

The limits of parallelism in adaptation due to domestication in the grasses

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October 4, 2018

Abstract

The selection of desirable traits in crops during domestication has been well studied. Many crops share a suite of phenotypic characteristics collectively known as the domestication syndrome. Previous work has demonstrated that, at least in some instances, parallel selection of orthologous loci across species has resulted in shared domestication traits. However, both demography and selection during domestication can place limits on the evolutionary potential for subsequent adaptation and reduce opportunities for parallelism. Here we review current knowledge regarding the extent of parallelism versus convergence during domestication and adaptation in the grasses and consider whether the dynamism of grass genomes (e.g., transposable elements, polyploidy, genome size), help these species overcome their legacy of domestication to achieve broad subsequent adaptation.

Introduction

Human societies rely heavily on domesticated crop species for survival. For example, considering crop production as a measure of consumption, in 2016 alone the United States produced 384 million tons of maize, China produced 211 million tons of rice, and Nigeria produced 6.9 million tons of sorghum [26]. Human reliance on crops has deepened over the last $\approx 10,000$ years, as crops have been continually selected by humans for traits including nutrition, yield, and other attractive features, a process that has also dramatically changed crop physiology. As such, domesticated crops are often radically different from their wild relatives. Notably, there are several traits beyond yield and nutrition that often distinguish domesticated crops from their wild progenitors [17], distinctions that are frequently shared even among distantly related crops such as maize and sunflower. These traits include apical dominance or lack of branching, loss of seed dormancy, loss of bitterness, and loss of shattering or seed dispersal (Table 1). This suite of shared traits is collectively known as the domestication syndrome [40].

But how can two vastly diverged species such as maize and sunflower (their last common ancestor was 150 MYA [12]) share the same domestication traits? Since these two species still share enzymatic pathways, perhaps orthologous genes or genes with similar physiological roles have been targeted by selection during domestication. Shared phenotypes caused by repeated modification of orthologs, is a phenomenon known as parallelism; parallelism is more likely to occur in

closely related species due to their similar complement of genes [86]. Conversely, it is possible for unrelated genes in different enzymatic pathways to give rise to similar traits, particularly when species experience similar selection pressures (either human or environmental), such as fruit/seed indehiscence in both dicot and monocot crops (reviewed in [18]). This phenomenon, known as convergence, is more likely to occur in substantially diverged species that contain fewer orthologous loci and pathways [107, 86].

After the initial wave of crop domestication yielded many of the aforementioned domestication syndrome traits, another level of differentiation ensued—the adaptation of crop species to varied environmental conditions during global expansion. A cultivar of maize bred for cultivation at sea level, for instance, may not necessarily thrive in the colder, higher UV environment of the Andes. Therefore, cultivators in the Andes must have looked for individuals in the existing domesticated maize population that were hardy under these new conditions. However, crop adaptation faced genetic limitations not experienced during domestication of wild progenitors [105].

Only a subset of genome-wide diversity was retained in initial domesticates and additional diversity was lost through subsampling events during crop expansion. Furthermore, selection on particular alleles coding for desirable traits (such as those comprising the domestication syndrome) often resulted in dramatic reductions in diversity in particular chromosomal regions. The effects of this loss of genetic diversity on the potential for adaptation has been documented. For example, a dramatic genetic bottleneck in the “lumper” variety of potato led to a catastrophic outbreak of *Phytophthora infestans*, resulting in the infamous Potato Famine in Ireland in the 1840s [36]. The Potato Famine demonstrated that by divesting a crop cultivar of its diversity, the cultivar also loses its ability to adapt to newly encountered environmental pressures, because the alleles that code for adaptive traits such as, for instance, disease resistance are lost.

This review will focus on the extent of parallelism and convergence in both crop domestication and adaptation and consider the extent to which early bottlenecks have affected the potential for parallelism and convergence during post-domestication adaptation. We will focus mainly on grass crops, since the major domesticates—maize, rice, sorghum, wheat, barley, and millet—include a range of divergence times conducive to adaptation and evolution of domestication syndrome traits through both parallelism and convergence. Grasses also share a certain amount of genomic dynamism, including polyploidization and transposable element activity, that provides diversity upon which selection can act. We examine the relationship between domestication and adaptive traits, how domestication bottlenecks reduce population diversity, and look at the ways in which the dynamic nature of grass genomes might potentially increase genomic diversity to facilitate adaptation despite bottlenecks during domestication and expansion.

