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Review article

Cereal landraces for sustainable agriculture. A review

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Abstract – Modern agriculture and conventional breeding and the liberal use of high inputs has resulted in the loss of genetic diversity and the stagnation of yields in cereals in less favourable areas. Increasingly landraces are being replaced by modern cultivars which are less resilient to pests, diseases and abiotic stresses and thereby losing a valuable source of germplasm for meeting the future needs of sustainable agriculture in the context of climate change. Where landraces persist there is concern that their potential is not fully realised. Much effort has gone into collecting, organising, studying and analysing landraces recently and we review the current status and potential for their improved deployment and exploitation, and incorporation of their positive qualities into new cultivars or populations for more sustainable agricultural production. In particular their potential as sources of novel disease and abiotic stress resistance genes or combination of genes if deployed appropriately, of phytonutrients accompanied with optimal micronutrient concentrations which can help alleviate aging-related and chronic diseases, and of nutrient use efficiency traits. We discuss the place of landraces in the origin of modern cereal crops and breeding of elite cereal cultivars, the importance of on-farm and ex situ diversity conservation; how modern genotyping approaches can help both conservation and exploitation; the importance of different phenotyping approaches; and whether legal issues associated with landrace marketing and utilisation need addressing. In this review of the current status and prospects for landraces of cereals in the context of sustainable agriculture, the major points are the following: (1) Landraces have very rich and complex ancestry representing variation in response to many diverse stresses and are vast resources for the development of future crops deriving many sustainable traits from their heritage. (2) There are many germplasm collections of landraces of the major cereals worldwide exhibiting much variation in valuable morphological, agronomic and biochemical traits. The germplasm has been characterised to variable degrees and in many different ways including molecular markers which can assist selection. (3) Much of this germplasm is being maintained both in long-term storage and on farm where it continues to evolve, both of which have their merits and problems. There is much concern about loss of variation, identification, description and accessibility of accessions despite international strategies for addressing these issues. (4) Developments in genotyping technologies are making the variation available in landraces ever more accessible. However, high quality, extensive and detailed, relevant and appropriate phenotyping needs to be associated with the genotyping to enable it to be exploited successfully. We also need to understand the complexity of the genetics of these desirable traits in

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order to develop new germplasm. (5) Nutrient use efficiency is a very important criterion for sustainability. Landrace material offers a potential source for crop improvement although these traits are highly interactive with their environment, particularly developmental stage, soil conditions and other organisms affecting roots and their environment. (6) Landraces are also a potential source of traits for improved nutrition of cereal crops, particularly antioxidants, phenolics in general, carotenoids and tocol in particular. They also have the potential to improve mineral content, particularly iron and zinc, if these traits can be successfully transferred to improved varieties. (7) Landraces have been shown to be valuable sources of resistance to pathogens and there is more to be gained from such sources. There is also potential, largely unrealised, for disease tolerance and resistance or tolerance of pest and various abiotic stresses too including to toxic environments. (8) Single gene traits are generally easily transferred from landrace germplasm to modern cultivars, but most of the desirable traits characteristic of landraces are complex and difficult to express in different genetic backgrounds. Maintaining these characteristics in heterogeneous landraces is also problematic. Breeding, selection and deployment methods appropriate to these objectives should be used rather than those used for high input intensive agriculture plant breeding. (9) Participatory plant breeding and variety selection has proven more successful than the approach used in high input breeding programmes for landrace improvement in stress-prone environments where sustainable approaches are a high priority. Despite being more complex to carry out, it not only delivers improved germplasm, but also aids uptake and communication between farmers, researchers and advisors for the benefit of all. (10) Previous seed trade legislation was designed primarily to protect trade and return royalty income to modern plant breeders with expensive programmes to fund. As the desirability of using landraces becomes more apparent to achieve greater sustainability, legislation changes are being made to facilitate this trade too. However, more changes are needed to promote the exploitation of diversity in landraces and encourage their use.

diversity / disease / yield / quality / nutrition / breeding / genotyping / competition / cultivar degeneration / whole-plant field phenotyping / non-stop selection / adaptive variation

Contents

1. INTRODUCTION

Elite cereal cultivars are derived from a relatively narrow germplasm pool and are predominantly well adapted to high input agriculture. However, climate change will bring ever greater challenges in response to both biotic and abiotic stresses. Together with pressures to move towards more sustainable agriculture, there is clearly a need to access and exploit a broader germplasm resource. Cereal landraces are just such a resource which could be very valuable and yet apparently underutilised in contemporary agriculture. Landraces have closer affinity with modern cultivars than wild species and can more easily be used as a foundation material in breeding programmes. During the course of the EU COST Action 860 "Sustainable variety development for low-input and organic agriculture" (2004–2008), a working group on cereal landraces was formed comprising a variety of scientific expertise, linked by common agreement on the potential value of landraces as a resource for contemporary agriculture. In this paper we therefore bring together a review of recent literature on multiple aspects of cereal landraces, offering insights and future direction for their more efficient incorporation and utilisation in agriculture for low-input as well for more favourable environments.

Various definitions of a landrace have evolved since the end of the 19th century. Owing to their complex nature, Zeven (1998) concluded that an all-embracing definition cannot be given. More recently, Camacho Villa et al. (2005) faced with the challenges this creates for inventory and conservation purposes, proposed the following working definition: "a landrace is a dynamic population(s) of a cultivated plant that has historical origin, distinct identity and lacks formal crop improvement, as well as often being genetically diverse, locally adapted and associated with traditional farming systems". They additionally recognised that although the above characteristics are commonly present, they are not always present for any individual landrace.

A distinction is made between landraces and modern, or so called elite, cultivars, the latter being the result of formal crop breeding programmes. It is useful to consider the implications of this from the genetic and breeding points of view. Modern cereal cultivars are almost always bred to be mono-genotypic as inbred or pure lines for self-pollinating species, or one-way hybrids in maize, and thus are genetically homogeneous. They are bred to exploit high-input environments with increased yield levels and with an emphasis on broad or wide adaptation. In the European Union (EU) and other International Union for the Protection of New Varieties of Plants (or UPOV (French: *Uion internationale pour la protection des obtentions vtégétales*)) countries, modern cultivars are accepted for commercial cultivation after they have passed through the Distinctiveness, Uniformity, and Stability (DUS) and Value of Cultivation and Use (VCU) systems of evaluation trials. In contrast, cereal landraces are genetically heterogeneous. They comprise a large number of distinct homozygous lines in the case of self-pollinating crops or, in the case of cross-pollinators like maize, are populations with more heterozygous components. An important difference between genetic heterogeneity and genetic homogeneity is that the former involves genetic competition among plants, whereas the latter lack such competition (Fasoula and Fasoula, 1997).

Landraces were the principal focus of agricultural production until the end of the nineteenth century with the arrival of formal plant breeding (Harlan, 1975). Then, in more favourable environments, gradual replacement during the early decades of the 20th century by selected component inbred lines and modern cultivars led to their virtual disappearance. However, their cultivation persisted in less favourable environments and despite earlier predictions about their imminent disappearance (Zeven, 1998), landraces still support subsistence farming worldwide. This persistence is not due to increased productivity levels (Almekinders et al., 1994), but because of their increased stability, accomplished through generations of natural and deliberate selection for valuable genes for resistance to biotic and abiotic stresses and inter-genotypic competition and compensation. The components of a genetically diverse population such as a landrace, have a disease buffering effect in reducing the pathogen spread (Frankel et al., 1995). Several important resistance genes were first identified in cereal landraces such as the durable *mlo* mildew resistance gene in Ethiopian barley landraces (Piffanelli et al., 2004) and later introduced into elite germplasm. In general however, elite cereal germplasm has very few durable resistance genes and little resistance to emerging or increasingly important diseases such as *Ramularia collo-cygni*, Fusarium disease complexes and rusts in general, a good example being the new race of stem rust (*Puccinia graminis*) Ug99. Therefore exploitation of landrace diversity to identify relevant resistance genes is an important goal. In addition, many cereal landraces are known to possess broad natural variation in valuable neutraceuticals, which has been inadvertently impoverished during the breeding of modern cultivars (Monasterio and Graham, 2000; Murphy et al., 2008).

The important issue of increased yield stability attributed to the inherent heterogeneity of landraces (e.g., Simmonds, 1979) is nicely described by Zeven (1998) as: "Yield stability of landraces under traditional low input agricultural systems is due to the fact that whatever the varying biotic and abiotic stress for each plant, one or more genotypes within the landrace population will yield satisfactorily". This emphasises the urgency for solutions to combat production problems encountered through lack of spatial and temporal uniformity, particularly in stress-prone or marginal environments. A longer-term breeding goal, described below, would include the incorporation of those desirable genes found in different landrace genotypes into one or few superior plants with elevated stability levels (Fasoula, 2008). However, a single genotype must express greater trait plasticity to compensate for its inability to exploit heterogeneity in spatial and temporal dimensions as flexibly as multiple genotypes (Newton et al., 2009).

Awareness that future increases in productivity may depend on improved yields in the high-stress environments, has focussed breeding on specific or narrow adaptation and on the need for conservation of genetic diversity (Cleveland et al., 1999). Conventional plant breeding has been successful in favourable environments and those which can be made favourable through interventions, but it is less successful in low-input environments, characterized by increased G × E interactions, or in organic farming systems. In these cases, participatory breeding approaches with the involvement of local farmers can have a significant and positive influence, as will be discussed. A renewed focus on cereal landraces for breeding purposes could ameliorate some negative consequences of modern agriculture and conventional breeding, such as the liberal use of high inputs, the loss of genetic diversity (Tilman, 1996), and the stagnation of yields in less favourable areas (Annichiarico and Pecetti, 1998).

The role of genebanks and on-farm conservation practices in preserving landrace genetic diversity is increasingly important, particularly since the pivotal involvement of local farmers is continually declining due to the changes brought about by modern agricultural and socio-economic practices. Studies on landrace genetic diversity are a prerequisite for efficient conservation and management, registration purposes and effective use of landraces in breeding programmes. The considerable advances in molecular genotyping and databasing technologies in recent years are beginning to make the variation and resources of landraces more accessible for exploitation. High-throughput genotyping enables genebank accessions with uncertain provenance to be elucidated and thereby enable validation of associated phenotypic data, making them much more useful. In the quest to bridge the phenotype-genotype gap (Miflin, 2000; Parry and Shewry, 2003) and exploit landrace variation, recent advances in genotyping and whole-plant field phenotyping methodology are discussed.

2. HISTORY OF CEREAL LANDRACES

The Fertile Crescent and Turkey (in Asia Minor) is known as one of the important centres of diversity of many field crops, particularly wheat and barley, and therefore has considerable genetic diversity. Plant domestication from this region over thousands of years has also resulted in the development of enormous diversity. Progressive adaptation to a wide range of environments, responding to various selection pressures including biotic, abiotic and human intervention, has resulted in characteristic intra-specific diversity and differentiation (Teshome et al., 2001) represented by many landraces with specific histories and eco-geographical origins. To better understand the importance of these resources it is necessary to highlight their history.

Archeobotanical data shows that the first domesticated wheat species were einkorn (*Triticum monococcum* ssp. *monococcum*) and emmer (*Triticum turgidum* ssp. *dicoccon*). These evolved from their wild relatives (*T. boeticum* and *T. dicoccoides* respectively) about 10 000 years ago (Heun et al., 1997). Both species were the staple food of the human population until the end of the Bronze Age when naked *Triticum* species became dominant in agricultural lands. In a recent expedition of the Hellenic Genebank, at the edges of the centre of diversity in the northern eastern part of Greece in Thrace natural populations of *Triticum monococcum* subsp. *boeticum* and *Aegilops speltoides* progenitors of the genomes A and B were found in co-existence and in situ conservation has been planned (Kotali et al., 2008).

Durum wheat (*T. turgidum durum*) has been of great historical significance, because it provided a range of sub-species that were cultivated widely across the globe for thousands of years (Feuillet et al., 2007). Durum wheat spread out from the Fertile Crescent and through southern Europe, reaching north Africa around 7000 BC (Feldman, 2001). It came into cultivation originally in the Damascus basin in southern Syria about 9800 BC (Zohary and Hopf, 2000). A second route of migration occurred through north Africa during the Middle Ages (Moragues et al., 2006a). The beginning of modern agriculture transformed durum landraces in obsolete 'cultivars' which were gradually replaced by today's elite cultivars where only a fraction of the crop diversity is exploited (Feuillet et al., 2007). Nowadays, wheat landraces are kept and maintained in germplasm bank collections around the world, but are grown in practice only in the more marginal agricultural environments of their origins.

Bread wheat (*T. aestivum* L. subsp. *aestivum* L.) first emerged in cultivated wheat fields approximately 5–6000 years ago (Zohary and Hopf, 2000), resulting from a hybridization between *T. turgidum* L and *T. tauschii* L. The D genome of bread wheat originated from *Aegilops tauschii* and carried alleles adapted to the more continental climate and thus enabled bread wheat to be cultivated over more extensive geographic environments than emmer wheat (Feuillet et al., 2007). The D genome also encodes proteins that restore the softness of the grain endosperm (Chantret et al., 2005) thereby improving bread-making properties. Use for leavened bread production has contributed to its migration to Europe and subsequent widespread cultivation around the world with the development of several different landraces with a diversity of local adaptations driven by different climates and agricultural practices. Hexaploid bread wheat accounts for approximately 90% of world wheat production today (Feuillet et al., 2007).

