

Review

New Approaches for Crop Genetic Adaptation to the Abiotic Stresses Predicted with Climate Change

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Abstract: Extreme climatic variation is predicted with climate change this century. In many cropping regions, the crop environment will tend to be warmer with more irregular rainfall and spikes in stress levels will be more severe. The challenge is not only to raise agricultural production for an expanding population, but to achieve this under more adverse environmental conditions. It is now possible to systematically explore the genetic variation in historic local landraces by using GPS locators and world climate maps to describe the natural selection for local adaptation, and to identify candidate germplasm for tolerances to extreme stresses. The physiological and biochemical components of these expressions can be genomically investigated with candidate gene approaches and next generation sequencing. Wild relatives of crops have largely untapped genetic variation for abiotic and biotic stress tolerances, and could greatly expand the available domesticated gene pools to assist crops to survive in the predicted extremes of climate change, a survivalomics strategy. Genomic strategies can assist in the introgression of these valuable traits into the domesticated crop gene pools, where they can be better evaluated for crop improvement. The challenge is to increase agricultural productivity despite climate change. This calls for the integration of many disciplines from eco-geographical analyses of genetic resources to new advances in genomics, agronomy and farm management, underpinned by an understanding of how crop adaptation to climate is affected by genotype \times environment interaction.

Keywords: abiotic stress; climate change; landraces; wild relatives; genomics

1. Introduction

Both genomics and phenomics will assist the investigation of genetic variation in both crop landrace germplasm and in crop wild relatives. Novel genetic variation will be needed to extend the range of tolerances to high temperature stresses and to severe droughts in the crop growing period, that are predicted to be more extreme with climate change this century [1,2]. In particular, the incidences of extreme conditions are expected to exceed those currently experienced in the temperate-tropical cropping regions [3]. This poses a threat to world food security, especially for production of the annual staple food crops of the world; wheat, rice, maize, sorghum and potato. A range of other crops from grain legumes to clonally propagated tubers, are also expected to suffer yield declines, especially when extreme conditions occur in the reproductive period of grain crops or in the tuberisation period for root crops [4]. Anthesis and pollination in many crops are adversely affected by temperatures above 35 °C, and the critical temperature may be as low as 32 °C [5]. High night temperatures above 32 °C can impede gametogenesis and photosynthesis in rice [6]. In potatoes the initiation of tubers requires temperatures below 18 °C.

Severe moisture stress in the pre-flowering and the flowering periods reduces formation of florets as well as affecting fertilisation and seed set [7]. Grain size is also reduced by terminal drought in the ripening period. Where rainfall is lower due to climate change, the reduced cloud cover may lead to increased frequency of frost in the reproductive period with further loss of yield potential.

The rise in global world temperature is now expected to exceed 2 °C by around 2050 in the worst case scenario, and certainly before 2100. In the temperate—tropical latitudes this will result in shorter crop growth periods and reduced yield potential [8]. There are some positive aspects to the predicted climate changes. Cropping will become more feasible at high altitudes, and at high latitudes, with longer periods above freezing. There will also be a fertilisation effect for more efficient photosynthesis due to higher global levels of CO₂ from increased industrial, urban and agricultural emissions. However this productivity response is very unlikely to compensate for severe losses from the predicted spikes in temperature and moisture stresses and overall more unfavourable crop growth environments [2,3].

World population growth is on schedule to exceed 9 billion by 2050, as well as being increasingly urbanised, and competing with agriculture for water and land resources. Even as major crop production environments become less favourable for crops, over 70% more production will be required to provide adequate food, mainly on the same area of arable land [8,9]. But to achieve this there is an urgent need to identify novel genetic variation, for crops to tolerate the expected levels of abiotic stresses beyond those experienced under the natural selection of domesticated crops dating back 11,000–13,000 years [2].

Integrated genetic (long term) and agronomic (short and long term) innovations will be important to raise world food production [10,11]. Many complementary strategies in conservation agriculture, weed control and chemical fallowing, innovative irrigation with the use of raised seed beds and of sub-surface drip systems, tie-bunding across cultivation ridges and inter-crop relay planting for more intensive land use, are some of the options that could provide tailored whole farm management specific to local environments [10]. Switching to more stress tolerant crops may be an option for particular crop regions, for example pearl millet is more drought tolerant than sorghum [12], triticale and rye are more drought tolerant than wheat with different respective strategies for maintaining photosynthesis, or for recovering from drought [13], and short season hybrid pigeonpea is preferred over maize in parts of east

Africa [14]. A complementary option is to seek genetic variation for tolerance of abiotic stresses in both the domesticated crop gene pool and that of its wild relatives, for each of the important plant food species. This paper explores the opportunities available in the gene pools of crops and their wild relatives to use new genomic tools for the next phase of plant breeding, and selection of crops with increased yield potential for future target environments of greater variability and extremes of temperature and moisture stresses than exist today.