Domestication in the grasses

Grasses have often been studied as a cohesive genetic group [7, 29], and there are many reasons why they present a compelling system for studying crop domestication. The grass clade is thought to have arisen around 75 MYA [10, 55] with rice, wheat, barley, millet, maize, and sorghum arising sequentially afterward (Figure 1). Prior to the radiation of the grasses, however, a genome duplication event occurred approximately 70 MYA [83], which is shared among all grass crops (Figure

1). Subsequently, both maize and wheat have undergone additional, lineage-specific polyploidy events (Figure 1) [64]. These polyploidy events, followed by selective and ongoing fractionation, present an opportunity for grass genomes to evolve subfunctionalized homeologs; this, along with relatively high transposon activity (particularly in maize and wheat) that can give rise to functional mutation [110, 67], make the grasses a useful system for studying the potential for adaptation after a domestication bottleneck.

Additionally, most grass crops were domesticated within the latitudinal boundaries of the equator and 35° N [46, 33], featuring both wet and dry seasons [46], which means that many domesticated grasses shared similar environmental pressures such as temperature, precipitation and day length. However, each grass cereal has been cultivated in separate geographic locations, including maize (Americas), sorghum (Africa), rice (Asia), millet (Eurasia), and wheat and barley (the Middle East) [35], and, to some extent, approaches to domestication in these separate regions were guided by culturally distinct selection of traits. Taken together, these features make domesticated grass species especially conducive to the meaningful study of convergence and parallelism.

Grass crops share a number of domestication syndrome traits also observed in non-grass crop species (Table 1). However, some common domestication syndrome traits are notably lacking in the grasses, such as reduced toxicity, vegetative reproduction, and reduced defensive structures like spines and thorns—by and large the wild relatives of grass crops lacked these defense mechanisms. Likewise, some grass domestication syndrome traits are absent in non-grass crops, such as increased spikelet number and increased number of kernel rows, because these traits occur on structures that are not found outside the grasses.

An ever-increasing number of causal genes for traits in the domestication syndrome are being identified both within and outside of the grasses; these genes are summarized in Table 2 (modified from [63]). Grass domestication genes can be categorized based on whether they occur strictly within a species, share orthologs across the grasses, share orthologs within and outside of the grasses, or share orthologs entirely outside of the grasses (Column 3, Table 2). This gives us an opportunity to form hypotheses regarding the likelihood of parallelism and convergence for a certain trait based on its known orthology across taxa. For example, in column 8 of Table 2 we indicate whether a domestication gene is expected to be convergent or parallel, based on patterns of orthology. If a domestication gene is found only within a single species, it obviously cannot be selected in parallel. For instance, coloration in rice through selection on the *Bh4* gene may be expected to be convergent since this gene's influence on coloration appears to be specific to the rice species. On the other hand, the coloration gene *BADH2* is found in both rice and soybean, (Table 2), suggesting an example of parallel selection.

Given that we see examples of both parallelism and convergence during domestication, what might determine which prevails for a given trait? A review by Lenser and Theissen [63] sets out four examples of when parallelism might be favored over convergence: (1) Genes occupying a nodal position upstream of genes that affect domestication traits; (2) Genes involved in simple metabolic pathways, because only a minimal set of genes serves as a potential mutational target to change a given trait (such as *Waxy*, Table 2); (3) genes with fewer pleiotropic effects, such as the MYB genes (i.e. *DFR*) associated with changes in fruit or seed color; (4) domestication-related alleles that are already present at low frequency within a wild population. Parallelism also requires retention of orthologous genes throughout evolution and a lack of functional divergence. Therefore, loss of certain orthologs in wild relatives prior to the onset of crop domestication would make parallel domestication for some traits impossible.

Table 2 provides a starting point to predict which domestication genes are likely to be found across the grasses, which traits in the grasses are likely to be selected in parallel, and which are likely to be convergent. In addition to enhancing our basic understanding of the repeatability of evolution, this is useful if we wish to breed wild grass relatives for domestication traits, or create hybrids among existing cultivars, since we can now associate favorable phenotypes and QTL with orthologs across species by simple comparative genomics. But to what extent can this knowledge help us to understand how domestication has impacted a crop's ability to adapt to new environments and the extent to which adaptation is in parallel or convergent across crops?

Adaptation in the grasses

An adaptive trait is one that interacts or responds to the environment in a way that helps an organism to thrive. For domesticated crops, however, adaptive traits that reverse desired domestication phenotypes such as yield, fragrance, flavor, or reduced shattering would not be considered favorable; therefore, we will narrow the definition of an adaptive trait to one that interacts or responds to the environment favorably but does not detract from desired domestication traits. Perhaps it is also necessary to define what specifically is meant by “environment”. A straightforward (and admittedly simplistic) way would be to break “environment” down to discrete features, which can include, for example, the level of carbon dioxide in the air, the level of UV radiation, temperature, day length, humidity, rainfall, wind, soil nutrient load, and soil salinity. By dividing the environment into these discrete elements, we can address each element individually by asking what sort of adaptive trait we would expect to observe in response to each, how many of these adaptive traits are expressed in the same genetic pathways as known domestication genes, and which represent entirely distinct physiological processes. Selection during domestication on genes relevant to adaptation during expansion could constrain adaptation and affect the likelihood that adaptation to similar environmental conditions occurs in parallel across species.

