

GENETICS AND GEOGRAPHY OF WILD CEREAL DOMESTICATION IN THE NEAR EAST

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About 12,000 years ago, humans began the transition from hunter-gathering to a sedentary, agriculture-based society. From its origins in the Near East, farming expanded throughout Europe, Asia and Africa, together with various domesticated plants and animals. Where, how and why agriculture originated is still debated. But newer findings, on the basis of genome-wide measures of genetic similarity, have traced the origins of some domesticated cereals to wild populations of naturally occurring grasses that persist in the Near East. A better understanding of the genetic differences between wild grasses and domesticated crops adds important facets to the continuing debate on the origin of Western agriculture and the societies to which it gave rise.

STAND

A population of a species that thrives in natural habitats. In the simplest example, the single species that dominates a field of grass.

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About 12,000 years ago, a small group of humans made the shift from hunter-gathering to cultivating plants for sustained survival. The discovery of agriculture caused many changes in human culture — a phenomenon known as the Neolithic revolution¹. Agriculture strengthened the sedentary lifestyle, which led to the stratification of society and to the development of key technologies; so, knowing where agriculture arose is necessary for understanding early human culture. The first humans to pioneer farming practices lived in the Fertile Crescent^{2,3} — a region that spans modern-day Israel, Jordan, Lebanon and western Syria, into southeast Turkey and, along the Tigris and Euphrates rivers, into Iraq and the western flanks of Iran (FIG. 1). In the Fertile Crescent, agriculture allowed the development of a dense human population. The ability to store food surpluses and to feed non-farming specialists — in other words, a successful agriculture — catalysed cultural development in this region⁴.

Before the beginning of agriculture, the Fertile Crescent was rich in what are still the most essential natural resources for mankind: a natural abundance of wild animals and plants that provide a protein-rich

diet^{2,4}. The archaeological record shows that humans who settled in the region harvested the wild forms of cereals from natural STANDS before deliberate cultivation and domestication^{2,3,5}. Some, as yet unknown, factors prompted this crucial shift. One of the numerous proposed possibilities is that an ~1,000-year episode of a cold, dry climate — the Younger Dryas, 12,200–11,100 cal BP (calibrated years before the present)² — constricted or impaired the natural stands of cereals, thereby favouring communities that invested in agricultural activity^{2,6}. (See BOX 1 for a discussion of the need to use calibrated dates.) Regardless of its initial cause, the result of man's first farming experiments was the creation of a set of domesticated varieties of cereal, many of which are still in use in various parts of the world.

When discussing the origin of agriculture, it is important to distinguish between cultivation and domestication. The former entails the deliberate planting and harvesting of either wild or domesticated forms. Conversely, domestication is the process of genetic selection that, by altering key traits, transforms wild forms into domesticated varieties of crops. The transition from wild to domesticated forms of crops



Figure 1 | **Map of the Near East.** Note the Fertile Crescent (dashed red line) and the archaeological sites that are mentioned in the review. The Fertile Crescent is characterized by a variable topography, marked seasonality with cold rainy winters and dry summers, a history of fluctuating precipitation and a rich palaeoflora that is well documented in the fossil pollen record⁶. These features contributed to making this region the cradle of agriculture. In the Fertile Crescent, the Karacadağ region (KD) has been proposed to be in the ‘core area’ for plant domestication in the Near East²⁵.

RACHIS

The backbone of the ear (inflorescence), which bears lateral spikelets.

GLUME

The leaf-like structure that protects the seed in cereals. They can be tenacious (hard and not releasing the seeds, indehiscent) or soft (freely release seeds; naked seeds).

PHYTOGEOGRAPHY

The study of the geographical distribution of plant species.

mainly entails changes to three principal morphological features that make the crop easier to harvest: seed size, ear RACHIS stiffness and the ease with which the seed is released from its enclosing leaf-like structures (GLUMES) (BOX 2).

The study of crop domestication is multidisciplinary, as it combines the use of genetic, archaeological and PHYTOGEOGRAPHICAL approaches. Two independent lines of evidence indicate that western agriculture originated in the Fertile Crescent²⁻⁷. First, the current distributions of the wild progenitors of modern cereal species intersect in this region; these species include wild wheats (*Triticum urartu*, *T. boeoticum* and *T. dicoccoides*), wild barley (*Hordeum spontaneum*) and wild rye (*Secale vavilovii*)^{3,5,8}. Second, the seeds of the wild species occur in early archaeological sites of the region, followed in radiocarbon age and stratigraphic succession by the remains of domesticated forms^{2,3,5}. The study of the archaeobotanical properties of plant remains from archaeological sites reveals

Box 1 | Estimating the age of historical samples

The age of a sample can be determined by measuring its content of the carbon isotope ¹⁴C. The ¹⁴C content in individual rings of the so-called ‘continuous dendrochronological series’ (tree rings), which provides absolute ages in years, showed that the ¹⁴C content of the atmosphere has fluctuated during the past 10,000 years. Therefore, dates based on ¹⁴C content alone need to be calibrated by the dendrochronological factor to obtain ages as measured in calendar years. ¹⁴C dates that are calibrated by this factor are indicated as calibrated years before the present (cal BP). As a very rough estimate, cal BP are ~10% more ancient than uncalibrated dates^{2,5}.

when and where domesticated crops first existed. By contrast, phylogeographical approaches focus on the present-day wild species and populations, their relationships to cultivated crops, their distribution, their ecology and the trends in those morphological characters that are associated with plant domestication.

Archaeology can tell us when agriculture arose^{2,5,9}, but genetics is yielding answers to two equally important questions: where do we find the natural stands from which cereals were domesticated, and which genes are responsible for the traits that distinguish wild from domesticated forms? Answers to the question of ‘where’ agriculture began are coming from population comparisons using AMPLIFIED FRAGMENT LENGTH POLYMORPHISMS (AFLPs) from hundreds of loci. These give genome-wide estimates of genetic similarity¹⁰ and are pinpointing the wild stands that humans used during crop domestication^{11,12}. These, and other experimental methods (BOX 3), are giving us insight into the evolution of domesticated crops and the genetic architecture of the transition from wild to domesticated traits. The specific alleles that underlie salient domesticated traits are turning out to be a handful of HOMOELOGUES that were independently selected in different cereal species. Several important morphological features distinguish domesticated varieties from wild forms (BOX 2); these have helped to guide the identification of loci that contribute to these phenotypic differences and correlate them to the agricultural advantages that they bestow.

In this review, we describe recent progress in understanding the transition from wild to domesticated forms of wheat, rye and barley in geographical terms, while focusing on the genetics of morphological changes that have been induced by the domestication process.

Wheat: *Triticum* species

Ploidy changes have been quite common in cereal evolution, and wheat species are a good example of this (BOX 4). The ploidy levels of domesticated wheat species range from diploid ($2n = 14$) to hexaploid ($6n = 42$), and wheats of all ploidy levels have been domesticated at some time. In the following sections, we attempt to reconstruct the history of domestication of wheat species, on the basis of genetic and archaeological evidence.

The first wheat to be cultivated successfully was einkorn, a diploid species, although its cultivation began to be abandoned in the BRONZE AGE (for a timescale of archaeological eras, see BOX 5). At that time, humans intensified the cultivation of polyploid wheats, probably owing to their superior adaptation to warm climates and to the favourable harvesting properties of polyploid varieties that had naked seeds and soft glumes. Tetraploid varieties of domesticated wheat — some of which are still used — derive from a single tetraploid progenitor, *T. dicoccoides*. Early after the domestication of *T. dicoccoides*, free-threshing forms evolved from the less amenable HULLED genotypes. The wheat species with tetraploid genomes were subsequently involved in a fateful experiment: accidental crosses with a wild diploid species (*Aegilops tauschii*) gave rise to hexaploid

wheats. These comprise hard and bread wheat, which are most suitable for baking. Bread wheat has no wild hexaploid progenitor in nature; it is, therefore, a farming-associated natural hybrid that has since become the world's leading crop.

