



“Barley landraces: Ecological heritage for edaphic stress adaptations and sustainable production”



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ABSTRACT

Spontaneous mutation and natural selection pressure have contributed immensely to the genetic diversity of barley; a crop domesticated and grown since antiquity under diverse agro-ecological regions. Similarly, anthropogenic factors like cultural traditions and food preferences have also shaped the evolution of barley genetic diversity in the course of acclimatization under diverse ecosystems. Despite a rich genetic diversity, rapid depletion of barley genetic resources including the virtual extinction of several important landraces due to introduction of high yielding varieties and the loss of traditional farming systems remains a significant concern. Genetic gain in terms of higher grain yield and quality has obviously reduced the resilience of farmers' varieties and landraces to environmental stresses; that could in fact be explored as an important source of genes and traits for improving barley adaptability to adverse agro-climatic conditions. Unfortunately, landraces are not being fully exploited in barley breeding programs mainly due to lack of inadequate information. In this backdrop, this article attempts to present an overview of the historical trends in barley conservation and the plausible use of barley landraces in modern breeding programs to achieve sustainable production suited to the current needs.

Introduction

Expanding global population, set to cross 9.0 billion by the middle of this century, has placed an unprecedented pressure on global land and water resources to produce adequate food (FAO, 2009; Foley et al., 2011). It is unfortunate; however, that productive soils and good quality water are diminishing (d'Amour et al., 2017) and degrading (FAO and ITPS, 2015; Foley et al., 2011), increasingly pushing agricultural production to marginal lands suffering from different environmental constraints (FAO, 2011). There is evidence that increased consumption of energy and nutrient-dense food (e.g., meat and livestock products) (Alexandratos and Bruinsma, 2012; Tilman et al., 2002) would further accentuate the pressure on shrinking farmlands. With severe adverse impacts of climate change on farm sector including increased frequency of droughts and floods, soil and water degradation, sea level rise and disease outbreaks remaining virtually certain in the coming years (Kurukulasuriya and Shane, 2003; Schmidhuber and Tubiello, 2007), changes

in means and ways of food production while ensuring ecological sustainability remain absolutely essential (Tilman et al., 2002). The challenges confronting global agriculture have served as a wake-up call, leading to a growing emphasis on sustainable solutions that could simultaneously address the intertwined goals of adequate food availability, safeguarding the natural resources from degradation, improving the human health and reducing the adverse impacts of climate change (Gliessman, 1990; Horrihan et al., 2002; Lichtfouse et al., 2009; Wezel et al., 2014). More recently, ‘The 2030 Agenda for Sustainable Development’, adopted by the United Nations General Assembly in 2015, sets out an ambitious path for a peaceful and prosperous human future through a set of 17 interconnected and indivisible ‘Sustainable Development Goals’ (SDGs) (Gaffney, 2014). In so far as food and agriculture sector is concerned, the Food and Agriculture Organization of the United Nations has identified a set of 20 integrated actions that could contribute immensely to achieving the goal of a sustainable human society. It specifically underscores an urgent need for mainstreaming biodiversity

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conservation and protecting ecosystem functions by implementing a series of initiatives established in the United Nations Decade on Biodiversity (2011-2020) and the Aichi targets (FAO, 2018).