Barley (*Hordeum vulgare* L.) also became domesticated in the Fertile Crescent, about 10 000 years ago, migrated through Europe, and local agricultural practices and natural selection have led to locally adapted landraces (Jaradat et al., 2004). Valuable information about domestication of cultivated barley, ecogeographical diversity and relevant issues are found in the recent book on barley diversity by Bothmer et al. (2003). In archaeological records, oats, along with rye, were found as a weed contaminant of wheat and barley samples. As a cultivated crop oats was present on a significant scale towards the end of prehistory, mainly in northern European regions (Moore-Colyer, 1995). Domestication of oats is complex, with independent domestication occurring at each ploidy level (Harlan, 1977). Britain was the main area of cultivation of the hexaploid oats. Until the early 1900's cultivated germplasm was landraces adapted to local growing conditions. Nowadays, a large number of modern cultivars trace back to a restricted number of landraces, such as 'Kherson' from which 14 cultivars developed by re-selection and another 80 had 'Kherson' in their pedigrees (Wesenberg et al., 1992).

Maize (*Zea mays* L. ssp. *mays*) was domesticated from its wild progenitor teosinte (*Zea mays* ssp. *parviglumis*) through a single domestication event, in southern Mexico, between 6000 and 9000 years ago (Matsuoka et al., 2002). After this initial event, introgressions from other teosinte types may have contributed to the maize gene pool and thereby help explain the remarkable phenotypic and genetic diversity (Matsuoka et al., 2002). The same authors suggested also that from early diversification in the Mexican highlands, two paths or lineages of dispersal occurred. One path traces through western and northern Mexico into the south-western USA and then into the eastern USA and Canada. A second path leads out of the highlands to the western and southern lowlands of Mexico into Guatemala, the Caribbean Islands, the lowlands of South America and finally the Andean mountains. There is evidence that these two maize germplasm pools were introduced to Europe at different times and locations. The first introduction came from the Caribbean germplasm, and remained confined to southern Spain probably due to poor adaptation to the mboxEuropean conditions as late maturing populations (Brandolini, 1969). From the 17th century onwards, the north American flint populations, relatively insensitive to day length and with low temperature requirements for flowering, were introduced in northern Europe. Since the introduction of maize to Europe five centuries ago, cultivated populations have evolved under the different selective pressures imposed by the environment and farmers. Adaptation to many environmental niches of European countries for many years explains the large variability and number of landraces which can be observed today (Gauthier et al., 2002).

Clearly landraces have very rich and complex ancestry representing variation in response to many diverse stresses. These are vast resources for the development of future crops deriving many sustainable traits from their heritage. How these resources can be made accessible and exploited will be addressed below.

3. DIVERSITY AND GERMPLASM COLLECTIONS

3.1. Bread wheat landraces diversity

Bread wheat landraces are characterized by their diversity and heterogeneity. However, this genetic diversity needs to be described and measured if it is to be used effectively in breeding and management of plant genetic resources. Traditionally used markers for the description of landrace genetic diversity are morphological and agronomic traits known as descriptors and established by the International Plant Genetic Resources Institute (IPGRI) (IPGRI, 1985). Among them plant height, flowering and anthesis time, spikelet and leaf emergence (Motzo and Guinta, 2007), grain size (Ferrio et al., 2007), grain yield and weight, spikes per unit area (Moragues et al., 2006a, b) and harvest yield index (De Vita et al., 2007) are considered to be the most important ones, and have been successfully used in the phenotyping of bread wheat landraces. Besides IPGRI descriptors other morpho-physiological traits have also been used (Autrique et al., 1996; Nachit et al., 1988; Dencic et al., 2000). Even though morphological descriptors are highly heritable characters and expressed in all environments (Frankel et al., 1995), they are limited in number, and agronomic traits are affected by environmental conditions.

In recent years several physiological, biochemical, molecular and technological traits have been commonly used to characterise bread wheat landraces and to asses their importance as a resource and for food security. Among the biochemical and physiological markers, carbon isotope (13C) discrimination (Ferrio et al., 2007), biomass accumulation (De Vita et al., 2007; Moragues et al., 2006b), storage protein patterns (Gregová et al., 1999, 2004, 2006), High Molecular Weight (HMW) glutenin subunits polymorphism (Caballero et al., 2001) and mineral content (Oury et al., 2006) have been evaluated. Technological parameters, i.e. grain hardness, starch and protein content, viscosity (Igrejas et al., 2002) have been applied also, providing different approaches to the evaluation of landraces diversity and quality. Although biochemical and molecular markers allow fast screening of landrace diversity to detect useful variation for breeding programmes (Gregová et al., 2006) or management of the genetic resources in germplasm collections (Dreisigacker et al., 2005), they are complementary to but cannot replace morphological characterisation (Moragues et al., 2006a; dos Santos et al., 2009; Zeven, 1998). Major difficulties arise if one attempts to interpret molecular or biochemical data generated from germplasm accessions in the absence of their morphological characterisation (Gregová et al., 2006; Zeven, 1998). Overall a significant decrease of genetic diversity has been observed related to the replacement of bread wheat landraces by elite cultivars which appears to be associated with loss of some quality traits such us protein content and glutenins quality (Gregóva et al., 2006; Caballero et al., 2001). At the same there exist enormous gaps in our knowledge that needs to be fulfilled concerning landraces structure, within and among landraces diversity and useful traits.

3.2. Durum wheat landraces diversity

Durum wheat is a primary cereal crop in several regions of the Mediterranean Basin, including the southern peninsular of Italy (Motzo and Giunta, 2007), southern Anatolia of Turkey (Akar and Özgen, 2007) and southern Spain (Ruiz and Martín, 2000). Durum wheat has a great economic importance due to the long tradition of pasta making in Italy (De Vita et al., 2007) and bulgur making in Mediterranean countries (Akar and Özgen, 2007). Archaeological findings suggested that bulgur and cracked wheat could be distinguished as two basic ingredients of Mediterranean cooking and bulgur was known at least since the 3rd millennium BC (Valamoti, 2002). A screen of Madeiran and Canary Islands wheat accessions showed that durum accounts only for 19 and 15% of the germplasm collections respectively (Andrade et al., 2007).

In these and other regions, durum wheat landraces are cultivated by farmers to a very limited extent (Moragues et al., 2006a; dos Santos et al., 2009; Ruiz and Martín, 2000; Zhang et al., 2006; Cherdouh et al., 2005; Teklu et al., 2005; Kebebew et al., 2001; Ben Amer et al., 2001).

As in the case of bread wheat, durum landraces have been replaced in modern farming systems by elite cultivars. The studies performed to evaluate the diversity of durum landraces are predominantly based on germplasm collections that preserve accessions of populations abandoned by farmers. Such studies show the existence of considerable crop heterogeneity and genetic variability (Medini et al., 2005; Masum Akond and Watanabe, 2005; Teklu et al., 2005; Queen et al., 2004; Pagnotta et al., 2004; Alamerew et al., 2004; Kebebew et al., 2001; Ben Amer et al., 2001). Among the DNA molecular markers, Randomly Amplified Polymorhic DNA (RAPD) (Mantzavinou et al., 2005), microsatellites or Simple Sequence Repeats (SSRs) (Zhang et al., 2006; Hao et al., 2006), Amplified Fragment Length Polymorphisms (AFLPs) (Martos et al., 2005) and Restriction Fragment Length Polymorphisms (RFLPs) (Autrique et al., 1996) have been used to genotype durum wheat landraces. However, it is not always easy to determine which material authors have analysed. For example Ruiz and Martín (2000) showed that from 619 durum wheat entries of the Spanish Plant Genetic Resources Center (CRF-INIA (Spanish: Centro de Recursos Fitogenéticos - Instituto Nacional de Investigación Agraria)) collection, 428 were *turgidum* and 126 were durum accessions and claimed that they were representative of durum landrace diversity in southern Spain. However, no detailed information about the origin and sampling methodologies were given.

As a result of the increased economic importance of durum wheat, several breeding programmes aim to develop new cultivars and release old durum landraces (De Vita et al., 2007; D'Amato, 1989). In southern Italy local durum landraces of *Mediterraneum typicum* were cultivated until the beginning of the 1950 when a process of their replacement by modern cultivars began (Motzo and Giunta, 2007; Ruiz and Martín, 2000). As with bread wheat landraces, there has been a significant decrease of genetic diversity in this process which appears to be associated with some loss of quality traits (Oak et al., 2004; De Vita et al., 2007). Overall, it can be concluded that our knowledge on durum landraces need to be improved.

3.3. Barley landraces diversity

Barley landraces show stability under adverse climatic conditions. This is attributed to the heterogeneity present and that provides them with a buffering capacity. The 'within' as well as 'among' landraces diversity has been the subject of many studies, for example with respect to their agronomic traits, and morphological characters (Assefa and Labuschagne, 2004; Abdellaoui et al., 2007). Biochemical markers used for assessing diversity (Kolodinska Brantestam et al., 2003) or complementing morphological data include isozymes (Jaradat and Shahid, 2006) and hordeins (Demissie and Bjørnstad, 1997). Molecular markers used include restriction fragment length polymorphisms (RFLPs) (Bjørnstad et al., 1997; Demissie et al., 1998; Backes et al., 2003), random amplified polymorphic DNA (RAPDs) (Abdellaoui et al., 2007; Manjunatha et al., 2007; Papa et al., 1998) microsatellites or simple sequence repeats (SSRs) (Yahiaoui et al., 2008; Feng et al., 2006; Hamza et al., 2004; Jilal et al., 2008), amplified fragment length polymorphisms (AFLPs) (van Treuren et al., 2006; Assefa et al., 2007) and Inter-Sequence Simple Repeats (ISSRs) (Kolodinska Brantestam et al., 2004).

A controversial issue of genetic diversity studies in landraces is the loss of genetic diversity overtime, as different trends in genetic diversity changes have been observed for different countries. A study carried out on barley germplasm derived from the Nordic and Baltic countries using ISSRs showed that while there were no significant changes of genetic diversity observed during the last century in the northern parts of this geographical region a significant decrease was observed in the southern parts (Kolodinska Brantestam et al., 2004). Similar results were obtained when biochemical markers were employed (Kolodinska Brantestam et al., 2003).

3.4. Oat landraces diversity

Oat landraces or oat mixtures were widely grown in Europe until early 1900, while in the USA most cultivars developed up until the 1970s traced back to only seven landraces introduced from Europe (Coffman, 1977). Oat landraces had fairly uniform morphological characters but were heterogeneous for alleles that conditioned reactions to diseases. The 14 cultivars developed as a single-plant selection from the uniform morphologically landrace 'Kherson' referred to above (Coffman, 1977) differed mainly in reactions to diseases and, to a lesser extend, morphological characters. Furthermore, from a single plant selection in a potato field in Cumberland, United Kingdom, the short straw 'Potato Oat' was obtained from which a number of sub-cultivar selections were isolated. We might therefore expect a rather narrow genetic basis to be present but the number of cultivars developed from 'Kherson' and 'Potato Oats' indicates otherwise.

In a number of experiments with many genotypes, morphological characters were shown to possess great phenotypic plasticity in their environmental response (Diederichsen, 2008; Katsiotis et al., 2009). Diederichsen (2008) tested 10 105 entries, including landraces, over four years in a single location and found eight environmentally stable characters, while during the RESGEN CT99-106 project (Katsiotis et al., 2009), 1011 entries were tested in four diverse environments over three seasons but only two stable characters were found, namely panicle shape and kernel covering. In both cases the morphological diversity within the oat accessions did not differ between landraces and modern cultivars.

Using molecular markers non-landrace entries showed the same polymorphism as landraces, with the majority of the AFPLP marker variation (89.9%) residing within accessions of each country, revealing the success of oat breeding programmes in maintaining genetic diversity within elite cultivars (Fu et al., 2005). Finally, in a study among Canadian oat cultivars released between 1886 and 2001 using 30 SSRs, a range of increasing and decreasing patterns of allelic changes was observed at different loci and significant allelic decrease was detected in cultivars released after 1970 coming from specific breeding programmes (Fu et al., 2005).

3.5. Maize landraces diversity

Maize domestication resulted from a single event involving its wild progenitor teosinte (*Z. mays* subspecies *parviglumis*), introgression from other teosinte types and the segregation into two European germplasm pools (see above) between which much hybridisation occurred. The idea of hybridisation rather than a slow northward dispersion accompanied by selection for earliness is supported in the case of Spain and Portugal where many maize landraces are still cultivated. The Iberian maize germplasm display no close relationship with any American types, sharing alleles with both Caribbean and North American flints (Rebourg et al., 2003; Vaz Patto et al., 2004). Other studies have shown that maize landraces can be distinguished by morphological and agronomic traits (Pinheiro de Carvalho et al., 2008; Brandolini and Brandolini, 2001; Goodman and Paterniani, 1969), biochemical traits such as zeins (de Freitas et al., 2005) or molecular markers (Reif et al., 2005; Rebourg et al., 2001; Gauthier et al., 2002). More recently SNP markers have been increasingly applied to study useful landraces (Tenaillon et al., 2001). These studies also show that a significant landraces diversity well adapted to agro-ecological conditions still exist in several countries (Pinheiro de Carvalho et al., 2008; Vaz Patto et al., 2007; Brandolini and Brandolini, 2001; Ruiz De Galarreta and Alvarez, 2001).

