Genome Plasticity a Key Factor in the Success of Polyploid Wheat Under Domestication

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Wheat was domesticated about 10,000 years ago and has since spread worldwide to become one of the major crops. Its adaptability to diverse environments and end uses is surprising given the diversity bottlenecks expected from recent domestication and polyploid speciation events. Wheat compensates for these bottlenecks by capturing part of the genetic diversity of its progenitors and by generating new diversity at a relatively fast pace. Frequent gene deletions and disruptions generated by a fast replacement rate of repetitive sequences are buffered by the polyploid nature of wheat, resulting in subtle dosage effects on which selection can operate.

Wheat Domestication

The transition from hunting and gathering to agrarian lifestyles in western Asia was a threshold in the evolution of human societies. Domestication of three cereals—einkorn, emmer, and barley—marked the beginning of that process (6). Genetic relationships between wild and domesticated einkorn and emmer suggest that the region west of Diyarbakir in southeastern Turkey is the most likely site of their domestication (Fig. 2) (7–9). From this area, the expansion of agriculture lead to the dissemination of domesticated einkorn (T. monococcum, genomes AAABB) and domesticated emmer [T. turgidum subspecies (ssp.) dicoccon, genomes BBAA] across Asia, Europe, and Africa. Southwestern expansion of domesticated emmer cultivation resulted in sympatry with the southern subpopulation of wild einkorn (T. turgidum ssp. dicocoides, genomes BBAA). Gene expression changes between the northern domesticated emmer and the southern wild einkorn populations or emmer domesticated in the southern region resulted in the formation of a center of domesticated emmer diversity in southern Levant (Fig. 2) (9). The consequence was a subdivision of domesticated emmer into northern and southern subpopulations with an increase in gene diversity in the latter (9). Northeast expansion of domesticated emmer cultivation resulted in sympatry with Aegilops tauschii (genomes DD) and the emergence of hexaploid common wheat (T. aestivum, genomes AABBDD) (10) within the corridor stretching from Armenia to the southwestern coastal area of the Caspian Sea (11) (Fig. 2).

The genetic changes responsible for the suite of traits that differentiate domesticated plants from their wild ancestors are referred to as the domestication syndrome (12). In wheat, as in other cereals, a primary component of this syndrome was the loss of spike shattering, preventing the grains from scattering by wind and facilitating harvesting (Fig. 1). Abscission scars of einkorn remains from archeological sites in northern Syria and southeastern Turkey revealed a gradual increase in nonshattering einkorn spikes from 9250 to 6500 years before the present (BP), a discovery interpreted as evidence of a prolonged domestication period of cereals (13). The chromosome locations of the genes controlling shattering in einkorn are unknown, but in emmer wheat shattering is determined by the Br (brittle rachis) loci on chromosomes 3A and 3B (14) (Fig. 1).

Another important trait for wheat domestication was the loss of tough glumes, converting hulled wheat into free-threshing wheat (Fig. 1). The primary genetic determinants of the free-threshing habit are recessive mutations at the Tg (tenacious glume) loci (15), accompanied by modifying effects of the dominant mutation at the Q locus and mutations at several other loci (15). The recent cloning of Q, which also controls the square spike phenotype in common wheat, showed that it encodes an AP2-like transcription factor. The
mutation that gave rise to the $Q$ allele is the same in tetraploid and hexaploid free-threshing wheats, suggesting that it occurred only once (16).

Seeds of free-threshing wheat began to appear in archaeological sites about 8500 years BP (2, 17). The tetraploid forms of these Neolithic free-threshing wheats may be the ancestor of the modern large-seeded, free-threshing durum (Fig. 1), which is genetically most closely related to the Mediterranean and Ethiopian subpopulations of domesticated emmer (Fig. 2) (9). The first archaeological records of durum appeared in Egypt during the Greco-Roman times [reviewed in (2)].

Other traits of the wheat domestication syndrome shared by all domesticated wheats are increased seed size (Fig. 1, A and B), reduced number of tillers, more erect growth, and reduced seed dormancy. One gene affecting seed size is GPC-B1, an early regulator of senescence with pleiotropic effects on grain nutrient content (18). In some genotypes and environments, the accelerated grain maturity conferred by the functional GPC-B1 allele is associated with smaller seeds (19). Therefore, indirect selection for large seeds may explain the fixation of the nonfunctional GPC-B1 allele in both durum and T. aestivum (18). Except for $Q$ and GPC-B1, no other genes relevant to the wheat domestication syndrome have been isolated so far, and a systematic effort to do so is long overdue. Not only is this knowledge critical for understanding the genetic and molecular mechanisms of domestication, it is also possible that genetic variation at these same loci plays an important role in the success of wheat as a modern crop.