Additionally, it is important to note that selection for adaptive traits in crop species can be fundamentally constrained by demography during domestication, primarily due to the population bottleneck that frequently accompanies domestication. Domestication bottlenecks are a demographic process in which cultivators derive a domesticate from a subset of wild populations. This subsampling of diversity results in a stochastic, genome-wide reduction in diversity in the domesticate when compared to its wild relative. Genome-wide loss of diversity during genetic bottlenecks associated with both initial domestication and later crop expansion has been well documented (*e.g.*, [105]). Massive loss of nucleotide diversity during domestication is reported in domesticated bread wheat [41], maize (with an increase in deleterious alleles) [22, 105], rice [123], Sorghum [39], and barley [56] compared with wild relatives, demonstrating that loss of diversity is widespread in cultivated grasses and is a phenomenon that is distinct from uncultivated wild relatives. These results suggest that domestication itself is responsible for the loss of diversity, and because of this, attempts to adapt domesticated grasses to new environments could be constrained by recent demography. In summary, both demographic bottlenecks and selection during domestication can affect the likelihood that adaptive traits would be selected in parallel, since we propose that this depends on whether adaptive alleles are retained across taxa post-domestication.

Particular domestication traits described in Table 2 are also associated with adaptation during crop expansion. For example, the *Ghd7* gene in rice has been associated with agronomic traits such as grains per panicle, plant height and heading date; however, natural variants with reduced function allow rice to be cultivated in cooler regions [115], which is an adaptive phenotype. Another example of a domestication trait with an adaptive component is pigmentation. Loss of pigmentation has been favored in a variety of cereal cultivars, from rice to maize, as a cultural preference during domestication. As it turns out, pigment assists with UV tolerance in cereals and other plant species, particularly at high elevation [95, 37]. Therefore, pigmentation could lead to greater tolerance of UV radiation in cereals colonizing high elevation post-domestication [87]. Table 2 matches examples of adaptation traits to domestication traits, where probable, using the definition of adaptation as described above. Loss of allelic diversity due to selection during domestication may reduce adaptive potential when the same genes control domestication and adaptation phenotypes. Thus it may be less likely that genes that are selected during domestication would also be selected in parallel for adaptive traits.

In contrast, there are a number of adaptive traits unlikely to have a domestication component, since they appear unrelated to domestication syndrome traits. These include (but are not limited to) drought tolerance, cold tolerance, soil salinity, and pathogen defense. One example is the gene *ZmCCT9* in maize, which appears to be involved in flowering under the long days of higher latitudes. More specifically, a transposon insertion upstream of *ZmCCT9* in domesticated maize cultivars led to reduced photoperiod sensitivity, which has allowed domesticated maize to expand its range [43]. Another adaptive gene not expected to be associated with domestication (see Table 2) is the maize *ZmVPP1* gene, where an upstream insertion is linked to drought tolerance [106]. Since this gene has an ortholog linked to drought tolerance in Arabidopsis, *AVP1* [32], orthologs may exist elsewhere in the cereals as well. However, another drought-tolerance gene in rice, *OsAHL1* [120], does not appear to have a defined drought-tolerant ortholog in any other species at the time of this writing. Wheat and barley share a small family of cold-tolerance genes including *Wcs19* [13], *Wcor14* [102] and *Bcor14b* [15], all of which encode chloroplast-targeted COR proteins analogous to the Arabidopsis protein *COR15a* [96, 99]. The LEA protein orthologs *HVA1* and *Wrab 18/19* in barley and wheat, respectively, are also associated with cold tolerance [42, 21]. Transcript and protein levels of the barley *HvPIP2* aquaporin gene were found to be down-regulated in roots but up-regulated in the shoots of plants under salt stress [52]. *HvPIP2* has an ortholog in maize, *ZmPIP2-4* [122], and in spinach, *PM28A* [27]. There are also the ASR (abscisic acid, stress, and ripening-induced) genes that are associated with salinity tolerance in rice [50], *Setaria* (millet) [65], and tomato [57]. Because these genes have no known link to domestication, their orthologs may be more likely to be selected in parallel during adaptation, since they retain more diversity post-domestication. However, diversity across these loci was most certainly reduced due to genome-wide demographic effects of domestication bottlenecks, a factor that may have limited the extent of parallelism during adaptation in the cereals relative to more diverse, wild species.