In summary there are many germplasm collections of landraces of the major cereals worldwide exhibiting much variation in valuable morphological, agronomic and biochemical traits. The germplasm has been characterised to variable degrees and in many different ways including molecular markers which can assist selection.

4. GENEBANKS AND CONSERVATION OF CEREAL LANDRACES

Throughout the centuries farmers have been the major guardians of genetic diversity. The importance of these crop resources for agriculture and food security was stressed in the International Agricultural Congress at Rome in 1927 (Zeven, 1998). The extinction of traditional farming systems, the aging and exodus of rural population, globalisation, and environmental degradation, have led to extinction of many cereal landraces and much of this diversity has been eroded. As a consequence, during the last century most of this unique cereal biodiversity has disappeared and the information regarding traditional cultivars is presently very scarce. According to FAO (1998), it is estimated that 75% of the genetic diversity of crop plants was lost in the last century. The erosion of these resources results in a severe threat to the world's long-term food security. Although often neglected, the urgent need to conserve and utilize landraces genetic resources as a safeguard against an unpredictable future is evident (Hammer et al., 1999).

The first organised attempts to conserve landrace resources by growing them on farm, (in situ conservation) were made in Austria, during the 1930s (Zeven, 1996). Nowadays the germplasm collections are major guardians of landraces diversity. Increasingly the new tasks of these genebanks are related to the conservation of plant resources and the need to keep accessions representing the landraces diversity and genetic structure (van Treuren et al., 2006). Cereal landraces represents a group of populations, sharing common morphological and agronomic traits, geographical origin and history, and uses (Camacho Villa et al., 2005). These populations are often composed of several genotypes, which together make up the cereal landraces characteristics (Jaradat and Shahid, 2006). For these reasons the genebanks need to collect or conserve rare alleles and avoid genetic drift when accessions are sampled both during field collection and sample regeneration (Mantzavinou et al., 2005). Recently, enormous effort has been made to capture biodiversity being lost by collecting as many germplasm accessions as possible from different geographic regions, especially from the rich centres of diversity. However, it seems that in many cases the sampling strategies were inadequate and the data collected incomplete and scarce, and insufficient attention was paid to ensuring the maintenance of the collected material throughout the lifetime of the genebank reducing the utility of the resource (Sackville Hamilton and Chorlton, 1997). Based on this evidence concern was expressed about the erosion of genetic diversity of the landraces held in the genebanks. It became evident that the management and research on biodiversity requires renewed approaches (Hammer and Gladis, 1996; Hammer and Spahillar, 1998). This problem is increased by the scarcity of knowledge about landrace structure or by the varying understanding of landraces definitions. During the last few years genebank management procedures, such as collecting strategies and techniques, conservation methods, monitoring viability, and regeneration strategies aiming at maintenance of integrity and characterisation of the accessions have been improved by IPGRI (2003). However a major effort is still needed to standardize methodologies used by different genebanks (Engel and Visser, 2003).

A second major problem is the undetermined level of duplicates within and between collections. In order to improve conservation efficiency there is an urgent need to rationalise collections by identifying and minimising unnecessary duplication (Dobrovolskaya et al., 2005) and to develop germplasm core collections, a concept proposed by Frankel and Brown (1984). The first step in the identification of probable duplicates is based on the available passport data (Hintum and Knüpffer, 1995), followed by characterisation data such as agro-morphological, molecular and protein traits. There is an absence of research dealing with this problem and little information is accessible on global information systems. However, there are good examples of research where germplasm collections have been evaluated identifying specific agronomic or quality traits for breeding purposes (Pecetti et al., 2001; Raciti et al., 2003) or assessing accession duplications. For example, Ruiz and Aguiriano (2004) confirmed the existence of 90% of the duplications among 106 cases in durum wheat collections with 266 accessions, using their gliadin patterns. Agro-morphological traits and biochemical or molecular markers are important tools in accession descriptions which will help to fill in information gaps which would otherwise diminish the ability to exploit such material by farmers and plant breeders. In principle, the better managed and more comprehensive a collection, the more valuable it is. The European Co-operative Programme for Plant Genetic Resources (ECP-GR, http://www.ecpgr.cgiar.org/) is a good example of a successful collaboration which should help ensure the continued protection and conservation of cereal landraces through standardised procedures, compatible data documentation systems, and compatibility with European frameworks for better management, study and exchange of resources. Valuable collections of cereal landraces are held at several European and world genebanks (see World Information and Early Warning System (WIEWS) on Plant Genetic Resources for Food and Agriculture (PGRFA), http://apps3.fao.org/wiews/wiews.jsp).

The Convention on Biological Diversity (CBD, 1993) recognizes the contribution of farmers to the conservation and development of genetic diversity. Sharing of benefits and the concomitant increased recognition of the value of the resources are the most effective ways to promote conservation and to ensure the continued availability of plant genetic resources. There is a need to make an economic evaluation of genebank conservation including the issue of benefit sharing but this has not received much attention among those formulating legal measures for the implementation of the CBD. Conservation involves both preservation and evolution. Therefore, ex situ preservation alone cannot provide the lasting benefits that accrue from the conservation of habitats and ecosystems rich in biodiversity (Swaminathan, 2002). This interaction among genebanks and those that are motivated to preserve the traditional seeds will be fundamental to overcoming the problems facing genebanks with seed regeneration, such as genetic drift, contamination and loss.

4.1. On-farm conservation

Two prevalent methods to conserve plant diversity are in situ and ex situ conservation. In ex situ conservation the genetic resources are conserved outside of their natural habitat (or cultivation territory) in identified genebanks. Unfortunately, in the ex situ conservation methods the variability that has been collected remains static because the natural evolution process is not allowed to continue (Dhillon et al., 2004). In contrast, in situ approaches to conservation are at the level of ecosystems and natural habitats, and include the maintenance and recovery of viable population of species in their natural surroundings, or in the case of domesticated species, in the surroundings where they have developed their distinctive properties. This approach involves two methods, (1) the genetic reserve and (2) on-farm conservation (Hawkes et al., 2002). The former is defined as location, management and monitoring of genetic diversity of natural wild populations within defined areas for active long-term conservation, for example the natural conservation sites in the near-east where the wild *Triticum* species are conserved in their place of origin. On-farm conservation is the sustainable management of genetic diversity of locally developed traditional crop cultivars along with associated wild and weedy species or forms within traditional agricultural systems. Such in situ methods, including on-farm conservation, have an advantage over ex situ methods since they provide a natural laboratory for evolution to continue and help the continued gradual build-up of traits imparting adaptation to specific ecogeographical regions and those matching the requirements of local tribes, communities and populations. New and more adapted types evolve and thus diversity is augmented. The need for on-farm conservation of original landraces is one of the most important recent questions in plant genetic resource management (Dhillon et al., 2004).

The 'European Plant Conservation Strategy' (Council of Europe, Planta Europea, 2001), the 'European Community Biodiversity Strategy' (European Commission, 2000), the 'Convention on Biological Diversity' (Convention on Biological Diversity, 1992) and the 'International Treaty on Plant Genetic Resources for Food and Agriculture' (http://www.planttreaty.org) all stress the need to improve the efficiency of conservation techniques, particularly those related to in situ conservation of endangered crops and crop wild relatives. However, little progress has been made on the methodologies for on farm conservation of plant genetic diversity (Maxted, 2003), especially in case of cereal landraces. Although there is a general agreement between conservationists on the fact that landraces should to be conserved on farm, i.e. in the place of their natural origin (Kovács, 2006b), in practice this is often very difficult.

In situ conservation programmes were initiated in most European countries (Maxted, 2003), using participatory approaches (see below), but with limited success. The main problems were that the original places are no longer agricultural land, that traditional farming systems and knowledge has disappeared in the given region, or that the in situ conservation is not economic for the farmers and therefore they do not participate in such projects (Kovács, 2006b).

Some very successful in situ conservation strategies have been established in some neighbouring countries. In case of cereals, Turkey, Israel and other countries of the Fertile Crescent have active genetic conservation programmes (Jaradat et al., 2004). One of the first projects was established in Ammiad to conserve wild wheat and wheat and barley diversity in its place of origin (Anikster and Noy-Meir, 1991). However, in Europe there are few such good examples. For example, the AEGRO (AGRI GEN RES 057) project which attempts to promote an integrative approach for the conservation of crop wild relatives and landraces in situ and on farm, such us in the case of Avena landraces. The Scottish landrace protection scheme was set up in 2006 to compile an Inventory of identified landraces and traditional cultivars which are still being grown and used in agriculture in Scotland providing a safety net for the continued use of landraces by storing seed produced by each grower each year (N. Green and G. Saddler, SASA, Edinburgh, personal communication). The farmers are an aging population and the future of Scottish landraces depends on the continued regeneration of the landraces, so if seed harvest fails, the landrace would otherwise be lost.

Clearly much landrace germplasm is being maintained across the world both in long-term storage in major collections and on farm where it continues to evolve, both of which have their merits and problems. There is much concern about loss of variation, identification, description and accessibility of accessions despite international strategies for addressing these issues.

5. GENOTYPING AND PHENOTYPING

Although the diversity within landraces has been demonstrated to be a powerful means to improve barley yields in marginal environments in recent times (Ceccarelli, 1996), to fully realise and utilise the potential of such resources they need to be accurately and appropriately genotyped and phenotyped and the data made readily available in forms which can be easily interpreted by the plant breeding community.

The genetic structure of landrace collections, when linked to geographical and environmental data, may reveal genomic signatures of selection which are valuable information for breeding for specific environments, farming methods and users. For example, a collection of landraces was made in 1981 in Syria and Jordan from farmers who had been using their own seed for generations (Syrian Jordanian landrace collection (SJLC), Weltzien, 1988). These landraces, sampled from a gradient of agroecological conditions, showed a wide range of responses to drought stress as established by extensive field trials. Preliminary morphological evaluation revealed considerable variation between and within collection sites for many agronomically important characters (Ceccarelli et al., 1987) and disease reactions (van Leur, 1989). Russell et al. (2003) assayed genetic variability at 21 nuclear and 10 chloroplast microsatellite loci for a stratified subset of 125 barley landrace accessions from the SJLC collection, sampled from five different ecogeographical regions. Chloroplast polymorphism was detected, with most variation being attributable to specific differences between the five regions. A total of 244 nuclear alleles were detected, only 38 of which were common to the five regions sampled, most variation being within sites. There were strong associations between the chloroplast and nuclear SSRs and linkage disequilibrium, the non-random association of alleles, at both linked and unlinked SSR loci, clearly showing that these landraces have 'adapted gene complexes' which might be advantageous for breeding programmes and the genetic diversity and population structure was clearly driven by a drought gradient.

In another study of barley, Bjørnstad et al. (1997), compared cultivated accessions from Europe, north America and Japan with Ethiopian landraces, and found that the Ethiopian germplasm was significantly less diverse than the cultivated germplasm, but that it was also genetically more distinct. Similar studies to those in barley have been carried out in wheat and other cereals. Al Khanjari et al. (2007) surveyed Omani wheats using SSR markers and Stodart et al. (2007) used Diversity Array Technology (DArT®) markers to examine 705 accessions from the Australian Winter Cereals Collection and found much diversity, the latter study identifying Nepal as a unique gene pool of particular value.

An exciting development in the potential exploitation of landrace germplasm is the considerable interest in using association-based approaches to identify candidate genes or regions underpinning complex traits (Gaut and Long, 2003; Flint-Garcia et al., 2003; Gupta et al., 2005). Large-scale investigations of sequence variation within genes and across genomes have only just begun for plant species. Such studies are required to determine the distribution and extent of linkage disequilibrium, since this will determine the resolution power of association-based mapping strategies. From studies in other plant species it is clear that the natural decay of linkage disequilibrium with distance occurs at a considerably slower rate in inbreeding systems because effective recombination is severely reduced and genetic polymorphisms remain correlated over longer physical distances (Nordborg et al., 2002; Morrell et al., 2005).

