and environmental hazards at local, regional and global levels. As such, grasslands provide for essential ‘ecosystem services’ in addition to their more recognized roles as suppliers of healthy fodder for livestock. These ecosystem services include capabilities for the regulation of water capture and its release, so as to mitigate incidents of flooding, and to enhance opportunities for the acquisition of consistent water supplies with a quality that is safeguarded through effective retention of wastes and potential pollutants. In addition to this, grasslands also provide cultural services such as recreation, aesthetic enjoyment and spiritual fulfilment and support over time, services such as soil formation and protection, and biogeochemical cycles including C sequestration. Some analyses of existing grasslands imply that at least 100 t ha-1 of steady-state carbon sequestration in roots is routinely attainable ([Kell 2011](#_ENREF_257)).

The grasslands of the world face a range of challenges from climate change, including the effects of elevated atmospheric CO2, increasing temperatures, changes in precipitation regime and higher concentrations of ground level ozone. These factors threaten productivity, species composition and quality, livestock production and provision of ecosystem services within sustainable production systems. The research priorities for the future are to develop grassland species with improved (i) drought tolerance and enhanced water use efficiency, (ii) tolerance of saline soils, (iii) tolerance of floods and related consequences of changes in rainfall patterns, and (iv) nutrient use efficiency and forage quality. The greatest achievements thus far focus on recent work carried out on the key species of temperate grasslands, the ryegrasses and clovers. State of the art genomic approaches are beginning to be deployed for the genetic improvement of temperate grassland species. However, there is an urgent need for increased public sector resources to be dedicated to the development of new varieties of grassland crops for the tropics and sub-tropics. Genetic improvement should be complemented by research to explore the potential of introduced species and ecotypes, and allied with modeling of climate change scenarios to facilitate breeding targeted to the needs of the regions most affected. For temperate grasslands, it is essential to build on current advances and to ensure high quality crops persist when faced with increased environmental stress. In this regard, adapted “wild-type” relatives will, and are, playing important roles in supply of novel adaptive variation.

In managed temperate grasslands, the ryegrasses *Lolium perenne* and *Lolium multiflorum* are considered as the optimal species as they provide high yields of nutritious forage when grown in mixtures with white (*Trifolium repens* L) or red clover (*T. pratense* L). However, they lack resilience against abiotic stress. Even in mesic environments and under moderate stress conditions such as those common to the UK, significant yield reductions, with 1 tonne/ha/yr lost for every 50 mm soil water deficit can be observed ([DEFRALINK 2013](#_ENREF_123)). Genetic improvement of the ryegrasses, targeted at greater resilience to environmental perturbations is crucial. Whilst selection from with existing breeding populations is one approach, an alternative and potentially more successful approach is to exploit the genes for abiotic stress resistance that can be found in the more robust and stress-adapted *Festuca* (fescues) of which there are >500 species. Several *Festuca* species are capable of hybridising naturally with *Lolium,* and as hybrids have the potential to colonise harsh growing conditions e.g. *Festulolium loliaceum* (*Lolium perenne* x *Festuca pratensis*), which is adapted to waterlogged soils in water meadows. Synthetic *Festulolium,* developed through conventional breeding methodologies, are marketed either as amphiploid or introgressive forms. ([Humphreys et al. 2006](#_ENREF_226)) reviewed genetic advances in relation to grasslands at a time of climate change and described the unique capability within the *Lolium* and *Festuca* complex to exploit their practically inexhaustible supply of genetic variation in order to redesign grass genomes both for production, and resilience against abiotic stresses. Whilst the presence of more effective allelic variants and traits in certain *Festuca* species explain their greater stress tolerance compared with *Lolium*, it is now becoming apparent that as hybrids, positive *Lolium*/*Festuca* species’ genome interactions will enhance stress tolerance in certain cases further than that capable by either the parent species. For at least certain traits such as root development, *Lolium* and *Festuca* genomes interact positively to enhance root growth and leaf elongation during drought stress, leading to increased forage production under suboptimal water supply. Furthermore, the evolution and speciation within the *Lolium-Festuca* genome complex that has led to natural interspecific hybrids, with adaptations to colonize new and harsher environments, provide us with a “window” to understand how stress tolerance evolved in the *Poaceae* which we might reproduce in high quality grass cultivars experiencing climate change. This knowledge will also benefit other related crop species. Advances in genomics have revealed the macrosynteny between *Lolium* and *Festuca* species*,* the model grasses rice and *Brachypodium* and many cereals such as wheat and barley, enabling studies of comparative trait genetics and knowledge transfers across crop species and of mutual benefit. Detailed abiotic stress QTL studies both in *Lolium* ([Turner et al. 2008](#_ENREF_501)) and in *Festuca* ([Alm et al. 2011](#_ENREF_11)) have benefited from knowledge of their syntenic relations with other crop species and have identified orthologous gene loci for expression of equivalent traits. ([Abberton and Marshall 2005](#_ENREF_1)) reviewed progress in breeding clovers for temperate agriculture in light of future challenges from changes to agricultural production practices and the likely potential impact of climate change. Much as described for the *Lolium* and *Festuca* complex, they considered important traits and opportunities for introducing genetic variation into plant improvement programmes by introgressing traits from closely related species. Indeed, significant progress in improving resilience to moisture stress has been achieved through the development of interspecific hybrids between white clover and *Trifolium ambiguum*.

Perhaps the most important focus for future research of perennial grassland species will be on the genetics of root architecture and ontogeny, and the important effects of roots on soil structure and hydrology, and on water and nutrient capture. Both in *Festulolium* and in white clover, root growth and subsequence senescence have improved soil porosity and rainfall retention leading to increased soil reservoirs at times when rainfall is suboptimal, and have reduced overland flow that would otherwise lead to flooding following periods of extended and excessive rain. The potential to enhance deep rooting in grasses both as safeguards against droughts, for nutrient uptake, and for C sequestration are being investigated ([Kell 2011](#_ENREF_257)), with novel *Festulolium* hybrid combinations capable of providing rapid growth rates and extensive root systems demonstrating great potential. Full integration of new high-throughput phenomic and genomic technologies should allow improved root design to sustain crop production under stress and to provide an environmental service.

Another focus as a response to climate change for grass design should be heat tolerance. Pilot studies have identified the possible transfer of heat tolerance genes from a fescue species into ryegrass, capable of providing adaptations within living cells of ingested forage to the high temperatures found in rumen conditions that can lead to improved efficiency in ruminant nutrition. Strategies for improved conversion of N in the rumen that can lower greenhouse gas emission are considered a research priority in livestock agriculture. Future research should also focus on improved heat tolerance in alternative important forage grass species such as Timothy (*Phleum pratense*) and cocksfoot (*Dactylis glomerata*) and should take account of the impacts of increases in temperature on spreads of diseases such as crown rust and blast in ryegrass, with a focus both on the impacts such diseases have directly on grassland quality and yield for livestock agriculture and also the potential for infected ryegrass as hosts for increased fungal attack onto related cereal crop species such as wheat.

# 3 Strategies of Breeding for Climate Resilient Traits

*Henry Nguyen* and *David Edwards*

## 3.1 Introduction

World crop production is increasingly impacted by global climate change. Climate change is predicted to lead to more extreme agronomic conditions, including variations in temperature, precipitation, drought, floods, and the increased incidence of disease pests. These impacts on agriculture will have devastating effects on food security across the world, particularly when combined with the growing demand for food for the rapidly expanding human population. Reliable food production during the period of climate change will require substantial changes in crop breeding, farming practices and infrastructure.

The establishment of integrated agronomic and management approaches, along with strategies to improve crop adaptation to abiotic stress and yield stability under these variable environmental conditions is urgently required. These can most readily be achieved through advanced breeding approaches for the genetic improvement climate related agronomic traits. Recent advances in genomics, facilitated by novel DNA sequencing technologies, have made crop genome investigations easier, and enable rapid and precise dissection of the genomic basis for agronomic traits which can be applied to accelerate crop improvement ([Edwards et al. 2013](#_ENREF_140)). Crop breeding methods have advanced through the application of genomics technologies, and they are being widely adopted in breeding programs for both major and orphan crops ([Berkman et al. 2012](#_ENREF_36); [Tester and Langridge 2010](#_ENREF_479)). The development of platforms for data and information sharing in genomics, together with trait mapping for climate change and disease-resistant traits will accelerate the breeding for crop resilient traits. The integration of new frontiers in crop modeling, genome biology and phenotyping technologies increase the potential for narrowing the genotype–phenotype divide and will contribute towards crop improvement through ‘plant breeding by design’ ([Fridman and Zamir 2012](#_ENREF_165); [Yin et al. 2004](#_ENREF_548)).

In this section, various crop resilient traits including both abiotic and biotic components are discussed.

## 3.2 Flowering Time

*Alison Bentley, Kiyosumi Hori, Masahiro Yano, Andy Greenland and James Cockram*

Environmental alterations arising from climate change are predicted to have a major impact on crop production worldwide. Interpretation of the likely effects of these alterations in climate, particularly global warming and water availability, is needed to develop strategies for the development of crop varieties that maintain and continue to increase yield in the major crop growing regions of the world. Manipulation of flowering time is currently a key adaptation mechanism and will be increasingly important in years to come.

 Temperature influences crop development in concert with additional floral pathways such as day length (photoperiod), which collectively control floral transition through interconnected genetic pathways. Global warming will result in increased ambient temperature with unchanged photoperiods at given latitudes. Annual plants generally respond to increased temperatures with accelerated growth and development, having shortened lifecycles, less opportunity for photosynthesis ([Reynolds et al. 2010](#_ENREF_394)), a shorter reproductive phase, and lower yield potential ([Ainsworth and Ort 2010](#_ENREF_7); [Craufurd and Wheeler 2009](#_ENREF_114)). There is also an increased risk of damage to reproductive tissue caused by the coincidence of high temperatures and sensitive developmental stages. Acceleration of flowering in spring should also occur due to increased temperatures following the coldest days of winter ([Cleland et al. 2007](#_ENREF_97)). In temperate regions flowering is a function of vernalization (the prolonged period of cold, non-freezing temperatures required for subsequent competence to flower), spring heat and photoperiod. Any subsequent delay in the fulfilment of vernalization requirement (due to acceleration of spring) could result in later flowering, although this may be masked by increased spring temperatures ([Yu et al. 2010](#_ENREF_550)).

Cereal yields in mid- to high-latitude production areas are predicted to increase with global warming, promoting crop production despite reduced yields at lower latitudes ([Ainsworth and Ort 2010](#_ENREF_7)). This prediction, however, is based on maintenance of existing levels of yield improvement, which are currently around 1% per year for cereal crops in Europe ([Mackay et al. 2011](#_ENREF_310)). However, rates of yield increase for all major cereal crops are declining ([Fischer and Edmeades 2010](#_ENREF_158)). A major breeding challenge is to arrest this decline and produce varieties that take advantage of the positive aspects of climate change whilst offsetting negative impacts, with genetic combinations of traits that are robust to inter- and intra-seasonal variation in water and temperature. To deliver the required sustainable increases in crop production, such germplasm must perform not only in suboptimal conditions, but remain responsive in favorable years ([Reynolds et al. 2010](#_ENREF_394)). Detailed knowledge of the interplay between the genetic control of flowering, allelic variants, epistatic interactions and phenotypic variation in varied growth conditions is necessary in order to identify breeding targets for climate change scenarios.

Recent seasonal temperature increases have resulted in reduced yield potential and grain quality in rice (*Oryza sativa*) production areas ([Ishimaru et al. 2012](#_ENREF_233); [Jagadish et al. 2008](#_ENREF_241); [Yamakawa et al. 2007](#_ENREF_544)). Rice is a short day plant, flowering when the photoperiod is shorter than a critical day length ([Izawa 2007](#_ENREF_239)). Although manipulating flowering time to avoid stress periods is a strategy for minimizing such losses, developmental re-programming via alterations in the function of floral pathway genes often results in deleterious changes to growth and yield potential. There are, however, a number of rice genes with utility for use in flowering time-specific breeding programs for adaptation in specific environments. ([Ebana et al. 2011](#_ENREF_137)) performed QTL analyses in 12 populations derived from crosses of the *japonica* cultivar ‘Koshihikari’ (a common parental line) with numerous cultivars originating from various regions in Asia, revealing a comprehensive series of QTLs involved in natural variation in flowering time. They clearly demonstrated that a limited number of loci [*Hd1*, *Hd2*, *Hd6*, *RFT1*, *Ghd7*, *DTH8* (*Ghd8:Hd5*), and *Hd16*] explained a large part of the varietal differences in flowering time ([Ebana et al. 2011](#_ENREF_137)). In rice, most of the major genes involved in flowering time have been cloned. This is an advantage in targeted breeding as MAS can be effectively deployed, and specific alleles introgressed allowing manipulation of flowering time to suit future agricultural environments. It should be noted that gene interactions also play an important role in flowering time in rice ([Izawa 2007](#_ENREF_239); [Yano et al. 2001](#_ENREF_547)) and the genetic background of a cultivar must be considered when planning which genes to combine (pyramid) to manipulate flowering time.

Unlike rice, the related Poaceae crops wheat (*Triticum aestivum*) and barley (*Hordeumvulgare*) are long-day responsive, and possess a vernalization requirement (in winter cultivars). Empirical selection through time has allowed optimization of wheat and barley flowering to ensure maximum yields in a given region. Farmers and breeders have selected a complex of genes controlling the transition to flowering, through selection for differing vernalization requirement (*VRN* genes), photoperiod sensitivity (*PPD* genes), as well as additional smaller effect earliness *per se* (E*ps*) loci. For example, analysis of known photoperiod-insensitive mutant alleles in near-isogenic lines (NILs) of bread wheat have shown that the *Ppd-D1a* allele markedly reduces flowering time in short days, with the *Ppd-A1a* durum allele also having a strong effect, followed by a moderate earliness conferred by the *Ppd-B1a* copy number variant ([Bentley et al. 2011](#_ENREF_35)). Further work has shown that combining the *Ppd-D1a* and *Ppd-A1a* alleles produces earlier flowering than either *Ppd-D1a* or *Ppd-A1a* in isolation in NILs assessed in short days ([Shaw et al. 2012](#_ENREF_442)).

Barley possesses an additional major photoperiod response locus, termed *PPD-H2*, probably encoded by the *FLOWERING LOCUS T-*like gene *HvFT3* ([Faure et al. 2007](#_ENREF_149)). If *HvFT3* orthologues were present in wheat, the identification and consolidation of recessive alleles at all three homoeologous genes into one genetic background would provide a novel source of useful flowering time variation of particular relevance to a warming climate, allowing floral repression in the winter without the need for a strong vernalization response.

Altering flowering time through manipulation of major genes in rice, wheat and barley breeding programs provides strategies to adapt elite varieties to the prospect of shorter, hotter, drier growing seasons. However, work is still required to understand the effect of flowering time on yield potential across environments and climate change scenarios. In addition, the potential utility of loci of minor effect and/or which affect various stages of reproductive development could offer the ability to shorten or lengthen various phases of the process, thereby fine-tuning flowering to suit particular regional climatic conditions, and to adapt to any changes in these conditions.

## 3.3 Drought Adaptation

*Antonio Costa de Oliveira, Henry Nguyen, Babu Valliyodan, Roberto Tuberosa and Rajeev Varshney*

Since the beginning of agriculture, mankind has coped with drought, the major abiotic stress affecting crop productivity globally. The first farmers had to set their fields close to water sources or depend of rain, which in many regions can be unreliable. The rapid growth of the human population has caused a movement of agricultural activities to marginal and more drought-prone areas, and at the same time demanded higher yields to feed growing population. Therefore, scientists from many disciplines are called to improve plant response to drought and to improve the water use efficiency (WUE) of crops. The frequency and intensity of drought episodes have increased in the last decades, a likely consequence of global climate change and temperature increase in some regions of the planet. The impact of drought stress can be variable, depending on its timing, duration and intensity ([Serraj et al. 2005](#_ENREF_434)). The effects of deforestation, overgrazing and industrialization have been felt as early as the seventeenth century, known as "Sahel drought" ([Held et al. 2005](#_ENREF_213)). Today, with advances in remote sensing techniques, climate-yield predictions can be obtained for the major crops through simulation ([Lobell et al. 2008](#_ENREF_299)) and scientists have become increasingly aware that genotypes better adapted to future climate changes are urgently needed. In this scenario, the combination of modern genomics techniques, with genetic approaches and reliable phenotyping platforms will be essential. Approaches that apply the molecular dissection of QTLs, marker-assisted backcrossing, marker-assisted recurrent selection and genome-wide selection will be key to such success ([Mir et al. 2012](#_ENREF_331); [Zhang 2007](#_ENREF_556)).