Certain adaptive traits are less likely to have orthologs, even in closely related species. These include pathogen resistance and stress response. While there are examples of shared orthologs for pathogen defense and stress response genes in the grasses (Table 2), by and large, genes that code for traits involved in plant defense and stress response are frequently orphan genes, or genes that are specific to a particular lineage and share no defined orthologs with any outgroup [112]; reviewed in [1]. Orphan genes tend to be very dynamic, arising and becoming lost much faster than

their basal counterparts [30]. Orphan genes often propagate through trans duplication [30, 1]; therefore, movement of these genes to a new region whose local euchromatic status can confer novel expression patterns to the mobilized gene can be a strong source of adaptation, especially since it has been shown that stressful environments can stimulate activation of transposable elements [6, 71] reviewed in [79], and this is one way that crop species might be able to escape the legacy of reduced diversity due to domestication in order to adapt. If an adaptive trait such as pathogen resistance is dependent on these orphan-type genes, which quite often are unique even in individual cultivars within the same crop species, then we would not expect to see parallel selection of this trait at the allelic level in cereal adaptation, since each species—indeed, each cultivar—would be expected to have its own unique, "outward-facing" suite of orphan genes that would confer environmental adaptation convergently to its niche.

We have postulated that the likelihood of parallelism vs. convergence in an adaptive trait may be dependent upon whether the adaptive trait is also associated with the domestication syndrome and whether, given the nature of the adaptive trait, causal genes are likely to be orthologous across taxa. We also hypothesize that the plasticity of a crop's genome due to transposon activity and recent polyploidy may play a role in governing these dynamics. We have seen that grasses tend to have relatively active transposons, and this transposon activity may permit a higher mutation rate in cereals [110]. In Table 2, several adaptive phenotypes are due to a transposon insertion somewhere in the functional region of a gene, such as *ZmCCT9* and *ZmVVP1* in maize. However, a comprehensive review of TEs and plant evolution [68] suggests that our understanding of the role of transposable element activity in crop adaptation is largely anecdotal and might be overstated, but perhaps can be better elucidated by harnessing the recent advances in genomics such as more sophisticated TE annotation protocols, whole-genome sequencing, and comparative algorithms. Using these advances in genome biology, a recent study by Lai and coworkers found that transposon insertions may have played an important role in creating the variation in gene regulation that enabled the rapid adaptation of domesticated maize to diverse environments [62]. Transposable elements may also result in meaningful differences in genome size across crop species. Transposons are known to contribute to the expansion of genome size in maize and other plant species [100] reviewed in [68]). A recent review [74] suggests that larger genomes may affect the process of adaptation by increasing the number and location of potentially functional mutations, thus expanding the regulatory space in which functional mutations may arise. This could increase the likelihood that a given ortholog could be selected in parallel for adaptive traits, despite losses of diversity experienced during domestication.

Genome duplication events can result in homeologs that may undergo subfunctionalization or neofunctionalization and give rise to adaptive loci. Neofunctionalization of homeologs is widespread in maize [44] and in bread wheat [84], which have both undergone recent, lineage-specific polyploidy events (Figure 1). To some extent, it can be predicted which homeolog in a post-polyploid cereal is likely to be adaptive. It is known that of the two retained post-polyploidy subgenomes in maize, one undergoes less fractionation and is more highly expressed than the other (i.e. the dominant subgenome) [113, 92], and there is evidence that fractionation is biased not only in maize, but in wheat as well [20]. Schnable and Freeling found that of the characterized genes that have a known mutant phenotype, the majority are on the less fractionated subgenome [93]. Many of these genes, such as *tb1*, *Waxy*, *Opaque2*, and several starch synthesis and coloration genes not in Table 2, have a domestication syndrome phenotype in maize. Additionally, recent work has suggested that the genes on the more highly expressed subgenome in maize contribute more to phenotypic

variation than the less expressed subgenome across a wide variety of traits, including those linked to adaptation [90]. Indeed, two genes associated with adaptive phenotypes in maize from Table 2, *ZmVPP1* (drought tolerance) and *ZmPIP2-4* (soil salinity) are both found on the less fractionated subgenome [93]; and genes associated with adaptation phenotypes such as disease resistance have also been observed on the more dominant subgenome in [90]. Parallelism in recent polyploids, therefore, may be more likely within the more dominant subgenome.