Several studies have shown that land use change, habitat destruction and intensive agricultural practices often lead to the loss of biodiversity in ways that many locally adapted species critical to the ecosystem functions and services could disappear over time (Gonthier et al., 2014; Mattison and Norris, 2005; Pascual and Perrings, 2007). Gradual loss of agro-biodiversity reported from both developed (Renard et al., 2016; Schröder et al., 2007) and developing (Khumalo et al., 2012; Upreti and Upreti, 2002) regions of the world is often also accompanied by an erosion of traditional ecological knowledge (TEK) and local farming practices (Singh et al., 2014) that in turn reduce the capacity of local communities in securing healthy food and environmental services. Crop wild relatives and landraces, important constituents of agro-biodiversity, continue to face the risk of depletion world over. Many studies have shown that arresting the loss of such genetic resources and their mainstreaming with the modern farming systems remains crucial to tide over a multitude of food and environment related issues (Dempewolf et al., 2014; Ford-Lloyd et al., 2011; Jarvis et al., 2008). Barley has been used in diverse ways since antiquity; including use as human food and livestock feed and in malt production. Legend has it that gladiators used barely as a key ingredient of their diet to gain strength, stamina and to accelerate the healing of wounds (Curry, 2008). It is possible that Carl Linnæus considered this particular use of barley while designating it as *Hordeum vulgare*, as name *Hordeum* derives from Latin name for gladiators (*hordearii*). Being one of the major crops of the Old World agriculture and based on archaeological evidences, barley was first used primarily for food (Grando and Macpherson, 2005). Since time immemorial, deliberate selection of preferred genotypes by the farmers coupled with spontaneous mutation and natural selection have contributed to rich variation in primitive landraces. Over the past one and a half century, these landraces were harnessed as the base material in modern genetic improvement programs (Von Bothmer et al., 2003). It is estimated that of the total global production, a bulk (60–70%) is used as livestock feed, and 30–40% for malt production. Hardly 2–4% production is used directly as food and about 5% as seed (Newman and Newman, 2008). Currently, about 147 million tons of barley is produced from 47 million hectares of land with average productivity of about 3.0 ton/ha (FAO, 2017). Barley (*Hordeum vulgare*), one of the oldest cereal crops, is widely grown in marginally productive soils across the world. Despite a high concentration in temperate areas and the high altitude regions of the tropics and subtropics; wide adaptability of barley crop to varying agro-ecological situations, particularly those suffering from relatively harsh environmental conditions, is well documented (Nevo, 1992). Available evidence suggests that barley crop was first domesticated around 10,000 years ago from its wild relative (*Hordeum spontaneum*) in the Fertile Crescent (Badr et al., 2000). The fact that barley crop is grown widely under low input conditions in areas suffering from a range of edaphic constraints points to the high adaptability of genus *Hordeum* to edaphic stresses defined herein as the growth and yield limiting effects of various soil-related constraints occurring either alone or in combination. As the climate change induced anomalies in crop growing conditions intensify, adverse impacts of such edaphic stresses on soils and crops are likely to magnify manifold in the foreseeable future with fragile agro ecosystems like drylands likely to be hit hard. Like other crops, drought and salinity are the two most prominent edaphic constraints causing considerable yield losses in barley throughout the globe. It is estimated that depending on agro-climatic conditions, stress intensity and other factors, drought and salinity impacts can diminish 20–50% of the potential barley yields (Shrivastava and Kumar, 2015). Globally, nearly 20% of the total cultivated area and about one third of the total irrigated area is salt-affected. Further, global salinized area is expanding by about 10% annually due to various natural and anthropogenic causes (Jamil et al., 2011). Waterlogging is also a severe limitation to profitable barley production in several high rainfall zones (Van Gool and Vernon, 2006). Unlike wheat and oats, barley is more susceptible to waterlogged conditions (GRDC, 2016b) as