Recently sequence diversity and patterns of linkage disequilibrium were investigated across a 212 kb region in cultivated, landrace and wild barley to determine the impact of inbreeding and evolution history (domestication and selection) (Caldwell et al., 2006). High levels of association were found to stretch across the whole region in the cultivated sample, with linkage disequilibrium values extended across the entire 212-kb region. In contrast, linkage disequilibrium and its significance decreased as a function of increasing distance in both landraces and wild barley (Fig. 1). These contrasting patterns exist despite similar levels of inbreeding and most likely reflect different population histories associated with the occurrence of bottlenecks and selection within the domesticated germplasm. Therefore, large linkage disequilibrium regions in cultivated, low-resolution whole-genome scans could be deployed to identify candidate gene regions; this would then be

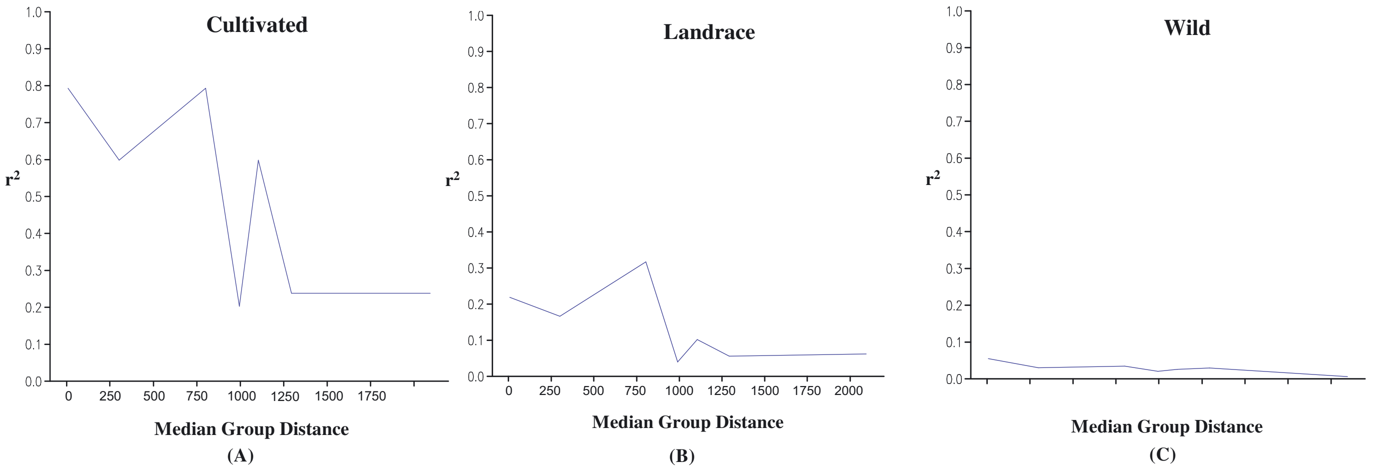

Figure 1. Plots of linkage disequilibrium as measured with the commonly used statistic (r^2) (y axis), which is based on the allele frequencies at two loci as a function of distance in kilobases (kb) (x axis) for the (A) cultivated, (B) landrace, and (C) wild samples (Caldwell et al., 2006).

complemented by fine-scale, high-resolution linkage disequilibrium mapping utilising landraces and wild barley to identify candidate genes.

5.1. Genotyping technology

The developments in association genetics have been facilitated through advances in DNA molecular marker technology reviewed above and by Buckler and Thornsberry (2002). An example of the latest technology is the high throughput Illumina ‘Golden Gate Assay’ SNP approaches which gives a high density of markers across many genotypes, enabling association genetic approaches to become highly effective. Such surveys provide information on genomic diversity, domestication and evolution, identify geographic regions, which contain high levels of diversity, and discriminate between groups of similar accessions. With the large amount of sequence information in barley, over 400 000 Expressed Sequence tags (ESTs), a platform was set up for high resolution genotyping known as Illumina Oligo Pool Assay (OPA) with 1536 Single Nucleotide Polymorphisms (SNPs) in each assay. Genes which are transcriptionally responsive to abiotic stress were chosen in particular for examining landrace populations.

A subset of the 176 landrace accessions from the SJLC referred to above were subjected to high throughput genotyping on the OPA platform and 72% of the 1536 SNPs were polymorphic and well distributed across the 7 barley chromosomes. Using the available phenotypic data also, whole genome association scans were used to identify and validate genes and markers linked to performance under drought stress (J. Russell et al., personal communication). Again five distinct groups clustering around key ancestors and regions of origin of the germplasm were identified, the accessions from North East Syria and South Jordan being particularly contrasting. Differences in the patterns of diversity between regions of origin were observed along the chromosome, highlighting selection signatures of adaptation to the environment and/or agronomic practices prevalent in these regions.

5.2. Genotype-phenotype association

Another example of strategies to combat drought stress using landrace germplasm is found in the work of Comadran et al. (2007) who identified barley genomic regions influencing the response of yield and its components to water deficits in a collection of 192 genotypes that represented landraces, old, and contemporary cultivars sampling key regions around the Mediterranean basin and the rest of Europe. They used a stratified set of 50 genomic and EST derived molecular markers, 52 of which were SSRs, and 1131 DArT® markers which together revealed an underlying population sub-structure that corresponded closely to the geographic regions in which the genotypes were grown. The population was phenotyped for yield at two contrasting sites in each of seven Mediterranean sites for two years leading to marker-trait associations to understand the genetic and physiological dynamics underlying barley domestication and intensive breeding carried out in the last century and its relation to adaptation to drought. The yields observed for individual genotypes ranged from 10 t/ha to complete failure of individual genotypes to produce any seed due to the stress. As this was a highly structured sample, after accounting for this in the analysis, multi-environment QTLs were detected most frequently on chromosomes 3H, 4H, 5H and 7H (Fig. 2). One of the encouraging findings of this study was the detection of significant genetic variation for yield in the eight severely stressed environments where the mean yield was less than 2 t/ha, with one of the most consistent genomic regions being that on chromosome 7H, where four out of the five significant associations came from the Jordanian sites with mean yield ranging from 0.3 to 1.2 t/ha. The detection of QTLs in the low yielding environments offers the

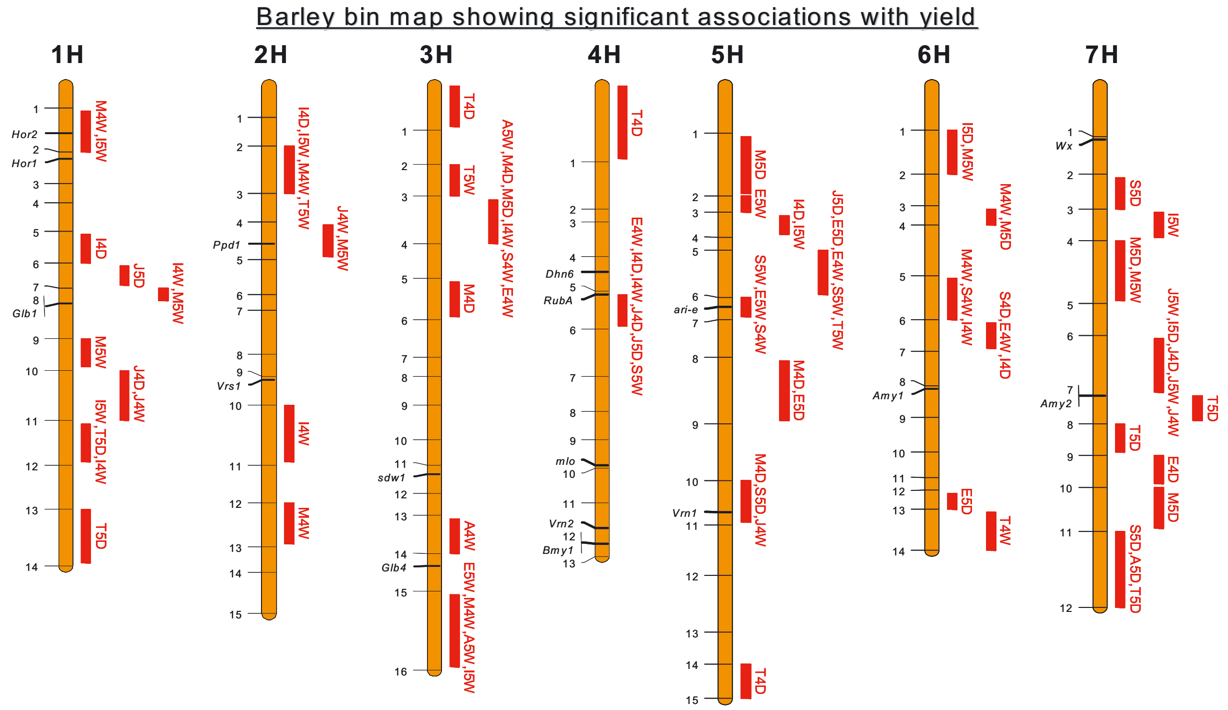

Figure 2. Barley chromosome 'bin' map showing the location of phenotypes associated with yield under drought stressed environment conditions.

prospect of developing Marker Assisted Selection protocols for yield improvement in such situations.

5.3. Accurate whole-plant field phenotyping for exploiting variation within landraces

In plant breeding literature, the term "phenotypic selection" is often used interchangeably with "visual selection", even though the two are not synonymous. With the current rapid advancements in high-throughput molecular genotyping technologies described above, it is becoming increasingly clear that the limiting factor in applying those powerful technologies to molecular breeding programmes is no more the capacity of genotyping, but the potential for accurate or precision phenotyping (Campos et al., 2004; Fasoula, 2004). Phenotyping becomes a particular challenge when moving from qualitative to quantitative traits, like yield and stability, which have the greatest interest for breeders (Thomas, 2003). A way to bridge the genotype-phenotype gap (Miflin, 2000; Parry and Shewry, 2003) is provided when the unit of evaluation and selection in plant breeding becomes the individual plant (individual genome) and the confounding effects of competition and soil heterogeneity on selection efficiency are addressed with appropriate experimental designs (Fasoulas and Fasoula, 1995, 2000).

Fasoula (2004) demonstrated a methodology for accurate whole-plant field phenotyping using the analysis of crop yield potential, i.e. yield, stability, and responsiveness to inputs (Fasoula and Fasoula, 2002, 2003) which resulted in extracting superior lines from breeder's seed of two local barley (cv. Athenaida) and durum wheat (cv. Kyperounda) cultivars of landrace origin. An excerpt of this analysis is presented in Table I.

Developments in genotyping technologies are making the variation available in landraces ever more accessible. However, high quality, extensive and detailed, relevant and appropriate phenotyping needs to be associated with the genotyping to enable it to be exploited successfully. We also need to understand the complexity of the genetics of these desirable traits in order to develop new germplasm.

6. NUTRIENT UPTAKE AND UTILISATION

Landraces have developed mostly in environments with low nutrients availability, and may therefore represent a source of variation for selection of varieties adapted to low fertiliser input cropping systems. While the literature on N and P uptake and utilisation of landraces is relatively rich, little has been documented for other nutritional elements. Landraces differ from elite cultivars in their heterogeneous genetic structure as well as for several typical morpho-physiological traits. However, the focus below will be on the morphological and physiological aspects associated with uptake and utilisation of nitrogen and phosphorus by cereal landraces.

The main factor determining nutrient uptake is the root system. This has been shown to be more developed in wheat landraces than in high yielding elite germplasm, especially semi-dwarf varieties (Siddique et al., 1990; Waines and Ehdaie, 2007). Good soil exploration by roots has been shown to be

Table I. Ranking of selected lines within the local Cyprus durum wheat cultivar Kyperounda, of landrace origin, based on the analysis of crop yield potential for accurate whole-plant field phenotyping, using the R-19 honeycomb design, capable to evaluate 19 entries. The original cultivar Kyperounda (control) was assigned the design code 19 and ranked second last in terms of mean yield per plant.

	Yield g/plant		Stability of performance		Responsiveness to inputs		Expected response to selection	
Line code	$\overline{x}$	%	$\overline{x}/s$	%	$(\overline{x}_{sel} - \overline{x})/s$	%	$\overline{x}(\overline{x}_{sel} - \overline{x})/s^2$	%
7	142.52^{a}	100	2.69	97	1.60	80	4.30	78
14	142.12^{ab}	100	2.28	82	1.76	89	4.01	73
5	140.87^{ab}	99	2.58	93	1.72	87	4.44	81
17	138.63^{ab}	97	2.78	100	1.78	90	4.95	90
Other intermediate lines								
6	123.26^{bcd}	86	2.44	88	1.77	89	4.32	79
13	123.09^{bcd}	86	2.29	82	1.72	87	3.94	72
3	116.89^{cde}	82	2.15	77	1.70	86	3.66	67
Kyperounda (19-control)	111.00^{cde}	78	2.03	73	1.67	84	3.39	62
8	101.10^{e}	71	2.44	88	1.78	89	4.34	79

essential for absorption of phosphorus (Gahoonia and Nielson, 2004a, 2004b) and nitrogen (Cox et al., 1985; Edwards et al., 1990; Feil et al., 1990; Laperche et al., 2006; Wieseler and Horst, 1994), though in the latter case the results are more divergent (Heuberger and Horst, 1995; Kuhlmann et al., 1989; Van Beem, 1997). Thus, appropriately selected landraces with well-developed root systems could be a source of variation for the improvement of nutrient uptake, but its use would require suitable methods for the assessment of the root system, which are still lacking.

Arbuscular mycorrhizas may considerably increase the active absorbing surface with minor cost for the plant, compared to the formation of roots and root hairs, enhancing P uptake and to a certain extent, uptake of other nutritive elements (Bolan, 1991). The degree of colonialisation has been shown to depend on the host genotype in wheat (Hetrick et al., 1993; Kapulnik and Kushnir, 1991; Manske, 1989, 1990; Manske et al., 1995) and barley (Baon et al., 1993). However, high colonisation rates are not always associated with correspondingly high symbiosis benefits for the plant as this also depends on the host genotype (Hetrick et al., 1993; Manske, 1989, 1990; Manske et al., 1995). There is evidence that certain landraces benefit more from symbiosis than high yielding elite cultivars (Kapulnik and Kushnir, 1991; Manske, 1990). Thus, improvement of the efficiency of symbiosis based on selected landraces might be possible.