The basic principles of coping with drought have to be drawn from the biochemical and physiological basis of crop production. One has to be careful to not confuse water use efficiency with drought resistance and high yield under drought stress ([Blum 2009](#_ENREF_48); [Blum 2011](#_ENREF_49)). According to ([Passioura 1996](#_ENREF_355)), grain yield is a partial function of WUE (Y = WU x WUE x HI), where Y is grain yield, WU is water use, and HI is harvest index. This has been used by breeders ([Reynolds and Tuberosa 2008](#_ENREF_393)) as an elegant way to convey this important message. However, some authors have stressed that WU and HI are more important than WUE as drivers of yield. WUE would be the transpiration efficiency (TE) measured at the leaf level and is determined by a delicate balance between stomatal activity, substomatal activity, CO2 concentration and transient photosystem activity ([Farquhar et al. 1989](#_ENREF_148)), and conflicting results have been found when trying to correlate WUE and yield ([Blum 2009](#_ENREF_48)). For these authors, efficient use of water - a set of constitutive and adaptive traits which drive the effective use of water (EUW) and not WUE should be used as a parameter for selecting drought resistant plants under most conditions of limited water supply. Indeed, many factors have to be taken into account to determine if a genotype is drought resistant: factors such as stomatal conductance, water leakage through the cuticle, nocturnal stomata opening and osmotic adjustment, which functions by (i) enabling leaf turgor maintenance at the same leaf water potential thus supporting stomatal conductance under lower leaf water status and (ii) improving root capacity for water uptake ([Ali et al. 1999](#_ENREF_9); [Blum 2005](#_ENREF_47); [Chimenti et al. 2006](#_ENREF_92); [Sellin 2001](#_ENREF_428)). Recently, the complexity of drought tolerance has been extensively reviewed ([Blum 2011](#_ENREF_49)). The point raised is that most experiments focusing on drought do compare different water status when different genotypes are subjected to the same periods of time without watering. Therefore, gene expression and metabolic function experiments should be standardized in order to compare plants and tissues with the same water status. Nevertheless, some examples of single traits conferring drought resistance are found in major crops, i.e., stay-green in sorghum and root depth in upland rice.

Transpiration efficiency is an important component of WUE. Increased transpiration efficiency can be obtained by either increasing biomass or photosynthesis by decreasing transpiration, or a combination of these traits. Often there are penalties associated with increasing or decreasing one trait. The challenge for physiologists and crop breeders is to increase photosynthesis and at the same time decrease transpiration

With the advent of molecular breeding, the identification of QTL and their use in the breeding programs may help develop new cultivars with improved drought tolerance. Recently, the ERECTA gene has been associated with transpiration efficiency in *Arabidopsis* ([Masle et al. 2005](#_ENREF_322)); expression of the ERECTA gene resulted in reduced stomatal frequency and conductance and greater photosynthetic rates, resulting in increased WUE under a wide range of water regimes.

Osmotic adjustment helps maintain higher relative leaf water content at low leaf water potential, and it is evident that this helps sustain growth while the plant is meeting the transpiration demand by reducing its leaf water potential. Osmotic adjustment sustains turgor maintenance and hence the yield-forming processes during moderate to severe drought stress. Osmolyte accumulation in roots can allow continued or even increased root development into deeper wet soil and can give a plant access to an increased water reservoir on which the crop can be grown and/or survive.

### 3.3.1 Maize

Drought has been and still is the main environmental factor curtailing maize production worldwide ([Cairns et al. 2012](#_ENREF_76)). The extensive yield reduction caused by drought in summer 2012 in the USA and also in some regions in Europe (e.g. Northern Italy) is a stark reminder of the potential socio-economic impact of drought.

In maize, similarly to other cereals, flowering is the most critical stage in terms of yield reduction caused by the occurrence of drought ([Duvick 2005](#_ENREF_133)). When drought occurs at flowering, silk extrusion is delayed and the interval between pollen shed and silking (i.e. anthesis-silking interval (ASI) extends. In turn, under drought conditions ASI shows a strong, negative correlation with grain yield ([Monneveux and Ribaut 2006](#_ENREF_336)). ASI has been the first trait to be targeted by marker-assisted selection in order to improve drought tolerance in maize using a genomics-based approach ([Ribaut et al. 2004](#_ENREF_395); [Ribaut and Ragot 2007](#_ENREF_396)). The negative association reported between the effects of QTLs that have been shown to influence both leaf elongation and ASI suggests turgor maintenance as a possible common mechanism accounting for the correlation ([Welcker et al. 2011](#_ENREF_531)). Extensive work has allowed for the mapping and cloning of major QTLs for flowering time ([Buckler et al. 2009](#_ENREF_67); [Salvi et al. 2007](#_ENREF_409)), thus enabling breeders to selectively target parental lines based on their haplotype at key regions controlling the transition from the vegetative to the generative phase. New mapping approaches (e.g. nested association mapping ([Buckler et al. 2009](#_ENREF_67); [Yu et al. 2008](#_ENREF_551)) and meta-analysis of biparental mapping data sets ([Salvi et al. 2011](#_ENREF_410); [Welcker et al. 2011](#_ENREF_531)) allow for a more refined and accurate genetic dissection of the loci controlling the adaptive response to drought. This information can also be used to model maize yield under different water regimes according to the genetic make-up of each genoype at major loci ([Tardieu and Tuberosa 2010](#_ENREF_477)).

Extensive work has also been carried out to investigate the role of root features in mitigating the negative effects of drought on maize productivity. Maize roots show a high level of developmental plasticity in response to environmental cues ([Ito et al. 2006](#_ENREF_237)), a clear example being provided by the interplay between abscisic acid (ABA) and ethylene in sustaining root elongation under conditions of water deficit which inhibit shoot elongation ([Spollen et al. 2008](#_ENREF_463)). Additionally, this plasticity ensures the optimization between the allocation of photosynthates to the root and its capacity to capture water as a function of the prevailing soil conditions. Notwithstanding the important role of roots for optimizing maize yield, the genetic factors that control root growth have only recently started to be unveiled with the use of mutants, and in some cases, gene cloning ([Hochholdinger and Tuberosa 2009](#_ENREF_220); [Taramino et al. 2007](#_ENREF_476)). Nonetheless, because the genetic basis of the variability of root architecture in cultivated maize is prevalently quantitative, the application of suitable genomics approaches is required to identify the relevant quantitative trait loci (QTLs). This, in turn, would enable breeders to apply marker-assisted selection for tailoring root architecture according to the ideotype perceived as optimal to maximize crop performance in the target environment ([de Dorlodot et al. 2007](#_ENREF_122)). QTLs for root traits have been described in a number of populations ([Hund et al. 2011](#_ENREF_227); [Ruta et al. 2010](#_ENREF_406); [Tuberosa et al. 2007](#_ENREF_497); [Tuberosa et al. 2011](#_ENREF_498); [Tuberosa et al. 2003](#_ENREF_499)) and in some cases the QTLs showed a concurrent effect on yield performance under drought conditions, e.g. on bins 1.06 and 2.04 ([Landi et al. 2010](#_ENREF_282); [Landi et al. 2007](#_ENREF_284)).

Among the morpho-physiological traits that influence the adaptive response of maize to drought, abscisic acid (ABA) concentration has been extensively investigated for its associated effects on yield. Excessive accumulation of ABA has been implicated as one of the factors that negatively influences reproductive fertility ([Boyer and McLaughlin 2007](#_ENREF_61)) and endosperm development ([Seiler et al. 2011](#_ENREF_426)). Several QTLs for leaf ABA concentration (L-ABA) have been identified ([Sanguineti et al. 1999](#_ENREF_416); [Tuberosa et al. 1998](#_ENREF_500)), the strongest one mapping on bin 2.04 which has also been shown to influence root architecture and yield ([Giuliani et al. 2005](#_ENREF_189); [Landi et al. 2007](#_ENREF_284)). Possible candidates for L-ABA include the genes involved in the biosynthesis and degradation of ABA, the intensity of the transduction signal associated with turgor loss, and/or genes controlling morpho-physiological features (e.g. root size and architecture, leaf angle, cuticular waxes, etc.) affecting water uptake and loss by the plant, hence its turgor. Accordingly, extensive overlap among QTLs for L-ABA and QTLs for leaf relative water content was reported by ([Sanguineti et al. 1999](#_ENREF_416)) with a consistently negative association between L-ABA and leaf relative water content, thus suggesting that under field conditions L-ABA mainly represents an indicator of the level of drought stress experienced by plants at the time of sampling. Notably, the evaluation of an historical series of maize hybrids released in the past 60 years has shown a significant decrease in the capacity to accumulate ABA in response to a given level of water stress ([Sanguineti et al. 2006](#_ENREF_415)) and, consequently, a negative correlation between the capacity to accumulate ABA at the seedling stage (a trait never selected for by breeders) and grain yield.

Recently, Syngenta and Pioneer-DuPont ([Cooper et al. 2014](#_ENREF_104)) deployed proprietary genomics-assisted approaches to select drought-tolerant maize hybrids (Agrisure Artesian™ and AQUAmax™, respectively). The superior performance of these maize hybrids in the severe drought that plagued the US corn belt in summer 2012 underlines their validity under dry soil conditions.

### 3.3.2 Wheat

Among all abiotic and biotic stresses, drought has the largest negative impact on wheat productivity. Between tetraploid wheat (*Triticum durum* L.) and hexaploid wheat (*Triticum aestivum* L.), durum is better-adapted to withstand drought in rainfed areas, particularly in the Mediterranean Basin, where ca. 75 and 50% of the worldwide acreage and production, respectively, are concentrated. The range of wheat cultivation spans areas with different levels of fertility, ranging from favorable conditions (e.g. temperate regions, with medium to high annual rainfall rate and/or irrigation in some cases) to dryland areas characterized by drought and high temperature stresses, with an increased occurrence of water shortage and heat waves during grain filling. In particular, terminal drought, the stress most commonly experienced by wheat grown in Mediterranean-like environments, negatively affects grain weight and grain volume weight ([Slafer et al. 2005](#_ENREF_455)), two pivotal yield-related traits for the milling industry. Notably, the Mediterranean Basin is one of the geographical regions where agriculture has been forecast to be at greater risk due to an increase in the frequency and severity of drought episodes ([Reynolds et al. 2007](#_ENREF_391)). Accordingly, due to the high variability in rainfall patterns, water shortage can also occur from sowing time in late autumn to early spring. In such cases, drought exerts even stronger negative effects on yield, for example by decreasing the number of fertile spikes per unit area at the crop establishment and tillering phases, as well as the number of grains per spike. Under such conditions, adaptation mechanisms, based on traits that allow the plant to escape (e.g. flowering date), avoid (e.g. root depth), and/or tolerate (e.g. osmolyte accumulation) the negative effects of drought, and influence the balance and competition between vegetative and reproductive organs, thus playing a major role in determining final crop performance ([Araus et al. 2008](#_ENREF_25); [Blum 1988](#_ENREF_44); [Reynolds and Tuberosa 2008](#_ENREF_393)) and yield stability ([Alvaro et al. 2008a](#_ENREF_15); [Alvaro et al. 2008b](#_ENREF_16); [Sanchez-Garcia et al. 2012](#_ENREF_411)).

Under conditions of low evapotranspiration, early vigor may be beneficial to optimize WUE in wheat and limit water loss due to evaporation from the soil surface, which would leave more stored water available for stages when soil moisture becomes progressively exhausted and its availability increasingly limits yield ([Richards 2000](#_ENREF_397); [Richards 2006](#_ENREF_398); [Slafer et al. 2005](#_ENREF_455)). Early establishment also reduces the occurrence of inhibition of stomatal conductance caused by root-borne signalling via xylem ABA ([Ren et al. 2007](#_ENREF_385)) due to shallow and superficial roots ([Blum 1996](#_ENREF_45)). However, it should be noted that excessively vigorous canopy development could cause early depletion of soil moisture. The optimal degree of vigour will thus depend on the environmental characteristics prevailing in the target environment. In Australia, early vigour has been successfully exploited to improve WUE and yield in wheat ([Rebetzke et al. 2007](#_ENREF_379)) and has contributed toward the release of cvs. Drysdale and Rees. The QTLs for the growth rate of wheat seedlings are being actively targeted at CSIRO (Commonwealth Scientific and Industrial Research Organisation, Australia) ([Spielmeyer et al. 2007](#_ENREF_462)).

Carbon isotope discrimination (Δ13C) measures the ratio of stable carbon isotopes (13C/12C) in the plant dry matter compared to the ratio in the atmosphere ([Condon et al. 2006](#_ENREF_101)). Because of differences in leaf anatomy and the mechanisms of carbon fixation in species with the C3 or C4 pathway, studies on Δ13C have wider implications for C3 species like wheat where the variation in Δ13C is larger than in C4 species, and has a greater impact on crop yield ([Condon et al. 2004](#_ENREF_102)). Commonly, but not always Δ13C is negatively associated with WUE over the period of dry mass accumulation ([Araus et al. 2002](#_ENREF_24); [Royo et al. 2008](#_ENREF_405)). The relationship between Δ13C and grain yield depends on the environmental conditions, the phenology of the crop and the plant organ (e.g. leaf or grain) from which the samples are collected ([Condon et al. 2004](#_ENREF_102)). High genetic variation for grain Δ13C has been reported in wheat([Turner 1997](#_ENREF_502)), with high heritability ([Merah 2001](#_ENREF_326)) and a low genotype x environment interaction ([Rebetzke et al. 2008a](#_ENREF_378)). For these characteristics, Δ13C is an attractive breeding target for improving WUE and yield, while the high cost required to measure each sample makes it an interesting candidate for MAS.

In wheat, canopy temperature depression has been widely used as a proxy to evaluate the water status of drought-stressed plants. Canopy temperature depression (CTD) as measured by thermal imaging is a highly integrating trait resulting from the effects of several biochemical and morpho-physiological features acting at the root, stomata, leaf, and canopy levels. In the field, wheat genotypes with a cooler canopy temperature under drought stress, or a higher CTD, use more of the available water in the soil to avoid excessive dehydration ([Blum 1988](#_ENREF_44); [Blum 2009](#_ENREF_48); [Blum 2011](#_ENREF_49); [Reynolds et al. 2007](#_ENREF_391); [Reynolds et al. 2009](#_ENREF_392)). CTD is useful mainly in hot and dry environments typical of countries with a Mediterranean climate. Measurements should preferably be made on recently irrigated crops on cloudless and windless days with high vapor pressure deficits. Under these conditions and provided that data are collected when the canopy is sufficiently expanded to cover the soil, CTD can be a good predictor of wheat grain yield ([Reynolds et al. 2009](#_ENREF_392)). In bread wheat, yield progress was found to be associated with cooler canopies ([Fischer et al. 1998](#_ENREF_157)) and significant genetic gains in yield have been reported in response to direct selection for CTD ([Brennan et al. 2007](#_ENREF_63); [Reynolds et al. 2009](#_ENREF_392)). The addition of CTD as a selection criterion in wheat nursery considerably improved the identification of the highest yielding materials ([van Ginkel and Ogbonnaya 2007](#_ENREF_511)).

In drought-stressed wheat, osmotic adjustment (OA) has been implicated in sustaining yield under conditions of water deficit in wheat ([Blum et al. 1999](#_ENREF_50); [Ehdaie et al. 2008](#_ENREF_142); [Izanloo et al. 2008](#_ENREF_238); [Serraj and Sinclair 2002](#_ENREF_433)). As soil moisture declines, OA favors turgor maintenance, and hence the integrity of metabolic functions. Importantly, OA can bias estimates of the value of relative water content, as has been shown in wheat and barley ([Boyer et al. 2008](#_ENREF_60)). Under severe dehydration, a higher capacity to accumulate osmolytes may help plants to better withstand a prolonged drought spell and recover more promptly upon rehydration. Similarly to other drought-adaptive traits, the trade-off between the metabolic requirements of OA and the potential benefits varies according to the dynamics and severity of the drought episodes.

