Tansley review

Barley: a translational model for adaptation to climate change

Ian K. Dawson¹*, Joanne Russell¹*, Wayne Powell², Brian Steffenson³, William T. B. Thomas¹ and Robbie Waugh¹,⁴

¹Cell and Molecular Sciences, James Hutton Institute (JHI), Invergowrie Dundee, DD2 5DA, UK; ²CGIAR Consortium Office, Montpellier Cedex 5, France; ³Department of Plant Pathology, University of Minnesota, St Paul, MN 55108, USA; ⁴Division of Plant Sciences, College of Life Sciences, University of Dundee at JHI, Invergowrie Dundee, DD2 5DA, UK

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Summary

Barley (Hordeum vulgare ssp. vulgare) is an excellent model for understanding agricultural responses to climate change. Its initial domestication over 10 millennia ago and subsequent wide migration provide striking evidence of adaptation to different environments, agro-ecologies and uses. A bottleneck in the selection of modern varieties has resulted in a reduction in total genetic diversity and a loss of specific alleles relevant to climate-smart agriculture. However, extensive and well-curated collections of landraces, wild barley accessions (H. vulgare ssp. spontaneum) and other Hordeum species exist and are important new allele sources. A wide range of genomic and analytical tools have entered the public domain for exploring and capturing this variation, and specialized populations, mutant stocks and transgenics facilitate the connection between genetic diversity and heritable phenotypes. These lay the biological, technological and informational foundations for developing climate-resilient crops tailored to specific environments that are supported by extensive environmental and geographical databases, new methods for climate modelling and trait/environment association analyses, and decentralized participatory improvement methods. Case studies of important climate-related traits and their constituent genes – including examples that are indicative of the complexities involved in designing appropriate responses – are presented, and key developments for the future highlighted.

I. Introduction

Barley (Hordeum vulgare ssp. vulgare) is cultivated globally, in both highly productive, high-input agricultural systems and in subsistence, low-input agriculture across a wide range of environments. It

*These authors contributed equally to this work.

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is an important source of feed and forage for livestock, and of food and drink for humans (Newton et al., 2011). Although production is currently greatest in high-income economies (e.g. France, Germany and Russia), it is a crop that spans the developed and developing world, with low- and middle-income economies also relatively large producers (e.g. Ethiopia, Iran, India, Iraq, Morocco, Syria and Turkey; FAOSTAT, 2014). Despite its global value, in recent decades yields have stagnated in several regions, including parts of Europe (Fig. 1). Even where yields have increased, they have generally not kept up with increases in wheat yields, as illustrated again by European data, partly as a consequence of the generally greater investment in wheat breeding, but probably also because of ‘inherent’ limitations in barley potential that are difficult to overcome. Somewhat worryingly, in southern European countries both wheat and barley yields have stagnated, a situation partly attributable to the emerging impacts of climate change (Brisson et al., 2010). All predictions indicate that these impacts will only be exacerbated in the future.

The threats to food security as a result of anthropogenic climate change (IPCC, 2013) include direct impacts on crop production from changes in water availability, salination and temperature, as well as indirect impacts from changes in disease and pest prevalence (Pérez-López et al., 2009; Högy et al., 2013; Yau & Ryan, 2013). These threats must be tackled through a variety of approaches that include different models of economic development, altered patterns of international trade and improved targeting of agricultural investments (Nelson et al., 2010). As a wide range of outcomes are possible, crops that are subjected to this range of influences are useful for understanding how to integrate research and development priorities (Olesen et al., 2011). With its wide environmental range, different end uses and wide variety of users, barley has emerged as an excellent model for both investigating and responding to the impacts of various climate change scenarios (Newton et al., 2011). For example, possible responses include avoidance (circumvention) of climate-related stress factors based on shifts in the cultivation of varieties adapted to planting in spring (‘spring’ types) versus autumn (‘winter’ types). A realistic danger, however, is that such a response simply hides the deeper complexities of climate adaptation. New introductions of tolerance or resistance traits may be required to facilitate shifts based on other abiotic and biotic pressures that have not been previously experienced. The interactions between climate change and other global challenges such as declining soil fertility and increasing human populations (Rockström et al., 2009) complicate these already complex issues, and highlight that multiple pressures must be addressed in concert (Newton et al., 2011).

In this review, we relate possible responses of agriculture to climate change using barley as a model. The varied environmental

![Fig. 1 Annual barley (Hordeum vulgare ssp. vulgare) grain yield data for the 50-yr period 1961–2010, according to FAOSTAT (2014). Data are arithmetic means across countries by geographical region, except in the case of Syria where data are extracted from the Asia/Eurasia mean to show the high inter-annual variability in reported yields there. Illustrative countries among the top 50 barley grain producers world-wide are included in the compilation (based on mean annual production values, 2003–2012, FAOSTAT figures). To be included, countries had to have data reported at FAOSTAT for every year of the time series. Trends in yield are indicated for regions. These show that in recent decades yields have stagnated in several important production regions, such as in parts of Europe. Data on wheat grain yields are also indicated for European regions. Countries included in regional compilations: northern Europe = Denmark, Finland, Ireland, Latvia, Lithuania, Norway, Sweden and the UK; southern Europe = Bulgaria, Greece, Italy and Spain; other Europe = Austria, France, Germany, Hungary, the Netherlands, Poland and Romania; Asia/Eurasia = Afghanistan, China (mainland), India, Iran, Iraq, Kazakhstan, Syria and Turkey; Africa = Algeria, Morocco, South Africa and Tunisia (Ethiopia, a country of interest because of its relatively high barley production, could not be included in the Africa group because only incomplete data are available at FAOSTAT). Note that for low-income nations, where much barley is produced under subsistence agriculture, yield data are likely to be less accurate than for high- and middle-income countries.](image-url)
production envelope of barley compared, for example, with wheat provides for numerous responses that can inform options for a wide range of other crops cultivated within the same envelope. The exploration of synergy between these options can shed further light on genetic-level responses to environmental change. From the widest perspective, almost all crops share the needs for improved tolerance to stress factors and for a reduction in the gap between potential and realized yields, and such research on barley is therefore generally informative (Newton et al., 2011). Lessons from barley are especially relevant to other cereals, particularly to other members of the Triticeae, including hexaploid bread wheat (Triticum aestivum), one of the world’s most significant food sources (FAOSTAT, 2014). Bread wheat has a more complex and larger genome than diploid barley that results from its origin by hybridization of three ancestor species. Consequently, the dissection and evaluation of adaptive traits in wheat is more difficult (Brenchley et al., 2012; IBGSC, 2012). Low chromosome number and ease of cross-breeding reinforce the utility of barley as a relevant biological model (Saisho & Takeda, 2011). Furthermore, farmer-participatory methods for genetic improvement have been widely studied in barley (Ceccarelli et al., 2013). These methods, which integrate decentralized and centralized approaches for genetic improvement, have been suggested as important for addressing climate-related stresses in crop plants, especially in low-income nations where farmers can afford few inputs, and where public and private funds for varietal development are limited.