**Success of Wheat as a Crop**

Domesticated wheat exemplifies the positive correlation between ploidy and success as a crop. In almost all areas where domesticated einkorn and domesticated emmer were cultivated together, it was domesticated emmer that became the primary cereal (2). Emmer remained the most important crop in the Fertile Crescent until the early Bronze Age, when it was replaced by free-threshing wheat (2). Although a free-threshing form of einkorn has been identified, it is not widely cultivated because of the association between soft glumes and reduced ear length in this diploid species (17).

The story repeated itself, with hexaploid T. aestivum expanding further than durum. Today, hexaploid T. aestivum accounts for most of the global wheat crop and is grown from Norway and Russia at 65°N to Argentina at 45°S (Fig. 2) (20). However, in tropical and subtropical regions wheat is restricted to higher elevations. Although the dominance of tetraploid wheat over diploid wheat potentially could be attributed to the greater robustness of tetraploid wheat, this does not explain the dominance of T. aestivum over durum. Durum often has larger seeds than hexaploid wheat (Fig. 1, C and D) and similar yield potential as that of hexaploid wheat under optimum growth conditions (table S1).

The vast majority of polyploid plants, including wheat, originated by hybridization between different species (allopolyploid). Allopolyploidy results in the convergence in a single organism of genomes previously adapted to different environments, thus creating the potential for the adaptation of the new allopolyploid species to a wider range of environmental conditions. This has clearly been the case for hexaploid wheat, which combines the D genome from Ae. tauschii with the AB genomes from tetraploid wheat. Compared with tetraploid wheat, hexaploid T. aestivum has broader adaptability to different photoperiod and ver- nalization requirements; improved tolerance to salt, low pH, aluminum, and frost; better resistance to several pests and diseases; and extended potential to make different food products (table S2).

This does not mean, however, that gene expression in an allopolyploid is the summation of gene expression in its diploid ancestors. Nonadditive gene expression has been reported in numerous artificial allopolyploids [reviewed in (4, 21)]. Rapid and stochastic processes of differential gene expression (22) provide an additional source of genetic variation that could be important for the successful adaptation of new allopolyploids.

There are detrimental aspects to polyploidy as well. Polyploid speciation is accompanied by a polyploidy bottleneck (5), in which the small number of plants contributing to the formation of a new polyploid species constrains its initial gene diversity. Because only a few Ae. tauschii genotypes participated in the origin of T. aestivum (23, 24), its D-genome diversity is expected to be limited.

Recent advances in the understanding of the dynamics of gene diversity during domestication and the subsequent evolution of polyploid wheat are reviewed in the following sections to reconcile these opposing effects of polyploidy and to shed light on the mechanisms by which T. aestivum has come to be one of humankind’s most important crops (Fig. 2).

**The Capture of Preexisting Diversity**

Domestication is accompanied by domestication bottlenecks, resulting in reduced gene diversity [reviewed by (25)]. A study using 131 restriction fragment length polymorphism (RFLP) loci showed that gene diversity values in cultivated emmer were 58% of those observed in wild emmer across its entire geographic distribution (9). A similar estimate (51%) was obtained for nucleotide diversity (26). For comparison, nucleotide gene diversity values in domesticated maize and pearl millet are 57% (27) and 67% (28), respectively, of those present in their wild progenitors. That self-pollinating emmer has an approximately equivalent proportion of the genetic diversity of its wild ancestor as do cross-pollinating maize and pearl millet is surprising. Several lines of evidence indicate that gene flow between wild and domesticated

![Image](https://www.sciencemag.org/content/sci/316/5826/1863/F2.large.jpg)
emmer occurred in all places where the two were sympatric (9). Additionally, if the emmer domestication process took as long as that of einkorn domestication (13), even a slow rate of gene flow would probably be sufficient for domesticated emmer to capture a significant proportion of the genetic diversity of its wild relative.

Additional diversity bottlenecks occurred during the transition from hulled to free-threshing wheat (Fig. 1) and during the polyploid speciation of T. aestivum. A study based on 27 RFLP loci showed that diversity values in T. aestivum D genome are less than 15% of those present in populations of Ae. tauschii from Transcaucasia, reflecting the severity of the initial polyploid bottleneck (11). A similar estimate (7%) was obtained for nucleotide diversity (26). However, in the A and B genomes of T. aestivum, the average diversity at the nucleotide level was found to be 30% of that present in wild emmer (26, 29). This result suggests that difference in ploidy has presented only a weak barrier to gene flow from tetraploid wheat, including wild emmer, to hexaploid wheat (30), a result also supported by the discovery of hybrid swarms between wild emmer and common wheat (31). In summary, hexaploid wheat captured a larger portion of the natural gene diversity present in its tetraploid ancestor than of the diversity present in Ae. tauschii.