Among the morpho-physiological traits able to mitigate the negative effects on grain filling caused by post-anthesis drought, remobilization of water-soluble carbohydrates (WSC) from the stem and leaves has been shown to play an important and beneficial role ([Araus et al. 2002](#_ENREF_24); [Blum 1988](#_ENREF_44); [Blum 1998](#_ENREF_46); [Blum 2011](#_ENREF_49); [Rebetzke et al. 2008a](#_ENREF_378); [Reynolds et al. 2007](#_ENREF_391)). QTLs for stem-reserve remobilization have been reported in bread wheat ([Rebetzke et al. 2008b](#_ENREF_380); [Salem et al. 2007](#_ENREF_408); [Snape et al. 2007](#_ENREF_457); [Yang et al. 2007](#_ENREF_545)).

As to yield itself, a number of major QTLs have been described in drought-stressed wheat. In bread wheat, a major QTL located on chromosome 4A explained 27% and 17% of variation in yield under drought and heat stress, respectively ([Pinto et al. 2010](#_ENREF_360)). The same study also identified common QTLs for drought and heat stress traits on chromosomes 1B, 2B, 3B, 4B, and 7A. Additional QTLs for heat stress have been described ([Paliwal et al. 2012a](#_ENREF_351)). Yield QTLs were shown to be associated with components of other traits, supporting the prospects for dissecting crop performance under abiotic stress conditions into its physiological and genetic components in order to facilitate a more strategic approach to breeding ([Reynolds and Tuberosa 2008](#_ENREF_393)).

Durum wheat is well-adapted to rainfed areas of the Mediterranean Basin, where ca. 75% and 50% of the worldwide acreage and production, respectively, are concentrated. Its range of cultivation spans areas with different levels of fertility, ranging from favorable conditions (e.g. temperate regions, with medium to high annual rainfall rate and/or irrigation) to dryland areas characterized by drought and high temperature stresses, with an increased occurrence of water shortage and heat waves in late spring, i.e. during grain filling. Therefore, terminal drought, the stress most frequently experienced by wheat grown in the Mediterranean Basin, negatively affects grain weight and grain volume weight ([Slafer et al. 2005](#_ENREF_455)), two traits very important for the milling industry. Water shortage in Mediterranean environments can also occur from sowing time (e.g. late autumn) to early spring. In such cases, drought exerts even stronger negative effects on yield, for example by decreasing the number of fertile spikes per unit area at the crop establishment and tillering phases, as well as the number of grains per spike ([Alvaro et al. 2008a](#_ENREF_15); [Alvaro et al. 2008b](#_ENREF_16)). Under such conditions, adaptation mechanisms, based on traits that allow the plant to escape (e.g. flowering date), avoid (e.g. root depth), and/ or tolerate (e.g. osmolyte accumulation) the negative effects of drought, influence the balance and competition between vegetative and reproductive organs, thus playing a major role in determining final crop performance ([Araus et al. 2008](#_ENREF_25); [Blum 1988](#_ENREF_44)). It should be noted that the Mediterranean Basin is one of the geographical regions most densely populated, where agriculture has been forecast to be at greater risk due to an increase in the frequency and severity of drought episodes ([Reynolds et al. 2007](#_ENREF_391)). Compared to rice and maize, less work has been carried out in wheat to investigate root architectural features ([Manschadi et al. 2006](#_ENREF_316); [Manschadi et al. 2010](#_ENREF_317); [Richards 2006](#_ENREF_398)) and how the relevant QTLs may influence yield and yield stability across different water regimes ([Hamada et al. 2012](#_ENREF_205); [Ibrahim et al. 2012](#_ENREF_228); [Kadam et al. 2012](#_ENREF_254); [Ren et al. 2012](#_ENREF_386); [Sanguineti et al. 2007](#_ENREF_414); [Wasson et al. 2012](#_ENREF_529)).

In an elite RIL durum population, two major epistatic QTLs for yield *per se* (i.e. irrespective of flowering time), effective across a broad range of water regimes have been reported ([Maccaferri et al. 2008](#_ENREF_309)). Association mapping was used to dissect the genetic basis of drought-adaptive traits and grain yield (GY) in a collection of 189 elite durum wheat accessions evaluated in 15 environments which differ in water availability during the crop cycle and grain yield. For highly heritable traits (e.g. heading date, kernel weight, etc.) several significant marker-trait associations were detected across five or more (up to 13 for kernel weight) environments, with R2 values ranging from ca. 5 to 10%. As to GY, significant associations were mostly detected in one environment (56 markers) and decreased rapidly from two to five environments (from 20 to three markers, respectively) and with only one marker (*Xbarc197* on chr. 5A) found significant in six environments (ranging from low- to high-yielding). These results are probably due to the complex genetic basis of GY and its interaction with environmental conditions. The number of markers significantly affecting GY decreased considerably under drought conditions, suggesting a limited effectiveness of association mapping to identify loci for GY under low-moisture conditions, most likely because different genotypes can attain similar phenotypes via different morpho-physiological traits and corresponding gene networks. This is one of the reasons why QTLs, particularly for yield, often show strong genotype x environment interaction ([Collins et al. 2008](#_ENREF_100)). A more effective improvement of drought tolerance in wheat and other crops will require a multidisciplinary effort involving expertise of plant and soil scientists ([Mir et al. 2012](#_ENREF_331); [Tuberosa 2012](#_ENREF_494)).

### 3.3.3 Oilseed crops

Water stress and heat stress often occur simultaneously, but they can have very different effects on various physiological, growth, developmental, and yield processes. Although drought and heat stresses have been extensively studied independently, relatively little is known about how their combination affects crop productivity. The few studies that examined the impact of the combined effects of drought and heat stress suggested that the combination of drought and heat stress had a significantly higher detrimental effect on growth and productivity of crops than when each stress was applied individually ([Craufurd and Peacock 1993](#_ENREF_113); [Savin and Nicolas 1996](#_ENREF_419)). In addition, the combination of drought and heat stress was found to alter physiological processes such as photosynthesis, accumulation of lipids, and transcript expression ([Jagtap et al. 1998](#_ENREF_242); [Rizhsky et al. 2004](#_ENREF_399)).

In most crops, leaves senesce early in response to drought and heat stress, particularly when these stresses occur during the post-flowering stages of seed filling. Drought stress during early stages of embryo development increased the rate of abortion. Drought imposed at flowering can also decrease photosynthetic rates and thus decrease the amount of photosynthates allocated to floral organs, causing increased abortion. Lower seed-set under heat stress can be caused either by poor anther dehiscence, hence low numbers of germinating pollen grains on the stigma ([Prasad et al. 2006](#_ENREF_363)) ([Jagadish et al. 2007](#_ENREF_240))or because of decreased pollen viability ([Prasad et al. 2000](#_ENREF_362)) or ovule function ([Gross and Kigel 1994](#_ENREF_195)).

Both microsporogenesis (pollen development) and megasporogenesis (stigma development) are impaired by heat stress, resulting in lower seed-set ([Cross et al. 2003](#_ENREF_116)) ([Young et al. 2004](#_ENREF_549)). Pollen is known to be relatively more sensitive to heat stress conditions. The mechanisms responsible for pollen sterility, lower seed-set or early embryo abortion under heat stress are not clear and need further investigation. Different hypotheses that have been proposed as possible mechanisms responsible for decreased pollen viability under drought and heat stress include: (i) developmental abnormalities in anthers leading to dislocation of microspores prematurely ([Saini et al. 1984](#_ENREF_407)); (ii) dysfunction of tapetal cells because of abnormal vacuolization ([Lalonde et al. 1997](#_ENREF_279)); (iii) premature degeneration of tapetal cells and lack of endothecial development ([Ahmed et al. 1992](#_ENREF_6)); (iv) altered carbohydrate accumulation and metabolism ([Jain et al. 2007](#_ENREF_244)); and (v) oxygen starvation in the developing microspores which could lead to loss of gametophyte viability.

### 3.3.3.1 Soybean

Abiotic stresses such as high temperature, drought, salinity, cold and waterlogging often result in significant reduction in the yield of this economically important crop. Drought stress reduces yield in soybean, with the most sensitive stages being flowering and seed filling ([Claassen and Shaw 1970](#_ENREF_96)). Research has shown that temperatures of above 34/20°C (day/night) will reduce yields in soybean ([Dornbos and Mullen 1992](#_ENREF_130)). There are no studies showing the effects of a combination of drought and heat stresses, but under field conditions plants will experience both stresses at the same time. Heat stress decreases stomatal conductance and photosynthetic rate due to ultra-structural damage to chloroplasts, mainly disintegration of the chloroplast and plasma membrane coupled with dilation of the thylakoid membrane, causing premature leaf senescence and decreased activity of the antioxidant defense system ([Djanaguiraman and Prasad 2010](#_ENREF_127)).

Cultivars with larger root length densities and deeper rooting systems have been found to be more tolerant to drought stress conditions in soybean ([Hudak and Patterson 1996](#_ENREF_224); [Sloane et al. 1990](#_ENREF_456)). Plants with deeper rooting systems will have longer periods of access to water on a declining profile. Extensive root growth and distribution of roots will help explore larger soil volumes and thus may provide a plant with greater access to water and nutrients under drought conditions, and so deeper and more vigorous root systems help extract enough water under these environmental conditions.

A study evaluating drought avoidance mechanisms among soybean lines exhibiting genetic diversity in root system developmental plasticity in response to water stress identified candidate genes and regulatory pathways associated with the root growth and plasticity ([Yamaguchi et al. 2010](#_ENREF_543)). A major finding was the increased abundance of the key enzymes in the isoflavone biosynthesis pathway and their correlation with a substantial increase in isoflavonoid content at the primary root tip region, suggesting possible contribution to growth maintenance.

The slow wilting trait in soybean confers drought tolerance by helping the plant conserve water in the soil. Even though this trait has been found in several soybean lines, the mechanisms controlling slow wilting remain unknown. A study by ([Abdel-Haleem et al. 2012](#_ENREF_2)) detected a locus on chromosome 12 (Gm12) from PI 416937 explaining 27% of the variation in canopy wilting which could provide an efficient means to augment field-oriented development of drought-tolerant soybean cultivars.

### 3.3.3.2 Peanut (Ground nut)

Like other crop plants, drought and heat stress will effect stomatal conductance, transpiration rate and decrease photosynthetic rate in peanut. Peg elongation, which is turgor dependent, is delayed due to drought stress ([Boote and Ketring 1990](#_ENREF_57)). Pegs fail to penetrate effectively into dry soil, especially in crusted soils. Often, within 4 days of withholding water, the soil surface becomes too dry for peg penetration. Pod and kernel development are progressively inhibited by drought stress due to insufficient plant turgor and lack of assimilates. Yield reductions are greatest when stress is experienced during the period between pegging and pod development, and lowest with stress occurs between pod development and maturation ([Patel and Golakiya 1988](#_ENREF_356)).

The optimum air temperature for growth and development of groundnut is between 25 °C and 30°C ([Williams and Boote 1995](#_ENREF_535)). As in other crops, the reproductive phase of groundnut is more sensitive to heat stress than the vegetative phase ([Cox 1979](#_ENREF_111); [Ketring 1984](#_ENREF_258)), and studies have shown a reduction of up to 33% in the number of pegs and pods with exposure to a temperature of 35°C ([Ketring 1984](#_ENREF_258)), and heat stress will cause pollen sterility at flowering and loss of seed-set ([Prasad et al. 2000](#_ENREF_362)).

### 3.3.3.3 Canola

Canola demonstrates a similar pattern of stress response to other crops in that stressed at earlier growth areas stages exhibit recovery, whereas stress during pod development severely reduces most of the yield components ([Gan et al. 2004](#_ENREF_171)) with the highest yield reduction being when water stress occurred at flowering and then at pod developmental stages ([Sinaki et al. 2007](#_ENREF_448)). The flowering stage and pod formation stages are the most sensitive to drought. Studies have shown a reduction of 20 – 37% in grain yield and 29 – 44% in oil yield respectively ([Ahmadi and Bahrani 2009](#_ENREF_5)). Yield reduction is due to pollen sterility, embryo abortion and pod dropping during heat stress. Drought stress will result in a reduction in photosynthetic rate due to reduced stomatal conductance and transpiration. The down-regulation of farnesyltransferase beta (FTB) or farnesyltransferase alpha (FTA) in canola has been shown to confer drought tolerance to plants growing in the field ([Wang et al. 2005](#_ENREF_524); [Wang et al. 2009](#_ENREF_525)).

### 3.3.4 Rice

Rainfed rice areas occupy 11% of the global rice-growing area (IRRI, 2001). Global yield loss estimates reach 18 million tonnes or 4% of total rice production or US$ 3.6 billion nearly two decades ago ([Evenson et al. 1996](#_ENREF_145)). Currently, yield losses have been reported to be around 70 to 80 million tonnes in China only ([Luo 2010](#_ENREF_305)) and could easily reach 100 million tonnes worldwide. Considering an annual consumption of 100 kg/person (conservative estimate for Asian countries), losses by drought prevent the feeding of 1 billion people annually. Therefore, the targeting of traits that can improve drought tolerance is among the major goals of rice breeders. The Green Revolution has had a higher impact on irrigated rather than on rainfed rice due to six major reasons as pointed out by ([Fukai et al. 1999](#_ENREF_167)) (1) the coupling of photosynthesis and transpiration processes when matter is limited, hence the difficulty in increasing dry matter production and yield; (2) the interaction between nutrient availability and water stress, with even mild soil water deficits reducing availability; (3) incomplete understanding of the mechanisms of drought resistance; (4) the importance of phenology and yield potential as components of yield under limited water that override the effectiveness of drought-resistance characteristics; (5) large genotype-by-environment interaction (GxE) for yield, causing inconsistency in yield performance in different environments, and hence needing more testing in different locations and years; and (6) the different types of drought, and the different traits that may therefore be required for each drought type. High throughput phenotyping methods should also help to accelerate the development and release of drought resistant cultivars ([O’Toole 2004](#_ENREF_350)).

The first linkage map in rice was constructed by ([McCouch et al. 1988](#_ENREF_324)). Since then, several enriched maps have been developed using different sets of molecular markers ([Causse et al. 1994](#_ENREF_87); [McCouch et al. 2002](#_ENREF_325); [Wu et al. 2002](#_ENREF_537)). Following the publication of the first maps, QTL studies have been developed, focusing on different traits, among them drought tolerance. One has to consider the different types of droughts affecting rainfed rice, i.e., upland or lowland. Upland rice can experience mild drought stress throughout the season and occasionally a more severe stress between major rainfall events. Lowland rice, on the other hand, usually experiences some water accumulation, and drought can occur between major rainfall events when water disappears. Also, the severity and timing of the drought in relation to the stage of the crop should be considered. One typical case is terminal drought, which develops towards the end of the growing season, but can start sometimes before flowering. It is common in Northeastern Thailand and Southern India when monsoon rains cease before rice maturity and has a major impact on yield ([Fukai et al. 1999](#_ENREF_167); [Pandey et al. 2005](#_ENREF_354)).

At least 15 different populations have been mapped for drought tolerance in rice ([Kamoshita et al. 2008](#_ENREF_255)). Most of the mapping populations are derived from crosses japonica x indica types. Most of the studies point out that favorable drought related alleles come from japonica lines. Studies of the population CT9993 x IR6266, in which both parents are well adapted to rainfed rice-growing environments, 34 genomic regions were found with multiple QTLs for putative drought-resistance traits. From these, 4 regions were identified as key for yield or yield components under stress, and drought-tolerant component traits were identified across populations with interval lengths of 35-64 cM. The first important region resides in the interval R2417-RZ909 (64 cM) on chromosome 1([Kamoshita et al. 2008](#_ENREF_255)). This region has frequently been associated with grain yield, drought-resistance traits, and plant type traits ([Zhang et al. 2001a](#_ENREF_555)). These include QTLs for cell membrane stability ([Tripathy et al. 2000](#_ENREF_493)); osmotic adjustment ([Lilley et al. 1996](#_ENREF_295); [Robin et al. 2003](#_ENREF_400)), and many root traits ([Hemamalini et al. 2000](#_ENREF_214); [Nguyen et al. 2004](#_ENREF_348); [Price et al. 2002a](#_ENREF_366); [Yue et al. 2006](#_ENREF_554); [Zheng et al. 2003](#_ENREF_559)). Under well watered control conditions, QTLs for deep and thick root traits co-localized in this region ([Ali et al. 2000](#_ENREF_10); [Courtois et al. 2003](#_ENREF_110); [Kamoshita et al. 2002](#_ENREF_256); [Li et al. 2005](#_ENREF_293); [Ray et al. 1996](#_ENREF_377); [Yadav et al. 1997](#_ENREF_541)). Other QTLs co-localizing in this region are those controlling leaf water potential (LWP) and relative water content (RWC), leaf rolling and leaf drying ([Kamoshita et al. 2008](#_ENREF_255)), and integrated trait QTLs, such as delay in flowering time, panicle exertion rate, DRI, yield components and grain yield have been mapped to this region ([Lafitte et al. 2004](#_ENREF_277)); ([Kumar et al. 2007](#_ENREF_276); [Yue et al. 2005](#_ENREF_553)).