In the following sections of this review we explore specific resources that contribute to barley’s utility as a model for studying and devising responses to climate change that can then be applied to other crops. We describe predictive approaches used to indicate the impact of climate change on barley production, and the gaps that exist and that may impair our ability to respond to environmental change. We next summarize some of the key genes and traits that are involved in responding to particular climate-related stresses, and the diversity of these in the barley gene pool, with an emphasis on a range of biotic stresses. The penultimate section describes practical responses to climate change that incorporate different genetic improvement approaches. We conclude by highlighting particular areas for future research and development.

II. Barley resources for climate change interventions

1. Barley accessions including genetic stocks

Since the mid-1990s, progress in conventional plant breeding has slowed at least in part because the different allelic forms of genes needed for sustainable and resilient production are not found in elite crop varieties (McCouch et al., 2013). Recent opinion (Feuillet et al., 2008) has returned (see Harlan & Martini, 1936 for earlier recognition for barley) to the importance of genetically diverse landraces and wild relatives as sources of alleles to ensure the future efficiency and productivity of agriculture (McCouch et al., 2013). In elite barley cultivars, a particular feature is the lack of haplotypic diversity at centromeric regions because of limited recombination, with landraces and wild relatives a potential repository of alternative haplotypes (IBGSC, 2012). Given the large ex situ seed collections available globally for use by scientists and breeders, barley is an excellent model to explore the hypothesis that landraces and wild germplasm can contribute usefully to modern crop improvement. Although there is significant duplication, > 400 000 accessions of Hordeum are found in gene banks globally (Knüpfner, 2009) and a significant proportion are barley landraces presumed to be adapted to a wide range of environments. In addition, many accessions are of the fully inter-fertile wild progenitor of domesticated barley, Hordeum vulgare ssp. spontaneum (hereafter referred to as wild barley; other wild Hordeum species referred to below are described by their binomial) (GENESYS, 2014). Together, these accessions provide an enormous potential resource for allele mining. As an example, the majority of northwestern European spring barley varieties have broad-spectrum powdery mildew (caused by Blumeria graminis f. sp. hordei) resistance conditioned by a naturally occurring recessive resistance allele at the Mildew resistance locus o (Mlo) gene, mlo-11, that originated from a small number of Ethiopian landrace accessions. These landrace accessions were collected by German expeditions in 1937 and 1938, probably from the highlands in the southwest of the country (Jørgensen, 1992; Piffanelli et al., 2004). Ethiopian landraces are also an important source of the Yellow dwarf (Yd) virus resistance gene Yd2 (Burnett et al., 1995).

Barley has been a model for genetic and cytogenetic studies for over 80 yr (Smith, 1951; Ward, 1962). The effects of temperature on meiosis have been studied, providing an indication of the possible impacts of climate change on recombination (Higgins et al., 2012) and fertility (with, e.g. possible decreased yields). Numerous morphological and cytological mutants have been produced, with Knüpfner (2009) reporting > 25 000 genetic stocks, including wheat-barley addition and substitution lines that may facilitate the introduction of favourable traits such as salt and drought tolerance from barley into wheat (Molnar-Lang et al., 2014), and crucial composite cross populations (Allard, 1999; discussed in Section V). Mutant stocks generally have more extreme morphological and developmental phenotypes than natural allele series, and have recently become a powerful tool to facilitate proof of gene function (e.g. Ramsay et al., 2011; Houston et al., 2013; Mascher et al., 2014). Reverse genetics approaches such as targeting induced local lesions in genomes (TILLING; Colbert et al., 2001) for the identification of mutant alleles can be similarly informative, and transgenic genetic modification (GM) methods based on transcription activator-like effectors (TALE; Boch, 2011) or clustered regularly interspaced short palindromic repeats (CRISPR; Barrangou et al., 2007; Wang et al., 2014) technologies are exceptionally promising emerging alternatives.

Genetic stocks include lines containing chromosomal segments from the wild barley genome and Hordeum bulbosum introgressed into H. vulgare ssp. vulgare (e.g. Brown et al., 1988; Matus et al., 2003; Johnston et al., 2009; Honsdorf et al., 2014). Numerous efforts have been made to introgress favourable alleles from wild barley into breeding populations through backcrossing. These include those of Schmalenbach et al. (2008) to introduce resistance to powdery mildew and leaf rust (Puccinia hordei) and Kalladan et al. (2013) for the improvement of various agronomic traits under post-anthesis drought. The Australian barley variety Tantangara
carries resistance to leaf scald (caused by *Rhynchosporium commune* (formerly *Rhynchosporium secalis*)) introgressed from wild barley (Friedt et al., 2011), and wild barley accessions have been used routinely in the International Center for Agricultural Research in the Dry Areas’ (ICARDA’s) crossing programme for stress environments (Lakew et al., 2011, 2013; Cecarelli, 2014). In the case of *H. bulbosum*, in the secondary gene pool of the cultivated crop, important sources of disease and pest resistance, as well as abiotic stress tolerances, have been identified (e.g. Pickering et al., 1998, 2006; Morrell & Clegg, 2011).

Under the assumption that further beneficial alleles for crop improvement do indeed exist in landrace and wild barley material and in the wider *Hordeum* gene pool, the continued development and implementation of strategies for the efficient quantification and utilization of these resources are underway.

2. The development of genomic tools

Understanding barley genetic resources and using them efficiently are underpinned by the continued development of ever more powerful genetic tools and genomic information. In 2012, the International Barley Genome Sequencing Consortium delivered a barley genome sequence assembly with > 79,000 transcript clusters, including over 26,000 ‘high-confidence’ genes with homology support from other plant genomes (IBGSC, 2012). The haploid genome size is 5.1 gigabases and the genome contains a high proportion of repetitive DNA. As a result of its close evolutionary distance and extensive conservation of synteny, barley is a useful genomic model for wheat (Brenchley et al., 2012). The genome assembly was supported by a physical map consisting of a large library of barley bacterial artificial chromosomes (BACs) and BAC-end sequences (Ariyadasa et al., 2014). High-density, mapped single nucleotide polymorphism (SNP) arrays (e.g. Close et al., 2009; Comadran et al., 2012), and more recently exome (i.e. the gene coding part of the genome) capture arrays that facilitate reduced representation genome-wide re-sequencing by avoiding the vast amount of noncoding DNA in the barley genome (Mascher et al., 2013a, b, 2014), are now available. These provide for high-resolution genome-wide genetic profiling in a manner that is not yet possible for many plant species (IBGSC, 2012).