Einkorn: *Triticum monococcum*. Einkorn wheat — the earliest variety of cultivated wheat — has a diploid AA genome (TABLE 1) and was domesticated from its wild progenitor, *T. boeoticum*^{13,14}. Although einkorn was important for Neolithic agriculture, it is, today, a relic crop and is rarely planted or harvested. Its progenitor, *T. boeoticum*, occurs in the central and eastern parts of the Crescent⁵; it also colonizes SECONDARY HABITATS, and FERAL FORMS occur in the Balkans¹⁵. Wild and domesticated einkorn interbreed to generate fertile progenies. The kernels of *T. boeoticum* have been found in Epi-Palaeolithic (BOX 5) and early Neolithic sites (12,500 cal BP) of the central Fertile Crescent. Here, they are found together with plumper kernels (~10,500 cal BP), a proposed sign of domestication^{3,5}.

In the western Crescent, domesticated einkorn remains become abundant at ~9,500 cal BP (REF 8). Then the wheat appeared in Cyprus, Greece and the Balkans at ~8,000 cal BP (REFS 16,17) and, later, in Yugoslavia, Bulgaria and Hungary. Einkorn was important for the early agriculture of Central Europe (~7,000 cal BP) but, as mentioned above, its cultivation started to decline in the Bronze Age⁸.

The site of einkorn domestication was identified from the analysis of 288 AFLP marker loci in einkorn and its wild ancestor¹¹. The results indicated that wild, *T. boeoticum*, populations from the western foothills of the Karacadag mountains of southeast Turkey (FIG. 1) are more similar to einkorn than are other wild populations, which indicates that this was the centre of its domestication¹¹. However, the conclusions of that study have been challenged. For instance, Jones *et al.*¹⁸ argued that farming sites of the Jordan basin were better candidates for einkorn domestication, whereas Nesbitt and Samuel¹⁹ maintained that southeastern Turkey sites were the earliest ones (11,100–10,500 cal BP)³.

AMPLIFIED FRAGMENT LENGTH POLYMORPHISM

A mapping method in which genomic DNA from different strains is amplified by PCR using arbitrary primers. DNA fragments that are amplified in one strain are used as polymorphic markers.

HOMOEEOLOGUE

Chromosomes that share a common ancestor; although these might differ to some extent, they have a collinear molecular organization. Homoeologues can occur in different species, but can also coexist in the nucleus of polyploid species.

BRONZE AGE

An archaeological period starting ~5,500 cal BP in the Fertile Crescent. This corresponds to a later period in Europe.

HULLED, NON-FREE-THRESHING (NFT). Forms of cereal that have tenacious glumes.

SECONDARY HABITAT

A primary habitat is an ecological or geographical zone in which a given species is naturally endemic. The same species might subsequently colonize other areas (secondary habitats) as a consequence of human activities.

FERAL FORM

A population living in wild habitats that is derived from crosses between wild and domesticated genotypes.

SPIKELET

The part of the ear in grasses that contains 1–4 seeds and their surrounding glumes (leaf-like structures).

DISARTICULATE OR BRITTLE RACHIS

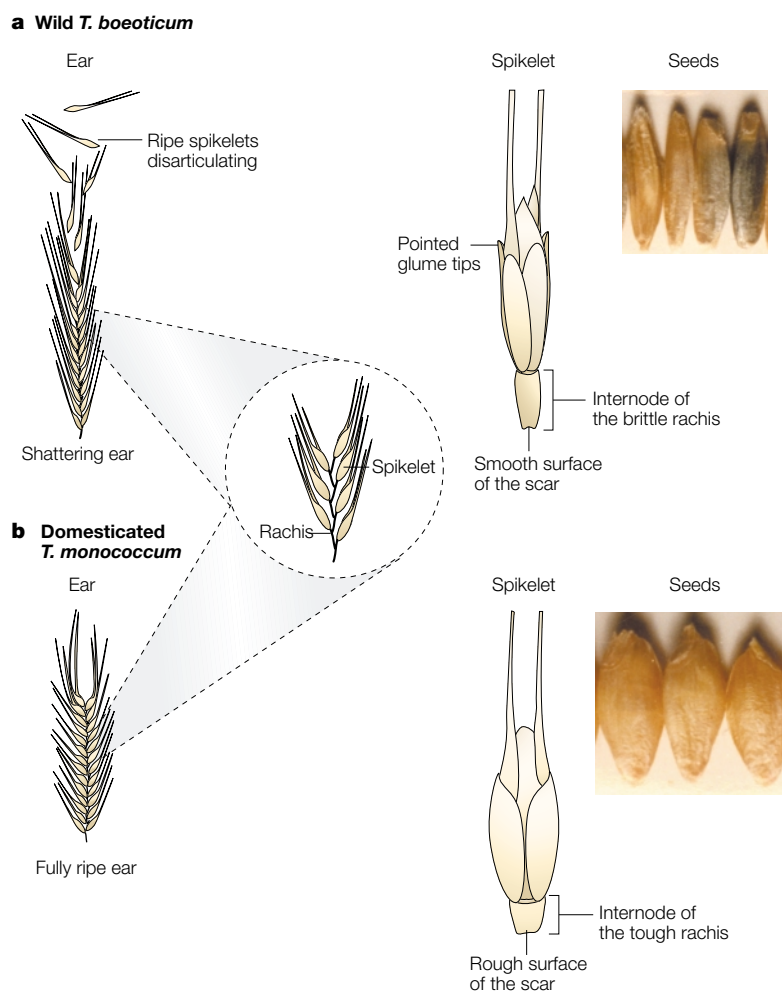
A rachis in which the ear disrupts at maturity into individual spikelets, each bearing a fragment of rachis.

TOUGH, NON-BRITTLE RACHIS

One that does not release spikelets at maturity. The ear can therefore be threshed to release seeds.

Box 2 | Phenotype of wild versus domesticated cereals and relevant terminology

The morphological differences that distinguish wild from domesticated cereals are crucial for understanding agricultural origins. A common complex of three basic characters emerged during the transition of all cereals from wild to domesticated forms (see figure). This is illustrated for einkorn wheat (*Triticum monococcum*), which was the first wheat to be domesticated. As for other cereals, domesticated einkorn wheat (b) differs from the wild form *T. boeoticum* (a) in three traits: first, the wild forms have small seeds, whereas those of domesticated forms are larger; second, the SPIKELETS of wild ears fall apart at ripening through fragmentation of the rachis (by shattering or DISARTICULATION), whereas the domesticated forms have a TOUGH RACHIS that holds the seeds together in a harvestable and threshable ear; third, the leaf-like structures that protect the seed (glumes) are attached tightly to the seed or are fused to it in wild forms, whereas they release the seed in the more advanced domesticated forms (which are therefore said to be free threshing or naked). Note that the ear of the species shown has two rows.



Nevertheless, excavations at early settlements near Karacadag, including at Çafar Höyük²⁰, Çayönü²¹, Nevalı Çori²² and Abu Hureyra^{23,24} (FIG. 1), have supported genetic evidence for the domestication of einkorn near the Karacadag range.

Adding to this debate, Lev-Yadun *et al.*²⁵ found that the ranges of several wild progenitors of various domesticated cereals and of legumes, such as pea, chickpea and lentils, intersect in a small region of southeast Turkey, circumscribing a core area that includes Karacadag (FIG. 1). This core might therefore be the cradle of agricultural innovation — a conclusion that is also supported by botanical remains in excavations and prehistoric finds²⁵. Domesticated wheats and barley were also present in several Neolithic sites in this core region at 10,500 cal BP (REF. 3). So, this specific area of the Fertile Crescent could have produced a master copy of various crops, from which new varieties have differentiated with time. This would be consistent with Daniel Zohary's model, based

mainly on cytogenetic data (BOX 3), that domesticated forms of founder crops have a single origin²⁶. The genetic evidence for a single origin of domesticated einkorn varieties from the wild progenitor species, *T. boeoticum*, on the basis of AFLP data, is shown in FIG. 2a.

Einkorn and its wild progenitor differ mainly in seed size and ear traits (BOX 2). The tough einkorn rachis, which makes it easier to harvest, arose from the disarticulate (brittle) *T. boeoticum* rachis during domestication. This trait is under the control of two genes that segregate 15 brittle to 1 tough rachis in the F₂ progeny of wild × domesticated crosses²⁷. Free-threshing einkorn varieties are uncommon; however, a free-threshing einkorn line was discovered in 1970 in a collection of the botanist Petr M. Zhukovskii²⁸. This line was used to show that the free-threshing trait is inherited as a recessive allele (soft glume, *sog*, with the *Sog* allele supporting tenacious glumes). Taenzler *et al.*²⁹ have mapped this locus to chromosome 2A in a

Box 3 | Experimental methods used in crop-domestication studies

The most important methods used to study the evolution and genetics of domestication are listed here.