Interestingly, this genomic region contains sd-1, a major gene that controls semi-dwarfism that is widely used by IRRI because of its strong association with harvest index and responsiveness to fertilizer ([Courtois et al. 1995](#_ENREF_108)). In silico analyses of this region have indicated 175 genes, with 16 candidates for drought response improvement ([Xu et al. 2005](#_ENREF_538)). Another important genomic region associated with drought response is located on Chromosome 4, in the interval RG939-RG620 (36 cM), mapped on the population CT9993/IR62266 ([Babu et al. 2003](#_ENREF_30)) under drought stress. This region is especially rich for root trait QTLs ([Boopathi et al. 2005](#_ENREF_56); [Champoux et al. 1995](#_ENREF_88); [Hemamalini et al. 2000](#_ENREF_214); [Kamoshita et al. 2002](#_ENREF_256); [Nguyen et al. 2004](#_ENREF_348); [Price et al. 2002a](#_ENREF_366); [Yue et al. 2006](#_ENREF_554); [Zhang et al. 2001b](#_ENREF_557); [Zheng et al. 2000](#_ENREF_560)) under well-watered and drought conditions. The co-location of QTLs for root traits and yield under stress have been observed in this region, probably because both parents of this population are medium to tall height and well adapted to rainfed rice ecosystems.

A third region important for drought QTLs is located on chromosome 8 in the interval RG978-RG598 (54 cM). This region contains QTLs for plant water status, grain yield, cell membrane stability, osmotic adjustment, leaf EW, rate of non-stomatal water loss and deep and thick root traits ([Boopathi et al. 2005](#_ENREF_56); [Champoux et al. 1995](#_ENREF_88); [Hemamalini et al. 2000](#_ENREF_214); [Kamoshita et al. 2002](#_ENREF_256); [Li et al. 2005](#_ENREF_293); [Lilley et al. 1996](#_ENREF_295); [Nguyen et al. 2004](#_ENREF_348); [Price et al. 2002b](#_ENREF_367); [Ray et al. 1996](#_ENREF_377); [Robin et al. 2003](#_ENREF_400); [Tripathy et al. 2000](#_ENREF_493); [Yadav et al. 1997](#_ENREF_541); [Zheng et al. 2000](#_ENREF_560)). The fourth important region for drought is in Chromosome 9, which is characterized by being rich in QTLs for root traits, but also shows association with plant water status and grain yield. This region also contains QTLs for deep and thick root traits, cell membrane stability, plant water status, leaf rolling and leaf drying, biomass, number of grains per panicle, relative spikelet fertility, and delay in flowering time ([Babu et al. 2003](#_ENREF_30); [Boopathi et al. 2005](#_ENREF_56); [Champoux et al. 1995](#_ENREF_88); [Courtois et al. 2000](#_ENREF_109); [Courtois et al. 2003](#_ENREF_110) ; [Gomez et al. 2005](#_ENREF_192); [Hemamalini et al. 2000](#_ENREF_214); [Jearakongman 2005](#_ENREF_248); [Kamoshita et al. 2002](#_ENREF_256); [Lafitte et al. 2004](#_ENREF_277); [Lanceras et al. 2004](#_ENREF_281); [Li et al. 2005](#_ENREF_293); [Nguyen et al. 2004](#_ENREF_348); [Price et al. 2002a](#_ENREF_366); [Price et al. 2002b](#_ENREF_367); [Robin et al. 2003](#_ENREF_400); [Tripathy et al. 2000](#_ENREF_493); [Xu et al. 2005](#_ENREF_538); [Yadav et al. 1997](#_ENREF_541); [Yue et al. 2006](#_ENREF_554); [Zhang et al. 2001a](#_ENREF_555); [Zheng et al. 2003](#_ENREF_559)).

There are, therefore, four regions consistently associated with drought response in rice. One frequently argues about the consistency of QTLs and their GxE interaction. Nevertheless, these four regions have stood above the average and should be part of a routine marker assisted breeding program for any drought concerned rice breeder. Current efforts in China have shown that WDR (water saving drought resistance) has been commercialized in two types: conventional varieties, such as Zhonghan 3, Huhan 3, Huhan 15, Handao 297, Zhonghan 209, and hybrid combinations, such as Hanyou 2 and Hanyou 3. Although improved performance under drought conditions can be achieved with these genotypes in low-middle-yielding fields, they still need to be improved for high-yield paddy fields in order to be competitive with top genotypes ([Luo 2010](#_ENREF_305)).

## 3.4 Cold Tolerance

*Mike Humphrey, Albert Abbott*

Winter-hardiness is the outcome of a seasonal shift between growth, quiescence, and assimilate storage in response to a cool temperate climate, and its level of effectiveness will vary on location. For example, a winter hardy plant in a maritime environment will not necessarily reproduce the same effect if transferred to a continental climate. The trait genetics may be further complicated in certain crops such as the outbreeding forage grasses of the *Lolium-Festuca* complex where the potential of a plant genome for cold-tolerance expression may in certain cases not be fully achieved ([Rapacz et al. 2005](#_ENREF_375)). In general, a tolerance to freezing-temperatures is the most important component for winter-survival, but also of considerable importance is the capability to withstand combinations of stresses due to desiccation, wind, ice-encasement, heaving, low light, snow cover, winter pathogens, and fluctuating temperatures, the relative importance of each depending on location. Resistance to desiccation through the maintenance of the integrity of cell membranes and retention of cellular water is essential, and it is unsurprising that the same genetic response to the onset of freezing temperatures is often found with drought or salinity stress ([Seki et al. 2002](#_ENREF_427)). Indeed, cold acclimation (CA) can frequently improve tolerance to a mild drought stress and *vice-versa* ([Thomas and James 1993](#_ENREF_481)). Several studies have established that major genes, or gene clusters, involved in the control of frost and drought tolerance are located on a region of the long arm of Triticeae group 5 chromosomes. Traits such as winter hardiness ([Hayes et al. 1993](#_ENREF_211); [Pan et al. 1994](#_ENREF_353)), vernalization response and frost tolerance ([Galiba et al. 1995](#_ENREF_168); [Sutka and Snape 1989](#_ENREF_472)) ([Laurie et al. 1995](#_ENREF_287)) , cold- and drought induced ABA (abscisic acid) production ([Galiba et al. 1993](#_ENREF_170); [Quarrie et al. 1997](#_ENREF_368)) , and osmotic stress-tolerance ([Galiba et al. 1992](#_ENREF_169)), have all been mapped to this region. Across the grasses and cereals, this chromosome region has been a major focus for genome studies and for crop improvement. It may well be as consequence of climate change from the perspective of future crop design that in many locations where winter temperatures are on the increase and favoring continued plant growth, and where this is accompanied by a decrease in winter rainfall, that unseasonal winter droughts will ensue, which will require a new breeding strategy for common stress-tolerance to both stress factors.

Development of winter hardiness requires exposure of plants to low, non-freezing temperatures, typically 0-10°C, and a shortened photoperiod. The majority of research studies for crop winter survival have focused on the key stage of CA through natural breeding, often employing wild-crop relatives ([Humphreys et al. 2007](#_ENREF_225)), currently the only crop improvement method available for many nations, or through genetic modification technologies ([Sanghera et al. 2011](#_ENREF_413)). Efforts have concentrated on inclusion of functional genes necessary for the induction of appropriate physiological mechanisms required to withstand exposure to freezing temperatures. For all crops to survive the winter, plants must engage mechanisms whereby sensitive tissues can avoid freezing or undergo cold hardening compatible with the normal variations of the local climate; co-ordinate the induction of the tolerance at the appropriate time; maintain adequate tolerance during times of risk; and properly time the loss of tolerance and resumption of growth when the risk of freezing has passed ([Guy 1990](#_ENREF_199)). For some locations and latitudes, should winter temperatures continue to rise, it may be necessary for breeding efforts to concentrate more on adaptation to short day-length rather than to a low temperature, both to achieve winter-hardiness, and also to avoid the normal vernalization requirement necessary for flower induction, an essential prerequisite for seed production and a crop yield.

Many physiological and biochemical changes occur during CA, including: slowed or arrested growth; reduced tissue water content; altered cell pH; protoplasm viscosity and altered photosynthetic pigments; reduced ATP levels ([Levitt 1980](#_ENREF_292)); transient increases in ABA ([Chen et al. 1983](#_ENREF_89)); changes in membrane lipids (Uemura and Steponkus 1994) ([Uemura and Steponkus 1994](#_ENREF_504)), accumulation of compatible solutes including proline, betaine, polyols and soluble sugars; and accumulation of antioxidants ([Tao et al. 1998](#_ENREF_475)). Considerable resources are necessary to sustain and protect plant metabolism under low temperature stress, and for recovery subsequent to the onset of more benign growth conditions. CA and freezing tolerance are the result of a complex interaction between low temperature, light, and photosystem II (PSII) excitation pressure. At low temperatures, plants have two principal difficulties. The first is maintenance of cell membranes in a fluid state. This can be compromised further by ice formation ([Thomashow 1999](#_ENREF_482)). The second relates to the thermo-dependency of photosynthetic electron transport and carbon fixation, which are slowed at low temperature ([Guy 1990](#_ENREF_199)). The PSII reaction center is the key site for the regulation of light energy, and also the main site of photoinhibitory damage. The redox state of PSII reflects fluctuations in the photosynthetic energy balance and so acts as a sensor of any environmental stresses that disturb that balance. Alien gene transfers have enhanced PS11 adaptation to freezing temperatures and have led to improved CA efficiency and to freezing-tolerance ([Humphreys et al. 2007](#_ENREF_225)).

The C-repeat binding factor (CBF) genes are key regulators of the expression of COR (cold regulated genes), which are conserved among diverse plant lineages such as eudicots and monocots. The CBF transcription factors recognize the cis-acting CRT/DRE (C-repeat/dehydration responsive element) element in the regulatory regions of COR genes ([Stockinger et al. 1997](#_ENREF_469)). Twenty CBF genes have been identified in barley (*Hordeum vulgare*), of which 11 are found in two tight tandem clusters on the long arm of chromosome 5H in the same region as the *Fr-H2* frost tolerance locus (([Skinner et al. 2006](#_ENREF_454)) ([Francia et al. 2007](#_ENREF_164)). An orthologous genomic region in *Triticum monococcum* contains similar CBF gene clusters located at the *Fr-Am2* frost tolerance QTL ([Miller et al. 2006](#_ENREF_330); [Vagujfalvi et al. 2003](#_ENREF_509)). In *Lolium perenne,* ([Tamura and Yamada 2007](#_ENREF_473)) mapped four *LpCBF* genes in a short interval on *Lolium*LG5, most likely syntenic with regions on *Triticeae* group 5 chromosomes. Studies of the organization of the CBF cluster in barley and wheat have shown that the number of CBF genes at the *Fr-H2/Fr-A1* locus may vary among cultivars with winter forms having a higher copy number of some CBFs ([Francia et al. 2007](#_ENREF_164)). ([Knox et al. 2010](#_ENREF_267)) . The co-segregation of the CBF gene clusters with the barley *Fr-H2* and wheat *Fr-Am2* frost tolerance loci, their role in cold acclimation ([Stockinger et al. 1997](#_ENREF_469))., and the association of transcript levels of CBF genes with frost tolerance loci ([Vagujfalvi et al. 2003](#_ENREF_509)) , makes them obvious candidates for one of the two major frost tolerance QTLs on Triticeae group 5 chromosomes. The locations of two frost tolerance/winter survival QTLs on the chromosome 5F of the forage grass *Festuca pratensis* correspond most likely to the *Fr-A1* and *Fr-A2* loci on wheat homoeologous group 5A chromosomes. One of these QTLs (*QFt5F-2/QWs5F-1*) has *FpCBF6* as a candidate gene shown to be rapidly up-regulated during CA ([Alm et al. 2011](#_ENREF_11)).

Using a targeted approach of achieving understanding of key regulatory mechanisms through crops of common ancestry, and using conserved genome regions and synteny, knowledge achieved through studies made in fully-sequenced model crops and organisms such as rice, *Brachypodium,* or *Arabidopsis* may be used in crop genome studies where researchers lack access to equivalent resources. A similar approach may be applied to the photoperiodic response where Triticeae group 1, 2, and 7 chromosomes have known genes and QTLs for photoperiodic response ([Bezant et al. 1996](#_ENREF_42); [Hayes et al. 1993](#_ENREF_211); [Laurie et al. 1995](#_ENREF_287); [Law et al. 1978](#_ENREF_288); [Pan et al. 1994](#_ENREF_353); [Scarth and Law 1984](#_ENREF_422); [Sourdille et al. 2000](#_ENREF_459); [Welsh et al. 1973](#_ENREF_532)) influencing adaptation and survival and which may be sought in other crop species.

## 3.5 Heat Stress Tolerance

*Anthony Hall*

Temperatures are projected to progressively increase several degrees C during this century. Many crops are currently grown in places where high temperatures are already reducing productivity. The few field studies that have been conducted indicate that increases in temperature can reduce grain yield of some cereals and grain legumes by from 4 to 14% per degree Celsius increase in temperature ([Hall and Ziska 2000](#_ENREF_203)). Consequently, the projected increases in temperature could substantially decrease productivity of these crops.

Current projections indicate that both day and night temperatures are likely to increase during this century. From the few definitive studies that have been conducted, increases in late night and early morning temperatures were more damaging than increases in day temperature. Pollen development and subsequent fertilization are particularly sensitive to high night temperature ([Hall 2004](#_ENREF_201)). Floral bud development and extent of flowering are also impacted by high temperatures. Controlled-environment studies demonstrated that the elevated atmospheric carbon dioxide concentrations expected during this century may not enable plants to overcome their sensitivity to high night temperature during reproductive development ([Hall 2011](#_ENREF_202)). This is consistent with the hypothesis that sensitivity to heat during pollen development is not influenced by the photosynthetic source strength. Consequently, substantial emphasis should be given to breeding for heat tolerance during reproductive development in the many crop species that could benefit from this trait.

In a few cases, annual crop plants have been bred that can tolerate high temperatures during reproductive development ([Hall 1992](#_ENREF_204)). This was performed by screening germplasm collections for heat tolerance during reproductive development and crossing the few tolerant accessions that were discovered with current cultivars. Progeny were selected with the ability to produce flowers and viable pollen, and set fruit and/or seed over several generations in appropriate hot field or glasshouse environments ([www.plantstress.com](http://www.plantstress.com)). Progeny were also selected for desirable agronomic traits. In cases where the heat-tolerant accession had few of the required agronomic traits, it was necessary to backcross to current cultivars one or more times to accumulate these desirable traits. Ideally, heat-resistant cultivars should not only have higher grain yields in hot environments but also similar grain yields as current cultivars in cooler environments.

Public plant breeding programs have developed heat-resistant cultivars of cowpea, common bean, tomato and Pima cotton that are more productive in hot environments than standard cultivars. Commercial plant breeding companies rarely divulge their methods, but from the available heat-resistant commercial cultivars it is clear they have had some success in breeding for heat tolerance during reproductive development in tomato and upland cotton.

In the past, very few public or commercial plant breeding programs gave any emphasis to breeding heat-resistant cultivars. For crops that are sensitive to high temperatures during reproductive development, including rice, sorghum, cowpea, common bean, peanut, tomato and pepper, but likely many more crop species, the way forward is for more plant breeding programs to give greater emphasis to breeding for heat tolerance during flowering.

