Review/Revue

Wheat domestication: Lessons for the future

La domestication des blés : leçons pour l'avenir

Gilles Charmet

UMR1095 génétique, diversité, écophysiologie des céréales, INRA Clermont-université, 234, avenue du Brézet, 63100 Clermont-Ferrand, France

A B S T R A C T

Wheat was one of the first crops to be domesticated more than 10,000 years ago in the Middle East. Molecular genetics and archaeological data have allowed the reconstruction of plausible domestication scenarios leading to modern cultivars. For diploid einkorn and tetraploid durum wheat, a single domestication event has likely occurred in the Karacadag Mountains, Turkey. Following a cross between tetraploid durum and diploid T. tauschii, the resultant hexaploid bread wheat was domesticated and disseminated around the Caucasian region. These polyploidisation events facilitated wheat domestication and created genetic bottlenecks, which excluded potentially adaptive alleles. With the urgent need to accelerate genetic progress to confront the challenges of climate change and sustainable agriculture, wild ancestors and old landraces represent a reservoir of underexploited genetic diversity that may be utilized through modern breeding methods. Understanding domestication processes may thus help identifying new strategies.

© 2011 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

R É S U M É

Le blé fut la première espèce domestiquée au Moyen-Orient, voici plus de 10 000 ans. Les approches combinées de la génétique moléculaire et de l'archéologie ont permis de retracer les scénarios les plus plausibles de ces évènements qui ont façonné la distribution de la diversité génétique des variétés actuelles. Pour les blés diploïdes (engrain) et tétraploïdes (blé dur), un seul évènement de domestication s'est produit dans les montagnes du Karacadag en Turquie. Une hybridation entre le blé dur tétraploïde et l'espèce diploïde T. tauschii, a donné le blé tendre hexaploïde, qui fut domestiqué et disséminé par les agriculteurs dans la région Caucasienne. Ces évènements de polyploïdisation qui ont facilité la domestication du blé ont provoqué de forts goulots d'étranglement génétiques, entraînant des pertes aléatoires d'allèles potentiellement adaptatifs. À l'heure où il devient urgent d'accélérer le progrès génétique pour faire face aux défis du changement climatique et de l'agriculture durable, les ancêtres sauvages et les populations locales représentent un réservoir de diversité génétique sous-exploité qui doit être mobilisé au travers de méthodes d'amélioration renouvelées. Comprendre les mécanismes de la domestication peut donc aider à inventer de nouvelles stratégies.

© 2011 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

Wheat is the most widely grown crop in the world, representing a major renewable resource for food, feed, and industrial raw materials. The world demand for food

Email address: Gilles.Charmet@clermont.inra.fr.

by an ever-growing population is expected to increase, by about 40% in 2030 [1]. Meeting this demand would require that agricultural land stabilizes at *ca.* 1.5 billion hectares [2] together with an annual yield increase of 2%, while yields have increased by only 0.9% per year over the past decade [1]. The situation is even worse in Europe (the first world producer) and particularly in France, where wheat yields have been stagnating since 1995, presumably because of unfavorable climatic conditions [3]. Domestication and crop improvement events have taken advantage of the genetic diversity of crops and their relatives. Hence, understanding the genetic bases of these events may help us imagine new ways to exploit untapped genetic resources and to accelerate genetic progress through modern breeding methods.

Cereals are amongst the first species to have been domesticated by man, at nearly the same time as dogs, sheep and cattle. Respective domestications occurred independently on all Continents. This paper will focus on the history of wheat, which was one of the first cereals to be domesticated in the Middle East and subsequently spread over the Old World during the Neolithic revolution. For plants, domestication is tte suite of anatomical domestication is the suite of anatomical and morphological changes that follows cultivation being oriented toward an adaptation to the new anthropized environment. In this sense, domestication is different from conscious cultivation, which began with related wild species [4]. Moreover, the discovery of fossilized remains on archeological sites does not allow ascertaining whether they were used for cultivation or for gathering. Molecular genetics tools may reconstruct the evolutionary scenarios of wheat domestication. This review addresses five questions about wheat domestication: why, when, where, how, and what the consequences are for today's agriculture.

2. Wheat is a polyploid series

As early as the late XIXth century, the first studies on biogeography of cultivated crops allowed identifying specific regions called the centers of origin [5,6]. For wheat, barley, pea and lens this center of origin is located in the Fertile Crescent, and more particularly in the mountainous regions that surround the fertile alluvial plains of the Tigris and Euphrates rivers [7]. Lessons from botany, archaeology and more recently from molecular genetics provided more elaborate and precise ideas about the geography and the chronology of the different events, which will be synthesized in the present paper. The case of wheat, however, is far more complex than that of barley or maize since the *Triticum* genus is made of several species with various ploidy levels, from $2 \times$ (14 chromosomes) to $6 \times$ (42 chromosomes).