Molecular markers

Various DNA-fingerprinting techniques have been used in recent years to reveal the existence of alternative alleles at DNA loci (encoded by the nucleus or organelles)¹⁰. Among them are restriction-fragment length polymorphisms (RFLPs), randomly amplified polymorphic DNA (RAPDs) and single-nucleotide polymorphisms (SNPs). RFLP and RAPD alleles are often due to sequence variation at restriction-enzyme recognition sites and primer-binding sites, respectively, but can also be due to length polymorphisms in the restricted or amplified region. As their name indicates, SNP alleles are single-nucleotide changes and can be detected in various ways (reviewed in REF. 103). Amplified-fragment length polymorphisms (AFLPs) can be detected through a PCR-based procedure, which avoids the many laborious steps that are involved in RFLP analyses. Here, DNA is usually digested with two restriction enzymes (one with a tetrameric recognition site and one with a hexameric) to yield fragments with overhanging ends; these are ligated to adaptors with primer-binding sites, which allows selective amplification of the fragment. The use of a labelled primer, usually for the hexamer site, yields a pattern of bands in a sequencing gel that is dense enough to reveal differences between fragments but simple enough to be interpreted¹⁰⁴.

Genetic distances

The fraction of alleles that differ between two individuals can be scored and used to determine genetic distances among closely related taxa. Various algorithms exist for this purpose, some of which infer distance on the basis of the presence or absence of characters, whereas others infer an estimate for the number of nucleotide substitutions that might have occurred between individuals in the restriction-site sequences¹⁰⁵.

Phylogenies

A phylogeny is a graph that depicts the relatedness of individuals, populations and species¹⁰⁶. Distance methods can be used to construct a tree from a matrix of pairwise genetic distances. A different approach involves constructing trees for populations on the basis of overall similarity of their allele frequencies; for example, at AFLP loci. In studies of plant-domestication genetics, phylogenies that are based on single genes are of very limited use, because the alleles at single nuclear genes are much older than the populations themselves. Instead, measures of genome-wide similarity, as provided by AFLP or SNP alleles, are more useful for unravelling domestication history.

Cytological methods

Genetic variation among related taxa can be assessed by comparing the organization of their chromosomes. Various inversions, duplications, translocations and ploidy changes are known to distinguish crop plants from their wild progenitors.

Genetics of domestication

Methods of Mendelian analysis, including the study of quantitative trait loci (QTL) by the use of molecular markers, are routine. To study the slightly more complicated genetics of polyploid species requires the use of special lines that are nullisomic (in which one pair of chromosomes is missing), monosomic (one chromosome is missing) or otherwise ANEUPLOID lines, or makes use of SUBSTITUTION LINES for classical marker segregation analyses^{107,108}. Several genes that underlie the traits that distinguish wild from cultivated cereals have been described using such tools and assigned to chromosomes (see TABLE 1).

ANEUPLOIDY

The presence of extra copies, or no copies, of some chromosomes.

SUBSTITUTION LINE

In polyploids, a new chromosome pair from a related species can be introduced, while eliminating the resident homoeologous pair. This generates a substitution line. When repeated for all chromosomes, the process generates a set of substitution lines.

Box 4 | **Polyploidy**

Variation in ploidy — a change in the number of chromosome complements — has had an important role in plant evolution. In related species, the chromosome number might vary as a multiple of an integer. For example, wheat species are characterized by a polyploid series with the basic chromosome number of seven. These species can have 14 ($2n$, diploid), 28 ($4n$, tetraploid) or 42 ($6n$, hexaploid) chromosomes. The chromosome complements of polyploid wheats are genetically redundant because they have originated from the synthesis of two or three genomes, as in the hexaploid wheats (genomes AA, BB and DD). The seven A chromosomes (1A–7A) of these wheats are related, through common ancestors, to homoeologous chromosomes B and D; that is, chromosomes 1A, 1B and 1D are SYNTENIC, as are 2A, 2B and 2D, and so on. Polyploidization is very common among flowering plants, in which up to 70% of all species might be polyploids¹⁰⁹, whereas among the GYMNOSPERMS it is rare (only ~5% of all species). Polyploidy arises mainly owing to the formation of unreduced gametes, which therefore have twice the expected number of chromosomes. When unreduced gametes from the same species make a zygote (autopolyploidy), the resulting progeny will have twice the original chromosome number. Unreduced gametes from different, but interfertile, species can also form a zygote (allopolyploidy). Newly generated polyploid species are often sterile owing to the formation of abnormal MULTIVALENTS during meiosis. However, in hexaploid wheat, the *Pairing homoeologous (Ph1)* gene on chromosome 5B suppresses the pairing between homoeologous chromosomes A, B and D^{110,111}. The loss of this chromosome or the mutation of the gene supports the exchange of genetic material between chromosomes A, B and D^{112,113}.

genomic position that has conserved synteny with the *Tenacious glumes (Tg)* loci of polyploid wheats, which contribute to the same phenotype (TABLE 1). Although in *sog* mutant plants the glumes that encase the grain are soft, the ears are very compact, which is a negative pleiotropic effect that has hindered the wide use of free-threshing einkorn varieties. The poor agronomic value that is associated with the compact ear (partial sterility and loss of spikelets) in free-threshing einkorn²⁹ explains why it is not widely cultivated. The genetic redundancy in the wheat polyploid genomes (discussed below) was the key feature that allowed the use of superior free-threshing forms.

Emmer and related tetraploid wheats. A further important step in the evolution of modern polyploid wheat varieties was the domestication of emmer, which is a tetraploid wheat, from its wild progenitor *T. dicoccoides*. Wild emmer, an AABB wheat (BOX 4) with its A genome from *T. urartu*^{30,31}, has brittle ears that shatter at maturity into spikelets that bear relatively large seeds. Unlike their wild progenitor, all domesticated tetraploid wheats have a non-brittle rachis, which is more amenable to harvest as the spikelets do not fall apart. Domesticated emmer wheat, *T. dicoccum*, has hulled seeds and the AABB genome that is common to other domesticated tetraploid wheats. Emmer was the most important crop in the Fertile Crescent until the early Bronze Age⁶, and domesticated forms are present at several early Neolithic sites, such as Tell Aswad (~10,800 BP)³². Domesticated emmer remains are present at Abu Hureyra from 10,400 BP (REF. 24), although the archaeobotanist Gordon Hillman²³ reports the presence of individual, apparently domesticated, grains in earlier layers of Abu Hureyra, Çayönü and Nevalı Çori,

which also indicate an early presence of the domesticated form^{21,22}. In later Pre-pottery Neolithic B settlements (BOX 5), domesticated emmer is abundant³³. Naked forms, such as the small grain *T. parvicoccum*³⁴, are also present in early Neolithic sites. The wheat used in ancient Egypt was emmer³⁵, and this wheat still remains in cultivation in Ethiopia. Of the different tetraploid wheats, however, the free-threshing *T. durum* (hard wheat) is the only one that is widely cultivated today.

The present geographical distribution of wild emmer is rather puzzling. In primary habitats (it rarely colonizes secondary habitats), it exists in two morphologically distinguishable types³⁶. The geographical distribution reported by Zohary and Hopf⁵ includes the western Fertile Crescent, its central part in southeast Turkey, and areas in eastern Iran and Iraq. Johnson³⁷ reports that, from southeastern Turkey to Iran–Iraq, the species is progressively substituted by the wild tetraploid wheat *T. araraticum*. This introduces a problem: *T. araraticum* has an AAGG genome and does not produce fertile progeny with *T. dicoccoides*³⁸, but the two are phenotypically indistinguishable. Johnson³⁷ raises doubts, on the basis of protein electrophoretic patterns, as to whether *T. dicoccoides* is present among the wild tetraploids in Iraq and Iran. On the contrary, vigorous stands of *T. dicoccoides* grow on the basaltic rocky slopes of the Karacadag mountains in southeast Turkey^{14,37}.