Selecting for a series of reproductive traits such as the ability to produce flowers and viable pollen, and extent of anthesis and fruit and/or seed set, has taken several years in those cases that have been reported. The few genetic studies that have been reported indicate that major genes may be involved in conferring tolerance to heat during early floral development and fruit set. Consequently, it could be possible to develop major DNA markers for heat tolerance during reproductive development whose use could substantially increase the effectiveness of breeding for heat tolerance, and some breeding programs are pursuing this goal. Since heat stress has similar effects on reproductive development in a range of different crop species it is possible that the major genes for heat tolerance during reproductive development in these different crop species could be similar. Consequently, there could be an advantage in collaboration among researchers developing DNA markers for heat tolerance who are working with different species. Collaboration would be particularly advantageous among scientists working on the various grain legumes, because for some of these species there are relatively few comprehensive plant breeding programs in the world.

For some major crop species, breeding for heat tolerance may be more complex. For example, studies in wheat indicate that high temperatures damage pollen development and seed set, but in addition, maintenance of stomatal opening and photosynthesis have been associated with heat resistance, i.e. higher grain yield in hot environments compared with current cultivars. In this case it may be necessary to breed for both heat tolerance during reproductive development and the maintenance of the photosynthetic source of carbohydrates. Combining many traits would be difficult, but there are many large wheat breeding programs in the world, and lines can be efficiently evaluated for yield using computerized mechanization procedures. Consequently for wheat, some progress might be made in increasing heat tolerance by selecting for grain yield among large numbers of lines grown in hot commercial production environments.

There is variation in the potential contributions that molecular studies might make to the genetic engineering of heat tolerance. Substantial funds have been devoted to studies of heat-shock proteins, but to-date there is virtually no evidence that this research has produced any genetic material or information that is of any value to plant breeders. In contrast, there has been insufficient research performed on apomictic breeding systems, yet they could substantially enhance heat tolerance during flowering and have additional benefits ([Jefferson 1993](#_ENREF_249)).

Reproductive processes such as pollen production and pollination are extremely sensitive to heat as well as other stresses including chilling and drought. Crop plants with an appropriate type of apomixis would be able to produce viable seed from maternal tissue without requiring either meiosis of the embryo mother cell or pollen production and pollination of the embryo and the endosperm. Sex would still be needed to permit the continual breeding of improved cultivars. This could be achieved by using facultative (switchable) apomixis systems, where the default state is apomyctic, and the breeder has methods to switch the sexual state on and off. For example, by using specific chemical sprays.

Apomictic breeding systems could have several advantages in addition to conferring tolerance to stresses that damage pollination. Apomixis would fix hybridity such that F1 hybrids would have true breeding seed. This would make possible the use of hybrid vigor in crops, such as wheat, rice and cowpea, where it is either difficult or not economically possible to exploit with current methods. Farmers could reuse this type of seed which would provide a significant advantage to poor farmers, but be of little interest to commercial plant breeding companies. Crops propagated vegetatively, such as most Irish potatoes and banana cultivars, would benefit from having apomictic cultivars because they could be propagated by seed avoiding major problems with disease transmission. Breeding programs would be accelerated by using apomyctic lines because they would confer the ability to fix heterozygous genotypes.

Many different plant species have some of the genes needed to develop facultative apomictic breeding systems in crop plants. Through genetic engineering it may be possible to create and transfer into crop cultivars the “cassette” of genes needed for facultative apomixis. This could be an extremely difficult task, but should be pursued by public research programs because it has the potential to revolutionize plant breeding and crop production.

Overall conclusions are that heat-resistant cultivars are needed now and will be more important in the future. Greater emphasis should be given to breeding for heat tolerance during flowering, the development of DNA markers for heat tolerance during flowering, and the development of apomictic breeding systems in crop plants.

## 3.6 Flooding and Submergence Tolerance

*Abdelbagi M. Ismail*

Global rainfall is expected to increase with global warming, causing more floods in the tropics as a consequence of increased heat waves, intensity of tropical storms, precipitation extremes, and sea-level rise ([Coumou and Rahmstorf 2012](#_ENREF_107)). Impacts of these changes on land use activities in the tropics have recently been witnessed in highly vulnerable areas, as in some low lying tropical deltas in Vietnam, Bangladesh, Burma and other countries. These deltas provide 30% to 70% of the national rice production in their respective countries, and any changes in flooding incidences and intensities will have substantial impacts on their food security ([Mackill et al. 2012](#_ENREF_311); [Wassmann et al. 2009b](#_ENREF_528)). Currently, floods are estimated to cost Asia alone more than US$1 billion in rice losses; and the impacts are probably worse for upland crops because they are more sensitive. Substantial efforts are therefore required to develop effective adaptation measures to halt further decline in crop productivity.

Waterlogging is a major problem for cereal production worldwide, as in sodic soils, soils affected by seepage from irrigation canals, and excess wetting due to rainfall or floods, especially if it rains after irrigation. Genetic diversity in waterlogging tolerance was reported in various crops, including wheat, barley, maize and oats ([Setter and Waters 2003](#_ENREF_436)), and diverse mechanisms have been associated with tolerance, categorized by ([Setter and Waters 2003](#_ENREF_436)) as associated with phenology and morphology; nutrition balances; metabolism, including anaerobic catabolism and anoxia tolerance; and post anoxia damage and recovery. Fortunately, the heritability of waterlogging tolerance seems relatively high in most crops, despite the complexity of the traits involved in tolerance, suggesting opportunities for genetic improvement. Flooding at any stage can severely damage all crops, except for some rice varieties, which thrive in flooded soils, thanks to an extensive aeration system through the well-developed aerenchyma tissue. However, rice is sensitive when partially or completely inundated for extended periods. Because of its adaptation to such semi-aquatic conditions, rice has been extensively used as a model crop in studies of traits associated with tolerance of flooding and low oxygen stress.

Early floods can lead to poor crop establishment, and transient complete submergence during the vegetative stage causes high mortality in rice. Even partial floods can be devastating if they persist for long durations, as in stagnant floods and deep water areas, where only landraces with certain adaptive traits can survive ([Mackill et al. 2012](#_ENREF_311)). Tolerance of flooding during germination and early seedling growth is essential for direct seeding, both in rainfed and irrigated areas, where even waterlogging is sufficient to cause considerable reduction in crop stand in all cereals because of the high sensitivity to hypoxia at this stage ([Angaji et al. 2010](#_ENREF_21); [Ismail et al. 2009](#_ENREF_234)). Substantial genetic variation was recently observed in the ability to germinate and establish in flooded soil. Tolerant genotypes are capable of catabolizing starch reserves in seeds germinating under hypoxia into simple sugars, and use them as substrates to generate energy via anaerobic pathways for the growing embryos ([Angaji et al. 2010](#_ENREF_21); [Ismail et al. 2009](#_ENREF_234); [Miro and Ismail 2013](#_ENREF_332)). Several QTLs originating from few landraces were identified, two of them with large-effects; on chromosome 9 (*qAG-9-2*; ([Angaji et al. 2010](#_ENREF_21)). and chromosome 7 (*qAG-7-1*; ([Septiningsih et al. 2013](#_ENREF_429)). These QTLs are being targeted for cloning and for use through marker-assisted breeding.

Transient flash floods that result in complete inundation of rice fields can occur any time, from crop establishment to harvest, and for durations of few days to over 2 weeks, often encountered more than once during the season in over 20 million ha in Asia each year ([Mackill et al. 2012](#_ENREF_311)). Recently, tolerant varieties carrying the *SUB1* locus became available. *SUB1* is a major QTL on chromosome 9 that has been cloned and the gene responsible for tolerance identified as *SUB1A-1*, an Ethylene Responsive Factor (ERF) gene that suppresses ethylene mediated responses under submergence, limiting excessive elongation and halting chlorophyll degradation. Both processes are essential to prevent carbohydrate starvation of the submerged plants. These varieties can survive 4 to 18 days of complete submergence, with yield benefits of 1 to over 3.5 t ha-1 (depending on flood duration and floodwater condition), compared to current farmers’ varieties, and without any undesirable effects on the features of the original varieties ([Bailey-Serres et al. 2010](#_ENREF_31); [Ismail et al. 2013](#_ENREF_236); [Mackill et al. 2012](#_ENREF_311); [Singh et al. 2009](#_ENREF_451)). Additional genes are being targeted to be combined with *SUB1* for higher tolerance.

Rice accessions with reasonable tolerance of stagnant floods (30-50 cm) were recently identified and work is in progress to unravel the genetics and physiology of tolerance. Numerous traits seem to be needed, including ability to tiller underwater; elongate sufficiently to keep pace with rising water; develop a sturdy stem to avoid lodging; and maintain sufficient leaf area above water for photosynthesis. Tolerant lines should also have large fertile panicles ([Singh et al. 2011](#_ENREF_452)). Deep water rice (>50 cm to few meters), on the other hand, has been studied extensively as a model type for shoot elongation in response to flooding. Recently, a large effect QTL on chromosome 12 was recognized as the major determinant of rapid internode elongation and was cloned, with two functional genes identified at this locus, called *SNORKEL1* and *SNORKEL2*. Like *SUB1A*, both are ERF genes, but control elongation in a manner opposite to that of *SUB1* ([Hattori et al. 2009](#_ENREF_210); [Xu et al. 2013](#_ENREF_540)). The availability of these genes will facilitate developing high yielding varieties for deepwater areas, and combining them with *SUB1* and with tolerance during germination and stagnant flooding could potentially provide more resilient varieties for current and future flood-affected areas. The progress made in rice could potentially be exploited to improve flood tolerance of other crop species.

## 3.7 Salinity Tolerance

*Abdelbagi M. Ismail*

Salt stress is a significant constraint for crop production in both inland and coastal areas, and is contributing to the loss of arable land in many countries. This is because of progressive salt accumulation resulting from excessive irrigation with poor quality water, coupled with poor or improper drainage, a fact likely to be aggravated by sea level rises in coastal areas and by global warming elsewhere ([Wassmann et al. 2009a](#_ENREF_527)). Several studies characterized responses mediated by salt stress in different plant species and highlighted the complexity of the mechanisms involved ([Ismail et al. 2007](#_ENREF_235)) ([Munns and Tester 2008](#_ENREF_342)). Rice, wheat and barley are among the most studied cereal crops, and in most cases, salt exclusion from active leaves was identified as a common mechanism, followed by others such as tolerance of high salt accumulation in leaf tissue.

Cultivated rice species are generally considered sensitive to salt stress, yet a handful of lines are known to be tolerant, and a small number of these have been used extensively as donors in breeding programs. However, these donors use many of the same physiological mechanisms and genes to confer tolerance. Generally, salt tolerance in rice varies with the stage of development, being relatively more tolerant during germination, active tillering and grain filling but most sensitive during early seedling stage and then during reproductive stages, and with weak association between the degree of tolerance at the two most sensitive stages. An inverse relation between shoot Na+ concentration and plant survival, growth, and grain yield is common in rice and other cereals ([Moradi and Ismail 2007](#_ENREF_337)) ([Ismail et al. 2007](#_ENREF_235)). Other traits associated with salt tolerance include sequestering Na+ in older leaves, leaf sheaths, and roots; maintenance of mineral nutrient homeostasis especially K+ and Ca2+; high selectivity for K+ and/or Ca2+ uptake over that of Na+; control over reactive oxygen species; accumulation of compatible solutes; and maintenance of photosynthetic carbon fixation. The importance of the apoplastic bypass flow in delivering Na+ to the xylem, thus reducing leaf Na+ concentration and improving tolerance, has also been reported ([Krishnamurthy et al. 2011](#_ENREF_273)). During the reproductive stage, tolerant genotypes strongly exclude salt from flag leaves and developing panicles. This complexity of tolerance highlights the need for combining useful traits, especially at sensitive stages, to develop varieties with sufficient tolerance for use by farmers. This can effectively be accomplished using modern molecular and genomic tools to combine functional alleles of genes controlling major tolerance traits.

Recently, we observed substantial genetic variation in salinity tolerance within both the cultivated *O. sativa* and *O. glaberrima* species. The predominant mechanisms of tolerance are associated with limiting salt uptake in active leaves and young tissue, but with considerable genetic variation among tolerant genotypes in the mechanisms that control leaf Na+ concentration. In few cases, some accessions were identified that display different mechanisms, such as high tissue tolerance ([Platten et al. 2013](#_ENREF_361)). This considerable variation in tolerance strategies reflects substantial opportunities for improving salt tolerance in rice and other cereal crops through genetic manipulation.

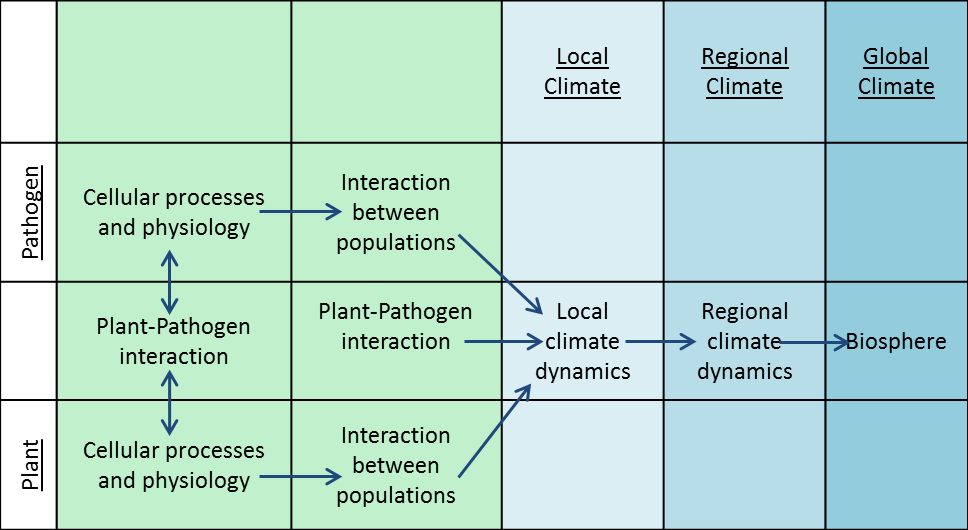
Few major loci and numerous minor ones were previously associated with various aspects of salinity tolerance. The best known for rice is *Saltol* on chromosome 1, identified in numerous studies ([Thomson et al. 2010](#_ENREF_484)), and a major gene, *OsHKT1;5* was identified at this locus ([Ren et al. 2005](#_ENREF_387)). In wheat, two members of the *HKT* gene family (including the wheat *HKT1;5* orthologue) have also been shown to co-localise with major QTLs ([Byrt et al. 2007](#_ENREF_73)). Apparently many other QTLs have been identified in rice and other cereals, and several of them are common across several mapping populations. Numerous genes have also been identified in various studies of salt stress responses, and many of them lead to improved tolerance when they are over- or under-expressed. Some even co-localize with QTL regions, but there has been no further success in using them for breeding tolerant cereal crops or in cloning additional QTLs. Current approaches involve using next generation sequencing (NGS) to target major QTLs for cloning, and to develop efficient SNP and *InDel* marker systems to manipulate these loci during marker assisted breeding (MAB).

The development of improved varieties with higher tolerance of salt stress has been a major and long-standing goal of many breeding programs. The substantial genetic diversity in tolerance of salt stress and in the mechanisms used by various crops to cope with increasing salt concentrations in soil and water, provides opportunities to enhance salt stress tolerance in cereal crops. However, this will require large investments to dissect and combine the genetic determinants of various traits. Developing such varieties that are highly tolerant of salt stress is a requisite to cope with the current worsening climatic conditions and to meet the urgent need for producing more food from marginal land and limited water resources.

## 3.8 Disease Resistance

*Jacqueline Batley*

Climate change may impact patterns of plant diseases in a complex manner, having either a positive, negative or no effect on individual plant diseases and the plant-pathogen interaction ([West et al. 2012](#_ENREF_533)). Current research suggests that climate variation will predominantly lead to increase losses from plant diseases, changes in the efficacy of current disease management strategies and in the geographical distribution of plants and their diseases. The climatic variables affecting the crop and pathogen include changes in temperature, rainfall and in the atmospheric chemical composition, predominantly elevated CO2 levels. These accelerate the reproduction time of many plant pathogens, increasing infection pressure ([Boonekamp 2012](#_ENREF_55)). For example, it has been calculated that changing climatic conditions will cause a 10-50% decrease in oilseed rape yield in the UK ([Boonekamp 2012](#_ENREF_55)). In other crop plants such as wheat, climate change may cause early anthesis, thereby increasing the probability of *Fusarium* earblight infections. Climate change may also affect the ability of plants to express resistance to pathogens. Experiments conducted by ([Huang et al. 2009](#_ENREF_223)) indicated a 45% increase in leaf lesions, when the surrounding temperature was increased by five degrees. This suggests that the expression and efficacy of *R* genes in host plants will be affected.