The availability of such powerful genomic approaches makes the identification of genome-wide gene-sequence-level genetic variation relatively straightforward in appropriately equipped laboratories. However, to rationally exploit this observed genetic diversity, it remains necessary to empirically evaluate alleles for their phenotypic effect in an appropriate genetic background, for example, by comparisons between near-isogenic lines. Mobilizing and tracking putatively advantageous variants has become much easier using a combination of molecular diagnostics for the target alleles and high-throughput genome-wide molecular markers (Comadran et al., 2012). For example, Wendler et al. (2014) applied exome capture-based re-sequencing, a custom multiplex SNP genotyping assay, and genotyping-by-sequencing, to reveal the precise location and extent of *H. bulbosum* introgressions into cultivated barley. Multi-parent populations such as nested association mapping (NAM; Yu et al., 2008) and multi-parent advanced generation inter-cross (MAGIC; Cavanagh et al., 2008) allow a population-based evaluation of allelic effects. Schnaithmann et al. (2014) demonstrated the use of a barley NAM population, HEB-5, to map quantitative trait loci for leaf rust resistance. The advent of more dense genetic and phenotypic data, and genetic approaches such as genome-wide association studies (GWAS), genomic selection and transcriptional profiling, provide alternative mechanisms to identify genes contributing resilience to abiotic and biotic stresses and deploy them in breeding programmes (Franks & Höffmann, 2012). The beauty of GWAS for an inbreeding crop such as barley is that, once different germplasm panels have been established and genomic data assembled, new phenotypic associations can be tested for in perpetuity without the need for further crossing programmes.

3. History of domestication

Applications of resources such as those discussed in the previous section extend beyond gene identification for future breeding. They are also powerful for investigating the evolutionary history of crops over past centuries and millennia (e.g. for barley, Morrell & Clegg, 2007; Lister et al., 2009; Russell et al., 2011; Forsberg et al., 2014). By revealing the processes and timings of domestication, germplasm flows and key domestication traits, such research is able to guide the trajectory of future domestimations in the context of climate change. In addition, because natural climate has varied markedly within the long period of barley cultivation and domestication (Fuller, 2007), it should be possible to relate early domestication stages and germplasm dispersals directly to past climatic fluctuations (Chen et al., 2014). Genetic data reinforced by prehistoric archaeobotanical information chart barley’s migration from its centres of origin in the Fertile Crescent and Central Asia, south into the Horn of Africa, north to Scandinavia, west around the Mediterranean to the western fringes of Europe and Africa, and further east into Asia (e.g. Harlan & Zohary, 1966; Harlan, 1975; Fuller et al., 2012). A crucial element of this research is that barley’s origins are predominantly hot and dry environments, so ancient samples are often well preserved in archaeological sites. This is to the extent that DNA can sometimes be extracted and amplified from seeds that are several thousand years old to reveal contemporaneous genetic structures (e.g. experiences with archaeological barley samples at Qasr Ibrim, Egypt; Palmer et al., 2009).

Such a thorough understanding of domestication processes as is available for barley has been established for only very few crops, usually because of limits in the available evidence in the archaeobotanical record (see Meyer et al., 2012; the authors reviewed domestication information for 203 major and minor food crops; for a discussion specifically on the domestication of grasses, see Glemin & Bataillon, 2009). In addition, although there has been displacement by modern varieties in some regions, older barley landraces still thrive in many locations, simply because they are preferred by local farmers. Causal links between adaptation to cultivation in these environments and sequence-level genetic variation have been described for traits such as flowering time and growth habit (e.g. Turner et al., 2005; Yan et al., 2006; Comadran et al., 2012; Zakhrabekova et al., 2012; explored further in Section IV).
III. Predictions for barley production and genetic resources based on environmental modelling

1. Modelling production of the barley crop

Barley yields are generally considered to vary less under changing weather conditions than those of wheat and most other small grains (Cossani et al., 2011; Newton et al., 2011). FAOSTAT (2014) yield data, however, indicate similar levels of response between barley and wheat, suggesting the resilience of barley grain production should not be overestimated (Fig. 1). Worldwide, FAOSTAT data show that the average yield of wheat since 2000 is 10% greater than that of barley and 34% greater in highly productive environments such as the UK. We interpret this as meaning that the lower resilience of other cereal crops is at least in part a function of their higher yield potential. Modelling barley production under future climate scenarios is imprecise because of the high dimensionality of climate, but a range of approaches has been taken considering CO₂ fertilization effects, temperature, water and other abiotic stresses (but not often biotic stresses), as illustrated by European examples (Trnka et al., 2004, 2011; Rötter et al., 2013). Rötter et al. (2013), in one of the most detailed analyses to date, combined agroclimatic indicators from gridded weather data with crop growth simulations to assess climate change impacts for spring barley production in Finland. The authors found that a combination of CO₂ fertilization and earlier sowing because of a warmer spring may lead to small yield increases for current barley varieties under most climate scenarios on favourable soils, but not under extreme scenarios and on poor soils. The practical outcome was a recommendation that producers use several different barley varieties given the uncertainty in projections. Trnka et al. (2011) undertook an analysis of climate change effects on agriculture covering the whole of western and central Europe, using spring barley as the reference ‘crop surface’ as it was grown across all the environmental zones investigated. Using the AGRICLIM model (Trnka et al., 2010), along with daily climatic data and a range of agroclimatic indices, they found clear signs of deteriorating agroclimatic conditions for many environmental zones. This was caused by increased drought stress and a shortening of the active growing season. The authors predicted that some European regions will become increasingly squeezed between a cold winter and a hot summer, and that there will be increased variability in climatic suitability. The authors suggest the need to diversify production as one means to improve resilience.

Other authors have modelled the effects of climate change on the quality of the barley crop. Erbs et al. (2010) demonstrated that an increase in CO₂ concentrations can result in lower protein content in the grain, while Högy et al. (2013) found that an increase of 2.5°C in soil temperature in heated field plots in Germany decreased grain starch content as well as yield for the spring barley variety Quench. By contrast, in the latter study, the amounts of some proteinogenic amino acids increased substantially, notably aspartate, glycine, alanine, arginine, valine and tryptophan. In another example, Anker-Nilssen et al. (2008) reported an increase in grain β-glucan content and the molecular weight of the water-soluble fraction of barley grain grown at higher temperature, leading to an increase in viscosity and hence potential problems in using the crop for brewing and feeding to mono-gastric animals. Thitsaksakul et al. (2012) reviewed gene expression studies on the effects of heat stress on key genes involved in starch metabolism and found that nearly all were down-regulated in barley. These studies indicate that tradeoffs between different components of grain quality for various uses may be required.

Crop modelling shows the advantage of barley breeders working in conjunction with a range of partners to identify what traits are required to combat climate-induced stresses in specific production regions, how these traits are likely to interact, and what other management approaches need to be put in place, such as a change in sowing date or the season of planting.

