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### *Application of genomics-assisted breeding for generation of climate resilient crops: Progress and prospects*

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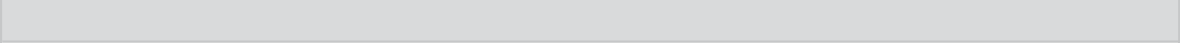
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# Application of genomics-assisted breeding for generation of climate resilient crops: Progress and prospects

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## Abstract

Climate change affects agricultural productivity worldwide. Increased prices of food commodities are the initial indication of drastic edible yield loss, which is expected to surge further due to global warming. This situation has compelled plant scientists to develop climate change-resilient crops, which can withstand broad-spectrum stresses such as drought, heat, cold, salinity, flood and submergence, and pests along with increased productivity. Genomics appears to be a promising tool for deciphering the stress responsiveness of crop species with adaptation traits or in wild relatives towards identifying underlying genes, alleles or quantitative trait loci. Molecular breeding approaches have been proven helpful in enhancing the stress adaptation of crop plants, and recent advancement in next-generation sequencing along with high-throughput sequencing and phenotyping platforms have transformed molecular breeding to genomics-assisted breeding (GAB). In view of this, the present review elaborates the progress and prospects of GAB in improving climate change resilience in crop plants towards circumventing global food insecurity.

**Keywords:** Climate change, crop improvement, stress tolerance, breeding, genomics

## Introduction

Three major events in agricultural history, namely domestication, displacement of native crops by major crops along with genetically limited introductions of non-native species, and intensification of agricultural production through the Green Revolution have contributed significantly towards reduced genetic and trait diversity within major crop species. Despite this decrease in crop diversity, global production of the major staple crops was increased in the last century (Fischer et al., 2009). This increase in productivity has largely been driven by conventional plant breeding coupled to intensification and simplification of production systems. This includes selection for edible yield and adaptation, and against yield reducing factors such as susceptibility to pathogens as well as 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 has led to the loss of certain genes which are responsible for efficiency or adaptation to stress(es) (Brown, 2003). This situation presents three potential challenges: (i) to modify the selection criteria to focus on efficiency or adaptation to stress(es) rather than total edible yield, (ii) to ensure the presence and efficiency of stress-tolerance genes and its exploitability in elite material and wider breeding germplasm, and (iii) to expand the use of minor crops, which may possess better nutrition quality, environmental sustainability or resilience and require lower inputs than major crops.

At present, global agriculture is facing a serious threat of climate change resulting in reduced productivity. Increasing food prices and greater global food insecurity are the outcomes of decreased productivity (FAO 2014) and this scenario, if persists, would lead to further increase in food prices in developed countries, and social unrest and famine in these regions. Climate change will affect food supply unless actions are taken to increase the resilience of crops as projections have shown a drastic decrease in the production of major cereals by 2020, including 9% for maize, 11% for rice and 14% for wheat (Hisas, 2011). Global warming, changes of

46 rainfall pattern and other extreme weather events may mostly contribute to this disaster, and the  
47 changing pattern of climate would result in increased attack of pathogens and pests. Moreover,  
48 the elevated CO<sub>2</sub> levels will reduce the nutritional quality of many crops, while some crops may  
49 become toxic due to changes in the chemical composition of their tissues (Dwivedi et al., 2013).

50  
51 Therefore, increasing the resilience of crops to climate change is the prime need to ensure food  
52 and nutritional security, which could be achieved through genetic engineering-based approaches  
53 or molecular breeding strategies. Genetic engineering allows direct transfer of beneficial gene(s)  
54 or manipulation of existing gene(s) in the crop of interest for generating expected phenotype(s),  
55 whereas breeding approaches involve the improvement of germplasm through introduction of  
56 novel alleles into target crops by breeding. Since genetic modification remains controversial in a  
57 number of countries though it serves as an invaluable tool in tailoring modifications to produce  
58 alleles and phenotypes beyond the range available through exploitation of existing genetic  
59 variation, molecular breeding could offer an easy-to-accept approach for crop improvement.

60

### 61 **Potential of genomics-assisted breeding in producing climate resilient crops**

62  
63 Genomics offers tools to address the challenge of increasing food yield, quality and stability of  
64 production through advanced breeding techniques. Applications of DNA markers to facilitate  
65 marker-aided-selection (MAS) for crop improvement have been proved successful in  
66 crossbreeding. Advances in plant genomics provide further means to improve the understandings  
67 on crop diversity at species and gene levels, and offer DNA markers to accelerate the pace of  
68 genetic improvement (Muthamilarasan et al., 2013). A genomics-led breeding strategy for new  
69 cultivars commences by defining the stress(es) that will likely affect crop production and  
70 productivity under a certain climate change scenario. Data from multi-environment testing  
71 provide an opportunity for modeling “stress-impacts” on crops and target populations of  
72 environments. Plant breeders and genebank curators will search for morphological and  
73 physiological traits in available germplasm that could enhance crop adaptation under such  
74 climate variability. In this regard, crop physiology may help define the ideotypes to be pursued  
75 for enhancing such adaptation. Moreover, the use of geographic information systems and  
76 passport data can allow identification of accessions for stress-prone environments, whereas the  
77 available characterization, including DNA fingerprinting, and evaluation data as well as mapping  
78 of desired genes or quantitative trait loci (QTL) will assist in selecting promising accessions for  
79 further screening against specific stress(es). Similarly, precise phenotypic assessments and  
80 appropriate biometric analysis will assist in identifying unique responses of a set of genotypes in  
81 a given phenological stage influenced by variation of weather patterns. This information will be  
82 further used in genomics-aided breeding approaches such as genome-wide selection of promising  
83 germplasm for further use in crop breeding aiming at both population improvement and cultivar  
84 releases.

85

86 Genetic mapping and QTL analysis and association genetics (AG) have accelerated the  
87 dissection of genetic control of agricultural traits, potentially allowing MAS, QTL and AG  
88 studies or direct calculation and genomic selection (GS) of high value genotypes to be made in  
89 the context of breeding programs. Until recently, AG and GS were hampered by the need for  
90 very high marker density coverage of the genome. Advancement of next-generation sequencing  
91 (NGS) methods has facilitated the development of large-scale, genome-wide, high-throughput



92 markers such as single nucleotide polymorphisms (SNP), insertion-deletions (InDels), etc. even  
93 in relatively research-neglected crop species. Discovery of novel genes/alleles for any given trait  
94 could be then performed through genotyping-by-sequencing (GBS) approaches. Similarly,  
95 genome-wide association study (GWAS) identifies the genomic regions governing traits of  
96 interest by performing statistical associations between DNA polymorphisms and trait variations  
97 in diverse collection of germplasms that are genotyped and phenotyped for traits of interest. NGS  
98 coupled with GWAS increases the mapping resolution for precise location of genes/alleles/QTL  
99 (Ma et al., 2012; Liu et al., 2013; Varshney et al., 2014).

