REVIEW PAPER

Exploiting genetic diversity from landraces in wheat breeding for adaptation to climate change

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Abstract

Climate change has generated unpredictability in the timing and amount of rain, as well as extreme heat and cold spells that have affected grain yields worldwide and threaten food security. Sources of specific adaptation related to drought and heat, as well as associated breeding of genetic traits, will contribute to maintaining grain yields in dry and warm years. Increased crop photosynthesis and biomass have been achieved particularly through disease resistance and healthy leaves. Similarly, sources of drought and heat adaptation through extended photosynthesis and increased biomass would also greatly benefit crop improvement. Wheat landraces have been cultivated for thousands of years under the most extreme environmental conditions. They have also been cultivated in lower input farming systems for which adaptation traits, particularly those that increase the duration of photosynthesis, have been conserved. Landraces are a valuable source of genetic diversity and specific adaptation to local environmental conditions according to their place of origin. Evidence supports the hypothesis that landraces can provide sources of increased biomass and thousand kernel weight, both important traits for adaptation to tolerate drought and heat. Evaluation of wheat landraces stored in gene banks with highly beneficial untapped diversity and sources of stress adaptation, once characterized, should also be used for wheat improvement. Unified development of databases and promotion of data sharing among physiologists, pathologists, wheat quality scientists, national programmes, and breeders will greatly benefit wheat improvement for adaptation to climate change worldwide.

Key words: Bottleneck, conservation, diversity, drought, durum wheat, heat.

Introduction

An autochthonous wheat landrace is defined as a traditional variety with a high capacity to tolerate biotic and abiotic stresses, resulting in high yield stability and an intermediate yield level under a low input agricultural system (Zeven, 1998). A landrace differs from a variety that has been selectively improved by breeders for particular characteristics. The

Fertile Crescent (the area known as the cradle of civilization surrounded by arid and semi-arid land in western Asia) was home to wild wheats and traditional varieties and other valuable crops of the modern world (Diamond, 2002). However, the migration process from the Fertile Crescent, as well as both natural and human selection, resulted in the development of local landraces. It is generally accepted that during the process of domestication and the spread of domesticated wheat, new adaptive traits suitable for new environments were selected (Charmet, 2011; Peng *et al.*, 2011). Primary targets were probably critical traits that facilitated harvesting and enabled the colonization of new environments, such as larger seeded, non-shattering plants (Fuller, 2007), or flowering time fit to the prevailing environmental conditions of the region (Cockram *et al.*, 2009). It has also been suggested that many other traits, such as plant height, number, and weight of spikes and grains, were co-selected by ancient farmers (Peng *et al.*, 2011). For durum wheat (*Triticum turgidum* L.), a diversification of the species into different subspecies occurred in several territories. This was the case in Spain, whose durum wheat landraces have been classified into three main inter-fertile subspecies, *dicoccon, turgidum*, and *durum*, which all share the same AABB genomic constitution (Ruiz *et al.*, 2012). Subspecies *dicoccon*, a hulled wheat for animal feed and human consumption, represents a primitive stage in crop evolution, and was gradually replaced by more advanced free-threshing types of ssp. *durum* and *turgidum*, which evolved from ssp. *dicoccon* (Zohary and Hopf, 1994). Cultivation of ssp. *dicoccon* was restricted to mountainous regions, while ssp. *turgidum* was grown in colder areas than ssp. *durum,* which was most widespread and better adapted to dry environments (Ruiz *et al.*, 2012).

Wheat landrace collections contain wider genetic diversity than most breeding programmes and this diversity includes adaptation to different conditions according to the place of origin. This characteristic has been exploited in some countries, where the first improved varieties consisted of selections of local landraces. One such bread wheat variety, 'Aragon 03', selected from the indigenous landrace population 'Catalan de Monte' (Gadea, 1958), was the leading variety in Spain during the period 1960–1976 due to its capacity for drought resistance (Royo and Briceño-Félix, 2011). Another variety, 'Turkey' (syn. 'Turkey Red'), a hard red winter wheat suited to cold regions, had a tremendous impact on wheat cultivation in the United States at the turn of the last century due to decreased winterkill, among other traits (Olmstead and Rhode, 2002). It quickly became the most widely grown wheat in the central Great Plains in the late 19th and early 20th century, transforming Nebraska into a predominantly winter wheat area. Such breakthroughs remain necessary to address the impact of climate change and risks to food security. Evidence suggests yield plateaus in some European countries (The Netherlands, UK, and France: Grassini *et al.*, 2013). However a significant improvement in wheat production will be required if demand from the growing human population, predicted by the United Nations to be more than 9 billion people by 2050 (http://www.fao.org/fileadmin/templates/wsfs/docs/expert_paper/How_to_Feed_the_World_in_2050.pdf), is to be met. The challenge for wheat breeders is to increase genetic gains in productivity at a rate not lower than growing demand, in combination with appropriate agronomy to minimize yield gaps and guarantee environmental sustainability. Analysis of spring wheat lines distributed by the International Maize and Wheat Improvement Centre (CIMMYT) between 1995 and 2010 has shown that average genetic gains in yield are still increasing; however, this study has also shown comparatively lower genetic gains in low-yielding environments (Lopes *et al.*, 2012a). The use of wheat landraces (which have the same genome as current wheat germplasm) for direct crossing and introgression of adaptive traits is an attractive breeding strategy when compared to more complex breeding approaches used in the deployment of synthetic wheat, which exploit genetic resources of wild species (Reynolds *et al.*, 2007). Despite recognition that landraces possess a useful source of stress-adaptive traits and wide allelic variation for most key traits, understanding how to exploit this genetic diversity is unclear and scattered. This review questions how this diversity can be exploited and made readily available for use by breeders and the scientific community. First, there is a discussion as to how a loss of diversity through breeding and associated bottlenecks occurred. Second, strategies to retain diversity are explored. Finally, ways of centralizing and unifying genetic resources and their potential associated traits for specific environmental conditions through the conservation of germplasm and the development of databases are proposed.