2. Abiotic Stress Tolerance in the Domesticated Gene Pools of Crops

Landrace populations or traditional local varieties with a diversity of types and polymorphic genetic variation have been selected through natural and manual selection for population complexes with specific adaptation to the range of seasonal crop environments in each locality [15]. Between 1976 and 2003, in response to shorter and less reliable growing seasons with less rainfall in Niger (part of the west African Sahel), natural and human selection in landraces of pearl millet has increased earliness, reduced plant height and shortened reproductive spikes [16]. Landraces need to be productive and reliable across the yearly variation in growing conditions especially if rainfed, or they will be replaced by other varieties or alternate crops, especially for low input sustainable agriculture on family operated small farms [17,18]. Thus landraces through their distribution across the myriad of local environments worldwide reflect natural selection for changes in allele frequencies at loci controlling fitness traits for local adaptation, and have much wider genetic diversity than the varieties generated by modern plant breeding [19,20]. In the last century scientifically managed plant breeding programs have enabled gains in productivity in many crops, through using a very high selection intensity for a small number of key traits (increased harvest index, improved plant architecture), very large breeding populations, the pyramiding of complementary pest and disease resistances, and high crop input responsiveness, for various target environments [6,21].

Accurate geographic positioning of the locations where both wild and landrace germplasm is collected is now possible with GPS data on longitude, latitude and elevation. World climate maps are freely available on the internet, with a local resolution down to 1 square km [22], providing 25 years of historic climatic data for a given location. This climatic data corresponds to the farm where a landrace population was collected [23]. The coefficient of variation and the means for key plant growth variables can be tabulated for over 25 years and separated between the vegetative and reproductive growth phases, for maximum and minimum temperatures, pre-season and in-crop rainfall, relative humidity, sunshine hours, day-length, frequency of frost and also the frequencies of extreme stress spikes [24]. This provides a climatic record of the location where a population mixture of locally adapted genotypes comprising the landrace survived, in part as a result of natural selection for tolerance of abiotic stresses [15]. Such selection would be affected by; the available genetic variation within a landrace; the balance among genotypes variously selected over different seasons; land race effective population size (may be shared by a village); occasional introgression over the long term from newly arrived introductions of other landraces [25]; accumulated mutations over hundreds of generations; and selection for survival under the combined effects of abiotic and of biotic stresses plus manual selection [20]. Analysis of the combined site data for a region/country/world identifies the particular collection sites with a history of extreme abiotic stress, thereby prioritising the corresponding landraces for potential verification of this

stress tolerance [23,26]. With this approach Li Ling *et al.* [24] short listed 61 pea accessions from 629 landraces in China, which survived under extremes of high temperature, drought, or frost in the reproductive growth phase. Both domestic and wild crop germplasm from locations with these stresses can be selected as candidates for potential tolerance to that stress, as a possible result of long term natural selection for survival either as a crop landrace population or as a wild relative.

Not all landraces from localities with a history of extreme stress are necessarily stress tolerant. Ehlers and Hall [27] screened 48 land races of cowpea (*Vigna unguiculata*) from the West African Sahel region to identify 2 with tolerance of high temperatures (up to 42 °C) during the reproductive phase. Although many had an early maturity escape mechanism, a small number exhibited high temperature tolerance with successful gametogenesis, fertilisation and seed set at temperatures above 40 °C in a desert environment. Such high temperature tolerance was also found in land races of vegetable cowpea (*Vigna sesquipedalis*) from northern India. These high temperature tolerances were verified under controlled growth cabinet conditions [28]. The use of geographic and agro-ecological information can assist in focussing the search for genes for stress tolerances from large genetic resource collections to just those landraces prioritised by respective collection environments with a history of extreme abiotic stresses. This can be augmented by appropriate sampling strategies [23]. The use of geographic mapping tools enables this search to be both more feasible and more practical.