2. Modelling the distribution of landraces and wild relatives

Ecological niche modelling of the distribution of wild barley is a useful tool for understanding past, and planning for future, climate impacts. Based on modelling the distribution under past, present and future climates using bioclimatic variables from WorldClim (2014) and a MaxEnt approach (Elith et al., 2011), Russell et al. (2014) identified potential refugial regions for the Last Glacial Maximum (LGM, c. 20 000 BP) that are candidate areas for sampling high genetic diversity in wild barley (Fig. 2). A major putative refuge identified in the eastern Mediterranean corresponded with high genetic diversity revealed in that region within the Wild Barley Diversity Collection (the WBDC; Steffenson et al., 2007; also see Jakob et al., 2014). Wild barley accessions from this environmentally-diverse refugial region are well represented in global gene banks (GENESYS, 2014) and are likely to be a particularly useful source of variation for response to abiotic stresses. Interestingly, comparing the modelled distributions of wild barley for the LGM and current climate indicates that range expansion has been mostly longitudinal (north–south), and this may be expected to limit adaptive variation in day-length traits in the gene pool needed for latitudinal (north–south) expansion (Diamond, 2002; but see Section IV). Turning to the future, the models of Russell et al. (2014) suggest that, by the 2080s, habitat for wild barley will be lost from large parts of Iran, (northern) Syria and (southern) Turkmenistan (Fig. 2). These regions could therefore be excellent targets for studying adaptation to abiotic stresses, either by observing in situ stands or by trials on gene bank accessions from the relevant locations. Time-series evaluation of populations would be a particularly effective approach for monitoring adaptation (Franks & Hoffmann, 2012). Few such studies have been undertaken for barley or other crop progenitors, although in an experiment in Israel, Nevo et al. (2012) examined wild barley populations sampled first in 1980 and then again in 2008. Accessions sampled in 2008 flowered significantly earlier under glasshouse conditions, which may be a climate-related effect (Craufurd & Wheeler, 2009). Extending ecological niche modelling to the wider Hordeum gene pool is also advantageous for providing further insights (Jakob...
et al., 2007, 2009, 2010), but to date examples where past, present and future modelling of distributions has been combined with the genetic analysis of extant stands are few.

Sophisticated modelling methods to analyse conservation gaps in gene pools of crop landraces and wild relatives are now available, which consider environment variables as well as taxonomy and geography, among other factors (Ramirez-Villegas et al., 2010; CWR, 2014). When these methods are applied to barley landraces, gaps in ex situ collections are apparent in large parts of Eurasia and elsewhere (GAP Analysis, 2014; although this analysis was limited by a low level of geo-referencing). Vincent et al. (2012) concluded that, to support the in situ conservation of wild Hordeum members, a reserve should be established in the Mendoza Province of Argentina, where most species richness is found. Maxted & Kell (2009) identified the in situ conservation of Hordeum chilense (in the tertiary gene pool of barley, but with a number of interesting characteristics for breeding, including high resistance to leaf rust; Patto et al., 2001) in central-southwest Chile and western Argentina as a priority. Future modelling of Hordeum conservation gaps could consider a much wider range of environmental variables such as soil properties, solar radiation, evapotranspiration indices and length of the growing period – data which can be readily obtained for geo-referenced accessions through open access online portals (e.g. FAO, 2014) – as well as a wider range of other types of information (Dawson et al., 2011).

Fig. 2 Potential wild barley (Hordeum vulgare ssp. spontaneum) distribution under current climate compared with distributions under past and predicted future climates, based on ecological niche modelling. (a) The current climate compared with the Last Glacial Maximum (LGM); areas lost and gained under current climate are indicated. Horizontal hatching indicates the region of highest allelic richness in a range-wide survey of genetic diversity based on the Wild Barley Diversity Collection and nuclear simple sequence repeat markers. High allelic richness corresponds with a putative refugial region from which many accessions of wild barley have been collected. (b) The current climate compared with the 2080s (A2 medium- to high-emission trajectory for global warming; data from CCAFS, 2014b); areas lost and gained under future climate are indicated. Comparing the LGM with the current climate, range expansion in wild barley appears to have been mostly longitudinal, with potential implications for the type of adaptive traits accumulated. The figure is adapted from Russell et al. (2014), where descriptions of the ecological niche modelling and genotyping methods are given.

3. The focused identification of germplasm strategy (FIGS) and environment–genotype associations

Statistical approaches have been developed to combine environmental and geographical data with trait information in the focused identification of germplasm strategy (FIGS). The assumption is that, when particular environmental parameters and adaptive traits are associated, then ecogeographical regions that are more likely to contain germplasm with specific attributes can be identified (Endresen, 2010). Based on an initial set of training samples, appropriate ‘best bet’ subsets of accessions can then be assembled for screening from more extensive germplasm collections. Alternatively, locations where new germplasm collections should be undertaken in order to try and locate a particular trait can be defined. Using FIGS, El Bouhssini et al. (2011) identified a subset of 510 from a total of 17 000 accessions of wheat for field evaluation of resistance to the Russian wheat aphid, a potential reduction of 97% for such testing. From this subset, 12 promising new sources of resistance to the pest were identified. In another example, Endresen et al. (2011) found FIGS effective for trait mining among wheat and barley accessions for resistances to wheat stem rust (Puccinia graminis f. sp. tritici) and barley net blotch (Pyrenophora teres f. teres), respectively.

To help understand the relationship between the environment and the genome, bioclimatic variable–SNP associations have been
analysed in the WBDC (Fang et al., 2014). These comparisons revealed associations with both temperature and precipitation variables for SNPs in genes on chromosome 2H that contribute to low-temperature tolerance and/or that are cold regulated, and with precipitation variables on chromosome 5H. Traditionally, most such association studies are based on population samples to establish genomic controls rather than individuals (e.g. the BAYENV software; Coop et al., 2010). In the case of barley, which is typically sampled as individuals rather than as populations, the construction of pseudo-populations or alternative methods of analysis are required (Hancock et al., 2011). In this regard, however, a number of barley population samples are already available that merit more research. The wild Barley1K collection from Israel (Hübner et al., 2009) and the famous collections from Evolution Canyon and elsewhere in Israel by Nevo et al. (1997, 2012) are notable examples. Other populations include the landrace collections made by Eva Weltzien in Jordan and Syria in 1981, when she sampled seeds from 100 individual plant heads in each of 70 different stands (Weltzien, 1988; studied e.g. by Ceccarelli et al., 1987; Russell et al., 2003). Perhaps most interesting of all are the wild and landrace barley populations referred to by Jana & Pietrzak (1988), where matched stands were sampled from each of 23 locations in Greece, Jordan, Syria and Turkey and characterized with isozymes. Further research on Jana & Pietrzak’s (1988) material is little reported, but it is held in the Plant Gene Resources of Canada collection (Fu & Horbach, 2012). Assuming that individuals can be clearly assigned into landrace and wild categories, these populations would be excellent candidates for association studies, because they provide an internal control for geographical structuring (i.e. location-specific paired stands) and the opportunity to test associations across barley categories coevolved at the same sites.