Wide genetic diversity in wheat landraces: what did we lose through breeding?

The Green Revolution, which occurred throughout the 1940s to the 1960s, led to the development of high-yielding, disease-resistant wheat varieties with dwarfing genes; these were lodging resistant and highly responsive to inputs. The success of these varieties is probably the most important event in the history of modern agricultural research and enabled such wheat-importing countries as India and Pakistan to become exporters. Currently, modern high-yielding varieties grown in major wheat environments have an assembly of genes or gene combinations pyramided by breeders. However, increasing reliance on relatively few varieties in most breeding programmes has led to the loss of well adapted, genetic diversity. It is well documented that selection targeted at individual loci will reduce genetic diversity within and around the selected loci (Tanksley and McCouch, 1997). Selection in modern breeding programmes acts simultaneously upon many loci, controlling a variety of traits under selection, and such selection would greatly reduce diversity throughout the genome as has been predicted (Tanksley and McCouch, 1997). Decreases in genetic diversity are often recognized as genetic bottlenecks imposed on crop plants during domestication and in modern plant-breeding practices, as explained below.

Bottlenecks for wheat diversity

There are two potential bottlenecks in wheat diversity. The first relates to the recent origin of common wheat (~8000 years ago: Cox, 1997) and the presumption that there are relatively

few tetraploid and diploid progenitor crosses. Hence, only a portion of the diversity of *T. dicoccoides* and *Aegilops squarosa* exists in common wheat. The second bottleneck relates to founder lines for local populations where breeding programmes often rely on a relatively limited number of parent lines in developing germplasm pools. In common wheat, this second bottleneck is believed to have reduced the population size by 6% (Cavanagh *et al.*, 2013). The second bottleneck helps to explain the value of germplasm exchange and the use of landraces. For example, while 'Turkey' was the landrace that greatly changed wheat production in the Great Plains, 'Cheyenne', released in 1933, and a selection from the landrace 'Crimea', formed the foundation line for the Nebraska gene pool. The impact of these two landraces on wheat improvement can be seen in the use of a major quantitative trait locus (QTL) for grain yield on chromosome 3A (Ali *et al.*, 2011; Mengistu *et al.*, 2012). First, the 3A QTL is most beneficial in the higher-yielding cropping systems of eastern Nebraska and neutral in the lower-yielding cropping systems of the western northeast (Mahmood *et al.*, 2004). 'Cheyenne' and many of the lines grown in western Nebraska do not have the favourable 3A QTL allele because it is not favourable in those environments. However, the majority of lines grown in the higher-yielding cropping systems in eastern Nebraska or under irrigation in western Nebraska contain the favourable 3A QTL allele. The favourable 3A QTL allele originates from 'Wichita,' a Kansas wheat released in 1954, which was most likely to have been obtained from 'Turkey', which also has this favourable QTL. This example highlights how genes from landraces are effectively deployed. In their original state they may have little or no effect. Where they have small effects, selection neither selects for or against them. Often the founder line genotype predominates, but the pay-off is a loss of diversity. However, where they have beneficial effects, selection will greatly increase their frequency. This example illustrates how germplasm beyond the founder line is incorporated through breeding.