3. Novel Genetic Stress Tolerance from Wild Relatives

A phenomenon known as a domestication bottleneck [29], or founder effect [30], took place with the domestication of crops from wild relatives [31]. Prior to the advent of agriculture food grains were collected direct from plants unless dispersed, or from the surrounding ground. Annual plants survived under natural selection through having efficient and effective dispersal mechanisms. These included; various forms of shattering or dis-articulation of seed from the flowering stalk such as seed pods twisting open to throw seed a short distance; awns to aid burial of seed; spines on seed coats to attach to passing animals; production of a many very small seed; or very hard/thick seed coats, which resisted digestion to enable seed dispersal through animal excreta, or delayed germination over a number of growth seasons [32]. In each environment, different plant species competed for survival with various modes of regeneration. The imperative was species survival with sufficient stored energy in the seed to enable germination of the embryo, and not on supplying a surplus of stored carbohydrates and proteins in seed to provide food and feed for humans and animals.

Selection for domestication was crop specific, but in grain crops typically required a shift in plant morphology and physiology; to retention of seed on plants for ease of harvest, to larger seed size so that agriculture became a more attractive food source than hunter-gathering, to a reduction in hard seed coats to allow reliable germination of annual crops, to improved nutrition and digestion, and for investment of more plant photosynthate in the seed rather than in vegetative growth [33]. Since these domestication traits were largely absent in the wild relatives there was a dependence on rare mutations to obtain the necessary major genes and quantitative variation for these traits. Such mutations needed to be observed and selected for, from natural recombinations of these different mutations, to enable successful both successful cropping and adaptation to local ecosystems [20,32]. The low level of cross-pollination in the self-pollinated crops (wheat, barley, rice, and the majority of grain legumes) largely isolated these crops

from their wild relatives [34]. For cross pollinated crops barriers to genetic exchange with their wild progenitors through differences in flowering time, inhibitors of cross compatibility, or differences in ecological distribution; tend to separate the respective gene pools [35]. Thus the resultant genetic variation that was transferred to crops from wild progenitors was very restricted by these rare events, a domestication bottleneck.

This bottleneck limited transfer of the genetic diversity for abiotic stress tolerances from the much wider genepools of the crop progenitors and of other wild relatives. The secondary and tertiary wild relatives of crops may be rich sources of desirable traits such as disease resistance [36], yield and agronomic traits [37], or of genes for regulatory and physiological stress tolerance mechanisms [38]. The much wider genetic diversity available in wild relatives offer the possibility of a breakthrough in the apparent yield ceilings in many crop breeding programs (or reduced rates of yield gains), as demonstrated with the pyramiding of yield promoting genes in domestic tomato to achieve a 50% yield gains in both irrigated and dry field conditions [39].

The wild progenitors often can still be found in the respective regions where a crop was domesticated, growing wild often in marginal habitats unsuited to agriculture with severe abiotic stresses, or sometimes even as a weed in cultivated crops [40], but there is a risk of erosion of some of this diversity with climate change [23]. Wild progenitors vary in their distribution, being restricted to a small region in Turkey for *Cicer reticulatum* the progenitor of chickpea [41], to a wide distribution of *Pisum sativum* subspp. *elatius* the wild progenitor of pea which preceded crop migration with the spread of agriculture, and to spread of the wild progenitor as a weed in the cultivated crop as for *Hordeum spontaneum* the wild progenitor of barley [42]. To different extents for each crop, an overlap in distribution with the progenitor plus other cross compatible wild relatives continued after domestication, and rare (in self-pollinating species) to occasional (cross pollinating species such as sorghum) introgression of both beneficial and detrimental genes from wild to cultivated has continued post domestication in many crops [43]. Now however, the gene pools of many domestic crops can be selectively broadened with manually directed genetic introgression from wild relatives for improved tolerances to abiotic stresses of drought, high temperature and frost especially in the reproductive phase [37,44]. These three stresses are likely to pose the most important challenges of climate change to agriculture.

Wild relatives survive on uncultivated ground in generally harsher environments. Wider genetic variation for tolerance of abiotic stresses, as a result of natural selection for survival with better seed set on the more tolerant plants, is more likely to be available in wild relatives than in the genepools of most domestic crops [32,40].