evidenced by moderate (~15%) to heavy (up to 80%) reductions in yield with the increasing duration and severity of waterlogging and the tolerance threshold of a particular variety (Zhou, 2011). Barley is also more vulnerable to sub-zero temperatures than wheat, particularly at the early seedling stage (Gomez-Macpherson, 2001). In Australia, where barley is grown on a large area, yearly losses in barley production due to frost damage are estimated to vary between \$33 to 100 million (GRDC, 2006, 2012). In marginal areas (e.g., arid lands), crops are often exposed to at least two stresses like drought and heat taking a heavy toll on economic yields (Savin et al., 1996). Similarly, in salt-affected lands, seasonal waterlogging (Datta and Jong, 2002) and boron toxicity (Goldberg, 1997) could be additional constraints to crop production. Besides curtailing the growers' incomes, less than expected barley yields also mean reduced supplies of malted barley for brewing (Stephanie et al., 2018). Barley varieties exhibit extensive variability in dry biomass, seed yield and malting quality traits, namely, β -glucan, α -amylase activity, soluble protein, refractive index, and free amino nitrogen under various edaphic stresses (Mahalingam, 2017). Various research workers revealed that terminal heat stress reduced the malt quality parameters such as starch, sucrose, β -glucan, malt extract, grain weight and starch quality though grain protein content increased under edaphic stresses (Table 1). Up to the late nineteenth century, barley cultivation was based almost entirely on locally adapted highly heterogeneous landraces and farmers' varieties. After advent of Mendelian genetics and the consequent emergence of systematic crop improvement methods, these locally adapted strains were gradually replaced by the high yielding improved cultivars (Nevo, 1992). This transition had apparently led to the erosion of genes and traits conferring ecological resilience to the landraces. Thus, genetic gain in terms of higher yields was achieved at the expense of reduced adaptability to various ecological stressors and a narrowing of the genetic base in the cultivated barley. Despite a noticeable shift towards improved cultivars, several farming communities transcending continental boundaries continue to retain the interest in barley landraces; due apparently to their better performance and compatibility with the local needs (Cleveland et al., 2000). As they are traditionally maintained by the farmers, landraces are seldom subject to genetic improvement for yield and quality (Scholten et al., 2009). They have an inherent capacity to provide sustained yields in low input and stressful agro-ecosystems (Zeven, 1998). Intra-specific diversity and differentiation in landraces within eco-geographical regions evolved from ancient agricultural practices and natural selection, as well as during the progressive adaptation to a wide range of ecosystems having the selection pressure of biotic and abiotic stressors (Teshome et al., 2001). Clearly, landraces are rightly recognized as the mainstay of sustainable food production; especially in areas suffering from various environmental constraints. Unique morpho-physiological and genetic traits enabling the barley landraces to withstand harsh agro-ecological conditions need to be harnessed for developing climate resilient varieties. It was found that barley landraces produced up to 61% more grain yield than improved cultivars under unfavourable growing conditions. In comparison, grain yields of improved cultivars were only 6–18% higher than landraces under optimum conditions (Ceccarelli, 1996). It is due to this reason that crop landraces and heirloom varieties continue to contribute nearly one fifth of the food grain produced in the marginal areas globally (Veteto, 2008). Identification of dwarfing gene like *uzu*, *sdw*, *ari-GP* and *denso* has revolutionized barley breeding programs in many countries. The allelic dwarfing genes *sdw1* of Diamant and *denso* of Triumph located on chromosome 3HL, and *ari-GP* of Golden Promise located on chromosome 5H have been used widely in the barley genetic improvement in Europe, North America and Australia. Similarly, *uzu* gene located on chromosome 3HL has been found useful in Southeast Asia (Ren et al., 2010). In the recent past, successful application of crop landraces in improving the food security began with the introgression of dwarfing genes in wheat; slowly paving the way for 'Green Revolution' and reflecting the enormous impact that landraces can have on world food production. It was the Japanese wheat landrace 'Shiro Daruma' possessing dwarfing genes (*Rht-B1* and *Rht-D1*) which provided a sound footing to the 'Green Revolution', resulting

Table 1
Effect of edaphic stresses on barley malt quality parameters.

Edaphic stresses	Quality parameters							References
	Starch	Sucrose	Protein	β -Glucan	Malt Extract	Grain weight	Starch quality	
Salinity	↓	↑	–	–	–	–	–	Bagheri and Sadeghipour (2009)
Drought	↓	↓	↑	↓↑	↑	S	↓	Macnicol et al. 1993, Coles et al. (1991); Morgan and Riggs (1981); Savin and Nicolas (1999); Afshari-Behbahanzadeh et al. (2016)
Terminal heat stress	↓	↓	↑	↓↑	↓	↓	↓	Savin et al., (1997), Wallwork et al., (1998), Savin and Nicolas (1999), Passarella et al., (2008), Mangelsen et al., (2011)

S: Stable; ↓: Decrease; ↑: Increase.

in the development of semi-dwarf wheat ‘*Norin 10*’ (Kihara, 1983). In this review, an attempt has been made to examine and compile the literature on the evolution of barley landraces, their usage in modern breeding programs with focus on developing climate resilient and abiotic stress tolerant cultivars.,