Allelic variation of genes recovered by going back to landraces

Cavanagh *et al.* (2013) highlighted the considerable germplasm exchange that has occurred within the wheat-breeding community. The increased spectrum of international agricultural research from the Consultative Group on International Agricultural Research (CGIAR) centres, particularly by CIMMYT, has enhanced the flow of germplasm worldwide, which in turn has favoured the use of beneficial alleles across environments. While the Green Revolution and the related spread of semi-dwarfing genes (*Rht-B1b* and *Rht-D1d*) are well known (Reynolds and Borlaug 2006), a third semi-dwarfing gene, *Rht8c*, provides an additional insight into the use of landraces. *Rht8c* is contained in 'Aka Komugi,' a Japanese landrace, and was used by Italian breeder Nazareno Strampelli to improve his varieties (Korzun *et al.*, 1998; Worland *et al.*, 1998; Ellis *et al.*, 2007). *Rht8c* does not affect coleoptile length, which is important in seeding wheat in dry regions or with variable planting systems in poor seed beds.

'Aka Komugi' also contains the photoperiod insensitivity gene (*Ppd_D1*, formerly *Ppd1*), which further reduces plant height by shortening the plant's life cycle and is valuable for adaptation in short-day environments (e.g. in Italy). In more northerly climates where a longer season occurs, daylight insensitivity is detrimental, and *Ppd_D1* is not used (Worland *et al.*, 1998). The 'Aka Komugi' landrace was the source of a different dwarfing gene than those used in the Green Revolution. This finding highlights the value of landraces as genetic resources; in this case its value was in part due to a second height-reducing gene (*Ppd_D1*), which was better adapted to the area where 'Aka Komugi' was initially used as a parent. As the value of *Rht8c* was determined and more broadly used, the second height-reducing gene (*Ppd_D1*) was not as valuable and was not incorporated (Gasperini *et al.*, 2012). Though not directly related to *Rht8c*, an additional finding was that initially a closely linked marker *Xgwm261* was assumed to be diagnostic for *Rht8* alleles. However, subsequent research (Ellis *et al.*, 2007) proved that *Xgwm261* was not always linked to *Rht8* and that *Xgwm261* was only diagnostic in lines derived from 'Aka Komugi' because the linkage disequilibrium still existed between the marker and the gene. The same can be said for resistance to pests and disease. As a pest arrives or is identified in a new country, breeders often screen landraces from the pest's original home for resistance genes for use in the development of new varieties. For example, the Iranian land races 'PI 1377397' (DuToit, 1989) and 'PI626580' (Valdez *et al.*, 2012) were used as parents for their resistance to the Russian wheat aphid *Diuraphis noxia* (Kurdjumov). The Russian wheat aphid is native to the Middle East and west Asia (Puterka *et al.*, 1993) and resistance to this pest has co-evolved there. As the aphid moved to or was identified in other locations, such as South Africa in 1978 and the United States in 1986 (Puterka *et al.*, 1993), plant breeders have searched the Russian wheat aphid's original location for sources of resistance. These sources of resistance and the genes that control these traits have been incorporated into modern wheat varieties. Hence, in much the same way that the pest has moved to new areas where a favoured crop is grown, breeders have moved resistance genes from their original home to the crop's new location and the pest has moved in tandem. These examples show how allelic variation of genes originally found in the wild, but gradually lost through domestication and breeding, have been recovered only by going back to landraces.

Strategies to retain diversity from wheat landraces

It is fully understood that landraces provide a rich source of genes, but at the same time plant breeders, who want to create new high-yielding varieties, tend to make crosses among elite lines where they have the highest likelihood of developing new varieties (Baenziger and DePauw, 2009). Similarly, although modern durum wheat varieties are more productive with a higher harvest index (Royo *et al.*, 2008; Fayaz *et al.*, 2013), less photoperiod sensitivity and fewer vernalization

requirements (Motzo and Giunta 2007), and with better over-all end-use quality than landraces (Nazco *et al.*, 2012), the nature of landraces, evolved and mixed through natural and artificial selection processes (Zeven, 1998), makes them the most genetically diverse of the cultivated lines. Mediterranean durum landraces represent a particularly important group of genetic resources because of their extensive genetic variability and their documented tolerance to drought (Kyzeridis *et al.*, 1995), resilience to pests, resistance to diseases (Talas *et al.*, 2011), and adaptability to low-input farming systems (Srivastava and Damania, 1989). Thus, landraces can be considered as likely sources of putatively lost variability and may provide new genes or alleles, which could be introgressed into modern varieties by hybridization. However, the importance of widening genetic diversity requires several actions in addition to hybridization within breeding programmes. These include monitoring genetic diversity and increasing the frequency of rare alleles using landraces in breeding programmes; finding 'new'' allelic variation for known functional genes among landraces; and promoting phenotypic characterization of landraces for adaptation to climate change and facilitating information sharing. These strategies are explained below in more detail.