Nitrogen-fixing bacteria in the rhizosphere are also important root symbiotic relationships for nutrient uptake, especially in Azospirillum species. These associations are also influenced by the host genotype and are particularly developed in several wheat landraces and wild ancestors originating from the southern Mediterranean basin (Kapulnik et al., 1983, 1985, 1987). Although the bacteria contribute to N nutrition of the host plants, the major benefit for the plant was from stimulation of root growth and thus drought tolerance (Kapulnik et al., 1983, 1985, 1987).

Landraces and old varieties are often later maturing than modern cultivars, especially those bred for dryer environments (Canevara et al., 1994). This may be of importance for the uptake of N in N-limited environments. If little or no N fertiliser is applied, N supply depends on mineralisation of soil organic matter, organic fertilisers and crop residuals. The time course of mineralisation is not always compatible with that of the crop's requirements (Panga and Lethaya, 2000) and varies greatly from year-to-year due to factors such as the weather and preceding crops. The potential uptake by cereal plants is mostly higher than the actual mineralisation in the soil, especially in the later growth stages (Baresel et al., 2008). Late-maturing genotypes may consequently absorb more N overall, and may therefore be better adapted to these conditions, if water availability is not limiting.

Under N-limited conditions, wheat landraces and varieties with a taller growth habit and lower harvest index have been shown to absorb and translocate more nitrogen into the grain than modern cultivars (Baresel et al., 2005). Figure 3 shows that old landraces and very old cultivars with similar morphological habit may absorb much more nitrogen under low-yielding conditions than modern cultivars and breeding lines. One reason might be greater pre-anthesis uptake and buffering capacity in genotypes with high vegetative biomass (Baresel et al., 2008), but this aspect has been little investigated. Nitrogen absorbed before grain filling is remobilised and then translocated to the grain after anthesis. Translocation efficiency might therefore also contribute considerably to efficient N utilisation. However, only small differences between genotypes could be detected in the absence of leaf diseases (Bertholdsson and Stoy, 1995; Johnson et al., 1967; Papakosta and Garianas, 1991; Pommer, 1990) and therefore genetic variation of translocation efficiency does not appear to offer much opportunity to improve N efficiency.

There are many possible combinations of environmental factors which determine nutrient availability and landraces generally reach their genetic equilibrium in environments with reduced nutrient availability and variable conditions from year to year. They therefore show many different adaptive types (Attene and Veronesi, 1991) and if maintained through

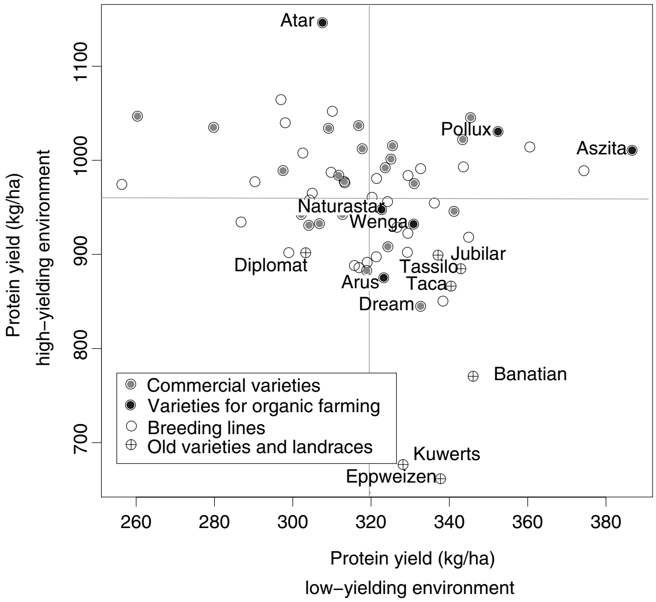

Figure 3. Protein yields of modern varieties and breeding lines, varieties bred for organic farming and landraces or very old varieties in an environment with high and low average protein yield, respectively. The latter group have relatively high protein yields in the low-yielding environments, but low performance in the high-yielding environments. Results of a linear regression analysis on 70 genotypes in 9 environments; see Baresel et al. (2005) for details.

on-farm conservation, will offer a valuable resource for finding ways of improving nutrient use efficiency without loosing genetic plasticity.

Nutrient use efficiency is a very important criterion for sustainability. Landrace material offers a potential source for crop improvement although these traits are highly interactive with their environment, particularly developmental stage, soil conditions and other organisms affecting roots and their environment.

7. NUTRITION AND QUALITY

Early landraces and wild species provide a broad representation of natural variation not only in agronomically important traits, but also in nutraceuticals, which have decreased during the breeding of modern cultivars. The nutritional status of the most important staple foods, such as the cereals is ultimately dependent on their metabolic composition (Galili et al., 2002). Nevertheless, while traits associated with yield and resistance have been the focus of most research, quality traits that are dependent on chemical composition are less well studied. There are some notable exceptions, such as protein content and structure of wheat cultivars and landraces (Láng, 2006; Rakszegi et al., 2006). Mineral content in modern wheat cultivars has significantly decreased including copper, iron, magnesiou, manganese, phosphorous, selenium, and zinc (Murphy and Jones, 2006). Looking for breeding sources for higher levels of iron and zinc has revealed that the highest levels can be found in landraces and low yielding genotypes (Monasterio and Graham, 2000). An ancestral wild wheat gene was found that accelerates senescence and increases nutrient remobilisation from leaves to developing grains. The gene was found in all wild emmer accessions and most domesticated emmer but not in durum lines or hexaploid wheat (Uauy et al., 2006). Cereal seed mineral content have been analysed in a wide range of cereal genebank accessions (Bálint et al., 2003) to find optimal sources to increase mineral content of modern wheat cultivars. Emmer wheat is a promising source of genetic variation for protein, zinc and iron content.

In bread wheat, the concentration of carotenoids is low, but they are more abundant in, for example, durum wheat, emmer and einkorn cultivars and landraces, having higher concentration in landraces then in cultivars (Panfili et al., 2004). Tocols, in contrast, are abundant both in bread wheat and durum wheat (Panfili et al., 2004). As carotenoid and tocol contents are independent traits (Hidalgo et al., 2006) that were not subject to conscious human selection and are selectively neutral, the wide range of natural variation still exists in the cereal genetic resources and landraces. In recent experiments bread wheat landraces, emmer and einkorn were found to be the best sources of tocols, while durum landraces and emmer were the best sources of carotenoids (Hidalgo et al., 2006).

Total phenolics in wheat varied both with cultivar and farming site (Gélinas and McKinnon, 2006). The phenolic compounds flavonoids, saponins, lignans and sterols are found in oat grain, but in minor quantities. Their concentrations are very low compared to avenantramides and tocols but have antioxidant and other bioactivitie properties (Peterson, 2004). Tocopherols and tocotrienols have higher concentrations in cultivars with high total lipids (Bryngelsson et al., 2002) and landraces of black oats have higher concentrations of antioxidants than elite cultivars (Mannerstedt-Fogelfors, 2001).

Maize contains appreciable amounts of carotenoids (Wurtzel, 2004) and has a greater total phenolic content and total antioxidant activity than wheat, oats or rice (Adom and Liu, 2002). In the maize kernel, tocopherol and oil content may be physiologically associated (Kurilich and Juvik, 1999) while the natural variation detected in maize landraces kernel pigmentation may be associated with increased availability of certain antioxidant compounds. White maize polyphenolics have shown to have antioxidant and anti-carcinogenic effects (Del Pozo-Insfran et al., 2006). Blue, purple and red-pigmented maize kernels are also rich in anthocyanins with well-established antioxidant and bioactive properties (Del Pozo-Insfran et al., 2006). Purple maize, that has been cultivated for centuries in the Andean Region, is a good example of this (Pedrechi and Cisneros-Zevallos, 2006).

In general, cereal landraces and old varieties are among the best sources of phytonutrients accompanied with optimal micronutrient concentrations. Grains, fruits and vegetables contain a broad variety of phytonutrients, which show a significant effect on reducing the incidence of aging-related and chronic diseases. Among the numerous antioxidant compounds present in these foods, grain fat-soluble antioxidants and their unique bioactive compounds play an important role in disease prevention. The additive and synergistic effects of such phytochemicals in fruits, vegetables and whole grains are thought to be primarily responsible for their health benefits.

Landraces are clearly a potential source of traits for improved nutrition of cereal crops, particularly antioxidants, phenolics in general, carotenoids and tocol in particular. They also have the potential to improve mineral content, particularly iron and zinc, if these traits can be successfully transferred to improved varieties.

8. BIOTIC AND ABIOTIC STRESS RESISTANCE AND TOLERANCE

The replacement of landraces by homogeneous cultivars entails a significant loss of genetic variation for resistance to biotic and abiotic stresses. Elite cultivars may not possess the combined resistances already present in the landrace that they are intended to replace. Also, landraces might be a good reservoir of resistance mechanisms other than the hypersensitive mechanism typically exploited in modern cultivars due to its simple inheritance and complete expression. Most of the studies cited and others are either screening for qualitative resistance or more detailed mapping of the major genes responsible. There are few studies of landraces for partial and polygenic resistance due to the increased resources needed to obtain quantitative data. However, such studies are needed to determine whether multiple sources of partial resistance from such sources offer genes more likely to be durable than those in the elite gene pools. Below we will review the biotic stresses for just wheat and barley where landraces have provided valuable sources of resistance, then disease tolerance and some abiotic stresses for cereals in general.

8.1. Wheat diseases

8.1.1. Septoria leaf blotch

The fungus *Mycosphaerella graminicola* (Fuckel) Schr. (sexual stage of *Septoria tritici* Rob. in Desm) or Septoria Tritici Blotch (STB) is currently a major disease of worldwide distribution. Most currently grown wheat cultivars are more or less susceptible to *M. graminicola*. The Italian landrace Rieti, an ancestor of many modern European wheat cultivars has been identified as very resistant to all studied isolates (Arraiano and Brown, 2006). The presence of *Stb6* gene in both European and Chinese landraces suggests that this gene has been present in cultivated wheat since the earliest times of agriculture (Chartrain et al., 2005). Resistance has also been found in Czech and Slovak landraces (Vechet and Vojácková, 2005).

8.1.2. Powdery mildew

Powdery mildew of wheat is a foliar disease caused by the obligate biotrophic fungus *Blumeria graminis* (DC.) Speer f. sp. *tritici* (syn. *Erysiphe graminis* DC. f. sp. *tritici* G. Marchal) that can cause loss in both grain yield and quality. Screening of old wheat cultivars, landraces and related species for resistance to powdery mildew started in the 1930's (Hsam and Zeller, 2002) and *Pm* genes have since been identified in many different, widely distributed wheat cultivars and landraces. Non-major gene resistance has been sought such as the durable adult plant resistance found in the landrace accession k-15560 (Peusha et al., 2002).

8.1.3. Fusarium Head Blight

There is little resistance available to the major disease Fusarium Head Blight caused by *Fusarium graminearum* Sch. although some has recently been identified in landraces (Zhang et al., 2000).

8.1.4. Bunts and smuts

Common bunts (*Tilletia foetida* (Wall.) Liro and *T. caries* (DC.) Tul.) are important diseases that are easily controlled by seed dressing, but might become more important in organic and low input agriculture. More than 15 resistance genes (*Bt1-15*) have been identified in wheat and the landrace PI178383, originally collected in Turkey, carries resistance genes *Bt-8, Bt-9* and *Bt-10* plus an unidentified factor (Goates, 1996). Resistance has also been reported in landraces of bread wheat (Hubert and Buertsmayr, 2006) and of durum wheat (Mamluk and Nachit, 1994). Karrnal bunt (*Tilletia indica* Mitra) is the most recently described smut of wheat and resistance has been identified in Indian landraces (Anon., 1943).

8.1.5. Rust diseases

Stem rust (*Puccinia graminis* Pers.) resistance transferred to bread wheat from Yaroslav emmer (*Sr2* complex) in combination with other genes seems to have provided the foundation for durable resistance to stem rust in CIMMYT germplasm (Roelfs, 1988) in the last 50 years. Sources of durable resistance to stem rust in durum wheat have been reported, like the durum wheat Glossy Huguenot, effective in Australia over the past 100 years (Hare, 1997). Interestingly, its resistance is also quantitative and based on a reduced number of pustules in adult plants and a delayed onset of disease. As indicated by Roelfs (1988), of the 41 known genes for stem rust resistance, 20 originated in species other than *T. aestivum* and *T. turgidum*; of the 35 known genes for leaf rust resistance, 12 originated in species other than *T. aestivum* and *T. turgidum*. Among the genes originating from *T. aestivum* for resistance to either rust, a number of these are from landraces (McIntosh et al., 1998). The recently reported spread of the stem rust race Ug99 and the dependence of so many elite cultivars of wheat on the *Sr31* resistance gene has spurred renewed interest in surveying landrace collections for novel resistance sources (Bonman et al., 2007).