100

101 In course of evolution, nature has evolved new genes, and shuffled and selected these genes in a  
102 wide range of environments to produce the diversity evidenced in wild species. In contrast, the  
103 selection and domestication of crops by humans is relatively recent, having occurred over the last  
104 10,000 years. During the domestication and breeding process, there has been a significant  
105 reduction of genetic diversity in major crops, alongside a selection for yield under highly  
106 managed agricultural environments. Currently, breeders are shuffling the combinations of  
107 relatively few alleles to produce enhanced combinations that provide increased yield and other  
108 attractive agronomic characteristics. In many large genome crop species, even this reshuffling  
109 process is limited by restricted recombination patterns within the species, leading to the  
110 consistent inheritance of blocks of genes, raising issues of linkage drag and fixed linkage blocks,  
111 which may not contain the best possible combination of alleles. Breaking down these linkage  
112 constraints will allow breeders to access novel combinations from within their current elite  
113 parents. The need to evaluate the genetics of the processes that allow genes to be recombined  
114 between parental genotypes in crops is a critical requisite. Genomics possesses the potential to  
115 increase the diversity of alleles available to breeders through mining of allied gene pools and  
116 genomes of crop wild relatives (CWRs). Genomics tools also enable rapid identification and  
117 selection of novel beneficial genes and their controlled incorporation into novel germplasm. In  
118 the next-generation genomics era, this technology will be used to safeguard the future through  
119 improved food security. Taken together, application of genomics for crop germplasm  
120 enhancement thus offers the greatest potential to increase food production in the coming decades.  
121 With continued rapid advances in genome technologies, the application of genomics to identify  
122 and transfer valuable agronomic genes from allied genepools and crop relatives to elite crops will  
123 increase in pace and assist in meeting the challenge of global food production.

124

## 125 **Genomics of climate resilience in major crops**

126

127 The following section summarizes the state of knowledge of the genetic blueprints of many  
128 leading crops, together with information about breeding needs and priorities related to climate  
129 resilience. Genomic tools and resources are widely available and being employed in most of  
130 these plants and will soon be ubiquitous, aiding 'MAS' strategies that can be successful even  
131 based only on phenotypic information. Knowledge of gene functions is less consistent,  
132 leveraging to varying degrees of the accumulated information from botanical models. However,  
133 even in model crops, the exact functions of most genes remain unknown, and exploring the  
134 variations conferred during angiosperm diversification represents an opportunity to identify a  
135 host of solutions to agricultural challenges.

136

## 137 **Cereals**

138

139 Cereals are a staple to billions and their production is increasingly threatened by the recent  
140 changes in weather patterns due to global warming, particularly in less-developed countries  
141 where the consequences of changing climate have devastating socio-economic impact. Reaching  
142 a level of cereal production sufficient to sustain an adequate level of global food security will  
143 require the effective integration of crossbreeding with ‘omics’ approaches that allow dissecting  
144 and more effectively manipulating the genetic make-up of adaptation to abiotic stresses  
145 (Langridge et al., 2011). In the past decade, genomics-based approaches have been extensively  
146 deployed to dissect the genetic make-up of abiotic stress adaptation and given the quantitative  
147 nature of abiotic stress tolerance, QTL have been the main target of research to identify the  
148 genetic loci regulating the adaptive response of cereal crops to unfavorable environmental  
149 conditions. This includes drought-adaptive traits (Serraj et al., 2009; Tuberosa 2012), root  
150 architecture (Wasson et al., 2012; Uga et al., 2013; Lynch et al., 2014), accumulation of water-  
151 soluble carbohydrates and their partitioning to storage organs (Landi et al., 2005; Salem et al.,  
152 2007; Snape et al., 2007; Rebetzke et al., 2008), abscisic acid concentration (Rebetzke et al.,  
153 2008; Rehman et al., 2011), stay-green (Yang et al., 2007; Borrell et al., 2014), canopy  
154 temperature (Lopes et al., 2014), and carbon isotope discrimination ( $\Delta^{13}\text{C}$ ) (Pinto et al., 2014).

155

156 Global warming is intimately associated with an increase in temperature that accelerates leaf  
157 senescence, disrupts starch accumulation and curtails yield, particularly when combined with  
158 drought. In wheat, a major QTL located on chromosome 4A explained 27% and 17% of  
159 phenotypic variance for reduction in yield under drought and heat stress, respectively (Pinto et  
160 al., 2014). The same study also identified common QTL for drought and heat stress adaptation on  
161 chromosomes 1B, 2B, 3B, 4B, and 7A. Yield QTL were shown to be associated with  
162 components of other traits, supporting the prospects for dissecting crop performance under  
163 abiotic stress conditions into physiological and genetic components in order to facilitate a  
164 strategic approach to breeding (Reynolds et al., 2008). Additional QTL with concurrent effects  
165 under both heat and drought conditions have been described by Wang et al. (2012).

166

167 In rice, the result of a study based on 227 intensively managed irrigated farms forecast a net  
168 negative impact on yield from the warming expected in the coming decades, and clearly show  
169 that diurnal temperature variation must be considered when investigating the impact of climate  
170 change (Welch et al., 2010). Higher temperatures are speculated to reduce rice grain yields  
171 through two main pathways: (i) high maximum temperatures that in combination with high  
172 humidity cause spikelet sterility, and (ii) increased nighttime temperatures, which may reduce  
173 assimilate accumulation (Wassmann et al., 2009).

174

175 Flooding is one of the abiotic stresses, whose frequency and intensity is increasing due to global  
176 warming and changes in rainfall patterns. Therefore, it is important to produce cereal crops with  
177 the ability to withstand the anoxic conditions associated with waterlogging and/or extended  
178 submergence. Among cereals, rice is more prone to submergence stress, which periodically  
179 affects approximately 15 million hectares of rain-fed lowland areas in Asia to cause annual  
180 losses in excess of US \$1 billion (Mackill et al. 2012). In rice, the *Sub1* QTL accounts for a  
181 major portion of variability for survival under prolonged submergence. Positional cloning of  
182 *Sub1* has revealed a cluster of three putative ethylene response factors (ERFs), namely *Sub1A*,  
183 *Sub1B*, and *Sub1C*. Further work unequivocally assigned the functional polymorphism to *Sub1A*

184 (Xu et al., 2006). Following the identification of *Sub1A* QTL, marker-aided backcrossing  
185 (MABC) was used to efficiently convert submergence-susceptible rice cultivars into tolerant  
186 cultivars in only three backcross generations. Accordingly, DNA markers were developed for  
187 introgressing *Sub1* into six popular cultivars to meet the needs of farmers in flood-prone regions  
188 (Bailey-Serres et al., 2010). This clearly demonstrate the effectiveness of MAS for introgressing  
189 agronomically beneficial QTL alleles into elite material. The success of this work is largely due  
190 to the major effect of *Sub1* QTL and the stability of its effect in different genetic backgrounds  
191 under submergence conditions. In maize, Mano et al., (2005a) identified QTL for adventitious  
192 root formation at the soil surface, one of the most important adaptations to soil waterlogging,  
193 which can severely impair root growth at an early stage, thus reducing the capacity of the plant to  
194 extract soil moisture at a later stage when water shortage is more likely to occur. Several QTL  
195 for adventitious root formation have been mapped, and a major QTL was mapped on  
196 chromosome 8 (Mano et al., 2005b).