Monitoring genetic diversity and increasing the frequency of rare alleles using landraces in breeding programmes

Sequencing is rapidly becoming so inexpensive that it will soon be possible to use it routinely in breeding programmes (Poland and Rife, 2012), e.g. for evaluation of genetic diversity (El-Basyoni *et al.*, 2013). Overall genetic diversity (including neutral or non-functional diversity) can be measured at two different stages: (i) to form core collections where genetic diversity is maximized with minimum repetition (Pessoa-Filho *et al.*, 2010); (ii) in the intermediate generations of a breeding programme to conserve genetic variability for selection in later generations (El-Basyoni *et al.*, 2013). Genetic diversity can be determined by the use of different data types, such as pedigree, morphological, and biochemical markers, and DNA molecular markers (Beaumont *et al.*, 1998; Li *et al.*, 2010; Vinu *et al.*, 2013). The first step toward identifying genetic diversity patterns in a given population is to estimate the similarity among genotypes. Various algorithms have been developed to estimate the genetic similarity among genotypes, as described in the literature (Beaumont *et al.*, 1998; Mohammadi and Prasanna, 2003; Kosman and Leonard, 2005; Aremu, 2011). Principal components analysis (PCA), principal coordinates analysis (PCoA), and multidimensional scaling (MDS) are three ordination methods that are also frequently used visually to represent genetic relationships among genotypes (Franco *et al.*, 2003). Principal components analysis [with 7710 Genotype-By-Sequencing (GBS) markers] was used to analyse a set of 2397 landraces from central and western Asia (Fig. 1). There is evidence that GBS markers are uniformly spaced across the chromosomes of wheat (Poland *et al.*, 2012); however, to avoid redundancy, markers with maximum missing values of 10%, minor allele

frequency lower than 0.05, and R^2 higher than 0.8 were discarded to avoid redundancy; missing values were input using an expectation-maximization algorithm. Fig. 1 shows how wide the diversity of landraces was as primarily related to geographical origin. Geographical origin has discriminated major groups (except for China, which has two distinct landrace groups) representing good evidence for local genetic adaptation to the place of origin.

In the area of diversity and genetic distance in populations, it is common to remove markers with minor allele frequencies (MAF). In studying and utilizing diversity, it is critical to recognize that MAF are part of the reservoir of genes that breeders need to access. In fact, under selection, MAF will greatly increase if the linked trait has commercial merit (Cavanagh *et al.*, 2013). Genome-wide association studies have recently been used for the discovery of markers associated with traits of interest (Lopes *et al.*, 2015); however, rare alleles are generally removed due to a limited population size (to keep an acceptable level of precision during phenotyping). Whether most of the variance for a specific trait is hidden as various rare alleles of large effect or as common alleles of very small effect is still not clear (Gibson, 2012; Romay *et al.*, 2013). New methodologies have been discussed in the literature via study designs and statistical tests for rare-variant association analysis (Lee *et al.*, 2013), but these will have to be tested in plants. Next-generation genotyping and sequencing technologies may facilitate future studies of uncommon and rare variants, while explaining an increased fraction of trait variation (Varshney *et al.*, 2014). Nested-association mapping (NAM) and multi-parent advanced generation intercross (MAGIC) approaches may also improve rare allele detection (Yan *et al.*, 2011). The use of landraces in the development of populations may greatly increase diversity and will change the frequency of alleles, making it possible to identify new alleles.