Conclusions

This review set out to explore how domestication has influenced the potential for subsequent adaptation in the grasses and the prospect of parallelism and convergence during both of these periods of selection. Demographic bottlenecks and targeted selection during domestication have removed potentially adaptive variation which may, in turn, affect the extent of parallelism observed during adaptation. We hypothesize that parallelism in adaptation is affected by: (1) whether an adaptive trait is related to the domestication syndrome; (2) the strength of the domestication bottleneck in a particular species; (3) whether an adaptive gene is orthologous across taxa; and (4) the level of plasticity across the genome. As demonstrated in Table 2, the causal loci underlying domestication and adaptation in the grasses are increasingly becoming clear. Comparative genomic analyses of cereals and their wild relatives combined with comparative studies of uniquely adapted populations will help further distinguish genes involved in these processes and characterize whether selection occurred in parallel. The genomic study of time-stratified archaeological samples will help further clarify the timing of selection and the extent to which parallelism in adaptation is conditioned on initial selection during domestication. Crops in the grass family have been very successful in adapting to a wide range of environmental conditions despite limitations in adaptive potential due to domestication, perhaps due to their active TEs, their history of polyploidy, and their large genomes. As the genetic basis of adaptation becomes more clear, genes involved in adaptation across both wild and domesticated grasses can be compared to fully evaluate the limits domestication places on parallelism in adaptation.

Authors' Contributions

M. Hufford devised the theme and general concepts of domestication, adaptation, and convergence vs parallelism. M. Woodhouse devised the sections relating to grass genome plasticity, orthology, and orphan genes. M. Woodhouse and M. Hufford contributed equally to the drafting and the editing of the article.

Competing Interests

The authors report no competing interests.

Funding

This work was funded by USDA grant USDA-ARS 58-5030-7-072.

References

- [1] Zebulun W. Arendsee, Ling Li, and Eve Syrkin Wurtele. Coming of age: orphan genes in plants. *Trends in Plant Science*, 19(11):698–708, nov 2014.
- [2] K. Asano, M. Yamasaki, S. Takuno, K. Miura, S. Katagiri, T. Ito, K. Doi, J. Wu, K. Ebana, T. Matsumoto, H. Innan, H. Kitano, M. Ashikari, and M. Matsuoka. Artificial selection for a green revolution gene during japonica rice domestication. *Proceedings of the National Academy of Sciences*, 108(27):11034–11039, jun 2011.
- [3] Kenji Asano, Tomonori Takashi, Kotaro Miura, Qian Qian, Hidemi Kitano, Makoto Matsuoka, and Motoyuki Ashikari. Genetic and molecular analysis of utility of sd1 alleles in rice breeding. *Breeding Science*, 57(1):53–58, 2007.
- [4] Torben Asp, Stephen Byrne, Heidrun Gundlach, Rémy Bruggmann, Klaus F. X. Mayer, Jeppe R. Andersen, Mingliang Xu, Morten Greve, Ingo Lenk, and Thomas Lübberstedt. Comparative sequence analysis of VRN1 alleles of lolium perenne with the co-linear regions in barley, wheat, and rice. *Molecular Genetics and Genomics*, 286(5-6):433–447, nov 2011.
- [5] James Beales, Adrian Turner, Simon Griffiths, John W. Snape, and David A. Laurie. A pseudo-response regulator is misexpressed in the photoperiod insensitive ppd-d1a mutant of wheat (triticum aestivum l.). *Theoretical and Applied Genetics*, 115(5):721–733, jul 2007.
- [6] T. Beguiristain. Three tnt1 subfamilies show different stress-associated patterns of expression in tobacco. consequences for retrotransposon control and evolution in plants. *PLANT PHYSIOLOGY*, 127(1):212–221, sep 2001.
- [7] J. L. Bennetzen and M. Freeling. Grasses as a single genetic system: genome composition, collinearity and compatibility. *Trends Genet.*, 9(8):259–261, Aug 1993.
- [8] Benjamin K. Blackman. Changing responses to changing seasons: Natural variation in the plasticity of flowering time. *Plant Physiology*, 173(1):16–26, nov 2016.
- [9] Benjamin K. Blackman, Jared L. Strasburg, Andrew R. Raduski, Scott D. Michaels, and Loren H. Rieseberg. The role of recently derived FT paralogs in sunflower domestication. *Current Biology*, 20(7):629–635, apr 2010.
- [10] YANIS BOUCHENAK-KHELLADI, G. ANTHONY VERBOOM, VINCENT SAVOLAINEN, and TREVOR R. HODKINSON. Biogeography of the grasses (poaceae): a phylogenetic approach to reveal evolutionary history in geographical space and geological time. *Botanical Journal of the Linnean Society*, 162(4):543–557, apr 2010.