The common ancestor of the grass (Poaceae) family, with putatively five chromosome pairs [8], produced a diploid ancestor of the Triticeae subtribe with seven chromosomes. As illustrated in Fig. 1, the first polyploidisation event occurred at 500,000–150,000 years BP
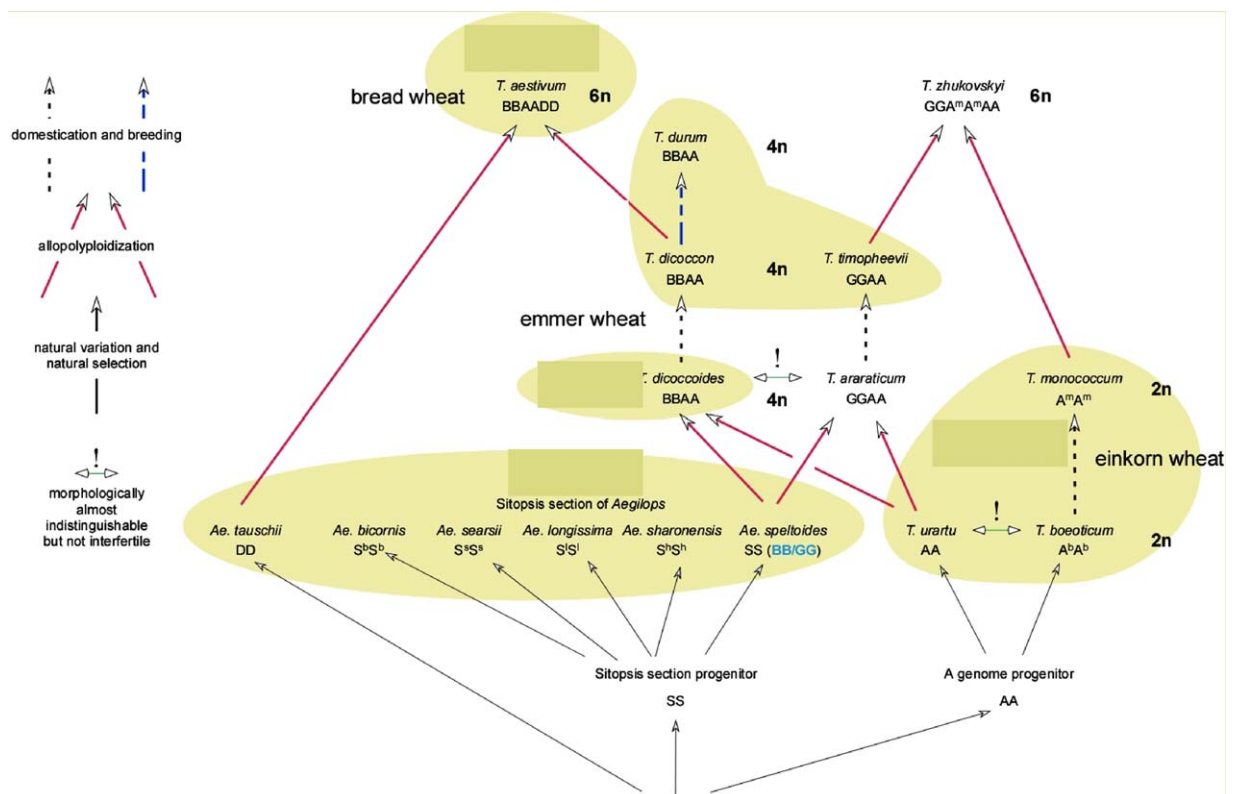

Fig. 1. Wheat evolution and events. Wheat (Triticum) and Aegilops species/taxa involved (from Kilian, pers. comm.).

(before present), between *Triticum urartu* (genome AᵘAᵘ) and an unknown, possibly extinct species closely related to *Aegilops speltoides*, thus creating a new amphi-tetraploid species with 14 chromosome pairs, namely *Triticum turgidum* L. *ssp diccocoides* (or *T. diccocoides*, genome AᵘAᵘ BB). This species was then domesticated and evolved as *T. turgidum ssp dicoccum* Schübl. (or *T. dicoccum*), which is the progenitor of durum wheat. The second polyploidisation event occurred about 10,000 BP, between the domesticated tetraploid *T. dicoccum* and the wild diploid species *T. tauschii* to give the hexaploid species (21 chromosome pairs) *Triticum aestivum* L. or bread wheat. *T. aestivum* is only known in its domesticated form, the widely grown bread wheat.

3. Why man turned to farming?

What are the reasons why modern man, *Homo sapiens*, a hunter and gatherer for 100,000 years, moved to plant cultivation and animal husbandry? Likely we will never know whether the demographic expansion pushed humankind to become farmers to increase food resources, or if the discovery of agriculture, by providing more food, enabled an increase in human population. According to ethnologists, the practice of primitive agriculture required an energy input (kcal) higher than that for hunting and gathering. Agriculture would thus not have been adopted for comfort but rather by necessity. However, this estimate of energy requirement is inferred from data on contemporary hunter-gatherers and might not be appropriate for Neolithic time. Moreover, it seems that the demographic expansion had started with the warming that just followed the last ice age about 13,000 BP, while the oldest remains of *T. diccocoides* in archeological digs are dated at about 19,000 BP [9]. Yet, the Old World agriculture was probably born in the Fertile Crescent, between 12,000 and 9,500 BP, during the Young Dryas period, characterized in the Middle East by winter frost and rainfall decline (11,000–10,300 BP). This period likely reduced available food resources and led human societies to cultivate the plant species they were used to gather [10]. The debate on the origins of agriculture will probably never end and the verity is probably a mixture of these two hypotheses. Agriculture might have been invented because natural resources were rarefied as a consequence of climate change and perhaps because of demographic pressure. It is not doubtful that a higher soil productivity (perhaps already associated to extended working time) allowed a higher fecundity, leading to demographic expansion, which in turn made a pressure toward higher productivity.