Finding 'new' allelic variation for known functional genes among landraces

While the importance of keeping diversity in breeding programmes has been well established, application may be questioned if this diversity does not address allelic variation for key priority traits in breeding programmes. Allele mining is a research field aimed at identifying allelic variation of relevant traits within genetic resource collections. For identified genes of known function and basic DNA sequence, genetic resources collections may be screened for allelic variation (Bhullar *et al.*, 2010) using different molecular technologies (Kumar *et al.*, 2010). Isolation of important alleles from landraces and other genetic resources has been referred to as a source of functional allelic diversity and differential allelic frequency in comparison to modern breeding lines (material selected through breeding but not yet a variety) and varieties. Bhullar *et al.* (2009) found new functional allelic diversity for resistance to powdery mildew using a strategic selection of bread wheat landraces. Similarly, new alleles for grain texture and quality have been identified in old Mexican and Mediterranean wheat landraces (Ayala *et al.*, 2013). Realizing the immense potential of the discovery of new alleles for
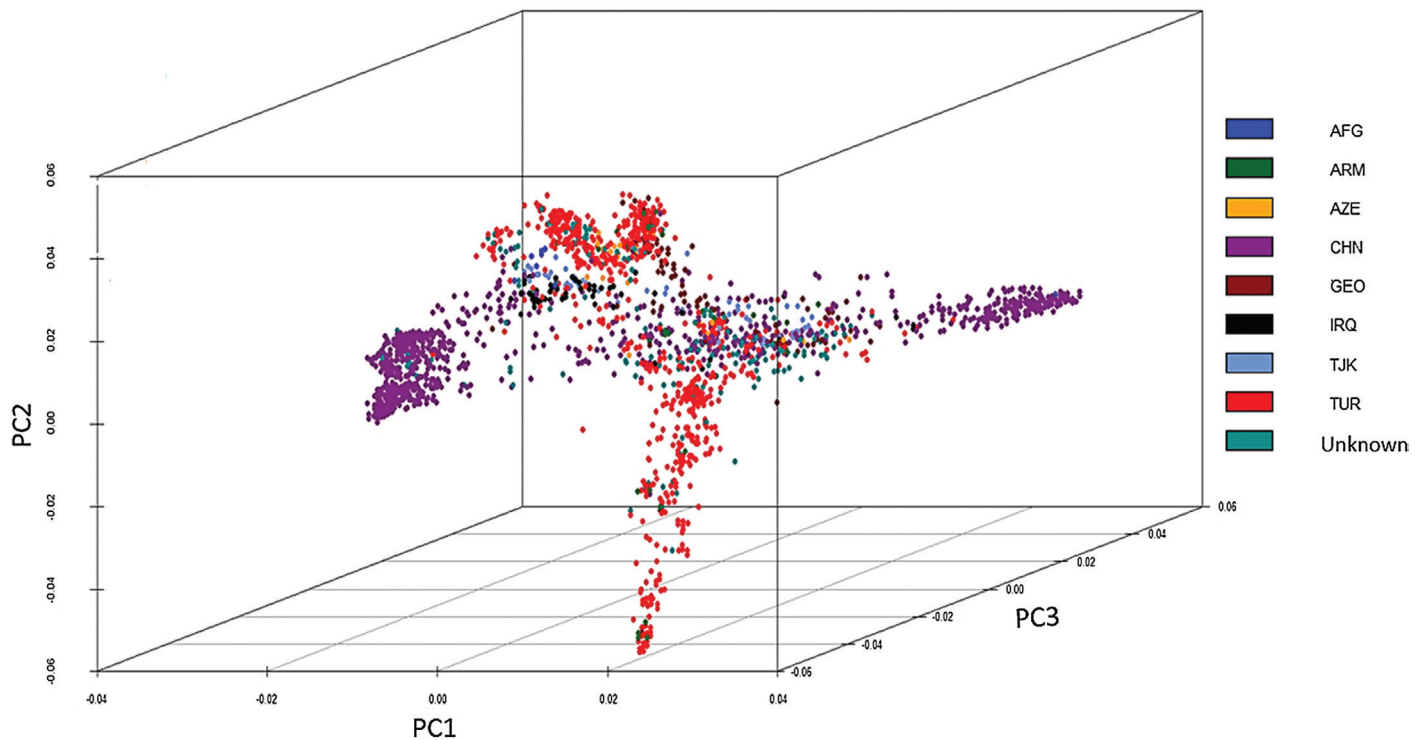
Fig. 1. Principal component analysis (PCA) of ~10 000 genotype-by-sequencing (GBS) markers run in a total of 3300 wheat landraces from Afghanistan (AFG), Armenia (ARM), Azerbaijan (AZB), China (CHN), Georgia (GEO), Iraq (IRQ), Tajikistan (TJK), Turkey (TUR), and unknown origin. This figure is available in colour at *JXB* online.

functional genes, efforts are underway to screen wheat collections in international crop research institutes (Kumar *et al.*, 2010). Once available, this information will be highly valuable for enriching the genetic diversity within breeding programmes. Discovery of new markers associated with key traits through genome-wide association studies (GWAS) will greatly benefit the scientific community, particularly after validation of important markers associated with complex traits. For example, the wheat association mapping initiative (WAMI), which has been genotyped with the 9K and 90K SNP chip, is now delivering a set of markers associated with complex traits (Lopes *et al.*, 2015; Sukumaran *et al.*, 2015).

Promoting phenotypic characterization of landraces for adaptation to climate change and facilitating information sharing

Kato and Yokoyama (1991) have shown that half of the variation for traits like heading time, photoperiodic responses, narrow-sense earliness, and vernalization requirements were explained by a geographical difference in origin. More recently, growth habit has been defined as one of the primary mechanisms driving local adaptation (Cavanagh *et al.*, 2013). This has important implications for the development of core collections for drought and heat tolerance, where selection based purely on geographical origin will unfortunately produce diversity primarily related with growth habit. However, growth-habit genes have been fixed in most commercial breeding programmes (Richards *et al.*, 2010) and this will not help in the development of more-tolerant breeding lines for