IV. Examples of important genes and traits under climate change

1. Abiotic stresses and climate change

In a recent review assessing barley’s resilience as a crop, Newton et al. (2011) described many of the genes that may be involved in responding to important abiotic and biotic stresses. In the current review, our purpose is to provide examples where research has involved the characterization of landrace and wild material, to exemplify the importance of the barley gene pool with respect to responses, rather than to provide a comprehensive survey. We also illustrate the complexities of responses by considering abiotic and biotic stress interactions. In Table 1, a number of genes related to abiotic stresses are listed, with information on landrace and wild barley characterization. The examples given that relate to vernalization requirement, photoperiod (day-length) sensitivity and flowering time illustrate the complexity of trait interactions in responding to climate-related stresses. The ‘funnel-like’ topology of flowering time regulation, where several environmental inputs converge and for which a variety of alternative upstream loci could be selection targets, has been extensively studied in Arabidopsis (Arabidopsis thaliana; Fornara et al., 2010; Weinig et al., 2014), and a broadly similar situation pertains for barley (the genetic basis for flowering cues reviewed by Andrés & Coupland, 2012). Comadran et al. (2012), for example, outlined how the winter growth habit lifestyle of wild barley was suboptimal as migration after initial domestication took place, with strong selection for acquisition of day-length insensitivity and loss of the vernalization requirement. They identified an association between time to flowering (as well as yield and thousand-kernel weight) and a chromosome location corresponding to the EARLIINESS PER SE locus EPS2. They identified EPS2 as the barley homologue of the Antirrhinum majus phosphatidyl ethanolamine-binding protein (PEPB) gene CENTRORADIALIS (CEN) and showed that alternative natural alleles were responsible for regulating time to flowering. By geographically mapping these alternative alleles, they concluded that variation in HvCEN was an important factor in enabling geographical range extension and was at least one component in the gradual differentiation between winter- and spring-sown barley gene pools. Interestingly, adaptation at EPS2 involved selection and subsequent enrichment of pre-existing genetic variants from within the wild barley gene pool, rather than the selection of mutations after domestication.

Wild barley is generally considered to exhibit a ‘winter’-type growth habit (Saisho et al., 2011). Similarly, ‘winter barley’ varieties are planted in autumn when the soil is warm and the first rains have fallen, establish quickly, survive relatively mild winters, and flower in spring before the heat of summer. Where winters are harsh, barley is generally planted in the spring (‘spring barley’), exploiting long and relatively mild summers, and flowers later. For the spring crop, predictions of elevated temperatures and lower rainfall under climate change during the summer growing season may adversely affect both yield and quality. Sowing winter (or facultative) barley in the autumn may then be beneficial, as the crop will mature earlier in the summer and effectively avoid drought (facultative barleys have a low vernalization requirement but remain ‘cold tolerant’; von Zitzewitz et al., 2005; see also Rollins et al., 2013 for an alternative situation). Partly as a response to this scenario, a number of traditional spring barley breeding programmes in the USA have initiated efforts in breeding winter/facultative types. The paradoxical challenge created by increased summer temperatures is, then, the need for the Upper Midwest USA to develop varieties with sufficient low-temperature tolerance (LTT) to survive long and extremely cold winters and variable spring weather conditions (von Zitzewitz et al., 2011; Fisk et al., 2013; TCAP, 2014). Surprisingly, considering their low latitude of origin, five WBDC accessions consistently survived in field trials over recent winters in Minnesota (Fig. 3). In Europe, the same scenario of increased summer temperatures and reduced rainfall has resulted in efforts to improve the melting quality attributes of winter barley varieties, so that they better compete with the spring barley types traditionally used for malting, but whose production is now threatened (IMPROMALT, 2014).

2. Biotic stresses and climate change

In common with other crops (Walters et al., 2012; West et al., 2012), a major effect of climate change will be to alter the incidence
Table 1  Illustrative examples of genes and sequences in the *Hordeum vulgare* gene pool that may play a role in climate-related responses to abiotic stresses for the barley crop

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<td><strong>Vernalization:</strong> Vernalization (VRN) genes VRN-H1, VRN-H2 and VRN-H3 interact to determine flowering response to temperature, involving up-regulation, repression and activation</td>
<td>Variation at these loci allows adaptation to a range of temperatures. For example VRN-H3 (HvFT1) links the photoperiod and vernalization pathways</td>
<td>Variation in the promoter, first intron and copy number of VRN-H3 influences flowering phenotype and is affected by day length. 102 North American spring, winter and facultative varieties were classified into seven different haplotypes for VRN-H3 based on promoter SNPs (Cuesta-Marcos et al., 2010). Yan et al. (2006) identified two VRN-H3 intron haplotypes, TC winter types and AG spring types. Casas et al. (2011) identified similar intron haplotypes geographically structured according to latitude in 159 Spanish landrace accessions (the Spanish Barley Core Collection). Copy number variation for HvFT1 observed in 49 spring/facultative – but not in 60 winter – European landraces (Loscos et al., 2014)</td>
</tr>
<tr>
<td><strong>Photoperiod sensitivity:</strong> Photoperiod (PPD) genes PPD-H1 and PPD-H2 regulate flowering time</td>
<td>Modifications to photoperiod response have allowed barley to flower under different day lengths and expand from its origins. Variation in response to day length means barley can flower earlier, avoiding increased summer temperatures and reduced water availability</td>
<td>Turner et al. (2005) identified 23 polymorphic SNPs, seven of which were nonsynonymous and distinguished between ppd-H1 (late flowering and nonresponsive to daylight) and Ppd-H1 (flowering under long days) alleles in 14 cultivars (seven late and seven early flowering) and 10 wild barleys (early flowering). Jones et al. (2008) discovered a further causative SNP at PPD-H1 in a set of 194 mostly European landraces, which accounted for observed variation in flowering time and showed a latitudinal cline in variation from south to north across the European continent. At PPD-H2, Casao et al. (2011) examined the distribution of dominant functional (generally associated with spring barleys) and recessive nonfunctional (associated with modern winter barley varieties) alleles in 159 landraces from the Spanish Barley Core Collection, which are mostly winter types. They observed the presence of the dominant (‘spring’) allele in the majority of landrace lines, at a much higher proportion than in modern winter varieties. This may represent part of an adaptation syndrome to Mediterranean conditions.</td>
</tr>
<tr>
<td><strong>Flowering time:</strong> controlled by genes including HvCEN and HvLUX1</td>
<td>Variation confers an advantage under different environmental conditions, particularly in latitudinal range</td>
<td>In a survey of 215 wild barleys, 184 landraces and 739 (more modern) cultivars, Comadran et al. (2012) identified 13 haplotypes at HvCEN, with three major haplotypes shared across the three barley categories. North–south and east–west gradients were observed in frequencies for the major haplotypes. In the circadian clock regulator HvLUX1, seven SNPs and six indels defined 16 haplotypes in a survey of 36 barley cultivars (including landraces) and 52 wild accessions (including <em>agriocrithion</em>). Greater variation was found in wild barley (contained all 16 haplotypes compared with two only in cultivars). This variation was not geographically structured (Campoli et al., 2013)</td>
</tr>
<tr>
<td><strong>Cold and frost tolerance genes:</strong> C-repeat binding factor (CBF) genes, including HvCBF1, HvCBF3, HvCBF4, HvCBF6, HvCBF9 and HvCBF14, are partially responsible for controlling tolerance</td>
<td>Key regulators genes. Major role in winter survival. Also involved in drought and salinity tolerance. Increase in copy number (Knox et al., 2010) important in adaptation?</td>
<td>Fricano et al. (2009) found reduced diversity at HvCBF3, HvCBF6, HvCBF9 and HvCBF14 in modern varieties (113 accessions) compared with landraces (76 accessions) and wild barleys (36 accessions). HvCBF1, HvCBF3 and HvCBF4 sequenced by Wu et al. (2011) in 188 Tibetan wild barley lines identified three, 8 and 13 haplotypes, respectively, including a specific HvCBF4 haplotype associated with salt tolerance</td>
</tr>
</tbody>
</table>
Table 1 (Continued)