An analysis of AFLP data at 204 loci has indicated that domesticated tetraploid AABB wheats are most closely related to wild emmer populations from southeast Turkey. In this study (H.O., A.B., R.S.-P. and F.S., unpublished data), 99 lines of wild emmer were used, which originated from Turkey, Israel, Jordan, Lebanon, Syria and Iran, as well as 19 wild emmer lines from Karacadag populations. The genetic profile of 15 out of the 19 Karacadag lines was consistent with their close genetic relationships to domesticated emmer. The analysis of AFLP allele frequencies also revealed that the Turkish wild emmer populations are more similar to domesticated tetraploid wheats than are other populations sampled (FIG. 3). Moreover, all lines of hulled emmer were included in a single group, and all hard, free-threshing wheat genotypes in another group, which indicates that each group had a single origin. The early splitting of the lineage that led to domesticated hulled and free-threshing wheat is consistent with the early appearance of domesticated tetraploid free-threshing wheats. This early split helps to explain the otherwise puzzling presence of domesticated grains that belong to both tetraploid and hexaploid free-threshing forms at Abu Hureyra and at other early Neolithic sites²⁴.

The genetic control of seed size in domesticated versus wild tetraploid wheats has been studied by generating *T. dicoccoides* substitution lines in *T. durum*^{39,40}. Kernel size is under complex polygenic control, and both positive and negative alleles (which contribute to an increase and decrease in kernel size, respectively) have been mapped to seven chromosomal regions (1A, 2A, 3A, 4A, 7A, 5B and 7B)^{39,40}.

SYNTENY

Collinearity in the order of genes (or of other DNA sequences) in a chromosomal region of two species. Homoeologous chromosomes are largely syntenic.

GYMNOSPERM

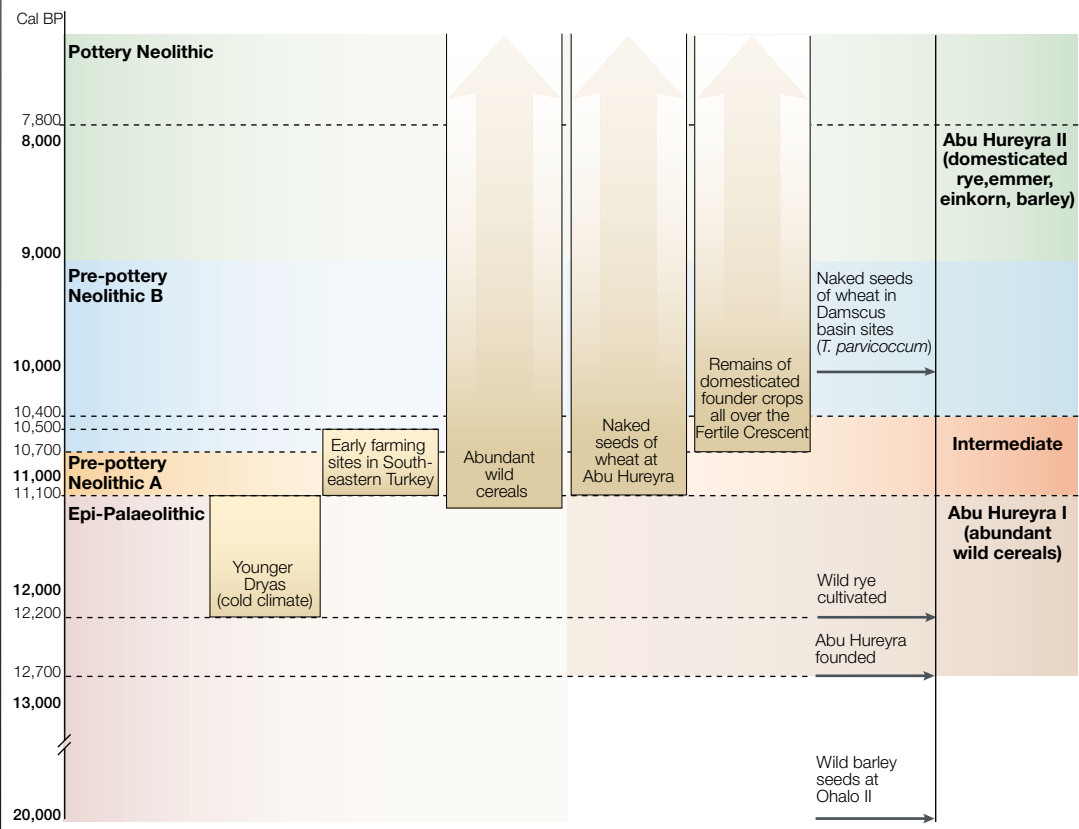
A non-flowering seed plant (for example, pine).

MULTIVALENT

The presence of more than two chromosomes synapsed in a unit during prophase I of meiosis; this is characteristic of many autopolyploids.

Box 5 | **A timescale of the major archaeological periods in the Near East**

The figure below shows the times of selected archaeobotanical events, including the duration of occupation of the Abu Hureyra site (FIG. 1). This is a particularly well-studied archaeological site that contains a wealth of plant remains that are very relevant to the origin of agriculture. The Near East archaeological periods shown in the diagram are reported in calibrated years before the present (cal BP), which is a more objective way of measuring the age of historical samples (BOX 1). Excavated sites of the Pre-pottery Neolithic A layers contain almost only wild seed remains, but domesticated forms start to appear at sites of Pre-pottery Neolithic B^{8,33,102}. The Younger Dryas period corresponds to ~1,100 years of cold climate that started at 12,200 cal BP (REF. 2).



Emergence of free-threshing wheats

Free-threshing wheats — tetraploid hard wheat (*T. durum*) and hexaploid bread wheat (*T. vulgare*) — represent the final steps of *Triticum* domestication. Although free-threshing seeds have not traditionally been used to identify early agricultural sites⁸, a partial revision of this assumption might be necessary². The appearance of the free-threshing phenotype can be illustrated with the comparative genetics of two hexaploid wheat varieties, *T. spelta* (a hulled wheat called SPELT) and *T. vulgare* (bread wheat, a free-threshing form). Understanding the origin of free-threshing wheat demands knowledge of how hexaploid wheats evolved. Both *T. spelta* and *T. vulgare* have an AABBDD hexaploid genome, although this is not found in wild species. McFadden and Sears⁴¹ showed that the progenitors of the hexaploids are the tetraploid *T. turgidum* (AABB) and the wild grass *Ae. tauschii* (DD). So, at some unknown time and place in the past, tetraploids hybridized with the diploid species and generated spelt-like hulled hexaploid wheats. The involvement of a domesticated tetraploid, *T. turgidum*, in this cross is

suspected, because the distribution range of *Ae. tauschii* does not overlap with the distribution of the wild tetraploid *T. dicoccoides*⁸. The AABBDD genome therefore probably stems from the anthropogenic expansion of tetraploid domesticated species into the distribution area of *Ae. tauschii*⁵. The southern Caspian basin is a likely place for this hybridization, because the *stangulata* subspecies, a form of *Ae. tauschii* (the D-genome progenitor) still grows in this area and was considered to be the actual donor (discussed in REFS 31,42). However, newer data, which were obtained using molecular markers, raise doubts about the direct participation of the *stangulata* subspecies in this event⁴³.

The most important gene that is involved in the evolution of free-threshing wheat maps to a complex locus known as the *Q* factor, which is located on the long arm of chromosome 5A⁴⁴⁻⁴⁶. In *T. vulgare*, the *Q* allele supports the formation of square-headed ears with good threshability. Pleiotropic characters of the *Q* allele are softening of the glumes, reduction of ear length, more spikelets per ear and toughness of the rachis — all features that are favourable to harvesting^{44,47}. Mutagenic

SPELT
A hexaploid wheat that is still sporadically cultivated in Europe, the grains of which are enclosed (hulled) in glumes.