drought and heat adaptation to climate change projections. Therefore, phenotyping and genotyping of landrace collections is crucial to further define and understand other traits of interest besides well known genes associated with vernalization and photoperiod responses. Work is being developed at CIMMYT (Turkey) to phenotype landraces from central and western Asia (selected from landraces in Fig. 1), where drought and heat are common events. The objective is to find new traits in landraces associated with tolerance to drought and heat. Fig. 2 and Table 1 show the evaluation of three basic traits, including thousand kernel weight (TKW), biomass at maturity, and grain yield, in three populations (population one with 251 varieties and breeding lines, population 2 with 291 landraces from several countries in central and western Asia, and population 3 with 236 landraces from Afghanistan). Table 1 shows basic information on experimental design and variance components of the field trials and it also indicates the range of variation (minima and maxima) for each trait in the different populations. Moreover, a common check was used in all trials and populations, in this case with check variety 'Karahan' (a locally well adapted variety). Landrace population 3 showed an increased percentage of genotypes with statistically significant higher TKW than check variety 'Karahan', whereas both populations 1 and 3 did not (see extended tail showing genotypes with the highest TKW in Fig. 2A and Table 1). Similarly, landrace population 2 showed an increased percentage of landraces with increased biomass (Fig. 2B) than check variety 'Karahan'. Finally for grain yield, only populations one and two showed statistically significant higher grain yield than check variety 'Karahan'
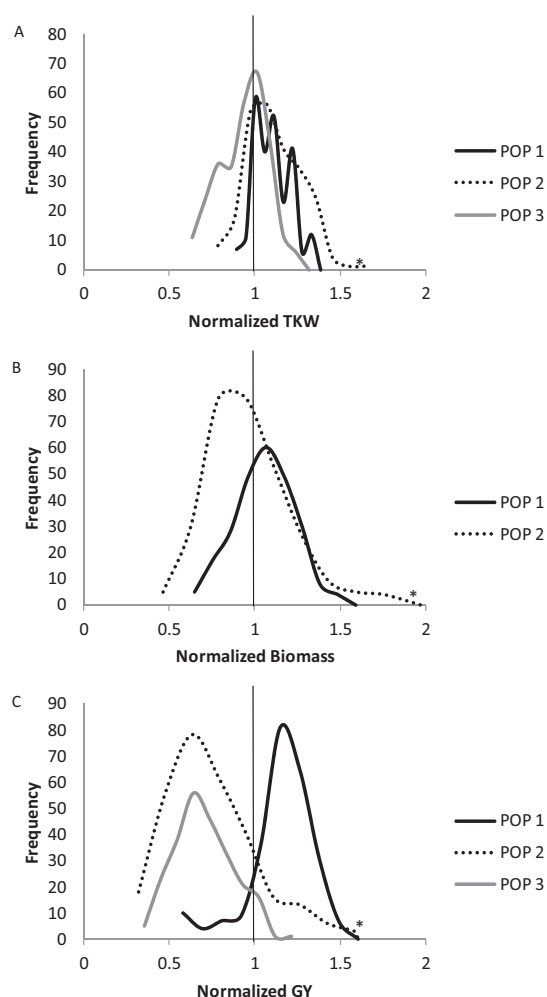
Fig. 2. Histograms of frequency distribution of (A) TKW, (B) biomass, and (C) grain yield (GY) parameters measured in wheat in populations 1, 2, and 3 (see Table 1 for details). All parameters were normalized against check variety 'Karahan'. Populations 1 and 3 were grown during the 2012–13 and 2013–14 wheat cycles in Konya; population 2 was grown in the 2013–14 wheat cycle in the same location. Biomass was not measured in population 3. Check variety 'Karahan' was randomly distributed (10% of entries) in each replicated trial for all three populations. *, populations where at least one genotype was statistically significant above the check variety.

(Fig. 2C). However, most breeding lines and varieties in population 1 were above the check variety 'Karahan', as shown by the frequency peak in Fig. 2C. In terms of biomass, this result indicates that selection for yield is linked to selection for smaller plants when comparing landraces with varieties and breeding lines. In fact, Richards *et al.* (2002) concluded that it is appropriate to focus on methods of increasing biomass and thereby crop photosynthesis genetically after observing that during the 20th century biomass remained stable. Similar results were recently observed by Pask and Reynolds (2013). However, biomass must increase without further increasing plant height, which may result in sensitivity to lodging in more favourable years. Moreover, increased TKW has been associated with increased grain yield in low and intermediate-yielding environments (Lopes *et al.*, 2012a) and this is an important trait for better performance. Landraces are probably an important source of allelic variation for biomass and

TKW that can be used in breeding; however, this will greatly vary across populations and terms of reference used in comparisons with varieties and breeding lines. Genome-wide association studies for the discovery of markers associated with biomass and TKW in core collections with fixed and known growth-habit genes of wheat landraces will be valuable for marker discovery.