The proportion of diversity captured by T. aestivum from both ancestors is likely to increase in the future, because modern wheat breeders, realizing the importance of expanding diversity for successful crop improvement, are starting to use synthetic wheats in their breeding programs (32). Synthetic wheats are produced by hybridizing different tetraploid wheats and Ae. tauschii genotypes and then inducing doubling of the genomes through colchicine treatment (32).

New Sources of Diversity

None of the plant genes that contributed to the domestication of diploid and ancient polyploid species (e.g., maize) discovered so far are null alleles (33), consistent with the view that domestication was achieved mostly through “tinkering” rather than “disassembling” or “crippling” key genes from wild relatives (33). In a young polyploid species like wheat, however, null mutations of one of the duplicate or triplicate homologous gene copies may have only subtle dosage effects and thus may appear as “tinkering” mutations with a potential to generate adaptive variation.

A null mutation of the GPC-B1 gene in the B genome of polyploid wheat illustrates this point. In tetraploid wheat, the GPC-B1 mutation caused a few days’ difference in maturity; whereas in diploid rice RNA interference (RNAi) of the rice GPC gene brings about almost complete seed sterility [Supporting Online Material (SOM) text]. Mutations in one of the three functional copies of a gene in hexaploid wheat are expected to have more subtle effects than in tetraploid wheat. This fact is illustrated by the higher tolerance to induced mutations of hexaploid wheat compared with tetraploid wheat (34). The fact that most of the 21 T. aestivum chromosomes can be removed to produce nullisomic plants exhibiting only minor phenotypic effects leaves no doubt of the buffering effect of polyploidy on gene deletions. This buffering effect is eroded in ancient polyploid species (SOM text).

The abundance of repetitive elements in the wheat genomes (about 83% repetitive) (35) greatly facilitates the generation of null mutations, either by insertion of repetitive elements into genes (36) or by gene deletions (37, 38). As in maize, genes in wheat are embedded within long stretches of nested retroelements and other mobile sequences (Fig. 3). Studies of microsynteny among orthologous chromosomal regions across the tribe Triticeae showed that the intergenic space is subject to an exceedingly high rate of turnover (39). For example, 69% of the intergenic space within orthologous VRN2 regions from T. monococcum and the A genome of tetraploid wheat (Fig. 3) has been replaced over the course of the past 1.1 million years (My) (SOM text).

These data, along with a comparison of orthologous regions in T. urartu and the A genome of tetraploid wheat (30), yield an average replacement of 62% ± 3% (SEM) of the intergenic regions during the first million years of divergence (Fig. 4 and SOM text). The model in Fig. 4 predicts correctly the very proportion of sequence
conservation observed among orthologous intergenic regions in the A, B, and D genomes of wheat (30, 40) and the complete divergence observed in comparisons of orthologous regions between wheat and barley (41, 42) (Fig. 4). To put the magnitude of this rate into perspective, inbred polyploids from both chinampaza and human genomes (6- to 7-My divergence time) equal less than 4% of the intergenic regions from these genomes (43, 44).

Studies documenting the impact of this remarkably high rate of DNA replacement on wheat genes are starting to accumulate. Insertions of repetitive elements within regulatory regions of the wheat VRN1 and VRN3 vernalization genes, as well as four large independent deletions within the VRN1 first intron, have been associated with the elimination of the vernalization requirement (45–48). A deletion upstream of the PPD-D1 photoperiod gene is associated with the widely distributed photoperiod insensitive allele (49). Such diversity in genes regulating flowering time is particularly relevant because of its large impact on wheat adaptability to different environments. Deletions have also provided increased diversity in wheat products. Puroindoline A and B gene deletions, which have become fixed in the A and B genomes, are responsible for the hard grain texture of pasta wheat. A polymorphism for a Puroindoline A deletion (or for a point mutation in Puroindoline B) in the hexaploid wheat D genome dramatically affects grain hardness, dividing wheat cultivars into those used for bread (hard texture) and those used for cookies and pastries (soft texture) (50). The Puroindoline genes code for proteins located in the surface of the starch grains that facilitate the separation of intact starch grains during milling (50).

The example in Fig. 3 shows two genes affected by deletions within a small genomic region, providing an additional example of the high frequency of gene deletions. Such deletions are fixed in polyploid wheat with an initial rate of 1.8 × 10⁻² locus⁻¹ My⁻¹, 10 times faster than the rate in wheat’s diploid ancestors (51). However, most deletions are still polymorphic and represent, together with point mutations, an important component of genetic diversity in polyploid wheat (52).