Table 1 | **Species and their derived forms**

Species names in this review (common name)	Biological species	Genome and ploidy	Ear and seed traits	No. of loci that support B vs NB rachis*	Alleles of loci that affect either glume or glume and ear rachis (chromosome)†	References
<i>T. boeoticum</i> (wild einkorn)	<i>T. monococcum</i> L. ssp. <i>boeoticum</i> Boiss.	AA	H, B	2	<i>Sog_A</i> (2S)	27
<i>T. monococcum</i> (cultivated einkorn)	<i>T. monococcum</i> L. ssp. <i>monococcum</i>	AA	H, NB	2	<i>Sog_A</i> (2S)	27,29
<i>T. urartu</i> (wild <i>T. urartu</i>)	<i>T. urartu</i> Tuman.	AA	H, B	2	–	–
<i>Ae. tauschii</i> (wild <i>Ae. Tauschii</i>)	<i>Ae. tauschii</i> Coss.	DD	H, B	1	<i>Tg_D</i> (2S)	51,52
<i>T. dicoccoides</i> (wild emmer)	<i>T. turgidum</i> L. ssp. <i>dicoccoides</i> Aschers.	AABB	H, B	2; polygenic	<i>Tg_{2B}</i> (2S), <i>q_A[§]</i> (5L), <i>Qft_{5A}</i> (5S), <i>Qft_{6A}</i> (6)	44,50,56,114,115, 116,117
<i>T. dicoccum</i> (cultivated emmer)	<i>T. turgidum</i> L. ssp. <i>dicoccum</i> Schübl.	AABB	H, NB	2	<i>Tg_{2B}</i> (2S), <i>q_A</i> (5L)	50,116
<i>T. durum</i> (hard wheat)	<i>T. turgidum</i> L. ssp. <i>durum</i> Desf.	AABB	FT, NB	polygenic	<i>tg_{2B}</i> (2S), <i>Q_A</i> (5L), <i>qft_{5A}</i> (5S), <i>qft_{6A}</i> (6)	50,51,56,114,116,118
<i>T. parvicoccum</i> (<i>T. parvicoccum</i> , archaeobotanical)	<i>T. turgidum</i> L. ssp. <i>parvicoccum</i> Kislev	(AABB)	FT, NB	–	–	–
<i>T. araraticum</i> (wild Timopheev's wheat)	<i>T. timopheevii</i> Zhuk. ssp. <i>araraticum</i> Jakubz.	AAGG	H, B	–	–	–
<i>T. timopheevii</i> (cultivated Timopheev's wheat)	<i>T. timopheevii</i> Zhuk. ssp. <i>timopheevii</i>	AAGG	H, NB	–	–	–
<i>T. spelta</i> (spelt)	<i>T. aestivum</i> L. ssp. <i>spelta</i>	AABBDD	H, NB	2	<i>Tg_{2B}Tg_D</i> (2S), <i>q_A</i> (5L), <i>Qft_{5A}</i> (5S), <i>Qft_{6A}</i> (6)	53,55,108,114,119
<i>T. vulgare</i> (bread wheat)	<i>T. aestivum</i> L. ssp. <i>vulgare</i> Host.	AABBDD	FT, NB	2	<i>tg_{2B}tg_D</i> , <i>Q_A</i> , <i>qft_{5A}</i> , <i>qft_{6A}</i>	44,48,51,116
<i>S. vavilovii</i> (wild rye)	<i>S. cereale</i> L. ssp. <i>vavilovii</i> Grossh.	RR (SS)	B	1	–	72
<i>S. cereale</i> (rye)	<i>S. cereale</i> L. ssp. <i>cereale</i>	RR (SS)	NB	1	–	72
<i>H. spontaneum</i> (wild barley)	<i>H. vulgare</i> L. ssp. <i>spontaneum</i> Thell.	HH	H, B	2	–	80,120
<i>H. vulgare</i> (barley)	<i>H. vulgare</i> L. ssp. <i>vulgare</i>	HH	H [#] , NB	2	–	78,80,120

Nomenclature is taken from REF. 5, with modifications. *Genes that affect rachis but not glume traits. †Subscripts indicate genomes. §Designated as *q2* in REF. 56. ||Allele inferred from genotype of wild emmer. ||Allele inferred from genotype of hard wheat. #The trait is under the control of the single gene *N* (recessive *n*, naked seeds)⁸⁰. *Ae.*, *Aegilops*; B, brittle rachis, ears disarticulating at maturity into spikelets; FT, free-threshing, soft glumes, shorter rachis internode, tougher rachis; H, hulled wheat, in the spikelet, the kernels of H wheats are covered by tenacious glumes, not easily separated from grains during threshing; *H.*, *Hordeum*; NB, non-brittle, non-brittle (tough) rachis that does not disarticulate at maturity; Q, Q factor; S., *Secale*; *Sog*, tenacious glumes; *T.*, *Triticum*; *Tg*, tenacious glumes.

disruption⁴⁸ of the *Q* gene in QQ hexaploid free-threshing wheat generated a *q* mutant phenotype, known as speltoid because *q* mutants have a morphology similar to that of spelt, which is a naturally occurring hexaploid hulled wheat (that has tenacious glumes) with a *qq* genotype. Free-threshing bread wheats, which are *Qq* heterozygotes, have intermediate phenotypes due either to dosage effect or to the interaction of two active alleles, *Q* and *q*. Because spelt has the *q* allele, Sears⁴⁴ was confident that the large *Q* allele found in free-threshing wheats derives from a form of *q* that retains some activity. In an elegant and important experiment,

Muramatsu⁴⁹ showed that *q* is active by using substitution and other aneuploid tetrasomic and trisomic lines of hexaploid wheat. These were used to create conditions in which chromosome 5A — on which *Q* resides — was present in a nucleus in variable amounts, which creates genotypes with 1–5 doses of either *Q* or *q* alleles. He showed that a square-headed hexaploid ear derives from either two doses of *Q* or five doses of *q*. In other words, *q* is also functional but is hypomorphic in comparison with *Q*. All free-threshing *T. durum* lines have the *Q* allele, whereas all hulled *T. dicoccum* or wild *T. dicoccoides* have *q*⁵⁰. This is taken as evidence that

Q emerged by mutation from hulled domesticated tetraploids. In the same genome, mutations at additional loci shaped the full expression of the free-threshing characteristic.

A second genetic system that controls the speltoid phenotype was discovered in synthetic hexaploids that were produced by crossing free-threshing tetraploids with the diploid and hulled *Ae. tauschii*. The hybrids were hulled⁵¹, even in the presence of the dominant Q allele. The suppression of the free-threshing character

is caused by a partially dominant *Tg* allele, on chromosome 2D of *Ae. tauschii*; *Tg* inhibits Q and leads to tenacious glumes. The conclusion is that free-threshing hexaploids have the genotype *tggtg,QQ*, whereas all tested *Ae. tauschii* lines have the dominant *Tg* allele. Later, Villareal *et al.*⁵² found that, in synthetic hexaploids, two genes (rather than *Tg* alone) affect glume tenacity, both of which are contributed by the D genome.

Rachis fragility and square-headed ears in free-threshing hexaploid wheats can assort independently. For instance, in experimental crosses with *T. spelta*, three genes segregate for rachis fragility, but only one, *q*, for tenacious glumes⁵³. Moreover, *q* and Q interact with genes on other chromosomes that also govern glume tenacity and rachis fragility⁵⁴. A further gene, located at 32 cM from *Tg*, on chromosome 2D, belongs to the system⁵⁵. When the free-threshing habit was studied in a *T. durum* × *T. dicoccoides* cross, the F₂ population showed a continuous distribution for the trait⁵⁶. F₃ lines were fingerprinted and four major quantitative trait loci (QTL) (2BS, 5AL, 5AS and 6AS; where S stands for short arm and L for long arm) were located on three chromosomes. The 2BS and 5AL QTL correspond, respectively, to the homoeologous genes *Tg* and Q of hexaploid wheats, whereby the *Tg*-like gene *Tg2* is located on chromosome 2B. So, the polygenic control of the free-threshing character in tetraploid wheats is based on the selection on new loci in addition to Q and *Tg*.

The findings summarized above reveal four important points. First, several genes contribute to the free-threshing phenotype. Second, some of these genes control both glume strength and rachis fragility, which indicates that the selection of a free-threshing ear improves the strength of its rachis. Third, alleles of these genes are frequently semi-dominant⁴⁸, and semi-dominance extends the selection for free-threshing to heterozygous phenotypes. Fourth, Q-like alleles shorten the ear, which contributes to the visibility of a mutant phenotype.