197  
198 Salinity is also an impact of global climate change, which affects over 20% of the world's  
199 agricultural soils and thereby affecting cultivation. In durum wheat (genome AABB), two major  
200 QTL have been shown to control Na<sup>+</sup> accumulation in shoot via Na<sup>+</sup> exclusion (James et al.,  
201 2006). Both exclusion genes represent introgressions from an accession of *Triticum monococcum*  
202 (genome AA). Remarkably, under standard conditions, durum wheat containing the salinity  
203 tolerant allele at *TmHKT1;5-A*, which is one of the two salt-tolerance loci showed the phenotype  
204 similar to durum wheat that lacked the beneficial allele at this locus. But under saline conditions,  
205 it outperformed its durum wheat parent, with increased yields of up to 25% (Munns et al., 2012).  
206 In barley, evaluation of a mapping population derived from a cross between a wild barley  
207 (*Hordeum vulgare* ssp. *spontaneum*) accession and cultivated barley (*H. vulgare*) allowed the  
208 identification of a major QTL capable of limiting Na<sup>+</sup> accumulation in the shoots under saline  
209 conditions (Shavrukov et al., 2010). In rice, several QTL for salinity tolerance have been  
210 identified (Wang et al., 2012) indicating that pyramiding by marker-assisted selection (MAS) of  
211 QTL can be applied to enhance salt tolerance of rice.

## 212 213 **Oilseeds and pulses**

214  
215 Oilseeds and pulses are major food crops, known for their unique protein and oil rich  
216 characteristics. Major biotic and abiotic stresses are the most serious production constraint for  
217 global oilseed and pulse production, and are predicted to worsen with anticipated climate change.  
218 Among the oilseeds, soybean has the highest protein content (40%) and the second highest oil  
219 content (20%). In spite of this importance, efforts are yet to be invested towards improving stress  
220 tolerance and other traits in soybean. *Phaseolus* beans are an essential part of the human diet and  
221 are a source of proteins, vitamins, and minerals (Gepts et al., 2008). Of the five domesticated  
222 *Phaseolus* species, common bean (*P. vulgaris* L.) is the economically important bean. Genetic  
223 studies and cultivar breeding in *P. vulgaris* have shown that heat and drought tolerance are under  
224 complex genetic control, although a single instance of a major gene has also been observed  
225 (Schneider et al., 1997; Asfaw et al., 2012). Selection of lines with improved drought adaptation  
226 has also been successful (Singh, 2007; Beebe et al., 2008; Urrea et al., 2009). Development of  
227 MAS methodology for drought adaptation has been initiated (Schneider et al., 1997; Asfaw et al.,  
228 2012) with the assistance of genomic resources developed through whole-genome sequencing of  
229 Andean (accession: G19833) (Schmutz et al., 2014) and Mesoamerican (accession: BAT93,

230 OAC Rex) bean genomes, and a bean breeder's genome toolbox and database  
231 (<http://phaseolusgenes.bioinformatics.ucdavis.edu/>).  
232

233 In case of chickpea and pigeonpea, several abiotic and biotic stresses pose a threat to high and  
234 stable grain yields. To overcome these production constraints and meet the growing demand for  
235 these crops, efforts at national and international levels have led to the development of large-scale  
236 genetic and genomic resources (Varshney et al., 2013a). These resources have been used to  
237 understand the existing genetic diversity and exploit it in breeding programs. In chickpea, several  
238 intra- and inter-specific genetic maps have been developed (Gaur et al., 2011; Gujaria et al.,  
239 2011; Thudi et al., 2011; Hiremath et al., 2012) and genomic regions responsible for different  
240 biotic stresses (Anbessa et al., 2009; Kottapalli et al., 2009; Anuradha et al., 2011), abiotic stress  
241 (Rehman et al., 2011; Vadez et al., 2012) and agronomic traits (Cobos et al., 2009; Rehman et  
242 al., 2011; Bajaj et al., 2014, 2015; Kujur et al., 2015a, 2015b; Das et al., 2015) have been  
243 reported. In pigeonpea, more than 3000 SSR markers (Saxena et al., 2010; Bohra et al., 2011;  
244 Dutta et al., 2011), ESTs (Raju et al., 2010), 454/FLX transcript reads (Dubey et al., 2011; Dutta  
245 et al., 2011), transcriptome assemblies (Dubey et al., 2011; Kudapa et al., 2012) and SNPs  
246 (Saxena, 2008) have been developed for their use in genomics-assisted breeding for crop  
247 improvement.  
248

249 The draft genome sequence of both Kabuli ([http://www.icrisat.org/gt-](http://www.icrisat.org/gt-bt/ICGGC/GenomeSequencing.htm)  
250 [bt/ICGGC/GenomeSequencing.htm](http://www.icrisat.org/gt-bt/ICGGC/GenomeSequencing.htm)) and Desi (<http://www.nipgr.res.in/CGWR/home.php>)  
251 chickpeas have recently been published (Varshney et al., 2013b; Jain et al., 2013). Similarly,  
252 International Initiative on Pigeonpea Genomics (IIPG, [http://www.icrisat.org/gt-](http://www.icrisat.org/gt-bt/iipg/Home.html)  
253 [bt/iipg/Home.html](http://www.icrisat.org/gt-bt/iipg/Home.html)) released the draft genome of pigeonpea (Varshney et al., 2012). These  
254 sequence data of chickpea and pigeonpea will assist in enhancing their crop productivity and lead  
255 to conserving food security in arid and semi-arid environments. Further, attempts have been  
256 made towards improvement of oilseed crops such as peanut (or groundnut) using genomics-  
257 assisted breeding. Large-scale genomic resources were developed during recent years to facilitate  
258 molecular breeding in peanut and QTL have been identified for stress adaptation related traits  
259 (Varshney et al., 2009; Gautami et al., 2012), rust and late leaf spot resistance (Khedikar et al.,  
260 2010; Sujay et al., 2012), and oil quality (Sarvamangala et al., 2011).  
261

## 262 **Millets**

263

264 Millets are small-grained graminaceous crops, well known for their water-use efficiency,  
265 excellent nutrient content, adaptation to a range of ecological conditions and ability to flourish in  
266 nutrient-poor soils. Foxtail millet, proso millet, pearl millet, barnyard millet, finger millet and  
267 kodo millet are few notable millet crops cultivated worldwide and of these, foxtail millet is  
268 considered as a C<sub>4</sub> crop model for studying the biology of other millets and biofuel grasses (Lata  
269 et al., 2013; Muthamilarasan and Prasad, 2015). Therefore, the Beijing Genomics Institute, China  
270 and the US Department of Energy - Joint Genome Institute have sequenced the foxtail millet  
271 genome (Zhang et al., 2012; Bennetzen et al., 2012). As foxtail millet serves as a rich source of  
272 genes, alleles, or QTL for genetic improvement of major cereals and bioenergy grasses, large-  
273 scale genomic resources were developed including simple sequence repeats (SSRs) (Pandey et  
274 al., 2013; Zhang et al., 2014), intron length polymorphisms (Muthamilarasan et al., 2014), eSSRs  
275 (Kumari et al., 2013), miRNA-based markers (Yadav et al., 2014) and transposable-elements

276 based markers (Yadav et al., 2015). Moreover, open access online databases such as foxtail  
277 millet marker database (FmMDB) (Suresh et al., 2014), foxtail millet miRNA database  
278 (FmMiRNADb) (Khan et al., 2014) and foxtail millet transposable elements-based marker  
279 database (FmTEMDB) (Yadav et al., 2015) have been constructed. In addition to development of  
280 these markers, their utility in population genetics, association mapping, comparative genomics  
281 and genomics-assisted breeding have also been demonstrated (Muthamilarasan and Prasad,  
282 2015). An allele-specific marker developed from an SNP in *SiDREB2* gene linked to drought  
283 tolerance in foxtail millet (Lata et al., 2011) is being used in allele mining and MAS for drought  
284 tolerance (Lata and Prasad, 2012; Lata and Prasad, 2013).