Adaptation to dry soils

Extended periods of soil moisture deficit and, in some areas repeated droughts; continue to inflict serious losses in commercial barley farming in several rain-fed agricultural areas across the globe. In Mediterranean countries, for example, drought periods coinciding with the end stages of plant life cycle often cause heavy yield reductions (Passioura, 1996). This is in contrast to the fact that barley crop is well adapted to arid conditions and its immediate progenitor (*H. vulgare* ssp. *Spontaneum*) flourishes even in desert soils (Zohary and Hopf, 1988). Such ecotypes have also been reported from the desert areas of Jordan (Jaradat et al., 1996). Two barley landraces grown traditionally in Syria i.e. ‘*Arabi Abiad*’ and ‘*Arabi Aswad*’ perform well in the regions with scarce rainfall. While the former is commonly found in areas having annual rainfall between 250 and 400 mm; the latter adapts well in regions having extremely low annual rainfall (<250 mm). Some adaptive traits enabling the black-seeded ‘*Arabi Aswad*’ landrace to adapt to harsh arid conditions include less vigorous early growth and maintenance of grain productivity under water scarce conditions. In comparison, the more drought tolerant white-seeded landrace ‘*Arabi Abiad*’ has a very short grain filling period. After twelve years of pure line selection, two black seeded pure lines i.e. ‘*Tadmor*’ and ‘*Zanbaka*’ were released by International Centre for Agricultural Research in the Dry Areas (Ceccarelli and Grando, 2000). Field experiments have also indicated better adaptability of ‘*Arabi Aswad*’ and ‘*Tadmor*’ to dry and hot conditions (Van Osterom, Ceccaralli and Peacock, 1993). ‘*Tadmor*’ plants were found to have a pale green leaf foliage and only about one third of leaf chlorophyll and carotenoids than other barley cultivars allowing them to endure the excessive irradiance through a passive reduction of the light absorbance and thus minimal photoinhibition (Tardy et al., 1998). Chinese landrace ‘*TX9425*’ could also be a valuable genetic resource for improving the drought tolerance of barley. Because repeated droughts are a major hindrance to successful barley cultivation in arid and semi-arid regions, genetic mapping for identifying the drought associated traits and genes remains a major area of interest to the barley breeders. A major QTL conferring drought tolerance was recently identified on chromosome 5H in the Chinese barley landrace ‘*TX9425*’ (Fan et al., 2015). The gene underlying this QTL was suggested to be 9-cis-epoxycarotenoid dioxygenase 2 (*HvNCED2*), which is involved in the synthesis of abscisic acid. Two candidate genes i.e. *HvCBF10B* and *HvCBF10A* underlying this QTL could be linked to drought tolerance in ‘*TX9425*’ (Reinert et al., 2016).

Adaptation to frost

Frost damage often curtails barley yields by inducing floret and spike abortion and by hampering the kernel development (Zheng et al., 2015). In Turkey, selection of highly frost tolerant lines from barley landraces

during 1940s was instrumental in expanding the area under winter barley: currently about 60% of the total barley production of Turkey comes from the winter crop and the remainder 40% from the spring crop. Again, introduction of such winter hardy cultivars has also led to the doubling of grain productivity compared to the spring cultivars. In Turkey, winter hardy landraces have widely been used as parents in barley breeding programmes (Akar et al., 2009). Frost tolerance loci (*Fr-H1* and *Fr-H2*), located on chromosome 5HL approximately 30 cM apart from each other in the parental mapping population (*Nure x Tremois*) are the key determinants of low temperatures tolerance in barley (Francia et al., 2004).

Adaptation to salinity stress

Barley is one of the most salinity tolerant cereal crops (Lacolla and Cucci, 2008). In general, six-rowed barley cultivars are more salt tolerant than two-rowed, hull-less than hulled, tall than semi-dwarf ‘*uzzu*’ and winter types than spring types. Such differences in salt tolerance of various barley types can be attributed to the differences in tissue tolerance and compartmentation. In addition to accumulation and tissue tolerance to the high levels of Na^+ , Na^+ exclusion is another important mechanism for salinity tolerance in barley. Ethiopian landrace ‘*Abyssinia*’ grown commercially for forage has been reported to be the most salt tolerant barley genotype to date (Abo-Elenin et al., 1981). Numerous Quantitative Trait Loci (QTLs) associated with salinity tolerance in barley have been identified (Wu et al., 2011). A major salinity tolerant locus i.e. *HvNax3* was identified on chromosome 7HS in a bi-parental population resulting from a cross between the wild barley CPI-71284-48 (*Hordeum vulgare* ssp. *spontaneum*) and the cultivar Barque-73 (Shavrukov et al., 2010, 2013). Position of this locus mapped on 13.9-cM interval between markers *Bmag914* and *HvSS1* on chromosome 7H genetic map, was most closely associated with the DArT marker *bPb-1209* and the microsatellite marker *GBM1519* (Shavrukov et al., 2010). A strong candidate gene *HVP10* has been proposed to underly the locus i.e. *HvNax3* and was found responsible to reduce shoot Na^+ accumulation by 10–25% in plants exposed to 150 mM NaCl (Shavrukov et al., 2013). This wild accession is capable of limiting Na^+ accumulation in the shoots under saline conditions. Another salt tolerant locus *HvNax4* (for *Hordeum vulgare* Na^+ exclusion 4) was identified on chromosome 1HL in the Algerian landrace ‘*Sahara 3771*’ (Loneragan et al., 2009). The locus *HvNax4* is different from the salt tolerant loci *Nax1* and *Nax2* in durum wheat, which do not reside on chromosome regions corresponding to barley 1HL. A candidate gene *HvCBL4* underlying the *HvNax4* locus is homolog of Arabidopsis *SOS3* (Rivandi et al., 2011). Recently, a major QTL underpinning salinity tolerance in landrace ‘*TX9425*’ was detected on chromosome 2H. The phenotypic variation due to this QTL was nearly 50% of total variation (Xu et al., 2012).