Durum wheat

Phenotypic characterization of durum wheat landraces has also been undertaken by various research teams. A study conducted with durum wheat landraces from 14 Mediterranean countries revealed that those that evolved and dispersed through the north of the Mediterranean basin (via Turkey, the Balkan peninsula, Greece, and Italy) had different physiological and yielding strategies than the ones that migrated from east to west through North Africa, the southern pathway by which durum wheat was dispersed throughout the Mediterranean (Moragues *et al.*, 2006a,b). One of the most interesting findings of this study was that the yield of landraces was primarily related to variations in grain weight in terms of the ones that spread through the northern pathway, but was related to the number of spikes per unit area for landraces dispersed through the southern route (Moragues *et al.*, 2006a). These contrasting yield-formation strategies are most likely to be related to the mechanism of durum wheat's capacity to adapt to different climatic conditions existing in the north and the south of the Mediterranean basin. It has been shown that during the wheat-growing period, temperatures, solar radiation, and potential evapotranspiration are significantly higher in the southern region, which additionally has less rainfall than the north (Royo *et al.*, 2014). These contrasting yield-formation strategies developed by landraces appear to have also been adopted by modern varieties as a mechanism of adaptation to their growing environment. The yield of commercial durum wheat varieties and inbred lines under warm and dry Mediterranean environments has been shown to be determined mostly by the number of spikes per unit area, whereas grain weight predominantly influences the yield in cool and wet environments (García del Moral *et al.*, 2003; Royo *et al.*, 2006). One reason for these contrasting adaptive strategies has been given in a recent study, which showed that high minimum temperatures and photoperiods before flowering restrict the number of grains per unit area, while low levels of radiation during grain filling limit the achievement of heavy grains (Villegas *et al.*, 2015). Yield reductions related to a low number of grains per unit area under high pre-anthesis temperatures have been mainly associated with an acceleration of spike growth (Fischer 2011), which results in a reduction of the potential number of florets (González *et al.*, 2011), and consequently in the number of grains per unit area, which is not fully compensated later by kernel weight (Foulkes *et al.*, 2011; Peltonen-Sainio *et al.*, 2007).

Landraces evolved on different sides of the Mediterranean basin have also been shown to differ in a number of other traits, which supports the conclusion that northern landraces are better adapted to the most productive environments, while

Table 1. *Basic statistics for grain yield, biomass, and TKW in populations 1–3*

Population 1	Years	h²	LSD	GEN	ENV	G×E	'KARAHAN'		Min.	Max.
Grain yield (gm⁻²)	2	0.28	124.2	<0.0001	<0.0001	<0.05	271.3		126.3	404.6
Biomass (gm⁻²)	2	0.10	267.7	<0.05	<0.0001	<0.05	820.6		460.6	944.8
TKW (g)	2	0.60	6.3	<0.0001	<0.0001	0.656	32.8		27.5	43.7
Population 2										
Grain yield (gm⁻²)	1	0.46	117.7	<0.0001	NA	NA	220.0		36.7	348.6
Biomass (gm⁻²)	1	0.20	361.7	<0.05	NA	NA	611.4		187.4	1075.6
TKW (g)	1	0.78	6.3	<0.0001	NA	NA	32.6		19.6	43.3
Population 3										
Grain yield (gm⁻²)	2	0.40	87.8	<0.0001	<0.0001	0.40	239.9		62.9	269.4
Biomass (gm⁻²)	0	NA	NA	NA	NA	NA	NA	NA	NA	NA
TKW (g)	2	0.77	7.0	<0.0001	<0.0001	<0.0001	32.6		34.8	50.7

Populations 1 (251 varieties and breeding lines), 2 (291 landraces from several countries in central and western Asia), and 3 (236 landraces from Afghanistan) were grown in a two-replicated alpha-lattice experimental design in Konya, Turkey. Populations 1 and 3 were grown during the 2012–13 (224 mm precipitation) and 2013–14 (251 mm precipitation) wheat cycles in Konya; population 2 was grown in the 2013–14 wheat cycle in the same location. Common check variety 'Karahan' was randomly distributed (10% of entries) in each replicated trial for all three populations. Years, number of years in which data are available; h², heritability; LSD, least significant difference; GEN, probabilities associated with variance components of genotype; ENV, environment; G×E, genotype by environment interaction (G×E) effects; 'KARAHAN', average of check variety 'Karahan' in each set of field trials; Min. and Max., minimum and maximum values in each population (without check variety 'Karahan'); NA, not available. For more information on data collection and associated methodologies see Lopes *et al.* (2012).

southern ones are more resistant to drought and the poorest conditions (Moragues *et al.*, 2006b). Increased water and heat stresses which occur in the spring in southern Mediterranean countries may have caused landraces adapted to these environments to reduce their cycle length to anthesis, when compared to those adapted to more northern environments (Moragues *et al.*, 2006b; Royo *et al.*, 2014), as a strategy to allow their grains to fill under more favourable conditions. Grain filling in wheat is supported by transient photosynthesis and the remobilization of stored non-structural carbohydrates accumulated before anthesis (Blum, 1998). In Mediterranean environments, current photosynthesis during grain filling declines as a result of the hot and dry conditions, and the translocation of stored reserves becomes particularly important for grain filling (Papakosta and Gagianas, 1991; Blum, 1998). The larger contribution of pre-anthesis assimilates to the grain yield of southern landraces when compared with northern ones (Moragues *et al.*, 2006b) may also be a symptom of their superior adaptation to drought. On the other hand, landraces dispersed from the northern region have a larger tillering capacity and lower number of grains per spike than those dispersed in the south, which, according to Duggan *et al.* (2000), may indicate a greater yield potential.