285  
286 In pearl millet, three major QTL for grain yield with low QTL  $\times$  environment interactions were  
287 identified across a range of post-flowering moisture environments (Bidinger et al., 2007). One of  
288 these major QTL accounted for up to 32% of the phenotypic variance of grain yield under  
289 drought. The effects of this QTL were validated in two independent MABC programs in which  
290 30% improvement in general combining ability for grain yield expected from this QTL under  
291 terminal drought stress was recovered in introgression lines, based on the information provided  
292 by the markers flanking the QTL (Yadav et al., 2011). Compared to other crops, research on  
293 millets is at initial stage. Being predominantly climate resilient crops, millets could serve as  
294 valuable source of novel genes, alleles and QTL for stress tolerance, which needs to be identified  
295 and characterized. The close phylogenetic relationships between millets and other cereals could  
296 enable the introgression of novel alleles, genes or QTL identified in millets for better agronomic  
297 traits into other cereals towards ensuring food security under changing climate.

298  
299 **Forest and fruit tree crops**

300  
301 Clones of trees, namely populus, pinus, abies, and eucalyptus are used in afforestation, as they  
302 are dedicated to the production of wood and other wood-derived products. Therefore, it is  
303 imperative to develop climate-change resilient clones or populations of these forest trees. Several  
304 procedures have been developed for high-throughput DNA genotyping and genome-wide marker  
305 identification in forest trees. The genome complexity reduction DArT (Alves-Freitas et al., 2011)  
306 and whole-exome capture using in-solution target enrichment (Neves et al., 2011) have been  
307 tested successfully for genome-wide marker identification needed for GS in *Pinus taeda*.  
308 Considering the importance of genome sequence for development of genetic markers, Conifer  
309 Genome Project (<http://www.pinegenome.org/cgp/>) has been launched with an aim of promoting  
310 advance genome research in loblolly pine (*P. taeda*; 21.7 Gbp/1C;  $n = 12$ ), white pines (*Pinus*  
311 subgenus *strobus*; 25.1 Gbp/1C;  $n = 12$ ), as well as *Sequoia sempervirens* (31.4 Gbp/1C;  $n = 3x$   
312 = 33) and Douglas-fir (*Pseudotsuga menziesii*; 18.6 Gbp/1C;  $n = 13$ ). An extensive genetic  
313 resources and gene catalog was developed for *P. taeda* and *Picea glauca* (white spruce; 19.7  
314 Gbp/1C;  $n = 12$ ) (<http://www.pinegenome.org/cgp/>). The GENOAK project  
315 (<http://urgi.versailles.inra.fr/Projects/GenOak>) aims to establish a high quality reference genome  
316 sequence for pedunculate oak (*Quercus robur*; 905 Mbp/1C;  $n = 12$ ). The *Eucalyptus grandis*  
317 (640 Mbp/1C,  $n = 11$ ) genome has been deciphered  
318 ([http://phytozome.jgi.doe.gov/pz/portal.html#!info?alias=Org\\_Egrandis](http://phytozome.jgi.doe.gov/pz/portal.html#!info?alias=Org_Egrandis)) and will benefit agro-  
319 foresters utilizing this fast-growing hardwood tree to support industries based on Eucalypt fibre  
320 and hardwood products, and the production of Eucalypt feedstock for cellulosic biofuels.

321 Importantly, this would assist in accelerating forest tree breeding for fast response to the need of  
322 adapted populations facing environmental modifications induced by climate change.

323  
324 Fruit trees are also as important as the pulse and cereal crops and climate-change resilient clones  
325 or populations of fruit tree crops are necessary to maintain the source of nutrients that help the  
326 daily intake of healthy food ingredients. Genomics-based breeding approaches, along with  
327 bioinformatics capability and other omics resources will be the essential components of perennial  
328 fruit crop breeding and particularly, to adapt their cropping to combat or mitigate climate change  
329 effects. Genome sequencing and annotation projects include perennial fruit crops such as apple  
330 (Velasco et al., 2010), banana (Velasco et al., 2007), cacao (D'Hont et al., 2012), grape (Argout  
331 et al., 2011), peach (Ahmed et al., 1992) and sweet orange (Xu et al., 2013). The advances in  
332 genome sequencing, along with high-resolution genetic mapping and precise phenotyping will  
333 accelerate the discovery of functional alleles and allelic variations that are associated with traits  
334 of interest for perennial fruit crop breeding. However, very less progress has been made in this  
335 aspect and particularly, enhancing climate resilience needs more attention. For achieving this,  
336 genetics and genomics methodologies could provide the toolbox for identifying genomic regions  
337 associated with the desired phenotype, and assist the selection from the wild genetic resources of  
338 the parental plants that will be intercrossed to provide the progenies for commencing breeding  
339 procedures for recurrent selection.

340

#### 341 **Genomics-assisted breeding strategies for climate resilient traits**

342  
343 Genomics-based approaches and NGS have ushered in sequence-based breeding strategies that  
344 will expedite the dissection and cloning of the loci controlling abiotic stress tolerance, while  
345 providing unparalleled opportunities to tap into wild relatives of crops, hence expanding the  
346 reservoir of genetic diversity available to breeders (Tuberosa et al., 2011; Edwards et al., 2013)  
347 (Figure 1). In view of the complexity and low heritability of yield, particularly under drought and  
348 other abiotic stresses, GS will provide the most powerful approach to raise the yield potential to  
349 the levels required to meet the fast-increasing global demand in cereal grain. However, MAS will  
350 remain a valid option for major loci or QTL, while QTL cloning will become a more routine  
351 activity facilitated through a more widespread utilization of high-throughput, accurate  
352 phenotyping (Araus et al., 2014), sequencing (Imelfort et al., 2009; Edwards et al., 2012), and  
353 identification of suitable candidate genes through 'omics' profiling (Gupta et al., 2013). Cloned  
354 QTL will provide novel opportunities for genetic engineering for abiotic stress tolerance and for  
355 a more targeted search for novel alleles in wild germplasm (Salvi et al., 2007). Even with the  
356 application of advanced genomics technologies, mitigating the negative effects of climate change  
357 on crop productivity will remain a daunting undertaking. This requires a multidisciplinary and  
358 integrated approach, which will eventually allow plant breeders to more effectively select crops  
359 that are more resilient to climate change and ensure a sufficient level of food security for the  
360 decades to come.