Adaptation to alkali stress

Soil alkalinity is also a major concern in many barley growing areas because crop is adversely affected when soil pH_s ranges between 8 and 10. In such soils, boron toxicity could diminish the grain yield by up to

17% (Sutton et al., 2007). Soil pH_s range in which soil is neither deficient nor excess in boron is quite narrow (Goldberg, 1997). In arid and semi-arid regions with low rainfall, soluble boron is only partially leached such that high boron concentrations persist in the sub-surface causing boron toxicity (Reid, 2007; Ryan et al., 1998). Tolerance to boron toxicity is linked with the ability a particular genotype to maintain low shoot boron concentrations (Yau and Ryan, 2008). Screening of 444 accessions of winter barley from Europe, West Asia and North Africa revealed that boron toxicity tolerance varied with the geographic origin (Yau, 2002). Algerian barley landrace 'Sahara 3771' grows profusely in boron rich acidic soils and thus could be a promising resource of alleles conferring boron tolerance. Despite high boron concentrations in the soil solution, its low accumulation in the vegetative tissues of 'Sahara 3771' seems to be due to efflux from the roots (Hayes and Reid, 2004). A major QTL on chromosome 4H and several minor QTLs underlying boron tolerance were identified in a population derived from the cross of the boron-tolerant Algerian landrace 'Sahara 3771' and boron-sensitive genotype 'Clipper'. Higher transcript levels of candidate gene *HvBot1* underlying the 4H QTL seem to improve boron toxicity tolerance in landrace 'Sahara 3763' (Sutton et al., 2007). The proposed role of the *Bot1* gene product is to limit the amount of boron entering the root and to increase boron removal from the leaves (Jefferies et al., 1999). Turkish winter variety 'Tokak' is among the most boron tolerant barley cultivars ever tested (Braun, 1995).

Adaptation to acidic soils

Soil acidity is a serious threat to agricultural production, affecting as much as 40% of the world's arable land and up to 70% of the world's potentially arable land (Hede et al., 2001). Aluminium toxicity (Al³⁺) commonly seen in acidic soils (pH below 5.0) is the main factor suppressing plant growth and yield (Davies, 1994) and, it can directly reduce the crop yields by up to 60% (Tang et al., 2003). Under acidic conditions, aluminium is solubilized to its ionic form and rapidly inhibits root elongation and subsequently the uptake of water and nutrients, causing significant reductions in crop yields (Foy, 1988; Von Uexkull and Mutert, 1995). Although one of the most sensitive cereals to aluminium toxicity, ample genetic variation for Al-toxicity tolerance exists in barley germplasm (Reid et al., 1969). Barley shows differential responses to Al-toxicity and soil acidity (Foy et al., 1965). Despite being potentially novel sources for improving the aluminium toxicity and acidity tolerance, barley landraces remain neglected and most of the research on Al-toxicity tolerance deals with elite cultivars or isogenic lines (Kochian et al., 2005). The sources of aluminium tolerance in barley are limited to old cultivars and landraces, and represent multiples alleles of a single locus (Nawrot et al., 2001). Physiological studies demonstrate a strong correlation between Al-toxicity tolerance and citrate secretion from roots with cultivars/lines rapidly secreting citrate from the roots likely to withstand Al-toxicity (Zhao et al., 2003). It has been shown that a major locus *Alp* on the long arm of chromosome 4H of landrace "Dayton" (Al-toxicity tolerant) regulates Al-tolerance in barley (Minella and Sorrells, 1992). Another study revealed that a single major gene *Pht* on chromosome 4H in barley landrace 'Scottish Bere' was responsible for tolerance to high soil acidity (Stølen and Andersen, 1978). Candidate gene *HvAACT1* which encodes a citrate transport protein located on the plasma membrane has been identified to underlie the Al-tolerance locus (Furukawa et al., 2007). Scottish landrace 'Bere', considered to be one of the oldest extant crop varieties in the United Kingdom (Scholten et al., 2009), is supposed to have been introduced via waves of Viking invasion from Scandinavia in the 8th century (Martin and Wishart, 2007; Theobald et al., 2006). Landrace 'Bere' needed far lesser inputs in comparison to improved cultivars of barley (Theobald et al., 2006) and produced good yields in nutrient-poor soils without extra dose of fertilizers (Scholten et al., 2009). In acidic soils, landrace 'Bere' produces more number of panicles and more grains per panicle than contemporary cultivars (Riggs and Hayter, 1975). In comparison to most of the barley