Model for the origin of free-threshing wheats. The origin of free-threshing wheats is still not completely resolved, but a good working model is presented in FIG. 4. The emergence of free-threshing tetraploids from wild emmer is straightforward (routes 1 and 2): mutant alleles of at least four loci with additive effects had to be combined⁵⁶. Some of these alleles might have already been present in the intermediate, *T. dicoccum*, populations. Next, the emergence of the hexaploid *T. spelta* might have followed route 3 (FIG. 4). Although *T. spelta* is genetically *TgTgqq*, it has additional alleles that favour hulled seeds and rachis fragility on chromosomes 2, 3, 5 and 6 (TABLE 1). In this sense, *T. spelta* is genetically buffered against the evolution of the free-threshing habit (that is, routes 3 and 5 of FIG. 4 have a lower probability than route 4 for the origin of the free-threshing hexaploid *T. vulgare*). A problem with route 4 is that hexaploid wheats would have at least two independent origins, one leading to hulled (spelt) and the second to the free-threshing form (bread wheat). Is this compatible with genetic and archaeobotanical evidence? Recent

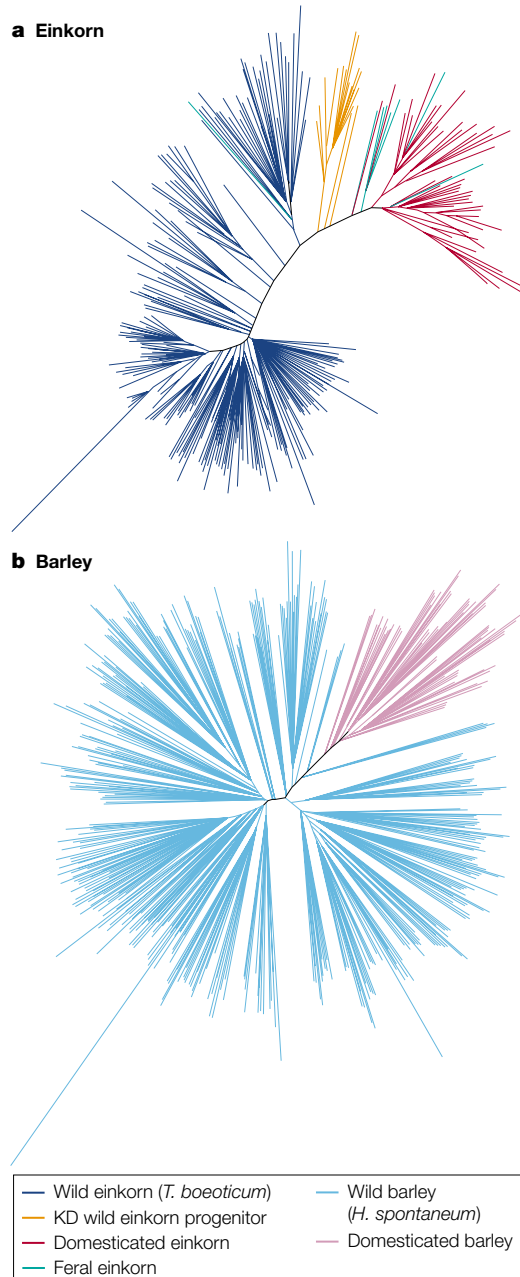


Figure 2 | **Phylogenetic trees showing a single origin for domesticated varieties of einkorn and barley.** The trees are based on amplified-fragment length polymorphism (AFLP) data from **a** | 288 loci and 388 accessions for einkorn (*Triticum monococcum*)¹¹ and **b** | 400 loci and 374 accessions for barley (*Hordeum vulgare*)¹². KD, Karacadag region.

results indicate that *Ae. tauschii* provided more than one allele at several loci of hexaploid wheats, as if the D genome had participated more than once in their evolution^{31,57–61}. Moreover, European spelts are molecularly distinct from Iranian spelts, in fact, so distinct as to indicate that they might have independent origins⁵⁸.

Zohary and Hopf⁵ suggested a Caspian origin of hulled hexaploid wheat, followed by an early emergence of free-threshing forms, which corresponds to routes 3 and 5 in FIG. 4. However, Nesbitt⁶², and Nesbitt and Samuel⁸, have pointed out problems with that model. The first of these problems is the questionable nature of hulled archaeobotanical remains in Transcaucasia that were cited as evidence for the spreading of *T. spelta* along the northern shore of the Black Sea to Central Europe. Here, spelt is archaeologically abundant. The problem is that spelt remains are absent in the ancient Near East sites⁶³. A second problem is the presence of internodes (BOX 5) from free-threshing hexaploids, which date from 9,700–8,600 cal BP (REF. 64), at Can Hasan III (REF. 65) and Çafar Höyük²⁰, in the absence of local spelt remains. Furthermore, already at Abu Hureyra I, rare rachis fragments and seeds of free-threshing hexaploids have been reported^{23,24}.

So, it is possible that the free-threshing trait in hexaploids was directly inherited from free-threshing tetraploids (route 4 in FIG. 4), which is compatible with the genetic evidence for an early emergence of free-threshing tetraploids. Naked seeds of domesticated tetraploids⁶⁴ are present from 10,000 cal BP in Damascus basin sites⁶⁶. Feldman⁶⁷ refers to Kislev's³⁴ *T. parvicoccum* as a candidate for those remains, but

this is questionable⁶². Route 4 requires the assumption that *Ae. tauschii* was more widespread in the Neolithic period than it is now. Feldman⁶⁷ suggested that *Ae. tauschii* penetrated fields of domesticated tetraploids as a weed. If this were the case, then European spelt would be the outcome of a later hybridization event⁴⁵. The idea that European spelt arose through introgression of a non-free-threshing emmer into stands of *T. vulgare*⁴⁵ is shown in route 6 of FIG. 4. From molecular evidence, European emmer (*T. dicoccum*) is, in fact, closely related to European spelts⁵⁸.

Although the precise details that surround the hexaploids are as yet unresolved, it is clear that once included in the agricultural package, free-threshing wheats followed a Mediterranean route to Europe. Around 8,000 cal BP, tetraploid forms were well represented in Mediterranean sites and in ~6,000 cal BP, free-threshing wheats were growing on the Northern foothills of the Alps⁶⁴.

Rye: *Secale cereale*

Less is known about rye domestication than about the other cereals. Rye did not become part of the collection of seeds that fuelled the agricultural revolution — possibly because of an inferior baking quality — and has received little attention in the literature on the origin of agriculture. However, on the basis of the excavation report of the Abu Hureyra site², rye can now be considered one of the founder agricultural crops in the Near East. Domesticated rye (*Secale cereale*) has large seeds and is non-shattering; in contrast to other early cereals, it is also self-incompatible, and the species includes other subspecies, such as *S. vavilovii* and two non-shattering weeds^{5,68}.

Several features implicate *S. vavilovii*, which, unlike domesticated varieties, is debated to have been an outbreeder, as the wild progenitor of rye^{5,23,69}. These include narrow kernels with brittle glumes, its presence in primary habitats and the fact that it is fully interfertile in crosses with *S. cereale*⁷⁰. Dense stands of the annual wild plant still exist on Mount Ararat (Turkey)⁷⁰ and on the Karacadag slopes⁷¹. Hillman²³ proposes that the wild species might have been present near Abu Hureyra during the Neolithic period, where it was collected together with other wild cereals, including *Secale montanum*. *S. montanum* is related to *S. cereale*, with which it crosses spontaneously⁵, but is distinguished by two chromosomal translocations. Experimental crosses between wild and cultivated forms have indicated that rachis brittleness is under the control of a single gene⁷².

Wild rye was reported to have been cultivated in the Epi-Palaeolithic (12,000 cal BP), 700 years after the establishment of Abu Hureyra²³. Interestingly, this dating is 1,000 years earlier than previously accepted for the beginning of intentional plant cultivation³. Hillman²³ believes that wild rye was cultivated before its domestication, based particularly on the finding at Abu Hureyra I of layered remains of weed flora, which is indicative of cultivated fields. Weeds and other plants rapidly colonize soil that has been disturbed by humans, and they occur at sites where agriculture was practised. In addition,

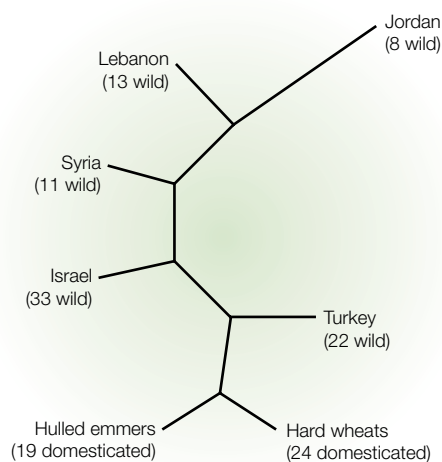


Figure 3 | Genetic similarities of cultivated tetraploid wheats (hulled emmer and hard wheat) to wild emmer populations from different regions. Amplified-fragment length polymorphism (AFLP) allele frequencies were calculated between lines of wheat from the geographical regions indicated. The tree shows that hard and hulled (domesticated) emmers each have a single origin and are more closely related to wild emmer progenitors in Turkey than those of other regions tested. All ten trees that were constructed gave the same topology as that shown here (H.O., A.B., R.S.-P. and F.S., unpublished data).