361

#### 362 **Flowering time and drought adaptation**

363  
364 Temperature influences crop development in concert with additional floral pathways such as  
365 day-length (photoperiod), which collectively control floral transition through interconnected  
366 genetic pathways. Global warming will result in increased ambient temperature with unchanged

367 photoperiods at given latitudes. Annual plants generally respond to increased temperatures with  
368 accelerated growth and development, having shortened lifecycles, less opportunity for  
369 photosynthesis (Reynolds et al., 2010), a shorter reproductive phase and lower yield potential  
370 (Ainsworth and Ort, 2010). There is also an increased risk of damage to reproductive tissue  
371 caused by the coincidence of high temperatures and sensitive developmental stages. Therefore,  
372 detailed knowledge of the interplay between genetic control of flowering, allelic variants,  
373 epistatic interactions and phenotypic variations in varied growth conditions is necessary in order  
374 to identify breeding targets for climate change scenarios.

375  
376 There are increasing number of germplasm resources including precise near isogenic lines  
377 (NILs) (Bentley et al., 2011; Bentley et al., 2013) as well as next-generation populations such as  
378 multi-founder populations (e.g., multi-parent advanced generation intercross populations), which  
379 have been developed in wheat (Mackay et al., 2014) and other crops to facilitate further research  
380 and validation of climate-smart crops. New variation incorporated into elite backgrounds from  
381 landraces, ancestral or wild crop relatives (e.g., [www.wheatisp.org](http://www.wheatisp.org)) also offers potential for  
382 discovery of functional variation for manipulating flowering time to suit future climate  
383 permutations. However, initial work should focus on understanding the effect of flowering time  
384 on yield potential across environments and environmental stresses. Identifying the potential  
385 utility of loci of minor effect and/or which affect various stages of reproductive development  
386 could offer the ability to shorten or lengthen various phases of the flowering process, thereby  
387 enabling fine-tuning of flowering to suit particular regional climatic conditions, and to adapt to  
388 any changes in these conditions.

389  
390 In case of drought tolerance, multi-disciplinary research is underway to improve plants' response  
391 to drought and water-use efficiency. With the advent of molecular breeding, QTL identification  
392 and QTL use in breeding programs assist in developing new cultivars with improved drought  
393 tolerance. In maize, extensive work has been carried out to investigate the role of root in  
394 mitigating the negative effects of drought. QTL for root traits have been described in a number  
395 of maize populations (Ruta et al., 2010; Tuberosa et al., 2011; Hund et al., 2011) in which some  
396 QTL showed a concurrent effect on grain yield performance under drought (Landi et al., 2005).  
397 Recently, Syngenta and Pioneer-DuPont deployed proprietary genomics-assisted approaches to  
398 select drought-tolerant maize hybrids (Agrisure Artesian™ and AQUAmax™, respectively)  
399 (Cooper et al., 2014). The superior performance of these maize hybrids in the severe drought that  
400 plagued the US Corn Belt in summer 2012 underlines their validity under dry soil conditions  
401 (Cooper et al., 2014). In wheat, yield QTL were shown to be associated with components of  
402 other traits, supporting the prospects for dissecting crop performance under abiotic stress  
403 conditions into its physiological and genetic components in order to facilitate a strategic  
404 approach to breeding (Reynolds et al., 2008). At least 15 different populations have been used to  
405 map drought adaptation in rice and four regions were identified as key for yield or yield  
406 components under stress, and drought-tolerant component traits were identified across  
407 populations with interval lengths of 35-64 cM (Kamoshita et al., 2008). The first region (on  
408 chromosome 1) was associated with grain yield drought-resistance traits, plant type traits (Zhang  
409 et al. 2001a), and QTL for cell-membrane stability (Tripathy et al., 2000) and osmotic  
410 adjustment (Lilley et al., 1992), and root traits (Robin et al., 2003). Second genomic region on  
411 chromosome 4 was rich in root trait QTL (Zheng et al. 2000; Hemamalini et al. 2000; Zhang et  
412 al. 2001b; Kamoshita et al. 2002; Nguyen et al. 2004; Boopathi et al. 2005) under well-watered

413 and drought conditions. The third region located on chromosome 8 contained QTL for plant  
414 water status, grain yield, cell membrane stability, osmotic adjustment, rate of non-stomatal water  
415 loss and deep and thick root traits (Zheng et al. 2000; Hemamalini et al. 2000; Zhang et al.  
416 2001b; Nguyen et al. 2004; Boopathi et al. 2005). The fourth important region for drought was  
417 located in chromosome 9, which was characterized by QTL for root traits, cell membrane  
418 stability, plant water status, leaf rolling and leaf drying, biomass, number of grains per panicle,  
419 relative spikelet fertility and delay in flowering time (Hemamalini et al. 2000; Tripathy et al.  
420 2000; Zhang et al. 2001a; Kamoshita et al. 2002; Price et al. 2002a, 2002b; Robin et al. 2003;  
421 Courtois et al. 2003; Babu et al. 2003; Zheng et al. 2003; Lafitte et al. 2004; Lanceras et al. 2004;  
422 Nguyen et al. 2004; Boopathi et al. 2005; Gomez et al. 2005; Jearakongman 2005; Li et al. 2005;  
423 Xu et al. 2005; Yue et al. 2006). Since these four regions are consistently reported to be  
424 associated with drought response and stood above the average, these regions should be part of  
425 marker assisted breeding program for drought tolerance in rice.

426

### 427 **Cold and heat stress tolerance**

428

429 Tolerance to freezing temperatures is the most important component for winter survival, but also  
430 of considerable importance is the capability to withstand combinations of stresses due to  
431 desiccation, wind, ice-encasement, heaving, low light, snow cover, winter pathogens, and  
432 fluctuating temperatures. Resistance to desiccation through the maintenance of cell membrane  
433 integrity and retention of cellular water is essential, and it is unsurprising that the same genetic  
434 response to the onset of freezing temperatures is often observed with drought or salinity stress  
435 (Yue et al., 2006). Indeed, cold acclimation (CA) can frequently improve adaptation to a mild  
436 drought stress and *vice versa* (Seki et al., 2002). Major genes or gene clusters involved in the  
437 control of frost and drought adaptation are located on a region of the long arm of Triticeae group  
438 5 chromosomes. Traits such as winter hardiness (Thomas et al., 1993), vernalization response  
439 and frost tolerance (Hayes et al., 1993; Galiba et al., 1995), cold- and drought-induced ABA  
440 production (Laurie et al., 1995), and osmotic stress-tolerance (Galiba et al., 1993), have all been  
441 mapped to this region. Across the grasses and cereals, this chromosome region has been a major  
442 focus for genome research and for plant breeding. It may well be as consequence of climate  
443 change from the perspective of future crop design that in many locations where winter  
444 temperatures are on the increase and favoring continued plant growth, and where this is  
445 accompanied by a decrease in winter rainfall, that unseasonal winter droughts will ensue, which  
446 will require a new breeding strategy for common stress tolerance to both stress factors.