- [11] E. Butelli, C. Licciardello, Y. Zhang, J. Liu, S. Mackay, P. Bailey, G. Reforgiato-Recupero, and C. Martin. Retrotransposons control fruit-specific, cold-dependent accumulation of anthocyanins in blood oranges. *The Plant Cell*, 24(3):1242–1255, mar 2012.
- [12] Chien-Chang Chang, Hsin-Liang Chen, Wen-Hsiung Li, and Shu-Miaw Chaw. Dating the monocot?dicot divergence and the origin of core eudicots using whole chloroplast genomes. *Journal of Molecular Evolution*, 58(4):424–441, apr 2004.
- [13] L. P. Chauvin, M. Houde, and F. Sarhan. A leaf-specific gene stimulated by light during wheat acclimation to low temperature. *Plant Mol. Biol.*, 23(2):255–265, Oct 1993.
- [14] Jordi Comadran, Benjamin Kilian, Joanne Russell, Luke Ramsay, Nils Stein, Martin Ganai, Paul Shaw, Micha Bayer, William Thomas, David Marshall, Pete Hedley, Alessandro Tondelli, Nicola Pecchioni, Enrico Francia, Viktor Korzun, Alexander Walther, and Robbie Waugh. Natural variation in a homolog of antirrhinum CENTRORADIALIS contributed to spring growth habit and environmental adaptation in cultivated barley. *Nature Genetics*, 44(12):1388–1392, nov 2012.
- [15] C. Crosatti, P. Polverino de Laureto, R. Bassi, and L. Cattivelli. The interaction between cold and light controls the expression of the cold-regulated barley gene cor14b and the accumulation of the corresponding protein. *Plant Physiol.*, 119(2):671–680, Feb 1999.
- [16] Aurora Díaz, Meluleki Zikhali, Adrian S. Turner, Peter Isaac, and David A. Laurie. Copy number variation affecting the photoperiod-b1 and vernalization-a1 genes is associated with altered flowering time in wheat (triticum aestivum). *PLoS ONE*, 7(3):e33234, mar 2012.
- [17] John F. Doebley, Brandon S. Gaut, and Bruce D. Smith. The molecular genetics of crop domestication. *Cell*, 127(7):1309–1321, dec 2006.
- [18] Yang Dong and Yin-Zheng Wang. Seed shattering: from models to crops. *Frontiers in Plant Science*, 6, jun 2015.
- [19] Yang Dong, Xia Yang, Jing Liu, Bo-Han Wang, Bo-Ling Liu, and Yin-Zheng Wang. Pod shattering resistance associated with domestication is mediated by a NAC gene in soybean. *Nature Communications*, 5(1), feb 2014.
- [20] N. A. Eckardt. Genome dominance and interaction at the gene expression level in allohexaploid wheat. *The Plant Cell*, 26(5):1834–1834, may 2014.
- [21] C. Egawa, F. Kobayashi, M. Ishibashi, T. Nakamura, C. Nakamura, and S. Takumi. Differential regulation of transcript accumulation and alternative splicing of a DREB2 homolog under abiotic stress conditions in common wheat. *Genes Genet. Syst.*, 81(2):77–91, Apr 2006.
- [22] A. Eyre-Walker, R. L. Gaut, H. Hilton, D. L. Feldman, and B. S. Gaut. Investigation of the bottleneck leading to the domestication of maize. *Proc. Natl. Acad. Sci. U.S.A.*, 95(8):4441–4446, Apr 1998.

- [23] Longjiang Fan, Liyan Quan, Xiaodong Leng, Xingyi Guo, Weiming Hu, Songlin Ruan, Huasheng Ma, and Mengqian Zeng. Molecular evidence for post-domestication selection in the waxy gene of chinese waxy maize. *Molecular Breeding*, 22(3):329–338, mar 2008.
- [24] S. Faure, A. S. Turner, D. Gruszka, V. Christodoulou, S. J. Davis, M. von Korff, and D. A. Laurie. Mutation at the circadian clock gene EARLY MATURITY 8 adapts domesticated barley (*hordeum vulgare*) to short growing seasons. *Proceedings of the National Academy of Sciences*, 109(21):8328–8333, may 2012.
- [25] Beatriz Fernandez-Marin, Ruben Milla, Nieves Martin-Robles, Erwann Arc, Ilse Kranner, Jose Maria Becerril, and Jose Ignacio Garcia-Plazaola. Side-effects of domestication: cultivated legume seeds contain similar tocopherols and fatty acids but less carotenoids than their wild counterparts. *BMC Plant Biology*, 14(1), dec 2014.
- [26] Commodities by country. <http://faostat3.fao.org/>.
- [27] Dimitrios Fotiadis, Paul Jenö, Thierry Mini, Sabine Wirtz, Shirley A. Müller, Laure Fraysse, Per Kjellbom, and Andreas Engel. Structural characterization of two aquaporins isolated from native spinach leaf plasma membranes. *Journal of Biological Chemistry*, 276(3):1707–1714, oct 2000.
- [28] F. Foucher. DETERMINATE and LATE FLOWERING are two TERMINAL FLOWER1/CENTRORADIALIS homologs that control two distinct phases of flowering initiation and development in pea. *THE PLANT CELL ONLINE*, 15(11):2742–2754, oct 2003.
- [29] M. Freeling. Grasses as a single genetic system: reassessment 2001. *Plant Physiol.*, 125(3):1191–1197, Mar 2001.
- [30] M. Freeling, E. Lyons, B. Pedersen, M. Alam, R. Ming, and D. Lisch. Many or most genes in arabidopsis transposed after the origin of the order brassicales. *Genome Research*, 18(12):1924–1937, oct 2008.
- [31] Tsutomu Furukawa, Masahiko Maekawa, Tomoyuki Oki, Ikuo Suda, Shigeru Iida, Hiroaki Shimada, Itsuro Takamure, and Koh ichi Kadowaki. The rc and rd genes are involved in proanthocyanidin synthesis in rice pericarp. *The Plant Journal*, 49(1):91–102, dec 2006.
- [32] R. A. Gaxiola, J. Li, S. Undurraga, L. M. Dang, G. J. Allen, S. L. Alper, and G. R. Fink. Drought- and salt-tolerant plants result from overexpression of the AVP1 h+pump. *Proceedings of the National Academy of Sciences*, 98(20):11444–11449, sep 2001.
- [33] Paul Gepts. Crop domestication as a long-term selection experiment. In *Plant Breeding Reviews*, pages 1–44. John Wiley & Sons, Inc., jun 2010.
- [34] Jason D Gillman, Ashley Tetlow, Jeong-Deong Lee, J Shannon, and Kristin Bilyeu. Loss-of-function mutations affecting a specific glycine max r2r3 MYB transcription factor result in brown hilum and brown seed coats. *BMC Plant Biology*, 11(1):155, 2011.