4. The contribution of archaeology

Archaeologists make inferences from the dating of fossilized remains of crops, mostly of grains that are the most easily conserved [11–14]. The main archeological sites are located in the Jordan Valley and the upper valley of the Tigris and Euphrates rivers, as well as in the mountainous regions of South-Eastern Turkey (Fig. 2). However, the archaeological sites that have been discovered may only represent a small and biased sample of the existing Neolithic villages, where domestication might have occurred. Moreover, most ancient sites experienced a long occupancy period, sometimes occurring in several waves during which wild types of wheat, barley, lens and pea grains were gradually replaced by domesticated forms. Morphological differences allow distinguishing brittle (i.e. wild) from non-brittle (i.e. domesticated) rachis, and hulled from free-threshing grains (Fig. 3) However, it is
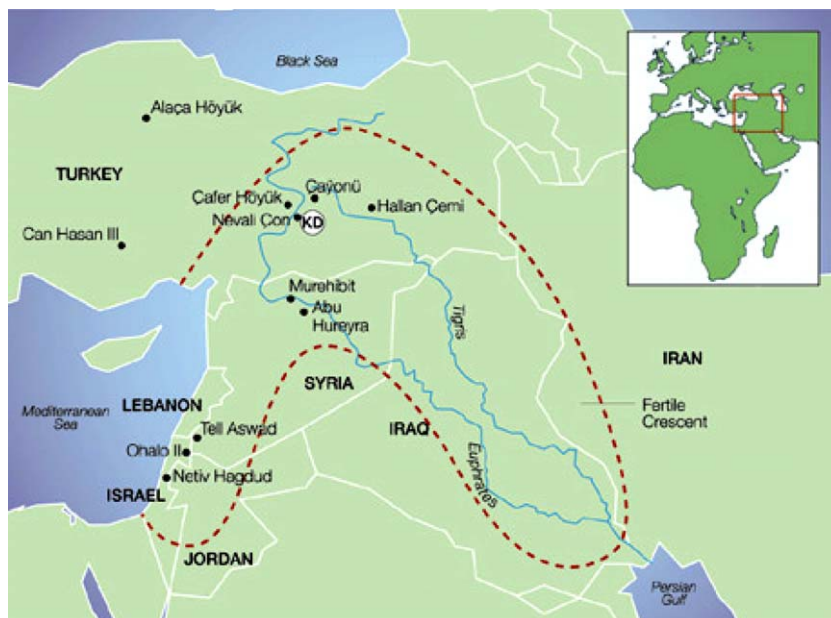

Fig. 2. After Salamini et al. 2002: The Fertile Crescent and the main archaeological sites (KD: Karacadag Mountains in Turkey).

Fig. 3. A major domestication trait: Brittle rachis of *T. diccocoides* (a) and non Brittle rachis of *T. dicoccum*.

generally difficult to differentiate the free-threshing durum and bread wheat remains.

For example, on the site of Abu Hureyra in Syria, a majority of wild grains were found for the period from 12,200 to 11,100 BP. Then a progressive substitution by domesticated grains could be observed for the period between 11,000 and 10,500 BP and finally domination by the latter forms is apparent during the period from 10,500 to 7800 BP. The domestication phase thus spread over several centuries and simultaneously concerned several species: einkorn (*Triticum monococcum*), emmer wheat (*T. dicoccum*), barley (*Hordeum vulgare*) and rye (*Secale cereale*) [13,15]. As a consequence of the limited sampling of sites and the relatively low accuracy of radiocarbon dating, archaeological research can only estimate ranges of dates for domestication in the Fertile Crescent. Genetic research established evidence for locating the cradle of agriculture in the Karacadag Mountains [10,16]. Indeed, most species that were cultivated prior to domestication originated from wild species naturally growing in this region, with the remarkable exception of bread wheat (see later). With the exception of rye, cereals are self-fertilized species. Gene flow via pollen and seed dispersion is limited in nature, which led to a high level of genetic differentiation among local populations. Then, provided that local populations of wild species did not migrate since the Neolithic period, populations most similar to domesticated species are the likely progenitors, thus revealing the primary domestication site(s). Moreover, since population expansion and migration leave imprints in the distribution of fossil DNA, it is possible to trace the migration routes of cultivated plants and to date such migrations [17], as is done for human populations [18].

5. The revolution of molecular genetics

These studies have been carried out during the last two decades since molecular biology has provided a huge number of molecular markers allowing a precise estimation of genetic similarities. For instance, Heun et al. [19] studied 338 accessions of *T. monococcum* from the Fertile Crescent and other geographic origins from Europe, including 68 domesticated accessions of *T. monococcum monococcum*, nine weedy accessions of *T. monococcum aegilopoides* and 194 wild accessions of *T. monococcum boeticum*. Using 228 Amplified Fragment Length Polymorphisms (AFLP) markers basically located in non-coding sequences and often assumed to be selectively neutral, these authors showed that the wild accessions most related to cultivated accessions originated from the Karacadag Mountains, thereby providing strong evidence for locating the cradle of agriculture in the Middle-East [16]. These results were later on confirmed by Kilian et al. [20], who also demonstrated that the diploid A genome donor of polyploid wheats, *T. urartu*, was actually genetically distinct from the wild *T. monococcum boeticum*, the progenitor of domesticated einkorn [21]. Einkorn was likely the first domesticated hulled wheat. It was one of the founder grain crops of Neolithic agriculture in the Near East, and a principal species of the early crop introduction in Europe. However, since the Bronze Age, its importance declined gradually and it is now a relic crop, only being sporadically grown.

Similar studies have been carried out on the wild forms of *T. diccocoides* and the domesticated forms of the tetraploid wheat *T. turgidum* [22]. These studies also used AFLP markers and disclosed that the wild populations from Karacadag Mountains were genetically close to old emmer wheats, suggesting a fate very similar to that of einkorn. Alternatively, Mori et al. [23] proposed a diphyletic origin for domesticated emmer, based upon two simultaneous primary domestication events occurring in the Karacadag Mountains and the Kartal region that is located 200 km west from Karacadag. This question was later solved by Ozkan [24] and Luo et al. [25]. By analyzing a larger sample of populations, these authors confirmed their first results and proposed an hypothesis to explain Mori's results in which the diphyletic origin of domesticated emmer would have arisen from a secondary introgression of some domesticated haplotypes from Karacadag into wild populations of Kartal, following their introduction by Neolithic farmers.