4. Ecological Screening by the Habitats for Collection of Germplasm

A systematic preliminary screening of both landraces (efficiently sampled as core or mini-core collections representing the species diversity (23)), and wild relatives, based on the growing season history of their respective habitats, provides a short list of selected germplasm for more intensive evaluation, in an efficient and strategic search for the required genetic tolerance of abiotic stress. Not all candidates for stress tolerance will have this characteristic, as some may have escape mechanisms such as very early flowering; indeterminacy; very low biomass; capacity to recover from short term stress spikes, or may represent the genetic remnants from a narrow genetic base as the species expanded to new

ecological niches [45,46]. Such escape mechanisms may suffice in current crop environments but may be inadequate to manage the more intense stresses predicted with climate change [2]. The chances of locating sources of genetic tolerance to abiotic stresses are greatly improved by the screening the environments of sites where germplasm was collected [23], noting that land race populations have wider genetic variance than conventionally bred varieties, and that wild relatives will have yet wider genetic diversity in most cases [20,31].

This approach, “survivalomics”, is useful to identify parental material for introgression of abiotic stress tolerance based on survival in extreme habitats. There may be extensive epistasis affecting the transfer of QTLs for stress tolerance from the wild into the domesticated genepool, and trait expression in a wild relative may not be an adequate guide to its expression in a domesticated genetic background [37]. The trait will need to be further evaluated after 1–2 backcrosses into the domesticated background, probably of an elite breeding line chosen as the recurrent parent [37]. Survivalomics searches through the natural selection history of habitats that helped determine a landrace population, a searching backwards strategy to locate sources of stress tolerances. The important issue thus becomes the optimisation of genomic tools to enable breeding and selection for these traits.

5. Genomics and Control Mechanisms for Stress Tolerance

New genomic tools such the use of a very density of genetic markers such as single nucleotide polymorphisms (SNPs) can provide genome-wide selection (GWS) in conjunction with genotyping of each individual in a segregating population [46]. Each marker has a breeding value based on phenotypes and marker genotypes, and summing the breeding values of all markers provides a genomic estimated breeding value for selection of superior individuals. This approach can be used to select backcross progeny from wild × domestic crosses using bi-parental population mapping to detect rare alleles of moderate effect which may be subject to epistasis [47]. Genomewide selection with molecular markers were used to simulate selection directly in F2 population from a cross of adapted × exotic maize for introgression of favorable alleles, to illustrate applicability to plant breeding programs re population sizes, number of selection cycles, and replication across different crop environments and years [48]. A high density of molecular markers has been identified for the wild progenitor of chickpea, *Cicer reticulatum*, which will facilitate exploitation of this source of diversity for crop improvement [49]. The combining of these approaches with bioinformatics helps to integrate various disciplines; structural genomics, transcriptomics, physiology and plant breeding, towards a more targeted and efficient plant breeding plus elucidation of heterosis and epigenesis, but the costs may be prohibitive for public breeding programs for self-pollinated crops [50]. Yet as new technologies become increasingly cost effective it is expected that the new genetic tools will enhance but not replace conventional breeding.

Stress tolerant regulatory loci occur across various species as variants of candidate genes or even as direct analogues [38,51]. Molecular tools are available to assist identification of critical genes for drought and for heat tolerance from crop wild relatives [23], such as analysis of known candidate genes, and application of comparative functional genomics in a genome wide search. Hundreds of adaptation and regulatory genes are known to affect crop responses to heat and drought stresses. These may be expressed by differences in protein levels or protein sequences detectable by respective mRNA levels. Drought up-regulated genes conferring resistance include dehydrins (*Hordeum spontaneum*), and DREB

in *Glycine soja* [38]. However a trait associated with drought or heat stress may actually be linked to a change in expression of another trait or even of a still unknown biochemical process. The molecular bases of various stress tolerance traits are not known in many species, despite documentation of a wide range of drought induced processes; e.g., anti-oxidant enzymes and compounds such as ascorbic acid, proline and mannitol which remove stress induced toxic reactive oxygen species molecules (ROS); osmoprotectant protein stabilisers in dehydrated plants; and heat shock HSPs/chaperones [38]. There is increased expression of heat protection genes in heat acclimated plants, than in non-acclimated plants exposed to a sudden heat spike. This corresponds to higher levels of mRNA of key heat protection genes. Adaptation to heat stress may depend more on the superior thermostability of key metabolic enzymes such as those for ROS removal, than the levels of stress protectant proteins.