- [35] Sylvain Glémin and Thomas Bataillon. A comparative view of the evolution of grasses under domestication. *New Phytologist*, 183(2):273–290, jun 2009.
- [36] S. B. Goodwin, B. A. Cohen, and W. E. Fry. Panglobal distribution of a single clonal lineage of the irish potato famine fungus. *Proceedings of the National Academy of Sciences*, 91(24):11591–11595, nov 1994.
- [37] Kevin S. Gould. Nature’s swiss army knife: The diverse protective roles of anthocyanins in leaves. *Journal of Biomedicine and Biotechnology*, 2004(5):314–320, 2004.
- [38] Julian R. Greenwood, E. Jean Finnegan, Nobuyoshi Watanabe, Ben Trevaskis, and Steve M. Swain. New alleles of the wheat domestication gene *Q* reveal multiple roles in growth and reproductive development. *Development*, 144(11):1959–1965, apr 2017.
- [39] M. T. Hamblin. Challenges of detecting directional selection after a bottleneck: Lessons from sorghum bicolor. *Genetics*, 173(2):953–964, apr 2006.
- [40] Karl Hammer. Das domestikationssyndrom. *Die Kulturpflanze*, 32(1):11–34, jun 1984.
- [41] A Haudry, A Cenci, C Ravel, T Bataillon, D Brunel, C Poncet, I Hochu, S Poirier, S Santoni, S Glémin, and J David. Grinding up wheat: A massive loss of nucleotide diversity since domestication. *Molecular Biology and Evolution*, 24(7):1506–1517, apr 2007.
- [42] Bimei Hong, Scott J. Uknes, and Tuan hua David Ho. Cloning and characterization of a cDNA encoding a mRNA rapidly-induced by ABA in barley aleurone layers. *Plant Molecular Biology*, 11(4):495–506, 1988.
- [43] Cheng Huang, Huayue Sun, Dingyi Xu, Qiuyue Chen, Yameng Liang, Xufeng Wang, Guanghui Xu, Jinge Tian, Chenglong Wang, Dan Li, Lishuan Wu, Xiaohong Yang, Weiwei Jin, John F. Doebley, and Feng Tian. *ZmCCT9* enhances maize adaptation to higher latitudes. *Proceedings of the National Academy of Sciences*, 115(2):E334–E341, dec 2017.
- [44] Thomas E. Hughes, Jane A. Langdale, and Steven Kelly. The impact of widespread regulatory neofunctionalization on homeolog gene evolution following whole-genome duplication in maize. *Genome Research*, 24(8):1348–1355, apr 2014.
- [45] Harriet V. Hunt, Hannah M. Moots, Robert A. Graybosch, Huw Jones, Mary Parker, Olga Romanova, Martin K. Jones, Christopher J. Howe, and Kay Trafford. Waxy phenotype evolution in the allotetraploid cereal broomcorn millet: Mutations at the *GBSSI* locus in their functional and phylogenetic context. *Molecular Biology and Evolution*, 30(1):109–122, oct 2012.
- [46] Subodh Jain. Crops and man. 2nd ed. 1992. by jack r. harlan. american society of agronomy, 677 s. segoe road, madison, WI 53711. 284 pp. \$34 hardcover. *American Journal of Alternative Agriculture*, 8(01):47, mar 1993.
- [47] Jong-Seong Jeon, Nayeon Ryoo, Tae-Ryong Hahn, Harkamal Walia, and Yasunori Nakamura. Starch biosynthesis in cereal endosperm. *Plant Physiology and Biochemistry*, 48(6):383–392, jun 2010.