Accordingly, a monophyletic origin of both diploid and tetraploid domesticated wheat is now considered as being the most likely hypothesis. We already mentioned that the two A genomes of diploid and tetraploid wheat originated from different wild species. Another wild tetraploid species, *T. araraticum,* with an AAGG genome composition resembling *T. dicoccoides* (though they are incompatible) has also been domesticated in the Caucasian region, being the progenitor of *T. timopheevi* whose cultivation has always been limited. Unlike wheat, cultivated barley (*Hordeum vulgare*) does seem to have a diphyletic origin. Here, wild populations of *H. spontaneum* in the western and eastern parts of the Fertile Crescent are the progenitors of European and Asian cultivated barley genotypes, respectively [26,27]. Thus domestication of wild species was at the center of einkorn (*T. monococcum*) origin, and *T. turgidum durum* grows today mostly in regions with summer-dry, relatively warm Mediterranean climate. As far as we know, there are no wild species of hexaploid *Triticum*, which is therefore a new species that evolved during *T. dicoccum* cultivation, when *T. dicoccum* crossed

with *T. tauschii*. Molecular genetics provided evidence for this event. Dvorak et al. [28], using molecular markers determined that the D genome of bread wheat originated from the subspecies *T. tauschii* var *strangulata*, which naturally grows in Northern Iran and the Trans-Caucasian region. Since *T. dicoccoides* does not naturally grow in this region, the only conclusion is that the hybridization had only been possible after the domestication of *T. dicoccum* and subsequent distribution by farmers who swapped agricultural technologies between the Karacadag region, Northern Iran and Transcaucasia, between 8000 and 7000 BP. The first studies based on molecular markers suggested a polyphyletic origin for hexaploid wheat [29,30]. However, the study of the promoter region of the *GluDy* loci encoding the high molecular weight glutenin subunits (storage proteins) brought evidence for a new diphyletic hypothesis [31]. Indeed these D-genome specific markers support previous studies suggesting the existence of at least two *Ae. tauschii* sources that contributed germplasm to the D genome of *T. aestivum*. *Ae. tauschii* from Syria and Turkey had relatively high nucleotide diversity and possessed all the major *GluDy* alleles, indicating that these populations are probably ancient and not the result of adventitious spread. The presence in the Turkish population of both of the shared alleles suggests that hexaploid wheat is likely to have originated in Southeastern Turkey or Northern Syria, within the Fertile Crescent and near to the farming villages where archaeological remains of hexaploid wheats were first found. A second and more recent hexaploidisation probably occurred in Northern Iran and Trans-Caucasia, where bread wheat would have appeared about 1300 years later [31]. However, the genotypic diversity of wheat landraces from this region is higher than that found in Turkey, suggesting that Trans-Caucasia is an important centre of secondary diversification. *T. tauschii* thrives in an area characterized by continental climatic conditions and is a successful colonizer of secondary, man-made habitats. It may have become a common weed in *T. dicoccum* fields where hybridization occurred. These features of the D genome donor may have contributed to the success of bread wheat and its broad range of adaptation under cultivated conditions. Experimental evidence indicates that the first hexaploid wheat had hulled grains, as for *T. aestivum* subsp. *spelta*. Indeed, artificial synthesis of *T. aestivum* by crossing tetraploid *T. turgidum* with diploid *T. tauschii* almost always results in hulled products, irrespective of whether the *T. turgidum* parent is hulled or naked. It is therefore difficult to infer which form (hulled or naked) hybridized with *T. tauschii* in Neolithic fields 8000 years ago.

6. Domestication syndrome and consequences of genetic bottlenecks

Man thus started to cultivate wild plant species adapted locally, likely plants of nutrional value possibly corresponding to the species he collected as a hunter and gatherer [4]. How did the traits that characterize the domestication syndrome manifest? By chronologic order, the first of these traits was the non-brittle rachis that has a simple monogenic determinism (Br for brittle rachis [32]). In a wild species, this trait causes a negative fitness due to reduced seed dispersion, progeny and species' success. Thus a non-brittle rachis mutation that could have appeared in a wild population would have likely been eliminated by natural selection. However, in a cultivated field such a mutation would confer a positive fitness if farmers preferred and nurtured plants carrying this trait. If harvest occurred after brittle-rachis plants had matured and dispersed seed, the seed pool would have been enriched with non-brittle types, which would eventually dominate the population. This seems to have occurred in archaeological sites, as indicated by the progressive replacement of brittle remains by non-brittle rachis types. Population geneticists have estimated the fitness of non-brittle over brittle rachis plants according to various parameters including seed set and seed dormancy, and they used this fitness in demographic models to estimate the time required for total replacement. Such total replacement would have taken 500–1000 years, which fits with the observations from archaeological sites [33,34]. The non-brittle rachis, which is governed by a single gene, could have dominated a population in cultivated fields without conscious selection by Neolithic farmers, simply because this trait would have been advantageous on farms where a portion of the harvested grains is retained as seed for the subsequent growing season, while tilling eliminates part of the seedlings born from brittle rachis plants.

The second trait, called naked grain, presents a slight fitness benefit over hulled grain (Tg, for tenacious glume [32]). This trait is associated with a shorter dormancy, which confers an advantage over the more dormant-hulled grains for germination and growth during optimal conditions. Although naked grains are preferred for their higher quality flour content for making bread, there is no evidence that the first farmer-millers sorted the naked from the hulled grains.

Naked-grain wheat has dominated hulled-grain wheat. However, today the hulled-grain cereals are marginally grown. It is worth noting that a common phenotype, namely non-shattering, can arise from independent mutations in different genes. Yet it was recently shown that the major threshability genes, namely *soft glume* (*sog*) in diploid *T. monococcum* and *tenacious glume* (*Tg*) in *T. turgidum diccocoides* originated from mutations at non-orthologous loci [35]. This case of convergent evolution is not so surprising as we have seen that the A genome of diploid and tetraploid wheat did not derive from the same donor species. Another mutation had a noticeable fate in durum wheat, but especially in bread wheat. Thus, the *Q* mutation (*Q* allele) is likely to be at the origin of the extraordinary evolutionary success of this species. This gene has been cloned and found to be homologous to the *APETALA 2* gene of *Arabidopsis thaliana* [36]. The *Q* allele affects a gene with pleiotropic effects on glume shape and glume tenacity, and on the shape of spike; consequently the spike is more compact with more flowers per spikelet, which increases the number of sinks for assimilate and thus potential yield (Fig. 4). The Q mutation seems to have appeared only once. It has a monophyletic origin. However,

Fig. 4. A major domestication trait: a) wild (qq) vs b) squared head (QQ). The Q allele affects a gene affecting spike shape of spike.

it is still unclear whether it appeared first in tetraploid wheat or in bread wheat with a secondary transfer to durum wheat. It seems that the *q* allele found in *T. aestivum spelta* with hulled grain appeared about 1000 years later than the first hexaploid wheat with naked grains [36]. Thus the Q allele appears to be the primitive allele in hexaploid wheat, possibly being inherited from a Q-tetraploid wheat that hybridized to *T. tauschii*. In any case, this mutation played a crucial role in the world distribution of durum and bread wheat. All extant 6 × naked wheat species carry the *tg/tg q/q* genotype.