genotypes showing poor adaptability in acidic soils, 'Bere' performs well under low soil pH conditions. Since chemical amelioration of acidic soil may not always be an economically feasible practice, emphasis has increased on developing barley genotypes with enhanced tolerance to acidity and Al-toxicity (Scott and Fisher, 1989). In UK and Orkney, 'Bere' is grown commercially for milling and flours for traditionally used for making bannocks and bread. Orkney grown 'Bere' grains are rich in minerals and nutraceuticals such as iron, iodine, magnesium, pantothenic acid, thiamine and folate. 'Bere' flour contains six times as much iodine and good amount of folate and dietary fibre compared to white wheat flour (Theobald et al., 2006)

Underuse of landraces in breeding programs

From ancient times, barley breeding was carried out by the farmers for specific adaptations and nutritional quality, leading to the evolution of landraces. However, in contemporary times, more emphasis was placed on high yield and tolerance to biotic stresses. In modern breeding projects, favourable alleles are selected and fixed repeatedly resulting in reduced genetic variability and thus minimizing the potential genetic gain. Evidently, introgression of potentially novel genes from landraces has received little attention compared to the widespread use of elite lines in the barley cultivar development programs (Rasmusson and Phillips, 1997). Less than potential use of the landraces in contemporary barley breeding programs may partly be attributed to the fear of linkage drag, loss of co-adapted gene complexes and the prolonged time needed for pre-adaptation or pre-breeding. Rapidly vanishing agro-biodiversity could pose severe obstacles to develop multiple stress resilient cultivars for coping with climate change related stresses (Ceccarelli, 2012; Frisone et al., 2011). Barley breeders, in order to accomplish the short-term breeding goals, rely almost solely on elite lines with which they are well acquainted (Sharma et al., 2013). Climate change is posing formidable risks to barley cultivation worldwide. Landraces showing adaptation to the stressful environments often out-yield the modern cultivars under unfavourable conditions. Accordingly, inclusion of landraces in the on-going barley pre-breeding programs seems to be a prerequisite for improving the adaptability to abiotic stress and grain nutritional composition for sustaining the global food and nutritional security.

Climate resilience of barley landraces

It is expected that climate change would affect the modern and traditional barley varieties differentially. Barley landraces; in and outside their centres of diversity, respond to climate change induced anomalies in a far better way than modern cultivars. In some parts of the world, modern varieties have limited acceptance in drought and salinity prone areas (e.g., Syria and Iraq) where indigenous landraces shows better adaptation (Ceccarelli et al., 1995). In Iran, barley is grown primarily for use as animal feed. Until recently, nearly 35% of the irrigated and more than 60% of rain fed barley growing areas of Iran were under landraces. Many important barley landraces such as 'Productive', 'Binam', 'Zarjo', 'Afzal', 'Sahand', 'Rihane' and other indigenous types (suited to both irrigated and rainfed conditions) have traditionally been grown by the farmers in harsh climatic conditions. Locally adapted indigenous races occupied an estimated 18% of the total irrigated and over half of the total rainfed barley area in Iran (Sarbarzeh et al., 2005). Given the huge agro-climatic diversity of Iran, a single improved cultivar or landrace is unlikely to be successful throughout the country. Barley cultivation in Eritrea still revolves around local landrace populations. The oldest landrace 'Abat' appreciated for its drought tolerance is still widely grown under rainfed conditions (Bereket, 2005). Tunisia is a secondary centre of diversity for barley and durum wheat (Vavilov, 1951). Over the centuries, early domestication and indigenous traditional knowledge have generated diverse barley landraces suited to varying food and feed needs. Barley landraces 'Martin', 'Rihane' and others are the main barley varieties grown in all the regions of Tunisia. While landrace 'Rihane' is grown

for food grains on more than 50% of the barley growing area, other landraces ('Souihli', 'Ardhaoui', 'Frigui', 'Beldi', 'Djebali', 'White Sfira' and 'Djerbi') are cultivated for use both as feed and food (Felah and Medimagh, 2005). The main reason behind widespread adoption of the landraces is the low adaptability of modern cultivars in harsh agro-ecosystems. Continual efforts led to the release of Turkish local landrace selection 'Tokak' in 1937 which occupied over 3 Million ha in Turkey till early 2000 and was also released as an improved cultivar under the name 'Sahand' in Iran (ICARDA, 1997). Most of the present-day high yielding Turkish barley cultivars had developed from 'Tokak' landrace (Kilian et al., 2006). Acclaimed barley landrace 'Batini' endemic to the coastal Batinah region of Oman, is still highly preferred by the subsistence farmers of Oman and the adjacent regions of the United Arab Emirates because of its high adaptability and tolerance to salinity (Abdullah et al., 2012). Similarly, primitive barley landrace 'Bere' highly tolerant to acidic soil condition and climatic aberrations and producing high quality malt is still grown widely in the Scottish islands of Orkney and Shetland (Mohan et al., 2016). Chinese hulless landrace 'Naigou', highly adapted to flooded situation of Northwest Yunnan, China is more suitable for commercial cultivation than other crops in areas suffering frequently from adverse weather conditions (Liu et al., 2019). Primitive barley landraces and their specific adaptations are summarized in Table 2.