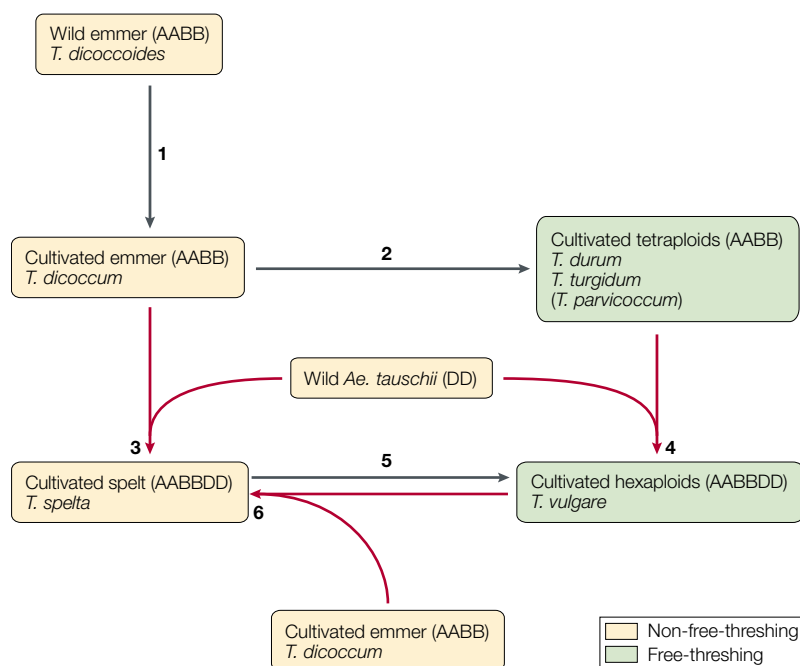


Figure 4 | **Models for the evolution of polyploid wheats under cultivation and domestication.** The red arrows indicate hybridization events; the black arrows show domestication events (see text for details). *Ae.*, *Aegilops*; *T.*, *Triticum*.

AWN

A bristle-like appendage that is seen on the glumes of many grasses.

SEED DORMANCY

A physiological condition of a viable seed that prevents germination, even in the presence of otherwise favourable germination conditions (for example, heat or moisture).

LANDRACE

A locally adapted strain of a species that is selected and adapted by farmers.

ACCESSION

A sample of plant material that is collected at a specific location and maintained in a seed bank.

HAPLOTYPE

An experimentally determined profile of genetic markers that is present on a single chromosome of any given individual.

GERMPLASM

The term used by breeders to refer to the collection of varieties and breeding lines.

INTROGRESSION

A process of recurrent backcrossing that leads to the incorporation of genes from one species into the gene pool of another.

Van Zeist and Casparie⁷³ have isolated wild rye seed remains from Murehibit (FIG. 1) that date from this earlier time (~11,500 cal BP). Domesticated rye appears at Abu Hureyra I and continues into Abu Hureyra II (10,400 cal BP)²⁴. Domesticated seeds reappear at only Can Hasan III, in South Anatolia⁶⁵, but disappear at other contemporary Near East sites. In the Bronze Age, rye is reported at Alaça Höyük, in Anatolia⁶⁵. Rye reached Europe probably through a northern route, and remains are present at sites dated to the Neolithic (Polish and Romanian cultures ~6,500 cal BP) and to the Bronze and Iron Ages. Today, rye is used for human food and in animal feed production.

Barley: *Hordeum vulgare*

Domesticated barley is a selfing diploid and evolved from the wild progenitor *Hordeum spontaneum*⁷⁴. Compared with domesticated barley, the wild form has narrower leaves, slightly smaller seeds, long stems and awns⁷⁵ and, when harvested before full maturity, can have a semi-brittle rachis (it is otherwise brittle)^{76,77}. In contrast to other cereals, the glumes of barley are fused to the seed, but a few domesticated varieties exist that have naked seeds due to the presence on chromosome 1 of a recessive allele of the gene *Naked caryopsis* (*N*)⁷⁸. The main differences between wild and domesticated barley are the acquisition of a non-brittle rachis, increased seed weight, and the appearance of six-rowed ears and naked seed varieties in the domesticated form. The six-rowed plants (BOX 2) have a recessive allele of the gene *V* (*Kernel rows*) and a dominant allele of the gene *Lateral floret fertility* (*L*)⁷⁹. Two tightly linked genes control brittleness of the rachis, but doubly recessive (*bt1*,

bt2), non-brittle rachis genotypes have never been isolated⁸⁰. SEED DORMANCY is a positive factor that secures the persistence of wild lines in nature⁸¹, and decreased seed dormancy has been selected during domestication. Domesticated varieties differ by the presence of alternative alleles at several QTL for this trait⁸².

The wild *H. spontaneum* colonizes primary habitats of the Fertile Crescent from Israel and Jordan to south Turkey, Iraqi Kurdistan and southwestern Iran. It behaves as a weed and colonizes secondary habitats in the Aegean region, as well as in Iran and central Asia¹⁴. This finding, in several geographically distinct locations of wild barley, has supported the view that barley had several centres of domestication^{83–85}. However, the once popular idea of a domestication centre in the Himalayas has to be excluded because the local Himalayan wild form (*H. agriocrithon*) was found to be a hybrid between wild and domesticated types^{86,87}.

The existence of two genes that control rachis brittleness has often been taken as evidence that barley was domesticated at least twice⁸⁰. However, AFLP data from 400 polymorphic loci studied in 317 wild and 57 diverse cultivated lines clearly indicate a single origin for all modern varieties and LANDRACES, including those from suspected secondary centres of domestication¹² (FIG. 2b). Data from chloroplast DNA^{88,89} are also consistent with a single domestication event. Unlike emmer and einkorn, which are believed to have originated in the Karacadag region, domesticated barley probably arose in the Israel–Jordan area: Badr *et al.*¹² showed that wild barley populations from this region are genetically more similar to domesticated forms than are ACCESSIONS from other regions. This conclusion is supported by genetic data: three major HAPLOTYPES for the gene *Barley knotted-like-3* (*Bkn-3*) were exploited to follow the flow of GERMPLASM from wild to domesticated lines of barley (FIG. 5b). This study showed that haplotype I is extremely rare in wild populations¹² but, when present, it is almost exclusively restricted to the wild populations of Israel. This haplotype I is pervasive in domesticated western germplasm (84%); domesticated barley subsequently migrated eastwards from the Fertile Crescent towards the Himalayas, during which process haplotype III replaced haplotype I. Indeed, haplotype III is most prevalent in the Himalayas and in most Asian wild forms (67%).

In terms of the distribution of barley, two-rowed, brittle-rachis forms of the wild *H. spontaneum* were found in the Fertile Crescent at Ohalo II, an early Epi-Palaeolithic site (18,000 uncalibrated BP)⁹⁰. In addition, wild barley is most abundant at Netiv Hagdud (~10,700 cal BP)⁹¹. In the Fertile Crescent, non-brittle barley remains are dated from ~10,500 cal BP onwards⁵. Naked barley seeds are the most abundant remains at Mehrgarh, in Pakistan (~7,400 BP), the oldest known agricultural settlement of the Indian subcontinent⁹², and similar varieties are still widely cultivated in the Himalayas. This central Asian *H. vulgare* is distinct from western germplasm, possibly owing to the INTROGRESSION by Asian *H. spontaneum* plants¹². The route followed by cultivated barley during its Himalayan diversification is summarized in FIG. 5b.