Events of the domestication syndrome may be considered as completed with the fixation of non-brittle rachis and naked-grain traits in cultivated fields. Then several other traits have progressively evolved in a favorable direction for farmers, namely flowering time and grain size. The mutations responsible for these changes have been fixed and concentrated, where they conferred agricultural benefits. However, when and where the voluntary selection of favorable traits by farmers occurred first is still unclear. Random mutation is an important contributor to phenotypic variation, but most mutations are more likely to be neutral or deleterious than advantageous. It has been postulated that polyploid species like wheat contain higher amounts of genomic DNA, including duplicated genes, thus being more prone to accumulating negative mutations. On the other hand, the duplicated genes will tolerate more mutations and thrive from a process termed subfunctionalization. Therefore, polyploid wheats have more opportunities to wait until a

favorable mutation occurs and becomes fixed. This genome plasticity is thought to be at the origin of the evolutionary success of polyploids, in wild as well as in cultivated species [37].

However, the success of wheat domestication is tempered by the degree of genetic variability in tetraploid and hexaploid species compared to diploid and tetraploid wild populations. Indeed, domestication and polyploidisation events likely involved a few plants, which led to a dramatic reduction of effective population size also called genetic bottleneck. The intensity of these bottlenecks and their effects on allelic diversity and distribution has been estimated by different methods based on molecular markers [38,39]. Using coalescent models of sequence evolution, such studies determined that the domestication of *T. dicoccum* from *T. diccocoides* had led to a bottleneck associated with a reduction in the effective population size of the domesticated species to about one third of that of the wild populations. However, spontaneous hybridization between domesticated forms and surrounding wild populations may have increased variability and attenuated the bottleneck effect [20]. More recently, even stronger bottlenecks occurred during the selection of modern varieties and therefore estimates of effective population sizes actually measure the effects of these two sources of bottlenecks (domestication then modern selection). This reduction of genetic diversity is even more pronounced for alleles exerting a strong positive selection (e.g., the Q allele) and for genes associated to selective genes by linkage disequilibrium (LD) that generally correspond to closely mapped genes.

Thus, domestication and later modern scientific selection of crop species in an increasingly anthropized environment was globally positive, as documented by the dramatic increase in yield, for example. However, domestication and selection had side effects, such as the loss of some favorable alleles, either because they were in LD with negative alleles at important adaptive genes, or simply by chance.

7. An urgent need to preserve and mobilize untapped genetic resources

With the food crisis of 2007, and perhaps the production losses in Russia and Ukraine noted in 2010, people became aware that food supply might be far from guaranteed. To provide food, feed and raw materials for biobased industries in a world of 9 billion people by 2050, the wheat demand is expected to increase from 621 mt to more than 900 mt [1]. This implies an annual production growth rate of 1.6% from 2005–2020, while it was limited to only 0.9% from 1985 to 1995. Moreover, the rate of yield increase has slowed down from 1995 to 2005 in nearly every country [1,40], being close to 0 in EU particularly in the major producing countries such as France, Germany and UK (Fig. 5). Although genetic progress was continuous at a rate of ~0.1 t/ha/year, this genetic progress has only been sufficient to compensate the negative effects of abiotic and biotic stresses, but not to allow a further increase in yield [3]. As most scenarios of climate change forecast a global increase of 2–4 °C, with increased
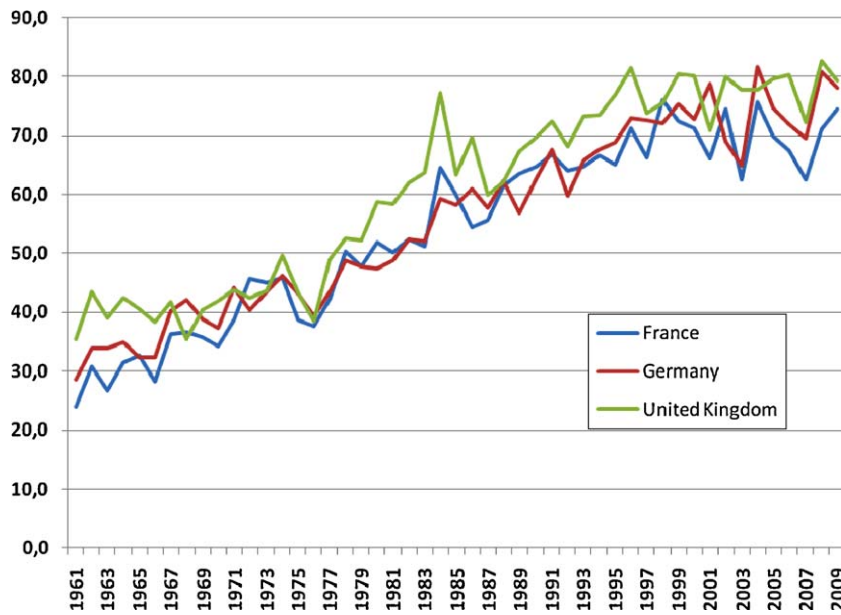
Fig. 5. Evolution of average yield (in quintals - 100s kg per hectare) in the three major producing EU countries.

variability and frequency of extreme events, the negative effect of climate change on wheat yield is expected to increase [41]. Moreover, there is a general consensus that this production increase should be achieved in sustainable farming systems, i.e. with less use of synthetic fertilizers, pesticides and fossil fuels, which were an integral part of the increased yields after 1930. Plant breeders must respond to these new strategies to develop more efficient varieties, being more productive and less resource-intensive. This unprecedented challenge will require the development of a new knowledge-based science and economy.