Regulatory genes are important in the simultaneous changes of the mRNA levels of many genes such as for ROS removal [38]. Drought response regulators may include signalling proteins, transcription factors which bind to cis-elements in promoters, proteins for post transcriptional regulation of RNA, and enzymes for abscisic acid synthesis. ABA (abscisic acid) pathways are important in plant response to drought stress. A wild tomato (*Solanum chilense*) which is adapted to extremely dry environments had a divergent haplotype structure in a dehydrin gene downstream in the ABA pathway attributed to directional selection [52]. Heat response regulators, such as some HSPs, can affect various regulatory proteins to result in changes to leaf morphology and to flowering time. There are many forms of heat shock factors variously up-regulated by heat and by drought, and over-expression of some can improve heat tolerance. DREB genes may also be up-regulated by heat. Many complex gene expressions, regulatory systems and specific adaptation genes, interact with heat and drought stresses currently experienced by crops in many environments and which are expected to be more severe as climate changes. Trait associated genes may not possess the allelic variation governing the trait expression, but reflect the allelic variation in an upstream regulator [38]. However positional cloning of a gene/regulatory sequence associated with a target phenotype does not conclusively prove that this is the causal sequence variant for a trait [46].

Differentially expressed genes associated with genetic variation for heat or drought have been investigated through their EST sequences using large array analyses for genome wide searches, however this is likely to be super-ceded with next generation sequence (NGS) technologies. Both approaches enable comparative functional studies of genes for stress resistance. Candidate genes for drought/heat adaptive traits in the domesticated gene pools of crops, such as for osmotic adjustment, transpiration efficiency, photosynthetic maintenance and water soluble carbohydrates have been identified [38]. But for the crop wild relative gene pools, gene transcripts may differ widely from those for crops, and array technology based on crop transcriptome sequences may not be suitable for its wild relatives. Yet such difficulties may be overcome with the increasing availability of sequences with a high density of markers for some crop progenitors such as *Cicer reticulatum* for chickpea [49], and *Aegilops tauschii*, the source of the D genome in the hexaploid bread wheat [53]. Genetic differences between crops and wild relatives are too large for mapping of differentially expressed functional genes for a trait QTL. Yet precision is improved if the physiological and biochemical bases of the trait are known [54].

With NGS, whole genome or gene-space sequencing data are available for many crops, plus transcriptome sequence data to provide large numbers of ESTs [50]. NGS technologies are rapid and relatively cheap, and many parallel reactions can be multiplexed for which bioinformatic tools

need further development. NGS resequencing is very useful for discovery of single nucleotide polymorphisms (SNPs) especially where a sequenced reference genome is available, and also for sequence assembly using bacterial artificial chromosomes for species with no reference genome available. NGS technologies can also be used for association mapping, wide crosses and alien introgression [55]. In particular NGS also allows additional molecular markers to be developed on a genome wide scale for wild germplasm enabling accuracy in tracing introgression of well defined segments from wild relatives. Knowledge of the gene region enables the use of NGS to screen germplasm collections to detect rare alleles in the domesticated gene pool and novel alleles in the wild gene pools [46]. Thus previous limitations of genetic markers for traits in wild relatives can now be addressed with NGS facilitating exploitation of this wild diversity for crop improvement.

While NGS technologies hold much promise, and a further “Third generation technology” is being developed, there are complications for allopolyploid genomes such as bread wheat made up of three related sets of homoeologous chromosomes, and canola (*Brassica napus*) with genome complements from two diploid domestic Brassica crops. In wheat genomic analysis and construction of a reference genome is confounded by homoeologous synteny and by repetitive transposon sequences in 75%–90% of the genome, with genic and low copy regions greatly interspersed by repeat sequences, thereby presenting challenges to genome sequencing [56]. Despite these difficulties the analysis of the bread wheat genome has now been achieved [57]. In Brassica there was an ancient triplication of the genome followed by diploidisation with very uneven loss of genome segments or genome fractionation. Thus the allopolyploid *B. napus* has complex presence-absence polymorphisms, and the subgenomes have a high level of plasticity with less structured patterns of gene loss compared with another reduced polyploid crop, maize [56]. Besides these complications, QTLs for stress and other trait expressions may not be stable across environments, and may be influenced by epistasis especially when there is a wide genetic distance between the QTL source and the introgressed genetic background [58]. Also such QTLs are affected by confounding expressions such as phenology affecting both drought response and grain yield relationships [46]. NGS and detailed data sets allow analysis of genic regions for tolerances of heat and other abiotic stress expressions at different stages of crop development, and better targeting of breeding opportunities.