Interaction between plants and pathogens in relation to the climate ([Garrett et al. 2006](#_ENREF_176)).

Where both crops and their associated pathogens are affected by climatic variation, they may be influenced by different combinations of selective pressures, and each may respond to these pressures at different rates. For example, a more aggressive strain of the pathogen can easily be selected during pathogenic regeneration accelerated by climatic changes. This, combined with decreased resistance in host plants, can lead to disease epidemics ([Boonekamp 2012](#_ENREF_55)). . For strategies to be identified for the development of climate resistant crops, our understanding of the host-pest/pathogen interaction must be improved, and the different effects of climate change must be separated. In addition, both direct and indirect effects of climate change must be considered, to determine how they affect the incidence and severity of plant diseases, including in the context of other factors that influence diseases and emergence of new diseases. Changes to farm practices and introductions of exotic material fall under this category. To date, research on the impact of climate change on plant diseases has been limited, with many studies focusing on the effects of a single atmospheric constituent or meteorological variable on the host, pathogen, or the interaction of the two, under controlled conditions. Whilst this work is a valuable base to start from, the combined effects must be studied. Recent developments in experimental, simulation and modeling techniques can be utilized to understand the impact of climate change and improve the capabilities for resilient crop breeding ([Caffarra et al. 2012](#_ENREF_75)).

Recent advances in genome sequencing and genotyping assays allow for many strategies at the genomics level which can be developed to understand the impact of climate change on plant disease. The newly available genome sequences for plants and pathogens provide the resources to study their co-evolution in response to climate change. An understanding of the co-evolution of genes responsible for virulence and resistance will lead to improved plant protection strategies and provide a model to understand plant-pathogen interactions in diverse species. Whilst it is important to understand the genomics of disease resistance in crop species, and how allelic differences are altering resistance, combining this with studies of wild germplasm or germplasm collections further allows the identification of novel variants. These variants can be used for the introgression of novel resistance genes into cultivated varieties, utlising the germplasm for breeding and developing new cultivars, or creating transgenics containing the advantageous genes. Sequencing the genomes of many individuals allows alleles to be identified that have increased resistance under the predicted climate changes.

Whole-genome analysis of *R* gene families within cultivated and wild varieties of a host species, made available by genome sequencing, may not only enable the identification of novel genes, but extensive phylogenetic and evolutionary analyses may also infer the nature of *R* and *Avr* gene product interactions under different climatic conditions.

Transcriptome sequencing of both the host and pathogens can be used to identify changes in gene expression in response to different stressors. Individual plants can be studied to identify the effects of different climatic variables on infection rates. Studies at the population level are important to identify the role of plant disease in ecosystem processes and the challenge of scaling up from individual infection probabilities to epidemics and broader impacts.

High throughput genotyping of many individuals can be performed using genome sequence data on many individuals to determine the advantageous across populations. This can be performed in a number of ways, depending on the capabilities of the laboratories performing the work. For example, by using the Illumina Infinium arrays, genotyping by sequencing through skim sequencing of the genomes, or sequence capture of the genes of interest.

In conclusion, the impact of climate change on disease resistance is difficult to predict and is likely to be variable depending on the crop and local environment. However, crop disease is an important factor when considering the impact of climate change on food production and intensive studies applying advanced genomics tools will be required to help ameliorate the impact of climate change on future cropping scenarios in relation to plant disease.

## 3.9 Insect Resistance

*Mehmet Cakir*

Insects are globally widespread, and often limit crop yields. Changing climate is expected to cause longer growing seasons in temperate regions of the world and hence this will affect the adaptation ([Stoeckli et al. 2012](#_ENREF_470)) and behavior ([Ma and Ma 2012](#_ENREF_308)) of insects, which will likely force them to spread into areas where they do not currently exist. Insects carry highly adaptable virulence genes. Changing habitat, including the deployment of new resistant varieties, forces insects to develop new virulence genes to survive in a given environment, and hence form a new biotype ([Haley et al. 2004](#_ENREF_200); [Tolmay et al. 2007](#_ENREF_490)).

Insects are known to be highly adaptive to changing environmental conditions.([Alford et al. 2012](#_ENREF_8)) demonstrated that the lethal temperature for *Myzus persicae* is highly plastic, and could be altered after acclimation over one generation. They concluded that aphids are greatly affected by the changing environmental conditions. In another study, the life cycles of the aphids were found to be affected by the climate change ([Finlay and Luck 2011](#_ENREF_155)). This study found that environmental conditions could induce a change from holocyclic to anholocyclic populations, illustrating the biological plasticity of the aphids.

The effect of heat waves and interaction of aphids with parasitoids were studied by ([Gillespie et al. 2012](#_ENREF_187)). They reported that the population growth of aphids was lower under heat waves (at 32°C and 40°C daily maxima), compared to environments with periodic hot days. The development time of parasitoids was also longer under heat waves. In another study, ([Ma and Ma 2012](#_ENREF_308)) found that aphids’ heat-escape behavior was significantly influenced by brief thermal history, implying that aphids make decisions to avoid heat stress based on the combination of temperature and exposure time, and escape before they were damaged by high temperatures. Above studies show that rises in global temperature and changes in other climatic factors could affect the way insects behave, propagate and evolve.

### The Application of Advanced Genomics Resources and Allied Gene Pools (AGPs) for the Improvement of Insect Resistance

The use of resistant varieties is proposed to be the best way to manage insect pests ([Burd et al. 2006](#_ENREF_70)). Breeding efforts have been hampered by a lack of genetic diversity and the complexity of transferring resistance genes into adapted backgrounds, as in most cases, resistance genes are found in wild plant relatives and land races. In some cases, the discovery of deleterious genes closely associated with the resistance genes, such as the *Dn7* gene that is found in the 1B/1R region of wheat ([Marais et al. 1994](#_ENREF_319)), has constrained the use of resistance genes with classical breeding approaches.

Current classical backcross breeding strategies are only amenable for the transfer of single genes. Knowledge of genetic variation, coupled with the availability of genetic tools will enable backcross breeding strategies to be more effective, facilitating the transfer of more than one resistance gene into adapted backgrounds.

The use of natural variation from wild relatives of wheat was recently reviewed by ([Broekgaarden et al. 2011](#_ENREF_64)). They stated that understanding allelic variants of resistance genes in wild relatives could provide a greater understanding of resistance mechanisms, as the current knowledge of insect R gene resistance mechanisms is not clear. Recent advances in wheat, barley and rice genome sequencing are now providing new opportunities towards understanding resistance genes and mechanisms ([Feuillet et al. 2008](#_ENREF_154); [Henry 2012](#_ENREF_215)) facilitating accelerated crop improvement ([Cakir et al. 2003](#_ENREF_77)).

Durable resistance through gene-stacking is proposed to be an effective strategy for crop management. The use of wild relatives, in conjunction with the second generation sequencing technologies will allow the rapid identification and characterization of new sources of resistance against insects, and will provide opportunities for breeding new varieties with durable resistance through gene pyramiding.

The screening of subsamples from major gene bank collections for insect resistance will be a key strategy for finding new sources of resistance to combat the effects of changing climate.

Recent molecular genetics research with various insects such as Russian wheat aphid, Greenbug, Sunn pest, and Hessian fly, all shown that resistance sources were most commonly identified from wild relatives of wheat ([Cakir et al. 2009](#_ENREF_78); [El Bouhssini et al. 2009](#_ENREF_144); [Liu et al. 2001](#_ENREF_298)) and barley ([Mornhinweg et al. 2002](#_ENREF_340)), collected from Central Asia. In the long term, the use of ‘untapped’ gene bank collections should provide sufficient sources of genetic variation against highly mutable insects. Significant progress in the identification of host resistance will only be possible through unlocking resistance gene blocks from the wild relatives of major crops such as wheat, rice and barley.

Recently developed genetic and genomic tools have been very useful to discover the genic regions relevant to insect resistance in cereals. In wheat, the 7D chromosome had been shown to be one of the “hot spots” harboring resistance genes for Russian wheat aphid (RWA) ([Cakir et al. 2012](#_ENREF_79)) and Greenbug ([Azhaguvel et al. 2012](#_ENREF_29); [Liu et al. 2001](#_ENREF_298); [Valdez et al. 2012](#_ENREF_510)), and the availability of chromosome sorting technology already allowed researchers to develop chromosome specific enriched libraries ([Doležel et al. 2011](#_ENREF_129)), targeting these resistance genes ([Simková et al. 2011](#_ENREF_446)). The availability of the chromosome 7D sequence ([Berkman et al. 2011](#_ENREF_37); [Berkman et al. 2013](#_ENREF_38)) will make it possible to undertake a detailed analysis using a targeted sequencing approach from a large number of wild relatives of wheat. Analyzing sequence variants from chromosome 7D will enable the comparison of these variants with phenotypic variation among wild relatives; hence this information will lead to the identification of resistance mechanisms and new resistance sources.

Barley chromosomes 1H and 3H consistently show strong associations with RWA resistance phenotypes ([Cakir et al. 2012](#_ENREF_79); [Mittal et al. 2008](#_ENREF_334)). The availability of sequence data from these chromosomes will provide a reference map (Neils Stein, pers. comm.) for any targeted genomic sequencing, transcriptome sequencing and sequencing by genotyping strategies. Recent RNAi technology, in conjunction with DNA sequencing technologies, is used for the identification of candidate genes, with subsequent application of transgenic technologies to enhance insect resistance in plants.

In conclusion, advances with DNA sequencing technologies and the sequencing of wild plant relatives and insect genomes, coupled with advanced genomic tools, will speed up the identification of new host resistance genes and key regulatory regions of the insect virulence genes towards the development of new plant varieties with durable insect resistance.

## 3.10 Nutrient Use Efficiency

*David Lightfoot*

### Environmental Issues

Nitrogen is an essential component in cellular physiology, with only oxygen, carbon and hydrogen being more abundant ([Andrews et al. 2004](#_ENREF_20); [Marschner 1995](#_ENREF_321)). Nitrogen is present in numerous essential compounds including nucleoside phosphates and amino acids, that form the building blocks of nucleic acids and proteins, respectively. In plants, nitrogen is used in large amounts in photosynthetic pigments, defence chemicals and structural compounds. However, inorganic N is difficult to assimilate. Dinitrogen in the atmosphere is highly inert. Reduction to ammonium requires the energy of a lightning bolt, petrochemicals, or 12 ATP dephosphorylations per molecule within a nodule or other anaerobic environment. Global warming may increase the frequency of lightning storms and hence raise NO concentrations. Warmer, more stressed crops will require more nitrogen fertilizers be applied and heavy rains will increase losses due to run-off.

Warmer days will cause more of the applied ammonium fertilizers to escape from the cell as ammonia gas. Photorespiration, increased by heat stress, releases 10 fold more ammonium than is assimilated from the environment, and plants only re-assimilate ~98% of this. Consequently, a haze of ammonia gas is found floating above a photosynthetic canopy. That ammonia may be lost on the wind or returned to the plant or soil by rains or dew falls. Any improvements to these nitrogen cycles ([Carvalho et al. 2011](#_ENREF_86); [Terce-Laforgue et al. 2004](#_ENREF_478)) can have a massive positive impact on the efficiency of agriculture, reduce its carbon footprint, and over geological time scales reverse some of the anthropogenic contributors to global warming.

The assimilation of ammonium has a second major problem associated with it. Ammonia is assimilated releasing one acidic proton per molecule ([Marschner 1995](#_ENREF_321)). There is enough flux to reduce the pH of even well buffered soils to concentrations that inhibit plant growth, both directly, and by the release of toxic concentrations of micronutrients (Al and Mn in particular). Reduction within a nodule or other anaerobic environment compounds this problem by releasing two protons per ammonium produced ([Indrasumunar et al.](#_ENREF_230) ; [Indrasumunar et al. 2011](#_ENREF_231)). Soil acidification is a worldwide problem on a massive scale.

Nitrates and nitrites provide a solution to the acidification problem, as their reduction to ammonium absorbs 3-4 protons ([Marschner 1995](#_ENREF_321)). So a pH balanced fertilizer should theoretically be a 4 to one mixture of ammonium and nitrates. Nitrates and nitrites are the ions produced by those lightning bolts that provide about 10% of the worlds reduced nitrogen each year. However, they are not without costs and problems. Nitrite is highly toxic to photosynthesis and respiration, and so must be immediately reduced to ammonium. Plants produce massive amounts of nitrite reductase for this purpose. Nitrate is benign, easy to store and transport and consequently is the major form of inorganic N found in plants. However, plants still produce 10 fold more nitrate reductase than is absolutely needed for assimilation, growth and yield ([Kleinhofs et al. 1980](#_ENREF_266); [Wang et al. 2000](#_ENREF_523)). Why this is remains unclear.

The major problem with nitrates and nitrates in the environment is that they are water soluble and so are rapidly leached from soils ([David et al. 1997](#_ENREF_121); [Lee and Nielsen 1987](#_ENREF_290)). So much is lost from agricultural soils, industrial activity and human waste treatments that the world’s rivers, lakes and oceans are significantly fertilized ([Burkholder et al. 1992](#_ENREF_71); [Cherfas 1990](#_ENREF_91)). Algae are the micro-organisms that benefit the most from this fertilizer. Unfortunately, they run low on other nutrients (P,K) and so produce toxins to kill other organisms to obtain the limiting nutrients through their decomposition. In addition, they absorb much of the waters oxygen at night killing even toxin resistant aerobes. Finally they bloom, blocking the light needed for photosynthesis by submerged organisms. Millions of acres of oceans are affected.

The major problem with nitrates in the human diet is that they are metabolized to a potent carcinogen (nitrosamine) in the acid of the human stomach problems ([Dykhuizen et al. 1998](#_ENREF_135); [Mirvish 1985](#_ENREF_333); [Moller et al. 1989](#_ENREF_335); [Tannenbaum et al. 1978](#_ENREF_474)). High nitrate, and so nitrosamine amounts in human diets are associated with many different cancers as well as fertility problems. However, nitrates are naturally excreted in human and animal saliva for the purpose of producing some nitrosamines in the gut. This is because the combination of acid and nitrosamine effectively kills many human and animal pathogens. *Helicobacter pylori* is one example. This microbe causes stomach ulcers that left untreated often become cancerous. *H. pylori* is endemic and became more abundant as lifestyles became more stressful. Consequently, several epidemiological studies found diets high in nitrate to be healthy in the 1990s and beyond whereas before that they were significantly unhealthy. Clearly, then the healthiest option is a low nitrate diet and low stress lifestyle. *H. pylori* and like pathogens and the lesions they cause are better treated with drugs than nitrosamines.

Microbes in the soil take up the bulk of all applied fertilizers before the plant can ([Cabello et al. 2004](#_ENREF_74); [Garcia-Teijeiro et al. 2009](#_ENREF_174); [Trenkel 1997](#_ENREF_492)). Ammonium can be assimilated or oxidized to nitrite, nitrate, nitrous oxide or dinitrogen by microbial activities. Plants have to absorb N from microbes by force, using highly efficient enzymes, or by trade through symbiosis (reviewed by ([Indrasumunar et al.](#_ENREF_230) ; [Reid et al. 2012](#_ENREF_383)). During symbiosis, the microbes are provided with sugars in return for ammonium. The microbes may be free-living in the rhizosphere or housed in specialized structures such as nodules. Symbiotic microbes produce a variety of chemical signals to elicit the delivery of sugars from the plants, and these systems are ripe for manipulation by biotechnology approaches.