As a consequence of positive selection during domestication and scientific breeding, modern varieties actually contain superior allele combinations for intensive cropping systems, as documented by the continuous yield improvement from 1920 to 1990 (Fig. 5). However, reduced diversity caused by genetic bottlenecks has diminished their potential to further evolve in a changing environment. The frequency of the most adapted alleles has increased, though many other potentially adaptive alleles have been lost [38,39].

Wild crop relatives and landraces are presumed to contain alleles useful for modern breeding programs [42]. Until now, wild wheat relatives have been used to incorporate new sources of resistance to diseases and pests, most being controlled by single genes. However, monogenic resistances are often overcome. A more durable resistance relies on quantitative (polygenic) genetics to sustain resistance against evolving pests. Moreover, traits associated with stress tolerance are probably polygenic and new strategies must be developed to exploit wild relatives for polygenic traits. Therefore, all hitherto neglected sources of allelic variation for genes controlling complex polygenic traits should be revisited. However, identification of useful target genes and alleles in wild

ancestor or primitive cultivars suffers from the problem of bias in human perception of important traits. In other words, we tend to investigate what we already think is important, such as disease resistance genes [43]. A newly appeared approach consists in genomic scans comparing diversity at molecular markers in wild vs. domesticated populations. Regions with significant reduction in gene diversity and extension of local LD provide evidence of selection imprinting. This approach gives an unbiased view about the type of genes that have played an important role in domestication, and might be further interesting in breeding for adaptation [44,45]. This illustrates how study of domestication processes at molecular level can help identifying novel target genes for future selection programs.

Usually backcross schemes are used to introgress wild chromosome segments carrying favorable traits into an adapted genetic background [46]. However, this strategy is less suitable for complex multigenic traits although molecular markers can help reducing time and cost of experiments [47,48]. An alternative is to mimic what happened in nature 10,000 years ago, and to give evolution a new chance to play with the allelic richness of wild species and old landraces. Indeed, if domestication occurred only once at a single place, the raw material from which modern varieties evolved only represents a small part of the available range of diversity present in the wild ancestor. Moreover, it is unlikely that this initial bottleneck has sampled the most valuable part of the diversity, but rather did it at random. The idea behind neodomestication is to give a new chance to wild species to give rise to domesticated forms of potential interest in breeding programs. This can be achieved by constructing a multiparental population from a broad genetic base and allowing it to evolve under natural selection pressure [49]. As the rate of allele frequency changes relies on cross-
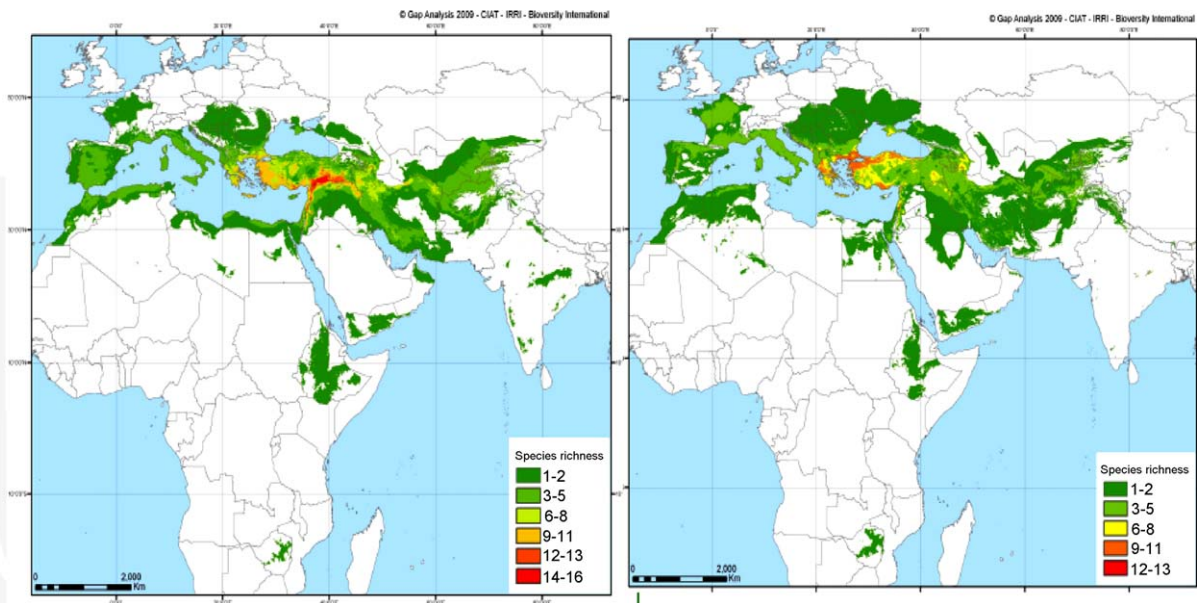
Fig. 6. Predicted evolution of wheat-related species richness indices between present (left) and 2050 (right).

fertilization, it is expected to be rather low in self-fertilized species, and introducing some male-sterility genes may be helpful. However, primary domestication lasted over at least half a millenary, while the urgent need of increasing yield is for the coming 50 years, which represents only 5–10 generation lengths in classical breeding schemes. Neodomestication would have to be much faster. Molecular genetics may provide tools for accelerated selection, which can be applied in the context of neodomestication. Genomic selection [50] consists of replacing phenotypic selection with a marker-based index selection (Genomic estimate of breeding value [GEBV]). Theoretically, genomic selection increases selection intensity and reduces the number of generations for selection. Moreover, dense molecular markers now offer the means to monitor the evolution of genetic diversity across generations of selection, and methods have been developed to balance genetic gain and drift, i.e. avoid diversity losses [51]. Again this is a lesson from the study of domestication and its consequences on crop genetic diversity. The advance of sequencing (www.iwsc.org) will soon provide the high throughput, high density and low cost genotyping tools required for implementing efficient genomic selection, which should also be used in neo-domestication experiments.