Durable resistance to leaf rust (*Puccinia recondita* f.sp. *tritici* (Eriks. & E. Henn.) D.M. Henderson and *P. triticina*

Erikss.) of wheat is thought to be more difficult to obtain than to stem rust but resistance against leaf rust has been identified that appears more durable than the norm. Resistance in the bread wheat cultivars Americano 44D, and Frontana, derived from resistant landraces, appears to be particularly durable. It appears that *Lr12* and *Lr13,* both genes for hypersensitive resistance that is expressed only in the adult plant stage, in combination with *Lr34*, are the basis of most of this resistance (Roelfs, 1988; Rubiales and Niks, 2000). Americano 44D, a Uruguayan landrace of unknown origin (called Universal 2 in Argentina), was used by Klein in breeding early Argentinean lines and is now considered another important source of durable resistance to leaf rust (Van Ginkel and Rajaram, 1992).

Durable resistance to yellow rust (*Puccinia striiformis* Westend.) has been described in wheat landraces from China, Italy and the Netherlands (Van Dijk et al., 1988; Zhang, 1995). Partial resistance combined with temperature-sensitive resistance have been suggested as the major components of the durable resistance found in old winter wheats in the Netherlands (Van Dijk et al., 1988). Sources of partial resistance to leaf rust have been recently reported in landraces from various origins (Fekadu and Parlevliet, 1997; Martínez et al., 2001a, b; Shtaya et al., 2006a, b).

Histological studies on interactions between plants and rusts can help both to discern the various resistance mechanisms and to combine them in a genotype in the hope to increase durability. The commonly used hypersensitivity resistance, typically conferred by single genes with race-specific effectiveness, is due to a post-haustorial defence mechanism. This type of resistance is very common in non-host interactions (Niks and Rubiales, 2002). It also is the mechanism responsible for the partial resistance of some wheat landraces to wheat leaf rust (Martínez et al., 2001c).

8.1.6. Aphids

Resistance to the Russian wheat aphid (*Diuraphis noxia* Kurd.) has been found in landraces of wheat from Iran and the former Soviet Union (Du Toit, 1987).

8.2. Barley diseases

8.2.1. Powdery mildew

In most barley growing regions powdery mildew (*Blumeria graminis,* (syn.: *Erysiphe graminis*) (D. C. Speer) f. sp. *hordei*) is very common. Intensive studies were carried out on barley landraces from Ethiopia (Negassa, 1985a, b), Jordan and Syria (Van Leur, 1989) and other countries of the Near East (Weltzien, 1988), Europe (Honecker, 1938), India (Freisleben, 1940), Japan (Hiura, 1960) and world-wide (Moseman, 1955; Nover and Mansfeld, 1955, 1956; Hoffmann and Nover, 1959; Rigina, 1966; Wiberg 1974a, b; Moseman and Smith, 1976; Czembor, 2002). The main history of incorporation of powdery mildew resistance genes in cultivated barley and the exploration of their genetic diversity in Europe is described by Wolfe and Schwarzbach (1978).

The situation regarding diversity of genes for partial resistance to powdery mildew in cereal landraces is less clear. However, many assessments of partial resistance to pathogens in barley have been made with powdery mildew (Wright and Heale, 1984; Asher and Thomas, 1983, 1984, 1987; Anderson and Torp, 1986; Carver, 1986; Heun, 1986; Geiger and Heun, 1989; Newton, 1990; Kmecl et al., 1995).

8.2.2. Rust diseases

Three rust species commonly occur on barley: leaf rust (*Puccinia hordei* Otth), stripe rust (*P. striiformis* West. f. sp. *hordei*) and stem rust (*P. graminis* Pers.: Pers. f. sp. *tritici* Eriks. et Henn.).

The origins of resistance sources were similar to those of mildew-resistant landraces from the Mediterranean region where both the host and the pathogen are indigenous and have co-evolved (Anikster and Wahl, 1979). Israel in particular is part of the centre of origin and genetic variation of wild native *Hordeum* species *H. vulgare* ssp. *spontaneum* Koch, *H. bulbosum* L. and *H. murinum* (Wahl et al., 1988; Kandawa-Schulz, 1996). Some interesting material has also been found in Azerbaijan and Turkmenia (Bakhteev collection) and Iran (Kuckuck collection) (Nover and Lehmann, 1974; Walther and Lehmann, 1980). Many studies described the activities in evaluation and in breeding for major genes and partial resistance (Clifford, 1985; Reinhold and Sharp, 1986; Yahyaoui et al., 1988; Khokhlova et al., 1989; Jin et al., 1995; Lukyanova and Terentyeva, 1997; Alemayehu and Parlevliet, 1997). Resistance against a new pathotype of *Puccinia hordei* with virulence for the resistance gene *Rph7* has been identified in barley landraces (Shtaya et al., 2006c).

Stripe rust is known in most of the barley growing regions. Screening for new sources of resistance has been carried out by many groups (Nover and Lehmann, 1966, 1970, 1975; Upadhyay and Prakash, 1977; Stubbs, 1985; Van Leur et al., 1989; Okunowski, 1990; Luthra et al., 1992; Hill et al., 1995). As with wheat rusts, much durable resistance is pre-haustorial and is known to be the mechanism responsible for the partial resistance of some barley landraces to barley leaf rust (Shtaya et al., 2006a, b). Sources of partial resistance to leaf rust (*P. hordei*) have been recently reported in barley and wheat landraces from Spain and from Fertile Crescent (Martínez et al., 2001a, b; Shtaya et al., 2006a, b).

8.2.3. Scald

Evaluations of barley for resistance to scald (*Rhynchosporium secalis* (Oudem.) J. J. Davis *f. sp. hordei*) have been carried out in many countries (Fukuyama et al., 1998; Yitbarek et al., 1998). Recent examples of such reports are: novel alleles at the *Rrs1* and other loci have been found for *Rhynchosporium secalis* resistance (Grønnerød et al., 2002; Bjørnstad et al., 2004).

8.2.4. Net blotch

Studies of landraces for resistance to net blotch (*Pyrenophora teres* (Died.) Drechsl. f. *teres*) have been carried out by many scientists (Schaller and Wiebe, 1952; Buchannon and McDonald, 1965; Gaike, 1970; Smirnova and Trofimovskaya, 1985; Proeseler et al., 1989; Lukyanova, 1990; Faiad et al., 1996). Sato and Takeda (1994) studied the variation of host resistance of 2233 accessions of the barley world collection and found sources of resistance in accessions from Ethiopia, North Africa and Korea. New sources with resistance to up to eight races of *P. teres* were found among Peruvian landrace accessions (Afanasenko et al., 2000).

8.2.5. Barley stripe

Many studies were conducted to identify new sources of resistance to barley stripe (*Pyrenophora graminea* Ito & Kuribayashi) including landraces (Baigulova and Pitonya, 1979; Nettevich and Vlasenko, 1985; Skou and Haahr, 1985; Van Leur et al., 1989; Su et al., 1989; Lukyanova, 1990; Bisht and Mithal, 1991; Ceccarelli et al., 1976; Kirdoglo, 1990; Skou et al., 1992, 1994).

8.2.6. Common root rot and spot blotch

Several germplasm collections have been evaluated and resistance to common root rot and spot blotch (*Cochliobolus sativus* (Ito & Kurib.) Drechsler ex Dastur) has been identified from several resources (Banttari et al., 1975; Velibekova, 1981; Rochev and Levitin, 1986; Lehmann et al., 1988; Lukyanova, 1990; Gilchrist et al., 1995; Semeane, 1995; Faiad et al., 1996).

8.2.7. The smuts

Three species of cereal smut attack barley: *Ustilago nuda* (Jens.) Rostr. (*U. segetum* var. *nuda*), *U. nigra* Tapke (*U. segetum* var. *avenae*) and *U. hordei* (Pers.) Lagerh. (*U. segetum*). Many studies on resistance to these pathogens were conducted (Shchelko, 1969, Nover et al., 1976; Damania and Porceddu, 1981; Onishkova, 1987; Dunaevskij et al., 1989; Surin, 1989; Lukyanova, 1990; Dubey and Mishra, 1992) identifying sources of resistance from landraces from Ethiopia, Yemen, Tibet, Canada and USA.

8.2.8. Fusarium complexes

Many scientists described differences in fusarium resistance between cultivars (Grigor'ev et al., 1988; Van Leur, 1989; Gu, 1989; Corazza et al., 1990; Khatskevitch and Benken, 1990; Lukyanova, 1990; Takeda, 1992; Filippova et al., 1993; Nelson and Burgess, 1994; Perkowski et al., 1995, 1997). Based on these reports it can be concluded that valuable sources of resistance were identified in the East Asian region landrace accessions in particular (Takeda and Heta, 1989).

8.2.9. Viruses

Yasuda and Rikiishi (1997) evaluated a total of 4342 barley accessions from the world collection on a field in Japan infected with strain I (Kashiwazaki et al., 1989) of BaYMV for resistance. The percentage of asymptomatic cultivars was highest among Ethiopian landraces followed by those from Japan. Cultivars showing severe disease symptoms were frequently found among Chinese, Nepalese, southeast Asian, north African, north American and European accessions. Field resistance to barley yellow dwarf was detected in several Ethiopian barleys (Schaller et al., 1964).

8.2.10. Aphids

The spring two-rowed barley RWA 1758 has been developed via selection from CIho 4165, a landrace originally collected in Afghanistan (Bregitzer et al., 2008).

8.3. Disease tolerance

A character much neglected in elite breeding programmes is disease tolerance, not least because of the varied definitions of the term and the difficulty of measuring it (Bingham and Newton, 2009). However, inter-specific variation has been found in cereals, for example powdery mildew-infected leaves of a wild oat showed a smaller reduction in net photosynthetic rate than a cultivated oat genotype under comparable infection severities (Sabri et al., 1997). The wild oat leaves also showed a slower rate of disease-associated senescence. In a comparison of wild and cultivated barley genotypes similar effects were reported (Akhkha et al., 2003) but the effect of this variation on tolerance at the scale of the crop canopy has not been determined. Several landrace accessions appear amongst the accessions screened for tolerance in barley (Newton and Thomas, 1994; Newton et al., 1998, 2000), though not disproportionately with more modern cultivars.

8.4. Abiotic stresses

Generally the genus *Hordeum* shows a high degree of adaptation to different stressful environments.

8.4.1. Drought tolerance

Drought is the most common abiotic constraint for stable barley production in rain-fed areas. Under Mediterranean conditions, water stress is particularly common at the end of barley life cycle (Passiuora, 1996). In comparison to other cereals, barley is well adapted to arid environments and the immediate progenitor of cultivated barley *H. vulgare* ssp. *spontaneum* can grow in desert condition (Nevo, 1992; Zohary and Hopf, 1998). Such ecotypes were identified in desert locations in Jordan (Jaradat et al., 1996). The study of drought stress on yield in Mediterranean environments noted above (Comadran et al., 2007) identified genomic regions in landraces that may be very valuable for combating such stress.

8.4.2. *Frost tolerance*

Selection of highly frost tolerant lines from Turkish barley landraces has resulted in conversion of spring based production into winter based and enlargement of winter sown barley production in the Turkish highlands since 1940. Today 60% of barley production has been provided by winter sown barley, yield has doubled and these landraces have been routinely and widely used as parents in many breeding programmes in Turkey (Akar et al., 2009).

8.4.3. *Salinity tolerance*

In the investigation of Abo-Elenin et al. (1981) 1163 entries were tested in the field and 777 in lysimeters. In this study 'Abyssinia' was the most tolerant. Mano et al. (1996) screened 6712 accessions for salt tolerance at germination. Accession variation showed a normal distribution and the most tolerant ones could germinate in sea water. However, six-rowed cultivars were more tolerant than two-rowed, hull-less than hulled, normal than semi-dwarf '*uzu*', and winter than spring. In another study Mano and Takeda (1995) evaluated 5182 barley cultivars for salt tolerance at seedling stage. Generally the geographical differentiation among tested accessions was not clear.

Tolerance to salinity is more frequent in bread than is durum wheat, as bread wheat has a salt-exclusion mechanism but durum does not. This was found in landraces originating from saline areas of the Middle East and is conferred by *Nax* genes which therefore could be incorporated into both durum and bread wheat (Munns, 2005).

8.4.4. *Acid and alkaline soils and tolerance to metal toxicity*

Cereal adaptation to acid and alkaline soils is limited by two major problems, the aluminium and manganese toxicity in acid environments and boron toxicity in alkaline ones. The soil acidity is a serious agricultural problem, affecting as much as 40% of the world's arable land and up to 70% of the world's potentially arable land (Kochian et al., 2005; Hede et al., 2001). Aluminium toxicity is a main growth and yield-limiting factor on soils with pHs below 5.0 (Davies, 1994), and can directly reduce yield by up to 60% (Tang et al., 2003). Amelioration of soil surface layer is not a reasonable solution in low input and organic agriculture, and because plant roots develop in lower acid layers to reach critical water and nutrient supplies. Selection and development of genotypes with enhanced tolerance to acid soils and toxic levels of aluminium is considered to be a more effective solution to this problem.