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Domesticated Nature: Shaping Landscapes and Ecosystems for Human Welfare

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Like all species, humans have exercised their impulse to perpetuate and propagate themselves. In doing so, we have domesticated landscapes and ecosystems in ways that enhance our food supplies, reduce exposure to predators and natural dangers, and promote commerce. On average, the net benefits to humankind of domesticated nature have been positive. We have, of course, made mistakes, causing unforeseen changes in ecosystem attributes, while leaving few, if any, truly wild places on Earth. Going into the future, scientists can help humanity to domesticate nature more wisely by quantifying the tradeoffs among ecosystem services, such as how increasing the provision of one service may decrease ecosystem resilience and the provision of other services.

Domestication of plants and animals may be the single most important feature of the human domination of our planet. Domestication involves the selection of traits that fundamentally alter wild species to become more useful to us. For example, wheat has been selected for larger and more seeds per plant, hatchery-raised trout are selected for rapid growth, and dogs have been selected for an ability to live and even communicate with humans (1).

Humans did not, however, stop with simply domesticating a few chosen species; we have domesticated vast landscapes and entire ecosystems. Moreover, just as domesticated plants and animals have predictable and repeatable traits among different species, domesticated ecosystems also reveal common traits. In particular, when humans tame nature they seek enhanced productivity, convenient commerce, and protection from predators and storms. However, along with domestication, there is often concurrent and inadvertent selection for maladaptive features in either species or ecosystems. For example, selecting for rapid growth in crop plants may result in plants with reduced investment in structural and chemical defenses (2). Similarly, hatchery trout that are selected for rapid growth often have smaller brains (3). Whereas plant and animal breeders are well aware that domestication involves tradeoffs in vigor, the notion of tradeoffs resulting from the domestication of entire landscapes has only recently received serious scientific attention.

Domestication has often been framed as the science aimed at protecting nature, and especially protecting nature from people. We restate here what others have already emphasized: There really is no such thing as nature untainted by people (4). Instead, ours is a world of nature domesticated, albeit to varying degrees, from national parks to high-rise megalopolises. Facing this reality should change the scientific focus of environmental science. Instead of recounting doom-and-gloom statistics, it would be more fruitful to consider the domestication of nature as the selection of certain desirable ecosystem attributes, such as increased food production, with consequent alteration to other ecosystem attributes that may not be desirable. Under this paradigm, our challenge is to understand and thoughtfully manage the tradeoffs among ecosystem services that result from the inescapable domestication of nature.

The Global Footprint of Humans

Domesticated nature in its simplest form means nature exploited and controlled. To that end, roughly 50% of the world’s surface area has been converted to grazed land or cultivated crops (5). More than half of the world’s forests have been lost in that land conversion (5). The whole notion of a “virgin rainforest” may be erroneous, with extensive prehistoric human activity evident in what were once thought to be untouched forests in the Amazon and Congo (6). In addition to clearing land for agriculture, humans target wild species for harvest or elimination. On every continent, humans have eliminated the largest mammals, leaving behind a fauna of smaller species (7).

Nature can be dangerous. To protect themselves and their domesticated animals, humans have been especially quick to kill predators, driving almost every large terrestrial carnivore in the world to near extinction (8). To protect property and lives, humans suppress wildfires (9). To reduce storm surges, humans fortify marine shorelines with jetties and sea walls. In Europe alone, 22,000 km2 of the coastline are artificially covered with concrete or asphalt, and where the coasts are severely retreating or eroding, over half are artificially stabilized by jetties or other structures (10). To control rivers for irrigation, hydropower, and flood mitigation, humans have built so many dams that nearly six times as much water is held in storage as occurs in free-flowing rivers (5).

Humans have so tamed nature that few locations in the world remain without human influence. Global maps of human impact indicate that, as of 1995, only 17% of the world’s land area had escaped direct influence by humans (4), as indicated by one of the following: human population density greater than one person/km2; agricultural land use; towns or cities; access within 15 km of a road, river, or coastline; or nighttime light detectable by satellite (Fig. 1). The huge magnitude of human impacts is recent, but the presence of impacts such as purposeful wildfires goes back thousands of years (9). The reality of the human footprint renders discussions about what areas of the world to set aside as wild and protected areas as somewhat irrelevant; more germane is a discussion of what tradeoffs we are willing to accept as a result of the domestication of nature.

The Tradeoffs of Domestication

There is no question that humans have been successful in their efforts to avoid predators, produce food, and create trade, thereby enhancing their well-being. Contrary to Malthus’s predictions, food production has kept up with, and even outpaced, human population growth (11). In South America, rangelands maintain 10 times as much herbivore biomass as natural ecosystems (12). This massive increase in food supply has been achieved by focusing efforts on planting and consuming a small variety of plants. As of 1999, barley, maize, rice, and wheat occupied almost 40% of global cropland (13). With these agricultural advances, the hand-to-mouth lifestyle of preagricultural humans has been