However, to make neodomestication possible for future generations, we need to preserve the reservoir of wild species and landraces. This is usually achieved with gene banks but *in situ* conservation is the best option for wild populations, as they continue to evolve with changing selection pressures. But the adverse effect of the expected climate change is threatening the survival of wild wheat relatives in their natural habitats of the Fertile Crescent. In this region biodiversity indices are pessimistic: the expected increase of drought period duration and severity (aridity index) may not permit wild wheat stands to

survive (Fig. 6 [52]). Thus, *in situ* preservation of wild *Triticeae* populations at the center of origin should be a priority.

Conflict of interest statement

The author has no conflict of interest.

Acknowledgements

References

[1] J. Dixon, H.J. Braun, P.P Kosina, J. Crouch, Wheat facts and futures, CIMMYT, Mexico, D.F., 2009.
[2] N. Movahedi, G. Paillotin, A. Neveu, Le monde manquera-t-il de terres pour nourrir les hommes du XXIᵉ siècle ? Académie d'agriculture de France, Paris, 2009.
[3] N. Brisson, P. Gate, D. Gouache, G. Charmet, F.X. Oury, F. Huard, Why are wheat yields stagnating in Europe? A comprehensive data analysis for France, Field Crop Res. 119 (2010) 201–212.
[4] E. Weiss, M.E. Kislev, A. Hartmann, Autonomous cultivation before domestication, Science 312 (2006) 1608–1610.
[5] A. de Candolle, Origine des plantes cultivées, Germer Baillllère, Paris, 1883.
[6] N.I. Vavilov, Studies on the origin of cultivated plants, Institut Botanique Appliquée et amélioration des plantes, Leningrad, 1926.
[7] R.J. Braidwood, H. Cambel, P.J. Watson, Prehistoric investigations in south-western Turkey, Science 164 (1969) 1275–1276.
[8] J. Salse, S. Bolot, M. Throude, V. Jouffe, B. Piegu, U.M. Quraishi, T. Calcagno, R. Cooke, M. Delseny, C. Feuillet, Identification and characterization of shared duplications between rice and wheat provide new insight into grass genome evolution, Plant Cell 20 (2008) 11–24.
[9] M.E. Kislev, D. Nadel, I. Carmi, Epi-paleolithic (19,000 BP) cereal and fruit diet at Ohalo II, Sea of Galille, Israel, Rev. Palaeobot. Palynol. 73 (1992) 27–67.
[10] F. Salamini, H. Ozkan, A. Brandolini, R. Schäfer-Pregl, W. Martin, Genetics and geography of wild cereals domestication in the Near East, Nat. Rev. Genet. 3 (2002) 429–441.

[11] D. Zohary, M. Hopf, Domestication of plants in the Old World. The origin and spread of cultivated plants in West Asia, Europe and the Nile Valley, Oxford Science Publications, Oxford, 1988.

[12] G. Willcox, The distribution, natural habitats and availability of wild cereals in relation to their domestication in the Near East: Multiple events, multiple centres, Veget. Hist. Archaeobot. 14 (2005) 534–541.

[13] D.Q. Fuller, Contrasting patterns in crop domestication rates: recent archaeobotanical insights from the old world, Ann. Bot. 100 (2007) 903–924.

[14] I. Kuljt, B. Finlayson, Evidence for food storage and predomestication granaries 11,000 years ago in the Jordan Valley, Proc. Natl. Acad. Sci. USA 106 (2009) 10966–10970.

[15] G. Hillman, S. Davies, Measured domestication rates in wild wheats and barley under primitive cultivation, and their archaeological implications, J. World Prehistory 4 (1990) 157–222.

[16] S. Lev-Yadun, A. Gopher, S. Abbo, The cradle of agriculture, Science 288 (2000) 1602–1603.

[17] S. Abbo, A. Gopher, Z. Peleg, Y. Saranga, T. Fahima, F. Salamini, S. Lev-Yadun, The ripples of "The Big (agricultural) Bang'": The spread of early wheat cultivation, Genome 49 (2006) 861–863.

[18] L.L. Cavalli-Sforza, P. Menozzi, A. Piazza, The history and geography of human genes, Princeton University Press, Princeton, 1994.

[19] M. Heun, R. Shäfer-Pregl, D. Klawan, R. Castagna, M. Accerbi, B. Borghi, F.F. Salamini, Site of einkorn domestication identified by DNA fingerprinting, Science 278 (1997) 1312–1314.

[20] B. Kilian, H. Özkan, A. Walther, J. Kohl, T. Dagan, F. Salamini, W. Martin, Molecular diversity at 18 loci in 321 wild and 92 domesticate lines reveal no reduction of nucleotide diversity during *Triticum monococcum* (einkorn) domestication: implications for the origin of agriculture, Mol. Biol. Evol. 24 (2007) 2657–2668.

[21] M. Heun, S. Haldorsen, K. Vollan, Reassessing domestication events in the Near East: Einkorn and Triticum urartu, Genome 51 (2008) 444–451.

[22] H. Ozkan, A. Brandolini, R. Shaefer-Pregl, F. Salamini, AFLP analysis of a collection of tetraploid wheats indicates the origin of emmer and hard wheat domestication in southeast Turkey, Mol. Biol. Evol. 19 (2002) 1797–1801.

[23] N. Mori, T. Ishii, T. Ishido, S. Hirosawa, H. Watatani, T. Kawahara, M. Nesbitt, G. Belay, S. Takumi, Y. Ogihara, C. Nakamura, Origin of domesticated emmer and common wheat inferred from chloroplast DNA fingerprinting. 10th Intern. Wheat Genetics Symposium, Paestum I (2003) 25–28.