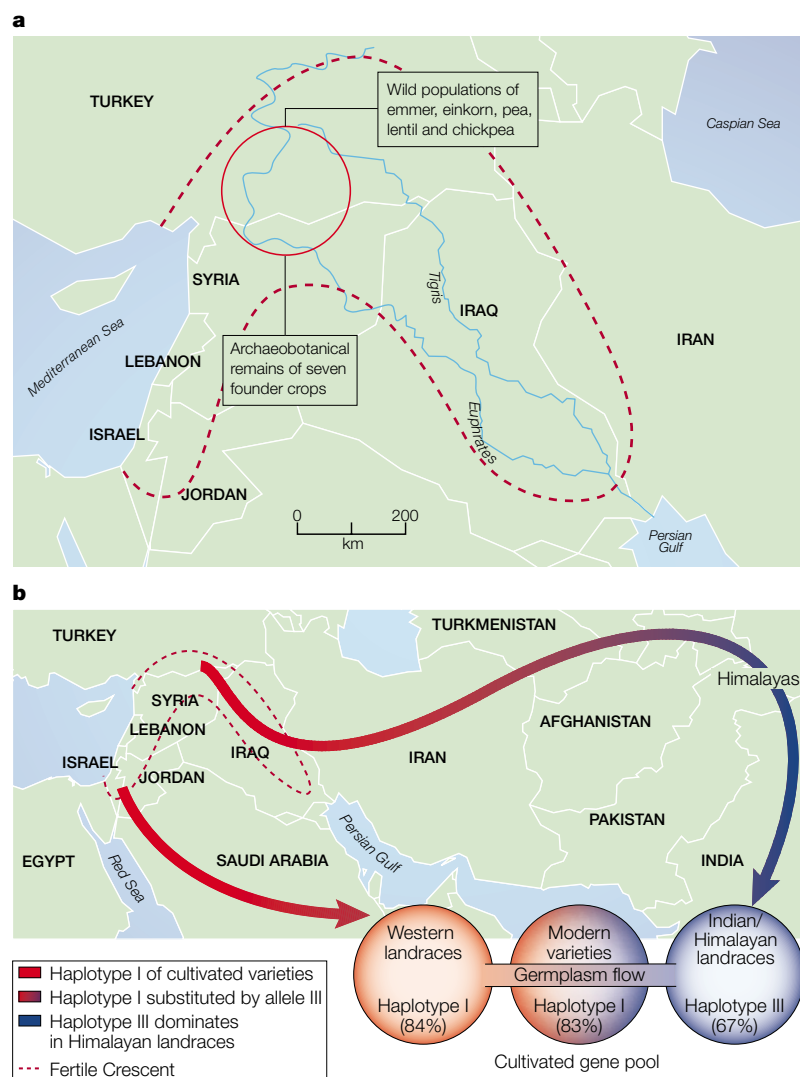


Figure 5 | Geography of early domestication and of later events during crop differentiation. **a** | The map summarizes the two kinds of data (phylogeographical and archaeological) that support the existence in the Fertile Crescent (dashed red line) of a ‘core area’ of domestication (red circle) (see also Lev-Yadun *et al.*²⁵). **b** | This panel summarizes the experiment of Badr *et al.*¹², which shows that, from its domestication in the western Fertile Crescent, barley moved eastwards and diversified in the Himalayas. This last route was monitored by following the flow of haplotypes of the *Barley knotted-like-3* (*Bkn-3*) gene from wild *Hordeum spontaneum* populations to cultivated germplasm. Haplotype I is pervasive in domesticated western varieties (present in 84% of varieties; lower red arrow), whereas haplotype III prevails in the Himalayan and Asian forms (present in 67% of varieties; upper arrow). The borders of the primary habitats of *H. spontaneum* are in the Fertile Crescent (dashed red line).

Whence agriculture?

Numerous factors, individually or in concert, could have provided the decisive impetus that sparked the transition from foraging to farming⁹³. Regardless of its cause, the precise window of time in which plant domestication occurred remains a question that archaeobotany has only in part answered⁹⁴. The archaeological record indicates that the origin of agriculture might have been a rapid process, possibly encompassing only the few hundred years that were needed to **FIX** relevant alleles of key genes and of their modifiers. How could these genes have been selected?

Before considering the models for how domestication could have occurred, it is necessary to return to the subtle but important distinction between cultivation (planting and harvesting seed for use) and domestication (altering the phenotype of a plant). Several scholars believe that plant domestication was a conscious and rapid process (discussed in REF 95); that is, humans selected and planted new phenotypes. According to this view, domestication coincided with the beginning of cultivation, and it was only when domestication was completed that cultivation became efficient. For diploid cereals, this view is compatible with the genetics of the simple morphological traits in which wild and domesticated forms differ; for example, naked seed in barley or rachis brittleness in rye. The alleles for these traits could easily have been exploited as soon as they appeared in the population. But for cases such as the *soft glume* allele — which supports free threshing in the diploid einkorn — negative pleiotropic effects might have prevented the successful cultivation of free-threshing varieties. In other words, a mutation at a single gene in a diploid might cause too extreme a phenotype to allow a fruitful use in domestication.

The most severe shortfall of the proposal that early farmers consciously selected plants with specific phenotypes is that it does not take into account the genetic basis of seed weight and (perhaps) seed dormancy. Whichever type of selection is adopted⁹⁶, repeated cycles of sowing and harvesting are an absolute necessity. These two domestication traits are polygenic not only in crosses in domesticated cereals, but also in the few examples of progeny from crosses between wild and domesticated forms that have been studied. By contrast, unconscious selection during a long phase of wild-plant cultivation can easily account for the origin of traits with polygenic inheritance. As its basic tenet, unintentional selection posits that the selection of alleles that confer domesticated properties is a by-product of the cultivation of wild plants. For example, it has been proposed⁹⁷ that domesticated emmer was the result of repeatedly harvesting brittle ears that disarticulate into a basket during harvest, while leaving mutant ears with tough rachis standing in the field. Such a protracted enrichment of alleles is also compatible with the domestication genetics of polyploid wheats.

There is also evidence that cultivation greatly preceded domestication during the origin of agriculture: the remains at Abu Hureyra reveal that wild rye was cultivated for a long time before it was domesticated². The excavation of this site also provides a link between archaeobotanical data and the Younger Dryas episode that started 500 years after the founding of the village (12,700 cal BP). The onset of a cool, dry climate might simply have forced the community to cultivate wild plants owing to their disappearance in nearby primary habitats^{4,5,23,98}. According to Hillman’s interpretation of the archaeological remains at this site²³, the adoption of domesticated plants and animals at Abu Hureyra was a gradual, step-by-step process. The semi-dominance of alleles of key genes that produced favoured domestication traits and the visibility of emerging phenotypes might

FIXATION
Increase in allele frequency to the point at which all individuals in a population are homozygous.

have positively reinforced domestication. Furthermore, a sedentary society with large settlements, such as Abu Hureyra I, Hallan Çemi Tepesi or Murehbit I (REF. 3) would have supported successful domestication.

If protracted cultivation before domestication should turn out to be the rule for other sites, how should we accommodate findings that indicate a founder effect for crop domestication in the Near East^{26,75,99?} Zohary's argument for a single origin for each Near East founder crop is strongly borne out by the genetic data summarized in this review. The apparently contrasting observations of the multi-regional cultivation of wild species versus the restricted regionality of crop domestication can be reconciled: in such a model, superior varieties of founder crops emerged in a core area and then moved throughout the region, displacing local genotypes.

Southeast Turkey was pivotal to the domestication of early einkorn^{11,100} and emmer³⁹ (H.O., A.B., R.S.-P. and F.S., unpublished data) (FIG. 3). Lev-Yadun *et al.*²⁵ have narrowed the area even further, suggesting that the region around Karacadag was in fact the core area

for plant domestication (FIG. 5a). In a more recent paper, the same authors³ cite circumstantial but convincing evidence in favour of a 'Turkish core' of plant domestication that started ~12,000 cal BP. An exception to the idea that all domesticated genotypes should trace to the same core region is the case of barley. As we have discussed, the genetic evidence assigns the origin of domesticated barley to Israel-Jordan¹². One possible way to reconcile such findings is that, in the early settlements of the western Fertile Crescent, wild barley was traditionally harvested more extensively than wheat^{8,101,102}. So, barley might have been domesticated in the Jordan valley with a technology invented in the core area. We will probably never know exactly who invented agriculture, but whoever they were, they solved an immediate local need and shaped the planet forever.

Update — added in proof

The unpublished study cited on p.433, p.440 and in FIG. 3 is now in the press and appears in the reference list as REF. 121.

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