447

448 The C-repeat binding factor (CBF) genes are key regulators of the expression of COR (cold  
449 regulated genes), which are conserved among diverse plant lineages such as eudicots and  
450 monocots. The CBF transcription factors recognize the cis-acting CRT/DRE (C-  
451 repeat/dehydration responsive element) element in the regulatory regions of COR genes  
452 (Stockinger et al., 1997). Twenty CBF genes have been identified in barley (*H. vulgare*), of  
453 which 11 are found in two tight tandem clusters on the long arm of chromosome 5H in the same  
454 region as the *Fr-H2* frost tolerance locus (Skinner et al., 2006; Francia et al., 2007). An  
455 orthologous genomic region in *T. monococcum* contains similar CBF gene clusters located at the  
456 *Fr-A<sup>m</sup>2* frost tolerance QTL (Miller et al., 2006; Vagujfalvi et al., 2003). Studies of the  
457 organization of CBF cluster in barley and wheat have shown that the number of CBF genes at  
458 *Fr-H2/Fr-A1* locus may vary among cultivars with winter forms having a higher copy number of



459 some CBFs (Francia et al., 2007; Knox et al., 2010). The co-segregation of CBF gene clusters  
460 with barley *Fr-H2* and wheat *Fr-A<sup>m</sup>2* frost tolerance loci, their role in cold acclimation  
461 (Stockinger et al., 1997), and the association of transcript levels of CBF genes with frost  
462 tolerance loci (Vagujfalvi et al., 2003) make them obvious candidates for one of the two major  
463 frost tolerance QTL on Triticeae group 5 chromosomes. The locations of two frost  
464 tolerance/winter survival QTL on the chromosome 5F of forage grass *Festuca pratensis*  
465 correspond most likely to the *Fr-A1* and *Fr-A2* loci on wheat homoeologous group 5A  
466 chromosomes. One of these QTL (*QFt5F-2/QWs5F-1*) has *FpCBF6* as a candidate gene shown  
467 to be rapidly up-regulated during CA (Alm et al., 2011).

468  
469 Conversely, many crops are currently grown in places, where high temperature prevails and field  
470 studies have indicated that increase in temperature reduces grain yield of cereals and legumes by  
471 4 to 14% per 1°C increase (Quarrie et al., 1997). Current projections indicate that both day and  
472 night temperatures are likely to increase during this century (Hall et al., 2000) and ideally, heat-  
473 resistant cultivars should not only have higher grain yields in hot environments but also similar  
474 grain yields as current cultivars in cool atmosphere. Public plant breeding programs have  
475 developed heat-resistant cultivars of cowpea, common bean, tomato and Pima cotton that are  
476 more productive in hot environments than standard cultivars. Commercial plant breeding  
477 companies rarely divulge their methods, but from the available heat-resistant commercial  
478 cultivars, it is clear that they have had some success in breeding for heat tolerance during  
479 reproductive development in tomato and upland cotton. In the past, very few public or  
480 commercial plant-breeding programs gave any emphasis to breeding heat-resistant cultivars. For  
481 crops that are sensitive to high temperatures during reproductive development the way forward is  
482 to give great emphasis to breeding and finding DNA markers for heat adaptation during  
483 flowering.

#### 484 485 **Submergence and salinity tolerance**

486  
487 Waterlogging is a major problem for cereal production worldwide, as in sodic environments,  
488 soils are affected by seepage from irrigation canals, and excess wetting due to rainfall or floods,  
489 especially if it rains after irrigation. Genetic diversity in waterlogging tolerance was reported in  
490 various crops, including wheat, barley, maize and oats (Kerr, 1986), and diverse mechanisms  
491 have been associated with tolerance. They are associated with phenology and morphology,  
492 nutrition balances, metabolism, including anaerobic catabolism and anoxia tolerance, and post-  
493 anoxia damage and recovery (Setter et al., 2003). Tolerance of flooding during germination and  
494 early seedling growth is essential for direct seeding of rice, both in rainfed and irrigated areas,  
495 where even waterlogging is sufficient to cause considerable reduction in crop stand because of  
496 their high sensitivity to hypoxia at this stage (Setter et al., 2003). Substantial genetic variation  
497 was recently observed in the ability to germinate and establish in flooded soil. Tolerant  
498 genotypes are capable of catabolizing starch reserves in seeds germinating under hypoxia into  
499 simple sugars, and use them as substrates to generate energy via anaerobic pathways for the  
500 growing embryos (Miro et al., 2013; Septiningsih et al., 2013). Several QTL originating from a  
501 few rice landraces were identified, two of them with large effects; on chromosome 9 (*qAG-9-2*)  
502 (Setter et al., 2003) and chromosome 7 (*qAG-7-1*) (Septiningsih et al., 2013). These QTL are  
503 being targeted for cloning and for use through MAB, which could eventually result high yielding  
504 rice cultivars for deep-water areas. Recently, tolerant rice varieties carrying *SUB1* locus became

505 available. *SUB1* is a major QTL on chromosome 9 that has been cloned and the gene responsible  
506 for tolerance identified as *SUB1A-1*. This gene encodes an ERF that suppresses ethylene-  
507 mediated responses under submergence, and subsequently limits excessive elongation and halts  
508 chlorophyll degradation. Both processes are essential to prevent carbohydrate starvation of the  
509 submerged plants. These varieties can survive 4 to 18 days of complete submergence, with yield  
510 benefits of 1 to over 3.5 t ha<sup>-1</sup> (depending on flood duration and floodwater condition), compared  
511 to current farmers' varieties, and without any undesirable effects on the features of the original  
512 varieties (Singh et al., 2009; Bailey-Serres et al., 2010; Ismail et al., 2013; Mackill et al., 2012).  
513 Additional genes are being targeted for submergence tolerance, and once identified they could be  
514 combined with *SUB1* for higher tolerance during germination and stagnant flooding. Further, the  
515 progress made in rice could potentially be exploited to improve flood tolerance of other crop  
516 species and provide more resilient varieties for current and future flood-affected areas.

517  
518 Progressive salt accumulation due to excessive irrigation with poor water quality coupled with  
519 poor or improper drainage results in high salt levels (Tuberosa, 2012). Numerous studies have  
520 characterized responses mediated by salt stress in different plant species and highlighted the  
521 complexity of the mechanisms involved (Munns et al., 2008). Studies have shown that few major  
522 loci and many minor ones were associated with various aspects of salinity tolerance. The best  
523 known for rice is *Saltol* on chromosome 1 (Thomson et al., 2010), which possesses a major gene,  
524 *OsHKT1;5* (Ren et al., 2005). In wheat, two members of *HKT* gene family (including the wheat  
525 *HKT1;5* orthologue) have also been shown to co-localize with major QTL (Byrt et al., 2007).  
526 Apparently, many other QTL have been identified in rice and other cereals, and several of them  
527 are common across mapping populations. In addition, numerous genes have been identified  
528 through functional genomics studies of salt-stress responses, and many of them lead to improved  
529 tolerance when they are over- or under-expressed. Some even co-localize with QTL regions, but  
530 there has been no further success in using them for breeding tolerant cereal crops or in cloning  
531 additional QTL.