Impact of landraces in barley improvement

Available evidence suggests that two-rowed barley was the oldest cereal domesticated by the humans (Harlan and Zohary, 1966). The wild barley, *Hordeum vulgare* ssp. spontaneum, is still widely distributed in the extremely dry areas of the Fertile Crescent. It is hypothesized that *H. spontaneum* contributes to the evolutionary processes of barley

landraces through continuous gene introgression (Russell et al., 2011). It is known that barley landraces not only out-yield the modern cultivars, but also produce satisfactory yields even under the extremely harsh conditions (Ceccarelli, 1994). Such hardy landraces maintain early vigour, earliness, plant height, long peduncle and have a short grain-filling duration (Acevedo and Ceccarelli, 1989). It is pertinent to mention, however, that the degree of association between each of these traits and grain yield under stress conditions is likely to vary from year to year, and that their relative importance depends on the timing, duration and intensity of the abiotic stress (Ceccarelli et al., 1991). Although landraces have been grown continually since the domestication of barley crop, adoption of improved cultivars in many countries pushed them to unfavourable and stress-prone environments (Li et al., 2012). Earlier research works on the landraces have shed light on their adaptation to low-input and stressful agro-ecosystems. The evaluation of pure lines extracted from Syrian and Jordanian barley landraces revealed a high degree of seed dormancy and variability in the requirement for vernalization (Weltzien and Fischbeck, 1990), reflecting that they could be potential sources of genes for such traits. Recently, rich genetic variation was noted in barley landraces with most of the landraces out yielding compared to modern cultivars in stressful environments of Spain (Yahiaoui et al., 2014). The discovery of abiotic stress tolerant alleles in barley landraces clearly shows the importance of conserving and exploring them as a means to identify beneficial alleles for enhancing adaptation and productivity in stress-prone environments. For example, Syrian landrace 'Tadmor' produced 1237 kg grain yield ha⁻¹ while the lines lacking 'Tadmor' in their pedigree produced only 604 kg ha⁻¹ grain yield under drought affected conditions (ICARDA, 2007) suggesting that chromosomal segments with a low frequency of recombination enhance adaptation to the stressful conditions (Gepts, 2006). In India, several salt tolerant barley varieties (NDB 1173, NDB 1445, RD 2552 and RD 2794)

Table 2
Primitive barley landraces along with their specific adaptation and genes/locus identified for specific traits.

Landrace	Region	Drought	Flood	Frost	Salinity	Alkalinity	Acidity	Gene/locus identified	Reference
Scots Bere	Scottish islands of Orkney and Shetland	-	-	-	-	X	X	A single major gene <i>Pht</i> , for high soil acidity tolerance mapped on chromosome 4H	Stolen and Andersen (1978); Scholten et al. (2009); Mohan et al. (2016)
Sahara 3771	Algeria	-	-	-	-	X	-	<i>HvNax4</i> locus for salt tolerance mapped on chromosome 1HL. Boron tolerance candidate gene <i>HvBot1</i> underlying the 4H QTL.	Rivandi et al. (2011) Jefferies et al., (1999); Hayes and Reid (2004); Sutton et al., (2007)
Nure	Turkey	-	-	X	-	-	-	<i>Fr-H1</i> and <i>Fr-H2</i> QTLs mapped on 5HL	Francia et al. (2004)
Dayton	USA	-	-	-	-	X	X	Al-toxicity tolerant gene <i>Alp</i> mapped on 4HL	Minella and Sorrells (1992)
TX9425	China	X	-	-	X	-	-	A major QTL (underlying two candidate genes i.e <i>HvCBF10B</i> and <i>HvCBF10A</i>) for drought tolerance was mapped on chromosome 5H. A major QTL for salinity tolerance detected on chromosome 2H.	Fan et al., (2015), Xu et al., (2012)
Wild barley CPI-71284-48	Australia	-	-	-	X	-	-	Salinity tolerant locus <i>HvNax3</i> identified on chromosome 7HS	Shavrukov et al., (2010); Shavrukov et al., (2013)
Tokak	Turkey	-	-	-	-	X	-	-	Braun (1995)
Arabi Aswad, Tadmor	Syria	X	-	-	-	-	-	-	Tardy et al., 1998
Abyssinia	Ethiopia	-	-	-	X	-	-	-	Abo-Elenin et al. (1981)
Abat	Eritrea	X	-	-	-	-	-	-	Bereket (2005)
Batini	Oman	-	-	-	X	-	-	-	Abdullah et al. (2012)
Bilara 2	India	-	-	-	X	-	-	-	Kumar et al., 2017
Martin, Rihane, Souihli, Ardhaoui, Frigui, Beldi, Djebali, white Sfira and Djerbi	Tunisia	X	-	-	-	-	-	-	Felah and Medimagh (2005)
Productive, Binam, Zarjo, Afzal, Sahand, Rihane	Iran	X	-	-	-	-	-	-	Sarbarzeh et al. (2005)
Naigou	China	-	X	-	-	-	-	-	Liu et al. (2019)
Duinian, Jianggai	China	X	-	-	-	-	-	-	Liu et al. (2019)