Cereal crops show very different responses to aluminium toxicity and soil acidity. The highest aluminium tolerance is detected among rye (Little, 1988), followed by oat (Slaski, 1992), wheat (Aniol and Madej, 1996), barley (Foy et al., 1965), and corn (Horst et al., 1997). Some experimental evidence shows a dramatic variation in aluminium tolerance among cultivars, which can be related to their genetic variability (Carver and Ownby, 1995). Landraces are important sources of this variability to improve the aluminium and acid soils tolerance in breeding programmes, but most research on aluminium tolerance has been carried out on elite cultivars or isogenic lines (Kochian et al., 2005) and there are very few studies to identify landrace tolerance for these traits (Pinheiro de Carvalho et al., 2003; Gudu et al., 2001; De Sousa, 1998; Cosic et al., 1994). Forty-eight accessions representing 16 Madeiran wheat landraces were screened for their aluminium tolerance using erichrome staining and root elongation (Pinheiro de Carvalho et al., 2003, 2004) and the accumulation of callose in the root types (dos Santos et al., 2005). The variability of landrace responses to the presence of aluminium and the existence of high performing accessions with better performance has been shown by comparison with elite cultivars such as Maringa. Durum wheat landraces show less variability and are moderately sensitive or tolerant to the presence of aluminium (Pinheiro de Carvalho et al., 2003; Cosic et al., 1994). De Sousa (1998) published a classification of aluminium tolerance of 76 wheat cultivars, including several landraces introduced in earlier twentieth century. The major sources of aluminium tolerance in wheat are considered to be originated from Brazil (Zhou et al., 2007). However, Stodart et al. (2007) and Zhou et al. (2007), through the screening of wheat accessions from different countries showed the existence of potential new sources of aluminium resistance among the landraces germplasm originated from Bulgaria, Croatia, India, Italy, Nepal, Spain, Tunisia, and Turkey. 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). The evaluation of corn germplasm, in two different studies screening of 76 accessions of unknown number of Kenyan maize landraces (Gudu et al., 2001) and 40 accessions of five Madeiran maize landraces (Pinheiro de Carvalho et al., 2004) also showed their high variability in aluminium tolerance, with several accessions presenting better performance then commercial standards.

The soil alkalinity also affects agricultural crops, growing in arable soils with pHs between 8 and 10. In barley, boron toxicity is directly responsible for yield penalties of up to 17% (Cartwright et al., 1984). The screening of 444 accessions of winter barley and 19 accessions of durum wheat, including landraces from Europe, west Asia and north Africa showed that boron tolerance is associated with geographic origin (Yau, 2002; Yau et al., 1995).

Landraces have long been assumed to be valuable sources of resistance to pathogens and the literature demonstrates that there is much to be gained from such sources. Transfer of resistance genes from landraces to modern cultivars is likely to be less problematic than from wild accessions.There is clearly also potential, largely unrealised, for disease tolerance and resistance or tolerance of pest and various abiotic stresses too including to toxic environments.

9. BREEDING: CONVERSION OF LANDRACES INTO MODERN CULTIVARS

In this section the advantages of breeding cereal landraces, the methodology of improvement and modifications of breeding assumptions will be proposed.

9.1. Yield-based selection

Breeding from landrace accessions is a strategy being used to improve yield and yield stability in less favourable agricultural system with lower input levels. Heritabilities are higher in more favourable than poor environments (Blum, 1988). The stagnation of yields in these areas (Annicchiarico and Pecetti, 1993) is mainly related to the narrow genetic base of the more recently bred, high-yielding cereals (Pecetti et al., 2002). Two different approaches may be followed to raise yields in the long-term: one is based on increasing yield potential of broadly adapted cultivars, while the other relies on the better exploitation of the adaptive features of genotypes by fitting cultivars to specific target environments (Acevedo and Fereres, 1993). Improvement of grain yield potential in small-grain cereals has traditionally relied on direct selection for this trait (Annicchiarico and Pecetti, 1998). Traditional breeding is based on a combination of bulk-pedigree method of selection, applied selection in the presence of stress, and use of adapted germplasm (Ceccarelli and Grando, 1997).

The opportunity to complement traditional breeding with use of indices of indirect selection for yield including sets of morpho-physiological traits, also known as an analytical breeding, has been put forward, especially for less favourable regions (Richards, 1982). There are two strategies in analytical breeding for identifying morpho-physiological traits usable as tools for selection (Fischer, 1981; Jackson et al., 1996). The first, called the ‘black box’ strategy, consists of assessing a germplasm pool for correlated response to yield gain deriving from selection for sets of putatively useful traits. The second, defined as the ‘ideotype strategy’, is based on the assessment of traits chosen a priori, through comparison in isolines or prediction of performance in crop growth models of different trait levels (Annicchiarico and Pecetti, 1998).

9.2. Adaptability

In landraces an understanding of the relationship between amount of genetic diversity expression of morphological and agronomic characters and adaptation to stress environments may elucidate whether the success of landraces in less favourable areas is due to a population buffering mechanism or to a particular architecture of morpho-physiological traits, or both. This may in turn clarify whether ‘pure line breeding’ is the correct approach for less favourable areas (Ceccarelli et al., 1987). Pure line breeding can be successful only if genotypes with a very high degree of phenotypic plasticity are identified.

Evans (1980) pointed out that selection for adaptation may result in yield increases but may not represent selection for greater yield potential. However, it has already been shown for durum wheat (Pecetti et al., 1992) and barley that some of the material selected under unfavourable conditions is able to retain its superiority in a more favourable environment (Ceccarelli et al., 1991). For barley the proportion was about 20% of the selected genotypes, and for durum wheat about 30%. In both cases such a proportion was higher than the proportion of lines selected under favourable conditions which were also able to perform well in a less favourable environments, and this is in agreement with previous observations (Pecetti et al., 1994).

Breeding for specific adaptation is particularly important in the case of crops predominantly grown in unfavourable conditions, because unfavourable environments tend to be more different from each other than favourable environments (Ceccarelli and Grando, 1997). The specific adaptation strategy may be explored on the basis of yield response of the germplasm pool that is representative of the available genetic base tested across a representative sample of sites within the target region (Annichiarico, 2002).

9.3. Conversion into density-neutral modern cultivars

Inter-plant competition, i.e., the unequal sharing of growth resources due to genetic (pre-existing) or acquired differences among plants, can be quantified by the drastic increase in the coefficient of variation (CV) of individual plant yields in the crop stand (Fasoula and Fasoula, 1997). The difference between the genetically heterogeneous landraces and the genetically highly homogeneous modern cultivars means that a landrace stand involves genetic competition among plants, whereas a modern cultivar stand is devoid of genetic competition. A systematic study of the relationship between yield and competitive ability within a bread wheat cultivar (Fasoula, 1990) found a high and significant negative correlation ($r = 0.94$). The study demonstrated that highly competitive plants, i.e., those yielding less at the ultra-low planting density (1 plant/m^2; absence of competition), out-yielded the low competitors in mixed stands, i.e., plants yielding more at the ultra-low density. Conversely, in pure stands, the performance of highly competitive genotype plants lagged behind that of the poor competitors.

Genetic heterogeneity, such as that found in landraces, involves genetic competition among plants, in addition to acquired competition, which is also encountered in stands of single genotypic cultivars. In principle, genetic competition can be eliminated when landraces are converted into desirable homozygous lines, but the acquired competition is more difficult to control. The intensity of acquired competition increases in marginal or low input environments, which possess inherent heterogeneity in the distribution of resources. The above offers an insight into the reasons that led to the eventual replacement of landraces by pure single genotype modern cultivars in favourable environments and their persistence in marginal environments. In favourable environments, competition in the crop stands is reduced because of elimination of both the genetic (single genotype) and the acquired (ample resources) components. This results in increased crop yields, reflected in the reduced CV of individual plant yields (Fasoula and Fasoula, 1997; Tollenaar and Wu, 1999).

Yields of modern single genotype pure cultivars can be either density-dependent as in the case of maize hybrids that yield optimally under high plant densities only (Duvick, 1992), or density-neutral, i.e., remain optimal under a wide range of plant densities. With appropriate breeding methodology, it is eventually possible to convert the density-dependent into more density-neutral cultivars (Fasoula and Fasoula, 2000; Tokatlidis et al., 2001). To effectively exploit landrace diversity for breeding purposes, it is important to appreciate the significance of creating more density-neutral genotypes, particularly for marginal environments, which usually suffer from drought stress. In drought-prone environments, the use of more density-neutral cultivars allows use of lower seeding rates, limiting the damage due to drought. A subtle point is the understanding that density itself is not a stress; it simply enhances the existing differences that lead to competition in the stand. Therefore, particularly in more uniform environments, it is possible to have a high yielding dense stand with reduced inter-plant competition, as measured by the reduced CV of individual plant yields.

There is a lot of evidence that mixtures can be valuable, especially when combining various disease resistances of the components. A word of caution is, however, presented as to the interpretation behind the phenomenon. In favourable environments, the evidence of yield stability due to heterogeneity is often counter-balanced by experiments and theory, indicating that increasingly homogeneous cultivars have higher yield potential across sites and years. A case in point is the well-known, superior stability of performance of the genetically homogeneous modern single-cross maize hybrids over the older genetically heterogeneous double-cross hybrids (Duvick, 1992), because the adverse effects of genetic competition are restricted by genetic uniformity. This hints to the non-universality of the superiority of populational (Allard and Bradshaw, 1964) buffering. However, the requirement for superior individual buffering is that genes conferring tolerance to the biotic and abiotic stresses are being gradually incorporated into a few or a single individual(s). Further, the cause of the superior stability of certain mixtures has been indicated (Fasoula and Fasoula, 1997) to mainly rest in the reduced stability of the individual components (quantified by the higher CV of single plant yields in pure stands), appearing as reduced under-compensation in the mixtures, mimicking the effects of true over-compensation (pseudo-overcompensation).

9.4. Seed degradation – cultivar degeneration

An additional detrimental effect of the negative correlation between yield and competitive ability relates to the observed landrace or cultivar "seed degradation". Zeven (1999) provides an interesting array of evidence about what he calls the often inexplicable seed replacement by traditional farmers. A traditional practice to combat seed degradation has been the periodic seed replacement of farmers' own seed with seed from elsewhere. Zeven (2000) reports a widely existing belief that the home-grown cultivar degenerates after several generations of re-sowing. He further states (Zeven, 2000) that most farmers do not actually perform traditional maintenance breeding; as they and their ancestors probably have experienced that traditional maintenance breeding does not result in a better crop. Apparently, "farmers must have thought that seed replacement was a better method to maintain the yielding capacity of their crops".

A proposed explanation for the practice of "inexplicable" seed replacement and the avoidance of traditional maintenance breeding by farmers relates to the consequences of the existing, but mostly unsuspected, negative correlation between yield and competitive ability. The problem of cultivar or landrace degeneration (Fasoula, 1990) can be addressed by applying the concept of non-stop selection (Fasoula and Fasoula, 2000) for superior lines at ultra-low plant densities. The outcomes of non-stop selection exceed that of conventional maintenance breeding (Fasoula and Boerma, 2007). Experimental data of honeycomb selection within breeder's seed of the old barley cultivar Athenais and the old durum wheat cultivar Kyperounda, both of local landrace origin, demonstrated the existence of useful adaptive variation persisting within homozygote lines, as well as the potentialities of non-stop selection (Fasoula, 2004).

Adaptive variation is genome-monitored, de novo and heritable across generations. It is directional and constantly released by the sensory mechanisms of the genome in response to environmental stimuli (McClintock, 1984; Rasmusson and Philips, 1997). This epigenetic variation stems from the interaction between genotype and environment (Goldberg et al., 2007) and allows profitable exploitation of limited resources and continual incorporation of gene variants for resistance to changing biotic and abiotic stresses. Continuous exploitation of adaptive variation is synonymous with the continuous genetic upgrading of landraces and cultivars.

Because of the reported negative correlation between yield and competitive ability, integration of yield and stability genes into fewer, improved genotypes is more efficient when the unit of evaluation and selection becomes the individual plant grown at ultra-low planting densities. When this negative correlation is considered at the level of the individual plant, it means that a plant possessing genes for high yield potential will also possess genes for low competitive ability. At the level of the variety crop stand, the negative correlation means that the greater the inter-plant competition in the stand, quantified by the yield CV of individual plants, the greater the crop yield reduction. At the level of selection and landrace/variety maintenance, it means that high competitors are selected at the expense of higher yielding genotypes. As a result, the variety eventually degenerates (Fasoula, 1990). This phenomenon offers a novel explanation for the previously reported practice of landrace seed replacement amongst traditional farmers and their avoidance of traditional maintenance breeding.

In summary, single gene traits are generally easily transferred from landrace germplasm to modern cultivars, but most of the desirable traits characteristic of landraces are complex and difficult to express in different genetic backgrounds. Maintaining these characteristics in heterogeneous landraces is also problematic. Breeding, selection and deployment methods appropriate to these objectives should be used rather than those used for high input intensive agriculture plant breeding.

10. PARTICIPATORY BREEDING

Participative approaches to agricultural research and development are now extensively used throughout the world to help define and address the practical research needs of farmers. They have proved useful in solving practical problems in complex and diverse farming systems characteristic of organic farming and low input systems. During the last few years participatory research divided into several different topics and in the field of plant breeding there are already many very different strategies like Participatory Varietal Selection, true or complete Participatory Plant Breeding (Witcombe et al., 1996) and an intermediate approach, Efficient Participatory Breeding (Morris and Bellon, 2004). The essential advantages of participatory plant breeding over conventional plant breeding involve: better targeting of local environmental conditions, better definition of selection criteria important to the end-users, faster and greater adoption of improved cultivars by the farmer, and increase or maintenance of genetic variability. Participatory plant breeding also gives voice to farmers and elevates local knowledge to the status of science (Ceccarelli and Grando, 1997).