### Plant Assimilations

Because soil particles do not naturally have many N containing minerals, and because N can be readily lost from the rooting environment, N is the nutrient element that most often limits plant growth and agricultural yields ([Duvick 2005](#_ENREF_133); [Specht et al. 1999](#_ENREF_461)). As noted above, nitrogen is found in the environment in many forms and comprises about 80% of the earth’s atmosphere as triple bonded nitrogen gas (N2). However, this large fraction of N is not directly accessible by plants and must be bonded to one or more of three other essential nutrient elements including oxygen and/or hydrogen through N-fixation processes, and carbon through N-assimilation processes ([Marchner 1995](#_ENREF_320)). Plants are able to absorb a little NH3 from the atmosphere through stomata in leaves, but this is dependent upon air concentrations. The ions NO3- and NH4+ are the primary forms for uptake in by plants. The most abundant form that is available to the plant roots is NO3- and the most abundant form in leaves is NH4+. The process of nitrification by soil bacteria readily converts fertilizer NH4+ to NO3- ([Trenkel 1997](#_ENREF_492); [Vitousek et al. 1997](#_ENREF_521)). Relative nitrogen uptake is also dependent on soil conditions. Ammonium uptake is favored by a neutral pH and NO3- uptake is favored by low pH. Nitrate also does not bind to the negatively charged soil particles; therefore, it is more freely available to plant roots, especially through mass flow of soil water than is NH4+, which binds to negatively charged soil particles and so moves primarily by diffusion. As noted above, the assimilation of NH4+ by roots causes the rhizosphere to become acidic, while NO3- causes the rhizosphere to become more basic.

Nitrogen uptake and assimilation summates a series of vital processes controlling plant growth and development ([Lam et al. 2003](#_ENREF_280)). Nitrate, nitrite and ammonium uptakes (and re-uptakes following losses) occur against massive concentration gradients that require lots of energy to generate and maintain. In agriculture plant are spaced sufficiently that they have an excess of captured light energy relative to the N and C supplies. Transgenic plants over-expressing low affinity nitrate uptake transporter Nrt1 increased the constitutive but not the induced nitrate uptake ([Liu 1999](#_ENREF_297)). Equally, plants transgenic with Nrt2.1 the high affinity nitrate transporter increased nitrate influx under low N conditions ([Fraisier et al. 2000](#_ENREF_163)). Transgenic plants expressing an ammonium transporter increased NUE ([Gupta et al. 2012](#_ENREF_198)). Glutamate receptors in transgenic plants provided better growth. Equally, the uptake of short peptides had positive effects. All these transport associated phenotypes would be desirable in agricultural production systems directed toward greater efficiency and lower environmental impacts, and a stack of the three transgenes would be of interest.

Nitrate acquired in the roots can be reduced in the shoot or the root, or even stored in vacuoles in the root or shoot for later assimilation. However, nitrate must be reduced to a useable form. This occurs via a two-step process catalyzed by the enzymes nitrate reductase (NR) and nitrite reductase to form NH4+. Both enzymes are produced in massive excess compared to the flux needed through the pathway, and mutants that reduce their amounts by 90% do not have phenotypes ([Kleinhofs et al. 1980](#_ENREF_266)). Equally, some transgenic plants over-expressing NR increased nitrate reduction but were not altered in phenotype ([Crete et al. 1997](#_ENREF_115); [Curtis et al. 1999](#_ENREF_119); [Djennane et al. 2002](#_ENREF_128); [Lillo et al. 2003](#_ENREF_296)) However, two studies of NR over-expressing transgenic plants did record altered phenotypes including; increased biomass, reduced drought stress ([Ferrario-Mery et al. 1998](#_ENREF_152); [Ferrario-Mery et al. 2002](#_ENREF_153)); and improved NUE and yield during N limitation ([Loussaert et al. 2008](#_ENREF_302)). These phenotypes would be desirable in agricultural crops. The coupling of NR to photosynthesis should be possible by transformation of plants with a ferredoxin dependent NR from cyanobacteria.

The ability to fix dinitrogen is restricted to the bacterial world, but is widespread among microbes ([Ferguson and Indrasumunar 2011](#_ENREF_151)). Many different *nif*gene families exist, suggesting selection for variation has been favorable for species. The activity of nif requires an anaerobic environment, so transferring the enzymes to plants will be difficult. To date, transgenics in this field are bacterial, as in hydrogenase enhanced microbes, or if plant, they are designed to improve the chances of nodule occupancy by improved bacterial strains. Strains that are most likely to set up nodule occupancy are rarely the most efficient nitrogen fixers. Plants also often fail to maintain effective nodules through flowering and pod set. Soybean and common bean for example have senescent nodules by flowering. Some species do have indeterminate nodules and it would be a valid goal of biotechnology to transfer this trait to major legume crops.

The N acquired as NH4+ does not require reduction upon uptake into the root, thus providing some energy savings to the plant over that of the NO3- form ([Marschner 1995](#_ENREF_321)). However, it does require assimilation to avoid loss, and at high concentrations (>10 mM) toxicity to the plant. Various studies have shown that under conditions of excessive NH4+ uptake, most plant species will transport this N source to the shoot, which is more sensitive to ammonium ions ([Barker and Mills 1980](#_ENREF_32)) .

One important process to build key macromolecules in any living organism is the acquisition and utilization of inorganic forms of nitrogen during metabolism ([Lea and Miflin 2011](#_ENREF_289)). Plants use amino acids as well as their precursors and catabolic products for important metabolic activities. Various other roles of amino acids include nitrogen storage and transport and the production of a very large number of secondary compounds including structural lignin compounds, light-absorbing pigments, phenolics and plant hormones. Plants convert the available inorganic nitrogen into organic compounds through the process of ammonium assimilation which occurs in plants by two main pathways. The first and primary pathway involves a reaction with glutamate to form glutamine which is catalyzed by glutamine synthetase (GS, EC 6.3.1.2) and requires an energy source of adenosine triphosphate (ATP). There are two isoenzymes of GS based on their location in the plant, either in the cytosol (GS1) or in the root plastids or shoot chloroplasts (GS2). Expressed in germinating seeds or in the vascular bundles of roots and shoots, the cytosolic form (GS1) produces glutamine for intracellular nitrogen transport. GS2 located in root plastids produces amide nitrogen for local consumption, while GS2 in the shoot chloroplasts re-assimilates photo-respiratory ammonium ([Lam et al. 2003](#_ENREF_280)). GS1 is encoded by a set of 3-6 paralogs in different crop species, so hetero-hexamers can form. However, the Kms hardly differ. Amino acid identity between GS1 isoforms is very high and is even similar to GS2. GS2 has a short peptide extension at the C-terminus that might be involved in regulation by phosphorylation. Alleles of the GS1 and GS2 encoding genes do exist that differ in their regulation. Alleles of GS appear to underlie QTL determining NUE and yield ([Canas et al. 2009](#_ENREF_83); [Cañas et al. 2010](#_ENREF_84)). Transgenic analyses have been made of GS2 but not GS1. Among 12 studies in 9 plant species, the phenotypes reported included enhanced accumulation of N, growth under N starvation, herbicide (PPT) tolerance, leaf-soluble protein, ammonia, amino acids and chlorophyll. Some genes and constructs though decreased growth; salt, cold and drought tolerance; seed yield and amino acid content. Therefore the use of GS transgenics in agriculture will be useful and desirable but only with careful attention to regulation and expression.

The glutamine molecules produced by GS are used by a whole series of trans-aminases to produce the 20 protein amino acids and some non-protein amino acids. Cardinal among the trans-aminases is the reaction catalyzed by glutamate synthase (GOGAT, EC 1.4.14) to form glutamate. There are two common isoenzymes of GOGAT including a ferredoxin-dependent GOGAT (Fdx-GOGAT) and an NADH-dependent GOGAT (NADH-GOGAT). While both forms are plastidic, the Fdx-GOGAT enzyme is predominately found in photosynthetic organs and the NADH-GOGAT enzyme is found more in non-photosynthetic tissues such as in roots and the vascular bundles of developing leaves ([Lea and Miflin 2011](#_ENREF_289)). An NADPH dependent GOGAT can be found in certain organs and in many bacteria. Plants transgenic with the NADH dependent plant GOGAT have been reported. Phenotypes included enhanced grain filling, grain weight, total C and N content, and dry weight. Phenotypes were very similar to the benefits reported from alanine dehydrogenase and asparagine synthase suggesting the transaminases are acting on a common pathway.

The second pathway for ammonium assimilation also results in the formation of glutamate through a reversible reaction catalyzed by glutamate dehydrogenase (GDH, EC 1.4.1.2), with a lower energy requirement than GS/GOGAT. There are also at least two forms of GDH that occur in plants that include an NADH-dependent form found in mitochondria; and an NADPH-dependent form localized in the chloroplasts of photosynthetic organs. In addition, there are enzymes capable of aminating reactions that resemble GDH (Turano, personal communication). GDHs present in plants serves as a link between carbon and nitrogen metabolism due to the ability to assimilate ammonium into glutamate or deaminate glutamate into 2-oxoglutarate and ammonium. However, due to the reversibility of this reaction, the assimilatory role of GDH is severely inhibited at low concentrations of ammonium. Additionally, GDH enzymes have a low affinity for ammonium compared with GS which further limits their assimilatory effectiveness. It has been suggested that the NAD-requiring form of GDH may be involved in carbon rather than nitrogen metabolism ([Coruzzi and Bush 2001](#_ENREF_106)), with glutamate catabolism providing carbon skeletons both for the TCA cycle and energy production during carbon or energy deficit. Alternate functions for GDH have also been proposed in which it has been assigned the role of re-assimilating excess ammonium, due to the limited ability of the GS/GOGAT cycle, during specific developmental stages ([Loulakakis et al. 2002](#_ENREF_301)), such as during germination, seed set and leaf senescence ([Coruzzi and Bush 2001](#_ENREF_106); [Kisaka and Kida 2005](#_ENREF_264); [Kisaka et al. 2007](#_ENREF_265); [Nadzan et al. 2007](#_ENREF_343)).

In contrast to plant GDHs, those found in microbes are very active in the assimilation of ammonium. Plants did not have the opportunity to incorporate this type of NADPH dependent GDH because the bacterial lines that gave rise to chloroplasts do not contain gdhA genes. The few cyanobacteia with GDH activity have acquired genes by transgenesis or cellular fusions. Transgenic plants in six crop species have been produced that express *gdhA* genes from 3 microbes. Phenotypes in plants include increased biomass, water deficit tolerance, nutritional value, herbicide resistance, N assimilation, NUE, WUE, amino acid and sugar content. GDH genes used in this way are being evaluated for commercialization. One problem faced by this and the alanine dehydrogenase transgenics is a dependence on soil type for some of the beneficial effects. GDH seems to provide a growth advantage on silty–loam clay soils common in the southern mid-west of the USA. In contrast, the alanine dehydrogenase transgenics seem to work best on sandy soils. Combining the technologies or altering their regulation might provide stable beneficial effects in many soil types and locations.

A variety of other enzmes exist that are capable of aminating reactions. Each will be a candidtate for over-expression in transgenic plants. Phenylalanine ammonia lyase has been used in many transgenic plants. Equally, the enzymes of cyanide assimilations (cysteine metabolism) might be more active than previousy thought and could be manipulated. Alteration of the enzymes of haem and chlorophyll biosynthesis might be tried again. The *E. coli hemA*ghene was functional *but hemB* became insoluble in plant chloroplasts (unpublished).

In conclusion, the assimilation of inorganic nitrogen is a key process in the productivity of crop plants, and there are many steps at which metabolic improvements can be made. In future, the ability to provide active nodules to non-legumes will provide an impetus for biotechnology. In addition, combining existing transgenes and new promoters for their regulation will provide for new avenues in crop improvement.

## 3.11 CO2 Sequestration

*Leland J. Cseke and Stan D. Wullschleger*

Carbon dioxide (CO2) concentrations in the earth’s atmosphere are increasing worldwide and will likely continue to rise, thus affecting biogeochemical cycles and ultimately climate change. In today’s world, most of the anthropogenic CO2 emissions result from the combustion of fossil fuels for energy production. While there are also natural sources of CO2 emissions, the increasing demand for energy, particularly in developing countries, underlies the projected rapid increase in global atmospheric CO2 concentration. Addressing the rising demand for energy without subsequently increasing CO2 emissions requires more than merely increasing the efficiency of energy production and usage. Carbon sequestration, the process where atmospheric CO2 is captured and stored away from the global carbon cycle, is likely to be a major tool for reducing CO2 emissions that originate from fossil fuel usage.

Combined with improved land and crop management practices, researchers have been developing a fundamental understanding of the molecular and cellular processes that orchestrate the conversion of carbon captured from the atmosphere into plant biomass that can sequester the carbon for many years. The plant traits that are involved in carbon sequestration are perhaps more complex than originally anticipated, and they are intimately connected with the surrounding ecology. Consequently, a deeper understanding of the biological processes, controlled by multiple genes and proteins, as well as how these processes interact between multiple organisms is critical to our ability to successfully improve carbon sequestration in biological systems. This makes the targeting and manipulation of pertinent traits all the more challenging.

Although the post-genomics era provides a unique opportunity to identify biochemical pathways and gene regulatory networks that underlie the rate-limiting steps in carbon acquisition, transport, and fate, few studies have assessed the consequence of breeding for enhanced carbon uptake, allocation, or storage in plant systems ([Cseke et al. 2009](#_ENREF_117)). Investments in plant genomics, transcriptomics, proteomics and metabolomics promise to identify and harness new approaches to increase biomass production, and the distribution of that biomass not only to above-ground leaves and stems, but also to the roots and recalcitrant pools of soil carbon in fast-growing trees and perennial grasses grown in managed plantations ([Garten et al. 2011](#_ENREF_177); [Jansson et al. 2010](#_ENREF_247); [Zhu et al. 2010](#_ENREF_562)).

Some of the more promising research targets improvements in light-use efficiency and photosynthesis (Long et al. 2006), improvements in overcoming the constraints imposed on plant productivity by temperature and drought ([Tuberosa and Salvi 2006](#_ENREF_496)), and improvements in root growth and nutrient uptake ([Hirel et al. 2007](#_ENREF_216)). The efficiency of the plants to access and uptake soil nutrients in particular is key to their ability to capture carbon and generate biomass. An improved understanding of such processes across a range of environments will improve the chances that manipulation of specific genes and proteins will translate to enhanced input of carbon to plant biomass and subsequently to soils via shoot and root litter. Gains in carbon sequestration might in turn be realized by improving our understanding of how the chemical composition of plant litter could impact the rates and magnitudes of carbon turnover in the soil.

Thus, another encouraging approach to improving carbon sequestration is to focus on harnessing plant-microbe interactions and the role these play in shaping plant nutrient uptake, biomass production, and the storage of carbon in the soils of terrestrial ecosystems. Recent studies have shown that the interaction between plants and beneficial soil microorganisms is a key component for biogeochemical cycling in soils beneath Miscanthus ([Mao et al. 2011](#_ENREF_318)) and for biomass production following inoculation of hybrid poplar with an endophytic, growth-promoting bacterium ([Rogers et al. 2012](#_ENREF_401)). When choosing targets for increased carbon sequestration, root associated microbes, including bacteria and mycorrhizal fungi, are appealing targets for eco-engineering. Microbes are typically much more tractable than genetically engineering plants. Many tree species tend to have very long juvenile periods that inhibit breeding programs, which are dependent on sexual maturity. Also, re-planting the landscape with genetically modified plants is likely to be daunting work, requiring many years for the plants to reach maturity and fix useful amounts of carbon. Thus, engineering the subsurface microbial population by addition of selected or modified microorganisms offers a promising alternative to alter existing plant ecosystems with a more rapid impact on stored carbon.

The application of modern system biology approaches and other advanced methodologies to improve the fundamental understanding of soil microbial communities and ecology will further the potential for enhancements in carbon sequestration. Information derived from such efforts will likely lead to new land management practices and organic matter production methodologies that can optimize microbial activities for the transformation and assimilation of soil nutrients specifically to enhance carbon sequestration and alleviate the negative impacts of our growing energy requirements.

## 3.12 Greenhouse Gas Emissions

*Michael Abberton*

Plant breeding has an important part to play in climate change mitigation as well as adaptation. Key areas are reducing emissions of greenhouse gases (GHG) and enhancing carbon sequestration. Livestock grazed grasslands have considerable potential for both.

Agriculture is a significant source of greenhouse gas emissions, particularly nitrous oxide from nitrogen inputs (not only fertilisers but also animal manures) and methane from ruminant animals, manures and rice production. These are both powerful greenhouse gases in terms of warming potential, and their release from agricultural sources has increasingly come under political and media scrutiny, particularly relating to livestock systems.

With respect to arable cropping, the major focus of plant breeding activity has been increasing nitrogen use efficiency (NUE), particularly with respect to applied N fertiliser. Increased use of legumes both in rotations and intercropping is a major need and requires both plant breeding for improved legume performance and to increase our understanding of competitive and facilitatory effects between species and the transfer of fixed N.