6. Synthesis of Plant Breeding, Genomics and Genotype × Environment Interaction

Plant breeding addresses the challenge of combining together heritable traits for improved yield, resistances to endemic diseases and pests, and product quality traits, to suit the production system of the target environment. This target environment can be very wide when new varieties have general adaptation [59], with relative stability in performance across locations and years with differing crop seasons. One of the most difficult challenges is to select and evaluate promising selections across a suitable range of environments, with the almost inevitable occurrence of genotype × environment interaction in which ranking of entries alters in different locations. This challenge will be magnified by climate change with a predicted wider and more extreme fluctuation of seasons, and the requirement for new varieties by 2050 to possess resilience to extreme spikes in abiotic stresses [2,3], notably in the Indian sub-continent and sub-Saharan Africa, and to a lesser but significant extent in other temperate to sub-tropical latitudes. Survivalomics breeding to reduce risk in extremes of temperature and drought,

plus selection for general adaptation to less reliable climates, will be key plant breeding challenges in the future. Wider genetic variation than currently available in domesticated crop gene pools will often be necessary to avoid replacement with alternative crops, with the largely unexploited genepools of crop wild relatives offering the most immediate prospects as exemplified in wheat and tomato [37,44]. Jordan *et al.* [60] describe a practical example of broadening the domesticated gene pool for quantitative traits, for a sorghum breeding program.

Early analyses of genotype \times environment interaction by regression analyses suggested that patterns of wide and of specific adaptation found in a worldwide barley germplasm collection reflected the natural selection history of the respective germplasm [59]. Adaptation has been more precisely described with three way analysis of Chinese adzuki bean (*Vigna angularis*) landraces \times multiple environments \times multiple traits. Accessions were clustered into groups with distinctive patterns of adaptation across geographically and climatically diverse sites, which reflected differences in both trait phenotype combinations and in the geographic origin of accessions [61]. The adaptation characteristic of an accession was defined by the group to which it belonged. There were differences among the adzuki adaptation groups in levels of genotype \times environment interaction across traits, which can also be interpreted as differences in plasticity [20,61]. Molecular analyses of Chinese pea landraces also displayed different genetic groups differing in geographic origins [62], and molecular analyses of faba bean landraces in China demonstrated clustering by geographic groups [63]. Variation in alleles for earliness in millet were associated with differences in rainfall, and earliness was correlated with both reduced height and shorter spikes, indicating a possible suite of traits for improved fitness and yield adaptation to drier environments [16]. It is possible that adaptation across environments can be defined genetically for many crops, explained in part by many underlying traits such as photoperiod response [64,65], and tolerances of soil moisture and of temperature stresses [24]. Thus if adaptation to target environments can be genetically characterized, possibly QTLs could be identified for various expressions of crop adaptation and plasticity [20]. The challenge is whether diverse genetic expressions for extreme drought and for heat tolerances can be selectively pyramided by strategic breeding to contribute the wide adaptation and plasticity for crops to cope with the predicted changes in world climate. It is important that development of such elite lines are planned now before 2050 in breeding programs tailored to each crop and target environment, to help crops adapt to climate change, rather than experience a lag in the development of appropriate research and development programs [11]. Overall there is the food security question of whether agriculture can meet the needs of future populations towards the end of the 21st century, particularly with the added complication of climate change.

7. Conclusions

New molecular tools such as NGS will assist in identifying the underlying components of stress tolerances in the domestic germplasm, and in the identification and introgression of novel stress genes from crop wild relatives. This is being systematically applied in the International Centre for Wheat and Maize Improvement (CIMMYT) wheat breeding program with managed field screening for tolerances of heat and drought stresses, to exploit both the domesticated and wild genepools [21,66]. For most crops the domestic germplasm has not been evaluated eco-geographically for identification of landrace collection sites likely to have had natural selection for tolerances of abiotic stresses, and likewise for the

wild gene pools which have been little explored for novel genes for stress tolerances. With strategically directed research there may be enormous scope to select for adaptation to extreme abiotic stresses in the domesticated gene pools of crops, and in the largely untapped germplasm resources of related wild gene pools, for exploitation of survivalomics to assist crop adaptation to climate change.

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