532  
533 Current approaches in this aspect involves using NGS to target major QTL for cloning, and to  
534 develop efficient SNP and InDel marker systems to manipulate these loci during MAB. The  
535 substantial genetic diversity in the tolerance of salt stress and mechanisms used by various crops  
536 to cope with increasing salt concentrations in soil and water provides opportunities to enhance  
537 salt-stress tolerance in cereals. However, this will require large investments to dissect and  
538 combine the genetic determinants of various traits. Developing such cultivars that are highly  
539 tolerant of salt stress is a requisite to cope with the current worsening climatic conditions and to  
540 meet the urgent need of producing more food from marginal land and limited water resources.

#### 541 **Host plant resistance to pathogens and pests**

542  
543  
544 The climatic variables including changes in temperature, rainfall and atmospheric chemical  
545 composition along with predominantly elevated CO<sub>2</sub> levels would accelerate the reproduction  
546 time of many plant pathogens and pests, thereby increasing their infection pressure on crop  
547 plants (Boonekamp, 2012). Climate change may also affect the ability of plants to express  
548 resistance to pathogens and insects. Experiments conducted by Huang et al. (2009) indicated a  
549 45% increase in leaf lesions in oilseed rape, when the surrounding temperature was increased by  
550 5°C. This finding suggests that the expression and efficacy of R-genes in host plants may be

551 affected where both crop and associated pathogen or pest are affected by climatic variation. This  
552 may be influenced by different combinations of selective pressures, and each may respond to  
553 these pressures at different rates. Improved understanding on the host-pest/pathogen interactions  
554 and knowledge on different effects of climate change is a requisite for the development of  
555 climate-resilient crops. To date, research on the impact of climate change on plant diseases has  
556 been limited, with many studies focusing on the effects of a single atmospheric constituent or  
557 meteorological variable on the host, pathogen, or the interaction of the two, under controlled  
558 conditions. Whilst this work is a valuable base to start from, the combined effects of biotic and  
559 abiotic stresses must be studied (Ramegowda and Senthil-Kumar, 2015).

560  
561 Recent advances in genome sequencing and genotyping assays allow for many strategies at the  
562 genomics level, which can be developed to understand the impact of climate change on plant  
563 diseases. The newly available genome sequences for plants, pathogens and pests provide the  
564 resources to study their co-evolution in response to climate change. An understanding of the co-  
565 evolution of genes responsible for virulence and resistance will lead to improved plant protection  
566 strategies and provide a model to understand plant-pathogen and plant-insect interactions in  
567 diverse species. Though it is important to understand the genomics of disease resistance in crop  
568 species, and how allelic differences are altering resistance, combining this with studies of CWR  
569 or germplasm collections further allows the identification of novel variants. These variants can  
570 be used for the introgression of novel resistance genes into cultivars, utilizing the germplasm for  
571 breeding and developing new cultivars, or genetic engineering with the advantageous genes.  
572 Taken together, it is obvious that the impact of climate change on disease resistance is difficult to  
573 predict and is likely to be variable depending on the crop and local environment. However, crop  
574 disease is an important factor when considering the impact of climate change on food production  
575 and intensive studies applying advanced genomics tools will be required to help ameliorate the  
576 impact of climate change on future cropping scenarios in relation to plant disease.

577

### 578 **Genomic engineering tools for targeted mutagenesis by editing genes for adaptation**

579

580 Plant breeders have been applying mutagenesis to induce genetic variation for increasing crop  
581 yield and later, the strategy has been used for improving the adaptability of crop plants. Initially,  
582 X-ray radiation was used as a mutagen since it was readily available to researchers (Muller,  
583 1927). Subsequently, gamma-ray radiation has been used to induce point mutations, although  
584 chromosomal mutation were also produced (Devreux and Mugnozza, 1964). From recent times,  
585 chemical mutagenesis is being practiced since they are easy to use, do not require any specialised  
586 equipment, and can provide a very high mutation frequency. Compared to radiation methods,  
587 chemical mutagens tend to induce SNPs rather than chromosomal mutations. Currently, chemical  
588 mutagens, such as Ethyl methanesulfonate (EMS) are being used to induce random mutations  
589 into the genome and have become a useful complement to the isolation of nuclear DNA from  
590 mutated lines by TILLING (Targeting Induced Local Lesions in Genomes) technology and  
591 screening of the M<sub>2</sub> population at the DNA level using advanced molecular techniques. Single  
592 mutations in specific genes for adaptation could be identified by cleavage of mismatched bases  
593 formed as a result of repeated melting and reannealing of PCR products amplified from a pool of  
594 alleles for the specific gene in a pool of DNA from a set (usually 8) of M<sub>2</sub> plants (McCallum et  
595 al., 2000; Caldwell et al., 2004). NGS can efficiently accelerate the identification of mutations at  
596 the whole-genome level. Promotor mutations and mutation in other regulatory elements

597 responsible for the downstream effect can be identified by qPCR, microarray and RNA-seq.  
598 Once a mutant allele is identified within gene(s) of interest, those mutations may be linked to a  
599 specific phenotype for stress resistance by backcrossing the mutant to the parental line. This  
600 TILLING approach is a reverse genetics procedure to associate a mutant allele to its phenotype.  
601 Of note, TILLING can also be used for a forward genetic approach by screening phenotypes for  
602 adaptation to stresses and then characterize the phenotype using a combination of whole-genome  
603 resequencing, linkage maps and microarrays, to gain a broad picture of gene expression changes  
604 due to the newly introduced SNPs compared to the original line.

605  
606 Other molecular tools and resources are now available for genome engineering and reverse  
607 genetics experiments in crop plants in order to implement precise manipulation of genetic  
608 building blocks and regulatory machinery that underlie yield improvement under stress condition  
609 and directly correct harmful mutations by genome editing (Hsu et al., 2014). Targeted genome  
610 engineering has emerged as an alternative to classical plant breeding and transgenic methods to  
611 improve crop plants and ensure sustainable food production (Belhaj et al., 2013; Osakabe and  
612 Osakabe, 2015). Currently, four types of engineered nucleases are used for genome editing:  
613 engineered homing endonucleases/meganucleases (EMNs) (Silva et al., 2011), zinc finger  
614 nucleases (ZFNs) (Townsend et al., 2009), transcription activator-like effector nucleases  
615 (TALENs) (Cermak et al., 2011), and CRISPR (clustered regularly interspaced short palindromic  
616 repeats)/Cas (CRISPR-associated)9 (Cong et al 2013; Mali et al 2013).