Plant breeding has the potential to reduce GHG emissions through alterations in the diet of ruminant animals (eg. cattle, sheep). Enhancing the efficiency of protein utilisation in the rumen may reduce nitrous oxide emissions arising from animal excreta, and there is also evidence that the composition of the diet (including secondary metabolites) affects methane emissions. Successful implementation depends on both knowledge of the genetic control of key plant traits and understanding of rumen processes. There is a need for more research at this interface and for plant breeding efforts centred on considerations of the farming system in its entirety.

There is growing evidence that genotypic differences in rice (root structure and exudates) may be important in observed difference in methane emissions, and these are therefore important breeding targets. Production of nitrous oxide in the soil is essentially a microbial process but it can be affected by plants. There is now a body of work on nitrification inhibitor chemicals derived from plants (biological nitrification inhibition, BNI), including a number of studies focused on chemicals derived from the forage grass *Brachiaria humidicola.*

It can be seen that grasslands-which cover large parts of the globe-are important with respect to GHG emissions, but they also have significant mitigation potential. This is largely through their capacity for carbon (C) sequestration in soil. The restoration of degraded grasslands and improvements in grazing management can lead to major enhancements in C sequestration potential, but plant breeding approaches (e. g, root structure, litter composition) and greater use of forage and tree legumes may also be important. In general, grasslands and forages have been greatly neglected in terms of plant breeding and research efforts, yet they are of immense importance to many of the poorest people in many areas of the world that are most likely to be affected by climate change.

# 4 Socio-Political Issues for Germplasm Exchange

*Michael Blakeney, John Bryant, and Stephen Hughes*

## Commodification of Germplasm and Traditional Agricultural Knowledge

Intellectual property (IP) laws confer exclusive exploitation rights upon those products of intellectual creativity, which society deems to be useful. Among the oldest categories of IP are patent rights, which protect inventions, and among the newest categories of IP are the rights of plant breeders to protect new varieties. Both of these categories of IP are relevant to the commodification of germplasm. Most countries IP laws allow the patenting of DNA and DNA fragments where some industrial utility can be identified. However, a recent U.S. Supreme Court decision prevents the patenting of naturally occurring sequences (<http://www.supremecourt.gov/opinions/12pdf/12-398_1b7d.pdf>). The modern biotechnological revolution has enabled the engineering of desirable genetic traits from useful local species which are identified through the guidance of traditional farmers or formal on-station evaluations. These include: (i) pest control traits such as insect, virus and nematode resistance as well as herbicide tolerance; post-harvest traits such as delayed ripening of spoilage prone fruits; (ii) agronomic traits such as nitrogen fixation and utilization, restricted branching, environmental stress tolerance, male and/or seed sterility for hybrid systems; and (iii) output traits such as plant color and vitamin enrichment. At the same time the inclusion of some of these traits in a breeding program can create a new and registrable plant variety.

The immediate socio-political significance of this IP activity is that the expense of securing international patent and plant variety rights is prohibitive to all but those in affluent industrialized countries. This means in the first instance that the biological resources from traditional agricultural countries can be appropriated by those with deep pockets in industrialized countries.

In recent years, patents have been granted in relation to genes which are important in relation to those stresses imposed by climate change such as drought, salinity and disease. Current statistics indicate that 9% of such patents are held by public sector institutions, contrasting with 91% held by the private sector. As is the case with biotechnological patenting generally, proprietary biotechnologies are concentrated in a few corporations. This level of market concentration gives cause for concern to those who espouse the positive role of competition.

This has obvious implications in those developing and least developed countries which will suffer the greatest impacts from climate change. The situation is exacerbated by the pattern of patenting in the life-sciences area, where innovators are often confronted by patent thickets, cross-licensing and patent pools.

In addition to the possible adverse impacts this market concentration might have upon the vigour of competition, the market dominance of these private corporations also has an important influence upon the sort of biotechnological research which is undertaken. For example, to what extent will the dominance of private corporations in agricultural research direct that research towards Northern concerns away from Southern food priorities. It has been estimated that only 1% of the research and development budgets of multinational corporations is spent on crops that will be useful in the developing world. Almost entirely neglected by these corporations are the five most important crops of the poorest, arid countries - sorghum, millet, pigeon pea, chickpea and groundnut.

## Biopiracy

The improvement of crops to withstand climate stresses will often involve the breeding of favorable traits or the insertion of beneficial DNA. In both cases, the source of the breeding stock or of the DNA will sometimes be germplasm that has been identified by persons from traditional communities and obtained from those communities.

The unauthorized appropriation of that source material is often described as “biopiracy”. The international controversy generated by incidents of biopiracy has encouraged the discussion of methods to deal with this practice. In most cases, this will involve the establishment of a regime where prior informed consent (PIC) is obtained from the source communities and where access to germplasm is based on the equitable sharing of benefits with source communities. As ([Jonge 2009](#_ENREF_251))points out, this provision is founded on a pragmatic ethic rather than an ethic of distributive justice (fare shares for all), which is to say that it is intended to induce participation with a promise of a return rather than to match the rights assigned to those of the formal system who might exploit the material. Hence we see a clear disparity between breeder’s rights and the notion of farmer’s rights. ([Jonge 2009](#_ENREF_251)) in his in depth inquiry into the principles of fair and equitable benefit sharing, Plants Genes and Justice, highlights the difficulty of administering any system of benefit sharing which involves a material return, given the very diverse nature of the materials and embodied knowledge which might be transferred, as well as the diverse and potentially indirect benefits which might accrue

So breeder’s rights assigned under IP regimes and farmers rights conceptualised under Convention on Biological Diversity (CBD) connote a barrier to cooperation between formal and informal seed systems, and further offer little incentive to informal systems to commit their working material to *ex situ* collections. ([Louwaars 2007](#_ENREF_303)) reports that public sector research centres in the developing world have drawn more extensively on the accessions than has the private sector, questioning the proposition that *ex situ* collections constitute more of a resource for speculative trait browsing than for adaptive diversification. At the same time, it seems that acquisitions of material from the *ex situ* collections has latterly shown a downward trend consistent with the expected burdens of negotiating material transfer agreements and a perceived general disincentive to invest in breeding within the ambient rights regimes ([Kingston 2007](#_ENREF_262)).

Probably the most important international precedent is the *Nagoya Protocol* on Access to Genetic Resources and the Fair and Equitable Sharing of Benefits Arising from their Utilization (ABS) to the CBD. The CBD was formulated in 1992 at the time of the Rio Earth Summit, and the Nagoya Protocol was formulated in October 2010, largely in response to the biopiracy issue.

The USA, in common with a number of bioprospecting countries, has not implemented the CBD and is hardly likely to implement the Nagoya protocol to the CBD. The countries of greatest biodiversity, and as a consequence the most profitable sources of useful germplasm are invariably the economically least developed. As a consequence, biopiracy involves the exploitation of the poorest countries by the most affluent. The scientific and academic communities are often complicit in this activity as there are many examples of universities in bioprospecting countries which have sought intellectual property rights in relation to germplasm obtained from source countries under the guise of bilateral research. It is important to assess the extent of biopiracy, its dimensions and the measures which have been or may be adopted to deal with this practice. This will include the formulation of research protocols.

## Traditional Knowledge

Useful germplasm is often identified with the assistance of traditional communities, or with the assistance of the healers or shamans within those communities. As this identification will invariably save many thousands of dollars of screening effort, it has been suggested that this kind of knowledge should be protected as a new category of intellectual property law. Since 2001, the World Trade Organization has been considering how its TRIPS Agreement might be amended to accommodate the protection of traditional knowledge (TK). Contemporaneously the World Intellectual Property Organization (WIPO) has been discussing the possibility of drafting an international legal instrument to mandate the protection of TK. In both fora, the industrialised countries, which are the principal beneficiaries of the utilisation of TK, are as unenthusiastic as they are to embrace access and benefit sharing under the CBD.

Beyond institutionally enacted provisions for IP protection discussed above, the regulatory environment associated with concerns over bio-safety erects an on-going significant hurdle to the development of novel traits and adaptive capacity by the plant breeding community (especially in Europe and Australasia) and also to international trade in seed. Interestingly, in relation to the intellectual property constraints governing the deployment of transgenic traits, it is anticipated that the proprietary knowledge embodied in regulatory dossiers will, as the corresponding patents expire, pose the most enduring barrier to distributed decentralized access to GM technologies and traits.

# 5 Education in plant breeding and genomics

*Rodomiro Ortiz*

## General Perspective

During the 20th Century, the conservation of plant genetic resources, through national, regional and international gene banks, became well-established, and today major collections are available for most crops. However, the use of this crop genetic endowment remains limited due to the lack of systematic research to provide a comprehensive framework for the efficient identification and introgression of beneficial variation for use in plant breeding. This needs to be achieved for both on-going priority traits and for novel added-value traits. The emergence of molecular genomic technologies and advances in computational systems provide opportunities to develop new more efficient approaches for plant breeding. The power of molecular genomics will be fully realized when used in combination with classical quantitative genetics to integrate and comparatively analyze phenotypic, pedigree, and genotypic information for important traits. Education in plant breeding should therefore emphasize research and training in the use of crop diversity; conservation and characterization; plus the development of methods for increasing the pace and scope of impact from seed-embedded technologies. This training will require a broad range of partnerships, which will facilitate leveraging of new resources to harness emerging knowledge.

The research agenda for hands-on training in plant breeding should range from crop biodiversity to bioinformatics, with the main focus on the analysis of genetic diversity of crops as well as the development of strategies for conservation and utilization of genetic resources in plant breeding, with breeding informatics as a primary supportive tool. Over the last century, assessment of variation in gene bank collections, and research into breeding and selection, has led to a vast accumulation of both knowledge and genetic resources. For example, many breeding programs have collated extensive amounts of historical phenotypic and genealogical information on their breeding lines, and some have conserved seed from these lines. However, rarely has this phenotypic data, derived from many years of multi-environment trials, been properly curated and integrated with genotype and site characterization data. The integration of interdisciplinary information resources and a comprehensive germplasm collection will facilitate the development of a new paradigm of knowledge-led plant breeding in which defined genomic regions will be the target for specific manipulation by plant breeding. Hence, all available data, although sometimes patchy, can be used for retrospective modelling to form the basis of developing simulation tools to optimize the design of breeding and selection systems of ongoing breeding programs. The main pillars for teaching plant breeding course(s) are proposed below.

Crop Biodiversity: Conservation, characterization and knowledge sharing: Developing evolutionary approaches for safe and dynamic conservation of the world’s crop heritage for future generations through further use in plant breeding; exploring improved techniques for the conservation of plant genetic resources and the assessment of crop diversity; understanding the rich genetic diversity of crops in the context of use in genetic enhancement, as the foundation for the development of dynamic core selectors; modeling genetic diversity in agricultural crop species and their wild relatives to determine the extent of variation, clustering of germplasm for sampling, and identifying potential areas for further search.

Genetic Variation: Targeted access and efficient utilization: Exploiting the untapped value of crop genetic resources through discovery of specific, strategically important traits required for current and future generations of target beneficiaries; analyzing genetic variation (including association mapping for gene discovery and gene re-sequencing for allele mining) of target traits in respective genetic pools to facilitate their further “smart” use in plant breeding; assessing innovative crop genetic enhancement methods that will lead to building “strategic germplasm blocks” through the utilization of unused “exotic” variation; finding eco-friendly bio-techniques that facilitate the genetic manipulation of plants

Breeding informatics, building a functional link between biodiversity and plant breeding: determining optimum use of molecular, genetic, phenotypic and genealogical data for “mining” germplasm collections; turning data into knowledge and skills by visualizing results of whole crop genome description that will lead to a better understanding of gene × genotype × environment interactions, of great use in plant breeding; simulating knowledge-driven breeding approaches for assisting genetic enhancement programs to choose the most appropriate parental genotypes, breeding systems and selection procedures; participating in enhancing crop information systems and informatics platforms through a holistic framework in which to orientate the development of such tools, especially to ensure overall biological interpretations

Education and Public Awareness: Advances in crop improvement will increasingly require professionals with holistic interdisciplinary skills. Integrated system-oriented thinking needs to be taught both at undergraduate and graduate levels. E-learning (through the use of web systems) should also become available as a supportive tool and reach students afar, especially through interactive modules allowing users to access knowledge and self-assess their performance. Likewise, awareness materials are needed to educate and sensitize the general public and policy-makers to the needs for conservation and sustainable use of crop genetic resources through plant breeding. This may lead to mobilizing resources for large national, continental and international research partnerships with public and private sectors.

# 6 Need for Collaboration

*Paul Gepts and Hannes Dempewolf*

The changing and uncertain future environment in which agriculture will be practiced, as well as the population increases on this planet in the next century, require a response to which crop improvement can certainly contribute. To a large extent, plant breeding has already been actively involved in developing new varieties with resistance to diseases and pests and tolerance to abiotic stresses. Therefore, this situation is not new for plant breeders. What is new, however, is the scope of the problem and its rapidity. If societies are to develop an adequate response at all to this supply and demand challenge, they will have to set up types of collaboration and collaborative mechanisms that reach well beyond the collaborations with which researchers are familiar now.

Different types of collaborative efforts should be envisioned, which are not mutually exclusive and not limited to: a) geographical and agro-ecological environments; b) multidisciplinary, including social sciences vs. natural sciences vs. agricultural sciences; c) basic vs. applied research; d.) public and private and e) education and training.

Global climate change and population increase are worldwide phenomena. Scientific findings and technologies developed in one region may be useful in other regions as well. An important caveat here is the both the stresses and their solutions can have an important local component. For example, not all heat stresses are created equal. Heat stress in dry vs. moist environments is likely to have different effects on plants, not to mention different interactions with intermittent or terminal drought stresses. The feasibility and efficiency of proposed solutions may also depend on local political and socio-economic conditions.

Some collaborative tools and data repositories that will be useful in this context have recently been made available or are currently under development. Examples include the recent establishment of the Global Agricultural Trial database (<http://www.agtrials.org/>), which is focused on evaluation data and could serve as an important source for phenotypic data from many different locations around the globe. Such collaborative databases have enormous potential for efforts such as genome-wide association studies. However, the use or establishment of common data standards and phenotyping protocols is essential to be able to exploit these databases to their full potential.

Some initiatives that aim to provide relevant tools and promote the use of establish standards, such as ‘The iPlant Collaborative’ (<http://www.iplantcollaborative.org/>), which focuses on the collaborative establishment of cyber-infrastructure and computational tools for plant science research, are promising. One of these tools is the Integrated Breeding Platform (IBP), which focuses on the development of informatics tools specifically related to plant breeding programs, such as field book development, data analysis, and simulation tools (<https://www.integratedbreeding.net/>).

Agriculture is practiced in widely different agro-ecological systems. These include monoculture, polyculture (e.g. systems that rely on crop-rotations or inter-cropping), conservation agriculture, and agroforestry, just to name a few. Most agricultural systems rely on crop diversity and plant genetic resources either directly as part of their agricultural management strategies, such as inter-cropping, or as a source for new alleles during crop improvement, such as genomic selection. Climate change will likely lead to an increased level of interdependence on plant genetic resources ([Fujisaka et al. 2009](#_ENREF_166)), further highlighting the need for collaborative efforts and pragmatic approaches to provide access and share the benefits of such resources on a global level.

Multidisciplinary collaborations include a combination of research approaches, involving not only scientists in the natural sciences but also those in the social sciences. The introduction of new technologies is not merely a technical issue but involves social, economic, and political aspects as well. The success in introducing new technologies meant to address climate change depends on effective interactions among scientists in these areas, but will also require input from stakeholders in civil society.

As argued by Jorgensen ([2012](#_ENREF_252)), a closer link between basic and applied research is necessary. While basic science can bring us new understanding to crucial biological, physical, chemical or socio-economic processes, this information alone does not guarantee the implementation of solutions. Implementation requires further applied research and outreach activities for the deployment of new technologies. A closer link between basic and applied research shortens the transit time between initial discovery and application.

Finally, the complexity of the problems to be addressed argues for a more multidisciplinary approach to education, which crosses disciplinary boundaries. Students will have to be exposed to the vocabulary, concepts, and approaches of different disciplines in order to function and be productive in a diverse work environment. They will also have to have international educational opportunities that expose them to real life research, development, and implementation situations in a variety of circumstances. This is not be unique to climate change research but seems to be more urgent in this situation.

# 7. Contributors

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