Very effective participatory plant breeding projects in cereals are active all over the world. In Europe in particular, a few participatory plant breeding projects are running with success either in cross-pollinated and self-pollinate cereals. In Portugal, the VASO (Vale do Sousa - Sousa Valley) project, running since 1984, is a maize Participarory Plant Breeding project developed to cover the needs of small maize farmers, with scarce land resources, in poly-cropping systems for human uses, particularly bread production (Moreira, 2006). Local germplasm is used, adapted to the local conditions over centuries of cultivation, quality being the first priority over quantity. This Participarory Plant Breeding project concerns mainly flint-type open-pollinated landraces with quality for the production of the traditional maize bread called ‘broa’. This quality depends on traits not present in the available commercial hybrid cultivars (Brites et al., 2008). ‘Broa’ production still plays an important economic and social role in Central and Northern Portuguese rural communities. Selection takes place at the farmers’ field by the farmer in close collaboration with the breeder.

The genetic diversity evolution through this participatory breeding project was evaluated using molecular markers and it was concluded that though interesting phenotypic improvements were achieved, the level of genetic variability was not significantly influenced and diversity was maintained (Vaz Patto et al., 2007). Several maize open-pollinated landraces were selected within this project with the joint collaboration of the breeder and the farmers. In Sweden, the Allkorn project, running since 1995, is a cereal Participarory Plant Breeding project for organic farming (Larsson, 2006). The goal of the project is to identify and find interesting cereal cultivars for organic farming in Sweden. Cultivars should be of high quality for human nutrition and be well adapted to local soils and climate. They should have good weed-suppressive traits as well as tolerance to diseases and pests. The farmer can select the best cultivar, from his point of view, from several quality cultivars that he has chosen from the project and tested in his own fields. The main aim of this breeding is not to conserve the cultivars but to develop them for the future use in organic farming all over the country. Cultivars of nearly all species of cereals which have historically been used in Sweden are tested in this project, namely *Triticum monococcum*, *T. dicoccum*, *T. spelta*, winter and spring wheat *T. aestivum*, winter and spring rye *Secale cereale*, hulless barley, spring barley, oats, and black oats. These cultivars have a broad diversity and cover primitive cultivars, older landrace cultivars and early Swedish breeding cultivars from 1900 to 1950, since in this early breeding period one of the parents of the cultivars was often a local landrace. The cultivars are selected each year for better adaptation to organic conditions. The idea is to form province groups of farmers that could help each other with seed supply, seed cleaning, shelling of spelt wheat, milling and selling. Regional production groups are formed for the local market with help of local mills and local bakers and the consumer can then find heritage cultivars from each region, country or province. The goal of this type of participatory research is empowering the farmers: supporting the formation of groups capable of assessing their own needs and addressing them either directly or through demands on research organisations.

In Hungary several Participatory Varietal Selection projects are running both in on farm cereal landrace conservation and organic farming research. The on-farm conservation Participatory Varietal Selection strategy is mainly connected with the regeneration of traditional Hungarian landraces and old cultivars which were maintained only in ex situ collections over the last 20 years. Several organic farmers are involved in such projects and their main interest is related to the traditional use of special local food and heritage farming in relation to agrotourism. In such Participatory Varietal Selection programmes, the Hungarian National Genebanks provide accessions to several farmers participating in the in situ conservation project, and the locations for long-term maintenance are chosen by all participants in order to try to find the optimal place (environmental condition) and landrace to maintain, considering the social background of the region too (Holly, 2000). In recent years new projects have been initiated in the field of Participatory Varietal Selection in Hungary. One of the biggest ones, entitled “Selection of suitable cultivars for organic farming” was carried out in a real Participatory Varietal Selection system in which most of the important stakeholders - the breeders, seed producers, farmers and end users - were involved in cultivar selection for several field crops, including wheat, barley, sunflower, pea, etc. (Kovács, 2006a). In this project breeding institutions provided both landraces and old and modern cultivars and farmers and end user made the cultivar evaluation independently of the providers' opinion in each locality taking into consideration the end users priorities (Kovács et al., 2006). A similar research programme is running for underutilised cereal species, such as einkorn, emmer and macha wheat in the country regions where such species were traditionally used. In this case the re-introduction of the forgotten species into modern agriculture it is important to exploit the genetic diversity which still exists in such cereals (Kovács, 2008).

A participatory breeding programme in tetraploid wheat was initiated in 2001 at INRA-Montpellier, France, based on a demand for organic pasta by the industry (Desclaux, 2005). The quality of the wheat cultivars being produced under organic conditions did not meet the requirements of the processing industry. To identify the main causes, a multidisciplinary public research team, bringing together plant breeders, soil scientists, ecologists, agronomists and sociologists was assembled to work in close collaboration with the farmers and end-users. The two main French territories involved were Camargue and Pays Cathare (Desclaux et al., 2002). The lack of cultivars adapted to low nitrogen conditions became apparent rapidly in such organic crop systems. The main aim of the on-farm and participatory breeding is to take on-board farmers preferences and to better target local environmental conditions by increasing and managing the genetic variability.

Old durum wheat cultivars, segregating or advanced pure lines and populations resulting from crosses between durum wheat and emmer or wild species were provided to the farmers by the breeders. Selection and evaluation are done in close collaboration and results are discussed between all the participants. Information is feed back and can lead to re-examination of the objectives of the breeding scheme (Desclaux, 2005). This French project is neither a farmer-led nor a formal-led project but it is led by both professionals and researchers and requires farmer's critical participation right from the first steps of the breeding scheme, i.e. it is collegiate and decentralised (Desclaux, 2005).

In the UK, a project for developing appropriate participatory methodologies for cereal seed production and cultivar selection under organic conditions has been established (Clarke et al., 2006). This project aimed to overcome the deficiencies of the UK official Recommended List of Cereals for organic farmers. In winter wheat comparative trials using cultivars and mixtures of cultivars were established at 19 UK farms the 2003/04 and 2004/05 seasons (Clarke et al., 2006; Jones et al., 2006). A collegiate participatory method was used to balance statistical rigour with farmer's objectives of managing a whole farm system. Participating farmers sowed the seed in large marked plots using their standard methodology within a field containing wheat. Researchers gained information from each of the farmers about their farming system, field and trial. These experiments showed the large variability of organic systems in the UK and the difficulty of selecting a single cultivar suitable for them all. This project also helped to develop a small core of trained farmers and researches which can be exploited in further participatory projects.

The diversity available within landraces is useful for breeding purposes in at least four different ways (Ceccarelli et al., 1987), including the release of the highest yielding lines as pure line cultivars, the utilisation of superior lines as parents, the evaluation of multilines built with a variable number of pure lines, and the identification of lines showing extreme expression of specific attributes.

Participatory plant breeding and variety selection has proven more successful than the approach used in high input breeding programmes for landrace improvement in stress-prone environments where sustainable approaches are a high priority. Despite being more complex to carry out, it not only delivers improved germplasm, but also aids uptake and communication between farmers, researchers and advisors for the benefit of all.

11. LEGAL ISSUES

Landraces as an important genetic resource have been included in international treaties and national decrees that protect and enhance their use in their local environment. The objectives of the convention on biological diversity are the conservation of biological diversity, the sustainable use of its components and the fair and equitable sharing of the benefits arising out of the utilisation of genetic resources. The objectives of the International treaty on plant genetic resources for food and agriculture (http://www.planttreaty.org) are the conservation and sustainable use of plant genetic resources and the fair and equitable sharing of benefits derived from their use, in harmony with the Convention on Biological Diversity, for sustainable agriculture and food security. The treaty promotes or supports, as appropriate, farmers and local communities' efforts to manage and conserve on-farm their genetic resources for Food and Agriculture.

In Europe the marketing of seeds of landraces and conservation of cultivars is ruled by the strict seed trade and cultivar protection laws. Cultivars have to meet the Distinctiveness, Uniformity and Stability standards to be registered legally. Agricultural crops have to meet the Value of Cultivation and Use criteria and to be listed on the "European common catalogue of cultivars of agricultural plant species" to be tradable within Europe. Combined with the extension of the intellectual property rights in the UPOV (French: *Union internationale pour la protection des obtentions végétales*) 91 act, the maintenance of agro-biodiversity on-farm and the conservation of local cultivars are generally threatened. According to the Biodiversity Action Plan for agriculture presented by the European Commission in 2001 "the conservation and improvement of in situ/on farm plant genetic resources also depends on the effective possibility of sustainable uses and on legislation which makes it possible to market diversified genetic materials".

The directive of conservation cultivars is still limiting the diversity of seed. The most recent draft of a directive of conservation cultivars has the same goals as the UPOV standards: Uniformity, stability and distinctness, but less documentation is needed to fulfil the requirements. Landraces are never uniform, neither are they stable. Therefore, landraces will not be allowed according to the directive of conservation cultivars. The directive of conservation varieties therefore applies for old out-dated approved cultivars, and will not contribute to the biodiversity of arable land (SANCO, 2006). An international commission has written a manifest on the future of seed in order to strengthen the movement toward sustainable agriculture, food sovereignty, biodiversity and agricultural diversity, to help defend the rights of farmers to save, share, use and improve seeds and enhance our collective capacity to adapt to the hazards and uncertainties of environmental and economic change (Shiva, 2007). The most recent European Union Commission Directive 2008/62/EC published on 20th June 2008 does provide for certain derogations for acceptance of agricultural landracs and varieties which are naturally adapted to the local and regional conditions and threatened by genetic erosion and for marketing of seed of those landraces and varieties.

Clearly legislation was designed primarily to protect trade and return royalty income to modern plant breeders with expensive programmes to fund. As the desirability of using landraces becomes more apparent to achieve greater sustainability, legislation changes are being made to facilitate this trade too. However, more changes are needed to promote the exploitation of diversity in landraces and encourage their use.

12. CONCLUSIONS

The position of cereal landraces as valuable genetic material in contemporary agriculture is gaining renewed importance. A lot of recent research effort has gone into collecting, organising, studying and analysing them with a primary goal being to incorporate their positive qualities in new cultivars or populations for a more sustainable agricultural production, particularly in response to recent climate changes. Positive attributes include landraces being a source of novel resistance genes or combination of genes with a good deployment strategy. Particularly important is the fact that resistance found in cereal landraces has been durable in many instances, in contrast to the gene-for-gene type of resistance that is usually encountered in modern cultivars. However, the durability may be associated with and dependent on deployment in heterogeneous populations.

A major part of this valuable landrace diversity is conserved in the world's gene banks network and should be exploited systematically for traits such as quality and specific adaptation to stress environments. The available genetic variation in adaptive responses to soil and climatic conditions conserved in landraces is little understood, known and even less used. More uniform and user-friendly documentation about collection and characterisation of landraces, either morphologically or with molecular tools, is needed to access this variation more effectively. Gene banks should aim at adopting a common concept of landraces and plan special inventories for them. The level of diversity should be monitored during their conservation so that the original level of variation is maintained. More studies are needed in order to investigate if their long-term maintenance by farmers resulted in increasing genetic variation.

New high-throughput genotyping platforms and phenotyping data in common databases will enable powerful association genetics approaches to be utilised for improvement and utilisation of landrace resources. Knowledge of linkage disequilibria in landraces compared with elite germplasm will help focus breeding for stress-adapted cultivars or populations. With the current rapid advancements in high-throughput molecular genotyping technologies, it is becoming increasingly clear that the limiting factor in applying those powerful technologies to molecular breeding programmes is no more the capacity of genotyping, but the potential for accurate or precision phenotyping. Particularly important and challenging is phenotyping for the so-called quantitative traits.

The renewed focus on cereal landraces for breeding purposes is also a response to some negative consequences of modern agriculture and conventional breeding, such as the liberal use of high inputs, the loss of genetic diversity, and the stagnation of yields in less favourable areas. To deliver this, participatory plant breeding and variety selection practices have emerged as a powerful way to merge breeders' knowledge and farmers' selection criteria, emphasizing decentralised selection in the target environments with the active participation of local farmers. Location-specific adaptation of these diverse landraces will be important for further selection at the farmer level. New strategies are emerging to produce "modern landraces" based on multiple cross populations of einkorn, emmer and bread wheat in combination with on farm site-specific selection to obtain highly adaptable populations for local and regional production.

The reported practice of the "inexplicable seed replacement" by traditional farmers is connected to the gradual seed degradation during landrace maintenance, brought about by the established negative correlation between breeding and competitive ability. Further enhancement of productivity and stability is achieved through practicing "non-stop selection" within landraces across the marginal production environments, to exploit the constantly released by the genome useful adaptive variation. The procedure and results of non-stop selection exceed those of conventional maintenance breeding, combating seed degradation and resulting to a constant cultivar upgrade. An additional essential breeding consideration is the creation of density-neutral landrace germplasm, since its use, particularly in marginal environments, permits lower seeding rates, limiting the damage due to drought.

The issues of conservation and sustainable use of landraces have been so far included in international convention treaties and directives which need to be implementated on European and national levels. In this review we have highlighted the value of landraces as resources for the future sustainability of cereal crop production, the methods to enhance their genetic makeup and avoid seed degradation, and emphasised the level of coordination and resourcing needed to realise their great potential.

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