A geographical pattern has also been identified regarding the overall grain end-use quality of durum wheat in Mediterranean landraces (Nazco *et al.*, 2012), which have large diversity for quality traits (Moragues *et al.*, 2006c; Nazco *et al.*, 2012). Genetic diversity based on allelic frequencies at glutenin loci has been shown to be greater in landraces than in modern varieties (Nazco *et al.*, 2014). Landraces from the eastern Mediterranean countries (Egypt, Turkey, Syria, Lebanon, Jordan, and Israel) have lighter grains and lower grain-filling rates than those from the western Mediterranean countries (Algeria, Italy, Morocco, Tunisia, Spain, France, Portugal, and Greece) (Nazco *et al.*, 2012). Both groups have similar gluten strength, although different allelic frequencies

of glutenin loci than those reported for landraces of southwest Asia and southwest Europe (Moragues *et al.*, 2006c).

Conservation of landraces

Conservation of all gene pools is a high priority for sustaining food security and coping with current and future climate change effects. Scientists have been sensitive to conservation for a long time and in the early 20th century, a Turkish scientist named Mirza Gökgöl collected and characterized wheat landraces from all over Turkey. Gökgöl identified about 18 000 types from which 256 new varieties were identified, and his descriptions and publications are still an important source of original wheat types in this part of the world. With all the diversity detected in these collections, Gökgöl was convinced that almost all wheat varieties existing in the world were present in Turkey and that Turkish landraces provided an endless treasure to breeders worldwide (Karagoz, 2014), as seen by the introduction of Turkish material in the United States (as described in the introduction of this paper). These early efforts by Gökgöl have been particularly valuable where the spread of high-yielding modern varieties grown under intensive systems have been replacing local varieties around the world. Exceptionally, Turkey and Iran serve as two examples where landraces are still cultivated, although in a very limited area, and this source of diversity may be lost sooner rather than later if not collected and conserved. Not only must landraces be conserved, but so should wheat varieties that have been replaced by new and more productive ones. Older varieties, due to the emphasis on landraces and more exotic materials, must not be forgotten, and older varieties, as well as other breeding materials, need to be conserved as a source of genetic diversity.

Despite the enormous efforts made by national and international programmes to conserve wheat diversity, eventually the conservation of germplasm and characterization of key

traits will provide specific information to breeders that will promote the use of genetic resources by the scientific community. Specifically, several challenges need attention: (i) dealing with duplication where tracking is lost when moving germplasm from one place to other, particularly if a unique notation is not used; (ii) genetic diversity of collections widely determined by DNA markers available in genebank facilities; (iii) diversity being well retained during collection through the use of molecular markers, visual observation, and by using internationally accepted conservation and characterization standards in seed genebanks; (iv) increasing *in situ* conservation; (v) functional multiplication programmes; (vi) organizing regular national or regional collection programmes with functional surveys that gather high quality information related to germplasm being collected; (vii) reliable 'passport' information being available with GPS coordinates; (viii) using internationally accepted data base management programmes in genebanks; (ix) providing a worldwide data system among genebanks; and (x) spreading research results in a database system linked with genebanks. These activities, once established, will greatly improve the targeted use of genetic resources and will help scientists and breeders strategically extract and use allelic variation for important traits.

Concluding remarks

Loss of genetic diversity has been recognized as a genetic bottleneck imposed on crop plants during domestication and through modern plant-breeding practices. Allelic variation of genes originally found in the wild but gradually lost through domestication and breeding has been recovered only by going back to landraces. Landraces with increased biomass and total photosynthesis and TKW have potentially new allelic variation that should be exploited in wheat breeding. Several strategies to retain diversity found in wheat landraces are available and must be implemented. The first of these is measuring diversity to form core collections where genetic diversity is maximized with minimum repetition and in intermediate generations of a breeding programme to conserve genetic variability for selection in later generations. The second is addressing the allelic variation for key traits in breeding programmes where the importance of keeping diversity has been well established. Allele mining for traits and alleles of interest (finding 'new' allelic variation for known functional genes, e.g. *Vrn* and *Ppd*, among landraces and linkages or pleiotropy between new alleles for known functional genes and grain yield) will be highly valuable for enriching the genetic diversity within breeding programmes. The third strategy is retaining phenotypic variation and related genetic association for specific traits through large-scale and precision phenotyping coupled with GWAS for the identification of new markers. Ultimately, the unified development of databases and promotion of data sharing among physiologists, pathologists, wheat quality scientists, national programmes, and breeders through linkages with genebanks will greatly benefit wheat improvement for adaptation to climate change worldwide.

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