[24] H. Ozkan, A. Brandolini, C. Pozzi, S. Effgran, J. Wunder, F. Salamini, A reconsideration of the domestication geography of tetraploid wheats, Theor. Appl. Genet. 110 (2005) 1052–1060.

[25] M.C. Luo, Z.L. Yang, F.M. You, T. Kawahara, J.G. Waines, J. Dvorak, The structure of wild and domesticated emmer wheat populations, gene flow between them, and the site of emmer domestication, Theor. Appl. Genet. 114 (2007) 947–959.

[26] A. Badr, K. Müller, R. Shäfer-Pregl, H. El Rabey, S. Effgen, H.H. Ibrahim, C. Pozzi, W. Rohde, F. Salamini, On the origin and domestication history of barley (*Hordeum vulgare*), Mol. Biol. Evol. 17 (2000) 499–510.

[27] P.L. Morrell, M.T. Clegg, Genetic evidence for a second domestication of barley (*Hordeum vulgare*) is at of the Fertile Crescent, Proc. Natl. Acad. Sci. USA 104 (2007) 3289–3294.

[28] J. Dvorak, M.C. Luo, Z.L. Yang, H.B. Zhang, The structure of the *Aegilops tauschii* genepool and the evolution of hexaploid wheat, Theor. Appl. Genet. 67 (1998) 657–670.

[29] L.E. Talbert, L.Y. Smith, N.K. Blake, More than one origin of hexaploid wheat is indicated by sequence comparison of low copy DNA, Genome 41 (1998) 402–407.

[30] D. Zohary, Monophyletic vs polyphyletic origin of the crops on which agriculture was founded in the Near East, Genet. Res. Crop Evol. 46 (1999) 133–142.

[31] R.J. Giles, T.A. Brown, *GluDy* allele variations in *Aegilops tauschii* and *Triticum aestivum*: implications for the origins of hexaploid wheats, Theor. Appl. Genet. 112 (2006) 1563–1572.

[32] J.F. Doebley, B.S. Gaut, B.D. Smith, The molecular genetics of crop domestication, Cell 127 (2006) 1309–1321.

[33] K. Tanno, G. Willcox, How fast was wild wheat domesticated? Science 311 (2006) 1886.

[34] M.D. Purugganan, D.Q. Fuller, The nature of selection during plant domestication, Nature 457 (2009) 843–848.

[35] S. Sood, The major threshability genes soft glume (*sog*) and tenacious glume (*Tg*), of diploid and polyploid wheat, trace their origin to independent mutations at non-orthologous loci, Theor. Appl. Genet. 119 (2009) 341–351.

[36] K. Simons, J.P. Fellers, H.N. Trik, Z. Zhang, Y.S. Tai, B.S. Gill, J.D. Farris, Molecular characterization of the major wheat domestication gene Q, Genetics 172 (2006) 547–555.

[37] J. Dubcovsky, J.J. Dvorak, Genome plasticity a key factor in the success of polyploidy wheat under domestication, Science 316 (2007) 1862–1866.

[38] J.C. Reif, P. Zhang, S. Dreisigacker, M.L. Warburton, M. van Ginkel, D. Hoisington, M. Bohn, A.F. Melchinger, Wheat genetic diversity trends during domestication and breeding, Theor. Appl. Genet. 110 (2005) 859–864.

[39] A. Haudry, A. Cenci, C. Ravel, T. Bataillon, D. Brunel, C. Poncet, I. Hochu, S. Poirier, S. Santoni, S. Glémin, J. David, Grinding up wheat: a massive loss of nucleotide diversity since domestication, Mol. Biol. Evol. 24 (2007) 1506–1517.

[40] M. Reynolds, D. Eaton, Symposium "Complementary strategies to raise wheat yield potential", CIMMYT headquarters, 2009.

[41] EEA technical report 7/2005.

[42] P. Reidsma, F. Ewert, A.O. Lansink, Vulnerability and adaptation of European farmers: a multi-level analysis of yield and income responses to climate variability, Reg. Environ. Change 9 (2009) 25–40.

[43] B.L. Gross, K.M. Olsen, Genetic perspectives on crop domestication, Trends Plant Sci. 15 (2010) 529–537.

[44] J.F. Storz, Using genome scans of DNA polymorphism to infer adaptive population divergence, Mol. Ecol. 14 (2005) 671–688.

[45] M.A. Chapman, C.H. Pashley, J. Wenzler, J. Hvala, S. Tang, S.J. Knapp, J.M. Burke, A genomic scan for selection reveals candidates for genes involved in the evolution of cultivated sunflower (*Helianthus annuus*), Plant Cell 20 (2008) 2931–2945.

[46] Y. Eshed, D. Zamir, Introgressions from *Lycopersicon pennellii* can improve the soluble-solids yield of tomato hybrids, Theor. Appl. Genet. 88 (1994) 891–897.

[47] F. Hospital, A. Charcosset, Marker-assisted introgression of quantitative trait loci, Genetics 147 (1997) 1469–1485.

[48] B. Servin, F. Hospital, Optimal positioning of markers to control genetic background in marker-assisted backcrossing, J. Heredity 93 (2002) 214–217.

[49] I. Goldringer, J. Enjalbert, J. David, S. Paillard, J.L. Pham, P. Brabant, in: H.D. Cooper, C. Spillane, T. Hodgkin (Eds.), Broadening the genetic base of crop production, CABI Wallingford, UK, 2000, pp. 245–260.

[50] T.H.E. Meuwissen, B.J. Hayes, M.E. Goddard, Prediction of total genetic value using genome-wide dense marker maps, Genetics 157 (2001) 189–1929.

[51] J. Hallander, P. Waldmann, Optimum contribution selection in large general tree breeding populations with an application to scot pines, Theor. Appl. Genet. 118 (2009) 1133–1142.

[52] H.K. Kafle, H.J. Bruins, Climatic trends in Israel 1970–2002: warmer and increasing aridity inland, Climatic Change 96 (2009) 63–77.