<table>
<thead>
<tr>
<th>Genes/sequences and overview of function</th>
<th>Importance for climate change adaptation</th>
<th>Examples of knowledge of genetic variation in advanced varieties, landraces and wild barley</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Drought tolerance: more than a dozen Dehydrin (Dhn) genes have been</strong> <strong>described. Several are up-regulated by dehydration. Some are induced by low-temperature stress</strong></td>
<td>Variation adaptive to drought conditions</td>
<td>Yang et al. (2009) sequenced Dhn1 for 47 wild barley individuals from Evolution Canyon (EC) in Israel. 45 SNPs were identified organized into 29 haplotypes that were differentiated across 'African' and 'European' slopes. Expression patterns related to SNPs in the promoter region. In further analysis at EC, Yang et al. (2011) identified 11 genotypes from 48 accessions tested with a 342-bp insertion 5′ UTR in Dhn6. The insertion showed a nonrandom distribution geographically and was associated with earlier up-regulation of Dhn6 following dehydration treatment. Holková et al. (2010) assessed allelic variation at Dhn4 and Dhn7 in eight spring and 22 winter cultivars from Europe. Indels were associated with frost tolerance, which was confirmed through test crossing. Kilian et al. (2006) tested 25 range-wide-sampled wild and 20 Turkish domesticated (including landrace) barley lines and found lower variation in domesticated material at Dhn9, with two haplotypes compared with 12 in wild accessions (the same disparity applied to other tested loci). Jakob et al. (2014) tested 275 range-wide-sampled accessions of wild barley and found 28 haplotypes in Dhn9 compared with nine haplotypes in 140 other barley accessions (advanced cultivars, landraces and three <em>agriocrithon</em>)</td>
</tr>
<tr>
<td><strong>Other examples:</strong> Small heat shock protein (HSP) 17.8 gene; Light-harvesting chlorophyll a/b-binding protein (Lhcb) 1 gene, which may be down-regulated under stress conditions; Eibi1, which codes for an ATP-binding cassette subfamily G full transporter protein</td>
<td>Plant tolerance to heat stress and other stress environments (HSP17.8). Increased photosynthetic efficiency (Lhcb1). Tissue protection from environmental stresses, particularly in drought-prone environments (Eibi1)</td>
<td>Xia et al. (2013) investigated HSP17.8 variation across 39 wild barley and 171 landrace accessions sampled widely from their ranges. 11 SNPs including 10 from the coding region (six mis-sense mutations and four synonymous nucleotide changes) formed nine haplotypes. Wild accessions exhibited greater diversity than cultivated barley. Xia et al. (2012) investigated Lhcb1 variation across 39 wild barley and 253 cultivars/improved genotypes (mostly landraces) sampled widely from their ranges. 17 SNPs formed 31 distinguishable haplotypes. Wild accessions exhibited greater diversity than cultivated barley. Ma et al. (2012) identified climatically clustered promoter haplotypes in Eibi1 representing transcription factor binding sites using 112 wild barleys sampled from a drought gradient in Israel. Evidence of regulation by gibberellin (GA), light and abiotic stresses</td>
</tr>
</tbody>
</table>

and intensity of barley diseases (Newton et al., 2011). The three factors that must be present for disease to occur are a susceptible host, a virulent pathogen and a favourable environment (the ‘disease triangle’; Agrios, 2005), and changes in climate can alter the distribution, incidence and severity of disease by influencing one or all of these. In the case of direct effects on the host, for example, disease resistance genes may be temperature sensitive, as exemplified by the complex of barley genes at the reaction to *Puccinia graminis* (*rpm*) 4-Mediated Resistance Locus (RMRL, formerly designated the *rpm4/Rpm5* complex) on chromosome 5H that confers wide-spectrum resistance to the wheat (*P. graminis* f. sp. *tritici*) and rye (*P. graminis*. f. sp. *secalis*) stem rust pathogens (Steffenson et al., 2009). The RMRL complex is critically important because it is the only source of resistance to the widely virulent African stem rust pathotype TTKSK (isolate synonym Ug99), to which over 97% of barley varieties world-wide are susceptible (Steffenson et al., 2013). In this case, at least one of the functional genes at the RMRL locus is extremely temperature sensitive and, coupled with the mesothetic reaction (i.e. the mixed range of different infection types occurring on the same leaf) that barley seedlings often exhibit to stem rust (Steffenson et al., 1993), this makes this host–pathogen interaction a good model for investigating the effects of subtle changes in temperature on disease development (Table 2). For the pathogen, temperature fluctuations can directly affect relative growth and reproduction, the timing of initial inoculum production for infection of crops at congenial growth stages, and survival during the off-season (West et al., 2012). With elevated temperatures, epidemics of stem rust...
earlier in the latter region, several cycles of pathogen reproduction and infection are effectively neutralized during the vulnerable post-heading period in early summer. Conversely, in the Upper Midwest region of the USA, powdery mildew and leaf scald are rarely observed in spring-sown crops, but are increasingly being observed in autumn-sown experimental trials (B. Steffenson, pers. obs.). Bi-parental and more recently multi-parental GWAS populations have been used to map resistances to biotic stresses in barley (e.g. Comadran et al., 2011; BCAP, 2014; TCAP, 2014; Thomas et al., 2014; as well as in the WBDC, of which more discussion later in this paragraph). Genes and quantitative trait loci controlling resistance to diseases including African stem rust, Fusarium head blight, spot blotch (Cochliobolus sativus), net blotch, leaf rust and powdery mildew have been successfully mapped (e.g. Massman et al., 2010; Berger et al., 2013; Zhou & Steffenson, 2013a,b, 2014). In the WBDC, variation for resistance/susceptibility has been phenotyped for several diseases including stem rust (pathotype TTKSK), leaf rust, net blotch and spot blotch; in each case, geographical trends in the distribution of resistant accessions are observed (Figs 4, 5). For example, all of the leaf rust-resistant accessions of the WBDC originated from the Fertile Crescent or North Africa and none from Central Asia. Interestingly, this corresponds with the habitat range of the main alternate host of the leaf rust pathogen, Star of Bethlehem lily (Ornithogalum umbellatum), which serves not only as a source of inoculum for infection of barley, but also as a platform for the generation of genetic variation in the pathogen, which undergoes sexual hybridization on it. It appears that long coevolution between the cereal, alternate host and pathogen has contributed to the high frequency of resistance found in wild barley accessions within the Fertile Crescent and North Africa. Similarly, barberry (Berberis spp.), the alternate host of P. graminis which causes stem rust, is found in Central Asia, where most of the resistant WBDC accessions are located. The geographical localization of resistance supports the use of FIGS (see Section III) for subsampling among a wider collection of wild barley accessions to enhance the efficiency of identifying new resistance (or, conversely, susceptibility) alleles. With the advent of greatly expanded SNP arrays, high-resolution mapping of these resistances in the genome through GWAS will be enhanced in wild barley over the cultivated crop because of the lower level of linkage disequilibrium in wild material (Caldwell et al., 2006).