617  
618 Sequence-specific nucleases (SSN) enable precise genome engineering by introducing DNA  
619 double-strand breaks (DSB) that subsequently trigger endogenous DNA repair by non-  
620 homologous end joining (NHEJ) or homology directed repair (HDR) recombination mechanisms  
621 in different species. Site-directed mutagenesis mediated via NHEJ can be achieved while HDR  
622 cause directed gene knock-in/correction at specific locations in the genome (HDR uses a DNA  
623 template to replace the DNA sequence at the break point). NHEJ functions throughout the entire  
624 cell cycle whereas HR is restricted to late S/G2 phases in the cell cycle. Therefore, NHEJ is the  
625 major DSB repair pathway in eukaryotes. Belhaj et al. (2013) and Osakabe and Osakabe (2015)  
626 display a clear illustration of genome editing assays in model (*Arabidopsis thaliana* and  
627 *Nicotiana benthamiana*) and crop (*Oryza sativa*, *Triticum aestivum* and *Sorghum bicolor*) plant  
628 species. These SSN effects generate targeted genome modifications including mutations,  
629 insertions, replacements and chromosome rearrangements and have been induced in a variety of  
630 important crops, such as rice, maize, wheat, barley and soybean. Each technology has advantages  
631 and disadvantages with regard to cost, ease of construction, efficiency of targeting, and  
632 specificity (Chen and Gao, 2014; Gao, 2015). Major advantages of ZFNs are related to the  
633 acceptance of the technology as no transgenic is produced because viral vectors have been used  
634 for expressing transiently the nuclease, which do not integrate into the genome. However, it has  
635 disadvantages such as difficulties to design the experiments, limited number of target sites, and  
636 the regeneration of juvenile and chimeric mutated plants when custom-designed nucleases have  
637 been delivered in tree explants.

638  
639 CRISPR was first discovered as an immune system of prokaryotes, which subsequently became a  
640 powerful tool for genome editing in eukaryotes (Gaj et al., 2013). It has emerged as an  
641 alternative to classical plant breeding and transgenic methods to improve crop plants. Plant  
642 transformation and co-expression of the Cas9 with a chimeric guide-RNA (gRNA) targeting a

643 GN19NGG motif in the gene of interest, results in a double-strand non-self DNA cleavage on  
644 both strands at a specific site near the protospacer adjacent motif (PAM) (Jinek\_et al., 2012;  
645 Gasiunas\_et al., 2012). The Cas9 from *Streptococcus pyogenes* (SpCas9) recognizes 5'-NGG-3'  
646 as the PAM sequence. PAM plays an important role in target binding and cleavage by the Cas9-  
647 gRNA complex. CRISPR/Cas9 has greater number of advantages, including the straightforward  
648 construct design and assembly and the achievement of high mutation rates, matching or  
649 exceeding those obtained with ZFNs and TALENs. Only 20 nucleotides in the gRNA need to be  
650 modified to recognize a different target making unnecessary the sophisticated protein  
651 engineering for each target that is crucial for the other SSN approaches.

652  
653 So far, the CRISPR-Cas9 technology has been applied in *A. thaliana* (Feng et al., 2013, 2014;  
654 Jiang et al., 2013; Li et al., 2013; Mao et al., 2013) *Nicotiana benthamiana* (Jiang et al., 2013;  
655 Nekrasov et al., 2013; Li et al., 2013), *Oryza sativa* (Feng et al., 2013, Jiang et al., 2013, Mao et  
656 al., 2013, Shan et al., 2013; Feng et al., 2013; Xie and Yang, 2013; Miao et al., 2013; Zhang et  
657 al., 2014), *Solanum lycopersicum* (Brooks et al., 2014), *Sorghum bicolor* (Jiang et al., 2013),  
658 *Triticum aestivum* (Wang et al., 2014), *Citrus sinensis* (Jia and Wang, 2014) and *Populus*  
659 *tremula x alba* (Zhou et al., 2015). Genes controlling traits of importance for adaptation have  
660 also been edited by CRISPR-Cas9 technology. gRNAs were designed to target three specific  
661 sites of the rice *OsMPK5* gene which encodes a stress-responsive rice mitogen-activated protein  
662 kinase and the targeted mutation of *OsMPK5* enhanced rice disease resistance (Xie and Yang,  
663 2013). Transgenic wheat plants carrying mutations in *TaMLO-A1* allele were susceptible to  
664 powdery mildew diseases (Wang et al., 2014). The bacterial blight susceptibility genes,  
665 *OsSWEET14* and *OsSWEET11*, were targeted for mutation at the promoter region in  
666 Arabidopsis, tobacco, sorghum and rice (Jiang et al., 2013). High CRISPR-Cas9 mutational  
667 efficiency was achieved for three 4-coumarate:CoA ligase (4CL) genes, *4CL1*, *4CL2* and *4CL5*,  
668 associated with lignin and flavonoid biosynthesis in *Populus tremula x alba* (Zhou et al., 2015).

669  
670 Moreover, accelerated breeding of crop plants carrying targeted gene mutation(s) without foreign  
671 DNA is possible using CRISPR genome editing. In fact, although transgene Cas9 and selectable  
672 marker integration is hemizygous, CRISPR editing at the target loci is biallelic. Therefore, in  
673 autogamous plants, self-fertilization of T<sub>1</sub> plants will provide 25% of the T<sub>2</sub> plants without the  
674 transgene but maintaining the edited gene in homozygosity. In self-incompatible or dioecious  
675 perennial woody trees, biparental hemizygous Cas9/sgRNA transformation and biallelic-edited  
676 gene can be produced. Controlled crosses between male and female primary transformants with  
677 confirmed biallelic mutations should produce transgene-free, biallelic mutants in 25% of the  
678 progeny (Zhou et al., 2015). Taken together, genome engineering for targeted mutagenesis by  
679 editing genes serves as a potential strategy for generating elite cultivars of crop plants with  
680 durable climate resilience.

## 681 682 **Concluding remarks**

683  
684 It is realized that the global climate change is going to impose a severe threat on agricultural  
685 productivity worldwide, and thereby challenging food security and nutritional security. Advances  
686 in technology, particularly transgene-based and molecular breeding technologies have facilitated  
687 the development of elite genotypes with durable adaptation to climate change. Noteworthy,  
688 crossbreeding coupled with genomics forms genomics-assisted breeding, which is playing a

689 significant role for developing climate change resilient crops. Excellent model organisms for  
690 climate change such as foxtail millet and green foxtail (for C<sub>4</sub> photosynthesis), *Brachypodium*  
691 (grass model) have been identified for deciphering traits that need to be decoded and introgressed  
692 in the crop plants. Advances in DNA sequencing technologies and the sequencing of CWR,  
693 along with advanced genomics tools will expedite the identification of novel genes and key  
694 regulatory regions of stress tolerance towards the development of new cultivars with durable  
695 resistance. Although, the impact of climate change on crop's resistance is difficult to predict and  
696 is likely to be variable depending on the crop and environment, genomics-assisted breeding  
697 could contribute significantly to reduce the impact of climate change on future cropping  
698 scenarios.

### 700 **Conflict of Interest Statement**

701  
702 The authors declare that the research was conducted in the absence of any commercial or  
703 financial relationships that could be construed as a potential conflict of interest.

### 705 **Author contributions**

706  
707 C.K. conceived and outlined the review; M.M., R.H., D.E., R.S., M.A., J.B., A.B., M.B., J.B.,  
708 H.C., M.C., L.J.C., J.C., A.C.O., C.D.P., H.D., S.E., P.G., A.G., A.H., K.H., G.T.H., S.H.,  
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717 [http://www.icrcgc.org/ncc\\_manuscript.docx](http://www.icrcgc.org/ncc_manuscript.docx).

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1280 **Figure legends**

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1282 **Figure 1:** Flow-chart demonstrating the steps involved in generating climate resilient crops using  
1283 genomics and next-generation sequencing technology.

Figure 1.TIF