were developed by cross-breeding for cultivation in salt affected soils. Oldest salt tolerant Indian barley cultivars i.e. 'Bilara 2' and 'Azad' originated from the crosses between 'Bahraich Local' and 'Rajasthan Local' landraces. Majority of the subsequently released cultivars descended from genetic recombination between parents of different landrace origin (Vishnu Kumar et al., 2017). In Egypt, barley is mainly grown under rainfed conditions in the north coastal regions and under irrigation in salt-affected regions facing limited supplies of the fresh irrigation water. Concerted breeding efforts over the decades led to the development of many abiotic stress tolerant barley varieties in Egypt. Some of these varieties originating from the crosses between cultivars selected from landraces include salt tolerant 'Giza 123', heat tolerant 'Giza 124' and drought tolerant 'Giza 125' and 'Giza 126'. (Ahmed, 2005). Chinese landrace 'TX9425' has two QTLs for drought tolerance (explaining 42% and 14% of variation, respectively) and one QTL for salinity tolerance (explaining 29% of variation) which are being tapped in barley improvement programs (Fan et al., 2015). A major gene i.e. *Bot1*, associated with tolerance to boron toxicity, has been delineated at 0.15 cM interval between markers xBM178 and xBM162 in barley landrace 'Sahara 3763' (highly tolerant to boron toxicity). It was introgressed into commercial barley cultivars using tightly linked markers (Sutton et al., 2007).

Conclusion and recommendations

Barley landraces are surviving from more than a millennium of evolutionary history and are well adapted to stressful agro-climatic conditions. Natural and artificial selection coupled with spontaneous mutations operating in environmentally harsh areas have contributed to the evolution of abiotic stress adaptive traits in barley landraces. Such landraces could be promising sources of genetic resources for novel genes and traits for developing multiple stress tolerant and high yielding barley cultivars. Over the decades, continued efforts of barley breeders to transfer adaptive traits/genes from landraces to elite genotypes and modern cultivars have met with little success; due apparently to problems of linkage drag, more residual heterozygosity and complex adaptive gene cassettes involved in metabolic pathways. Emphasis should be placed on increasing the yield potential of barley landraces without altering their adaptation: landraces need to be invariably used as recipient rather than as donor parents. However, advent of marker-assisted and omics-based tools offers a great opportunity to barley breeders for transferring gene(s)/QTLs from landraces to popular cultivars while minimizing problems like linkage drag. We put forth following specific recommendations for the best use of barley landraces in future genetic improvement programs for developing multiple stress tolerant and high yielding cultivars:

- 1 Advanced tools and approaches need to be harnessed for detecting the genes and QTLs (and their genetic sequences) underpinning abiotic stress tolerance in barley landraces.
- 2 In spite of exclusive focus on transferring genes from the landraces to the improve cultivars, there is a need to improve the genetic background of landraces themselves through conventional and molecular approaches.

Authors' contributions

RPS generated the idea and designed the framework of manuscript, GD and HS performed the literature search. The first draft of the manuscript was written by AK and all authors provided their critical views. AS edited the manuscript. All authors read and approved the final draft.

Compliance with ethical standards

Study was conducted following standard ethical protocols.

Ethical approval

This article does not contain any studies with human participants or animals performed by any of the authors.

Declaration of competing interest

All authors declare that they have none competing interest attached to this article.

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