V. Practical approaches for responding to climate change

1. Options to respond to change

The perceptions of farmers, researchers and policy makers condition responses to climate change. Olesen et al. (2011) gathered information on possible adaptation options in European agriculture, based on the views of agro-climatic and agronomy experts from 26 countries, ranging from Scandinavia to the Mediterranean. Their results indicated that farmers are active agents in responding to climate change, altering the timing of cultivation and selecting alternative crop species and varieties. In
only one-third of the countries covered in the survey, however, were farmers considered to have a good understanding of the consequences of change. The importance attributed in the survey to different adaptation measures to support spring barley production varied by geographical region and demonstrated the importance of multi-faceted, location-specific responses. The most consistently identified threats to production were rain at sowing and drought, with the former being more important in northern regions and rarely a problem in southern ones, whereas drought problems were only considered rare around the French and Iberian Atlantic coasts.

Some pragmatist crop breeders suggest that moving germplasm to more extreme latitudes may provide appropriate breeding material for more northerly or southerly climates, but, as alluded to in Section IV above, increased day-length variation as latitudes increase can be expected to interact with flowering time genes found in more equatorial germplasm, which may well result in a completely different growth pattern that may not provide a sustainable escape from drought. Furthermore, it is important to remember that Mediterranean barley varieties effectively escape drought rather than tolerate it. In the case of wheat, for example, Semenov et al. (2014) provided evidence to suggest that varieties from more Mediterranean-like regions are not inherently more drought tolerant than those from the UK, but that they are earlier and therefore more likely to escape severe effects. Assuming that interactions with flowering time genes are broken, climate analogue modelling can indicate appropriate sites where varieties from more equatorial latitudes should do well at more extreme latitudes as climate changes (CCAFS, 2014a). This allows planning for potential varietal redistributions and identifies novel production environments for which reallocations do not provide a solution (Ramirez-Villegas et al., 2011).

2. Evolutionary participatory barley breeding

In low-income nations where the potential for agricultural inputs to modify and respond to climate change is limited, decentralized crop improvement responses that maintain genetic diversity and widen resilience in landscapes have been advocated (Ceccarelli et al., 2001). How, though, can the gap between decentralized and existing centralized breeding approaches be bridged? This has been the subject of much discussion, as sometimes the two approaches have been considered to be in opposition (see discussion in Thro & Spillane, 2000; Bellon & Morris, 2002). In the case of barley, significant attempts have been made to develop a combined approach, which has then been applied in the Fertile Crescent region (Ceccarelli et al., 2003; Mustafa et al., 2006; Ceccarelli &

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**Table 2: Seedling infection types (ITs) of three barley (Hordeum vulgare ssp. vulgare) lines with or without the reaction to Puccinia graminis (rpg) 4-Mediated Resistance Locus (RMRL)**

<table>
<thead>
<tr>
<th>Time at 28°C/time at 18°C (h) after infection</th>
<th>Line SM89010 (no R genes)</th>
<th>Line QSM20 (carries RMRL)</th>
<th>Line QSM42 (carries RMRL)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Expt 1</td>
<td>Expt 2</td>
<td>Expt 1</td>
<td>Expt 2</td>
</tr>
<tr>
<td>0/350</td>
<td>3– 3 b</td>
<td>3– 3</td>
<td>0; 0;</td>
</tr>
<tr>
<td>16/334</td>
<td>3– 3</td>
<td>3– 3</td>
<td>0; 1–</td>
</tr>
<tr>
<td>28/322</td>
<td>3– 3</td>
<td>3– 3</td>
<td>0; 1 2–</td>
</tr>
<tr>
<td>40/310</td>
<td>3– 3</td>
<td>3– 3</td>
<td>1 2 0; 3–</td>
</tr>
<tr>
<td>52/298</td>
<td>3– 3</td>
<td>3– 3</td>
<td>2 1 3– 0;</td>
</tr>
<tr>
<td>64/286</td>
<td>3– 3</td>
<td>3– 3</td>
<td>3– 2 3 1</td>
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<tr>
<td>76/274</td>
<td>3– 3</td>
<td>3– 3</td>
<td>3– 3 2</td>
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<tr>
<td>88/262</td>
<td>3– 3</td>
<td>3– 3</td>
<td>3– 3</td>
</tr>
<tr>
<td>100/250</td>
<td>3– 3</td>
<td>3– 3</td>
<td>3– 3</td>
</tr>
<tr>
<td>112/238</td>
<td>3– 3</td>
<td>3– 3</td>
<td>3– 3 2</td>
</tr>
</tbody>
</table>

Lines were incubated initially at high temperature and subsequently at low temperature after infection with pathotype QCCJ of the stem rust pathogen (Puccinia graminis f. sp. tritici) (modified for barley by Miller & Lambert, 1955). They are listed in the order of their relative prevalence on leaves of the respective barley lines. Numbers with a minus symbol (e.g. ‘3–’) indicate lower sporulation than the classically described IT.

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Grando, 2007). Referred to as ‘participatory barley breeding’, the approach involves the deployment to devolved farmers of training populations developed centrally by breeders and scientists. Farmers are then involved in the testing of, and selection from, this material. When deployment is specifically in the context of environmentally-related adaptation, the epithet ‘evolutionary’ is sometimes appended to the name of the method. In this case, farmers chosen for involvement are positioned in multiple target environments that capture putative climate changes, and training populations are evaluated over a number of years, to capture variation in weather and climate (Ceccarelli, 2014). The principle is that, by undertaking selection in multiple environments, potential gains for particular environments are maximized through the exploitation of genotype–environment interactions, while at the same time selection takes proper account of the traits important to local farmers (Ceccarelli et al., 2013). According to the proponents of this approach, the method should be effective when crop production is limited by water availability, as then target environments can be very heterogeneous, and drought tolerance is dependent on multiple traits (Ceccarelli et al., 2007). Similarly, the approach is considered useful when the demand for specific varietal traits among producers is poorly understood and difficult to diagnose (Bhargav & Meena, 2014). Although commonly applied in low-income nations, the participatory approach does not need to
be restricted to such countries and has, for example, been applied recently to bread wheat breeding in France (Rivière et al., 2013).

A recent training population deployed to Middle Eastern and North African small-scale farmers under this type of approach consists of a mixture of barley seeds of nearly 1600 F2s constituted to contain very high genetic variation (Ceccarelli, 2009). In this instance, the role designated to farmers is not to undertake selection, but simply to collect and replant seed over multiple seasons, leaving the composite population to evolve under various climate pressures. Barley is predominantly a selfing crop (although the level of outcrossing varies by environment; Abdel-Ghani et al., 2004) and the evolution of new, adapted gene combinations in the field may therefore take time. The principle is similar, however, to that applied earlier by Harlan & Martini (1929) in the regeneration of seed from old-barley-variety composite crosses (e.g. Composite Cross II (CCII) synthesized in 1928, regenerated across many generations; see e.g. Allard et al., 1992; Saghai Maroof et al., 1994). The pioneering work of Allard and colleagues in evolutionary plant breeding using barley composite cross populations (reviewed in Allard, 1999; see also Suneson, 1956) provided an experimental system in which to examine and quantify adaptation to natural selection and the role of genetic diversity in relation to agronomic performance. These foundational studies resulted in a conceptual framework to develop approaches and resources to better understand the interactions between crops and environments, and identified the roles of breeding systems, selection, recombination, genetic drift and migration in shaping patterns of genetic diversity in relation to adaptation. Based on these long-term studies, theoretical support is given to the approach of Ceccarelli (2009) in distributing seed mixtures to farmers for regeneration purposes. In time, this approach should result in an increase in multi-locus genotypes with adaptation to abiotic and biotic stresses relevant for combating climate change.

As the high genetic diversity of extant barley landrace populations found in the arid and semi-arid Fertile Crescent remains after millennia of cultivation (Russell et al., 2003), it may be deduced that this variation supports production under marginal conditions (Grando et al., 2001). Such observations may provide a lesson for the use of mixtures to promote climate resilience in other crops and in other regions. Mixtures may extend beyond mixed-genotype varieties and inter-variety combinations to the practice of intercropping. In parts of East Africa, for example, a mixture of barley and wheat is sometimes grown together in ‘hanfetse’ cultivation, an

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**Fig. 5** Images of resistant and susceptible responses of *Hordeum vulgare* to four diseases important in the context of climate change for the barley crop. (a) Stem rust pathotype TTKSK. (b) Leaf rust pathotype 8. (c) Net blotch isolate ND89-19. (d) Spot blotch pathotype 1. In each case, the resistant response is on the left and the susceptible on the right. The distributions of resistant and susceptible responses in the Wild Barley Diversity Collection are given in Fig. 4.
approach that has been shown to reduce disease epidemics (Yahyaoui et al., 2004). Diseases can be reduced in mixtures through a combination of barriers presented by resistant plants, reduced densities of susceptible plants and induced resistance (Newton et al., 2011). There is, however, a reluctance to use mixtures in commercial, high-input agriculture because of problems (sometimes more ‘perceived’ than ‘real’; Walters et al., 2012) with harvesting and processing. Mixtures are therefore more applicable in production systems with low mechanization, unless differences within mixtures do not affect maturity and grain traits. Hybrids may also play a role, with greater yield stability on occasions reported for hybrids than for inbred lines (e.g. Mühleisen et al., 2014), and with the potential to combine two different resistance alleles at any one locus.

VI. Looking to the future

The combination of a barley reference sequence, the extensive research tools described in the preceding sections, and a strong international collaborative community of barley breeders, working with agronomists, crop modellers, pathologists and other researchers, provides a fertile environment for responding to climate change challenges. New genomic approaches may with other advances in targeting genes allow for more specific, localized responses to climate change that support resilience, while maintaining and enhancing productivity and quality, and facilitate the better deployment of existing varieties in modified and new climate spaces. By streamlining next-generation sequencing technology instrumentation and experimental pipelines, DNA methylation, histone modifications, chromatin accessibility and small-RNA transcripts (in different tissues) can be mapped onto the barley genome and related to phenotypic responses to environmental change. Sequence and epigenetic variation across the majority of the gene complement of barley can thereby be revealed, catalogued and made accessible to the breeding community. These data will be used to investigate signatures of selection, associations between molecular variants and adaptive traits, and potential variants that may have a role in plant improvement, among other phenomena. Such approaches are not unique to barley: the emerging international initiative DIVSEEK (2014) has been established to promote community-wide genomic-level characterization of the genetic resources of our crop plants as a critical component of a long-term strategy for enhancing sustainable crop production, through the intelligent use of natural genetic diversity (McCouch et al., 2013).

As the bottleneck in crop genetics and plant improvement has shifted over the last 10 yr from genotypic to phenotypic analysis (Varshney et al., 2011), an industry has emerged around new high-throughput precision phenotyping tools, both in ‘smart houses’ and in the field. These tools have been developed with the promise of increasing the rate of identification of trait–gene associations, particularly through the acquisition and interpretation of large-scale image-based phenotypic data. These methods are being applied to barley, for example, to understand drought stress responses (Honsdorf et al., 2014). Further large-scale association mapping studies are required using such high-throughput phenotyping, while developments are needed in how these methods can be used to measure climate-relevant traits. Innovative methods for studying genetic variation in root growth traits with regard to abiotic stresses are, for example, required (George et al., 2014). Bridging the gap between performance in controlled environments and performance under field conditions remains a potential problem for the exploitation of such resources, however. This is especially true for transgenic approaches where regulatory measures render field trialling difficult. One study of wheat compared lines transformed with the DEHYDRATION-RESPONSIVE ELEMENT-BINDING PROTEIN (DREB) 1A gene from Arabidopsis under a drought-inducible promoter to a null event with the nontransformed parent as a control. Under glasshouse conditions, transformants had a significantly better survival rate over a 23-d drought period than the nontransformed parent. This advantage was not, however, consistently translated into a yield gain for the transformed lines under drought stress in the field (Saint Pierre et al., 2012).

There are very few reports in the scientific literature of examples where a drought or temperature change mechanism has been transferred into a widely adopted variety using molecular approaches. Richards et al. (2010) listed a range of mechanisms to improve drought tolerance in wheat, but they still considered phenotypic selection to be more effective than marker-assisted selection. The developments in marker technology and GWAS noted above mean that markers can now be used at least as an effective negative selection tool to provide a pool of germplasm that is enriched for the frequency of potential drought tolerance alleles. Models that capture the dynamics of biological complexity, including gene interactions under different environmental and management influences, are under development and will underpin the development of crops adapted to future climates by supporting genomic selection for appropriate phenotypes (Hammer et al., 2016).

Recently initiated international projects such as WHEALBI (2014) are using exome capture tools to characterize carefully chosen panels of barley and wheat (in the case of WHEALBI, 500 accessions of each, including landrace and wild material) for climate-related adaptive traits. In parallel, the germplasm panels are being phenotypically evaluated in common garden trials in diverse environments across Europe. In the trans-national project CLIMBAR (2014), additional questions relate to climate change scenarios and, in particular, to epigenetic memory. It is known, for example, that the progeny of disease-infected plants can display epigenetic memories of infections (Boyko & Kovalchuk, 2011), and that epigenetic modifications are responsive to abscisic acid (ABA) and active in barley embryos (Kapazoglou et al., 2012, 2013). The objective of CLIMBAR is to establish if conditioning to environments that simulate climate scenarios for different parts of Europe in 2070 is epigenetically communicated to the next generation in barley plants.

Finally, it is important that improving yield under temperature and drought stresses does not neglect the quality of the barley crop. Reduced grain size under such stresses has been suggested to be caused by a greater decrease in carbohydrate deposition than protein deposition (Erbs et al., 2010; Högy et al., 2013), which would reduce the value of the crop as a source of energy. It is
therefore important that the whole barley research community is engaged in concerted efforts to produce stress-resistant barley varieties and provide a template that can be deployed in other crops.

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