- [48] Qiaojun Jia, Jingjuan Zhang, Sharon Westcott, Xiao-Qi Zhang, Mathew Bellgard, Reg Lance, and Chengdao Li. GA-20 oxidase as a candidate for the semidwarf gene *sdw1/denso* in barley. *Functional & Integrative Genomics*, 9(2):255–262, mar 2009.
- [49] H. Jones, F. J. Leigh, I. Mackay, M. A. Bower, L. M.J. Smith, M. P. Charles, G. Jones, M. K. Jones, T. A. Brown, and W. Powell. Population-based resequencing reveals that the flowering time adaptation of cultivated barley originated east of the fertile crescent. *Molecular Biology and Evolution*, 25(10):2211–2219, jul 2008.
- [50] Jounghsu Joo, Youn Hab Lee, Yeon-Ki Kim, Baek Hie Nahm, and Sang Ik Song. Abiotic stress responsive rice *ASR1* and *ASR3* exhibit different tissue-dependent sugar and hormone-sensitivities. *Molecules and Cells*, 35(5):421–435, apr 2013.
- [51] Ruangchai Juwattanasomran, Prakrit Somta, Sompong Chankaew, Takehiko Shimizu, Sugunya Wongpornchai, Akito Kaga, and Peerasak Srinives. A SNP in *GmBADH2* gene associates with fragrance in vegetable soybean variety kaori and SNAP marker development for the fragrance. *Theoretical and Applied Genetics*, 122(3):533–541, nov 2010.
- [52] Maki Katsuhara, Yoshiko Akiyama, Kazuki Koshio, Mineo Shibasaka, and Kunihiro Kasamo. Functional analysis of water channels in barley roots. *Plant and Cell Physiology*, 43(8):885–893, aug 2002.
- [53] Hiroyuki Kawahigashi, Masao Oshima, Tomotaro Nishikawa, Hisahito Okuizumi, Shigemitsu Kasuga, and Jun ichi Yonemaru. A novelwaxyallele in sorghum landraces in east asia. *Plant Breeding*, 132(3):305–310, apr 2013.
- [54] Makoto Kawase, Kenji Fukunaga, and Kenji Kato. Diverse origins of waxy foxtail millet crops in east and southeast asia mediated by multiple transposable element insertions. *Molecular Genetics and Genomics*, 274(2):131–140, aug 2005.
- [55] E. A. Kellogg. Evolutionary history of the grasses. *PLANT PHYSIOLOGY*, 125(3):1198–1205, mar 2001.
- [56] Benjamin Kilian, Hakan Özkan, Jochen Kohl, Arndt von Haeseler, Francesca Barale, Oliver Deusch, Andrea Brandolini, Cemal Yucel, William Martin, and Francesco Salamini. Haplotype structure at seven barley genes: relevance to gene pool bottlenecks, phylogeny of ear type and site of barley domestication. *Molecular Genetics and Genomics*, 276(3):230–241, jun 2006.
- [57] Zvia Konrad and Dudy Bar-Zvi. Synergism between the chaperone-like activity of the stress regulated *ASR1* protein and the osmolyte glycine-betaine. *Planta*, 227(6):1213–1219, feb 2008.
- [58] E. A. Koskela, K. Mouhu, M. C. Albani, T. Kurokura, M. Rantanen, D. J. Sargent, N. H. Battey, G. Coupland, P. Elomaa, and T. Hytonen. Mutation in *TERMINAL FLOWER1* reverses the photoperiodic requirement for flowering in the wild strawberry *fragaria vesca*. *PLANT PHYSIOLOGY*, 159(3):1043–1054, may 2012.

- [59] M. J. Kovach, M. N. Calingacion, M. A. Fitzgerald, and S. R. McCouch. The origin and evolution of fragrance in rice (*oryza sativa* l.). *Proceedings of the National Academy of Sciences*, 106(34):14444–14449, aug 2009.
- [60] Simon G. Krattinger, Evans S. Lagudah, Thomas Wicker, Joanna M. Risk, Anthony R. Ashton, Liselotte L. Selter, Takashi Matsumoto, and Beat Keller. Lr34 multi-pathogen resistance ABC transporter: molecular analysis of homoeologous and orthologous genes in hexaploid wheat and other grass species. *The Plant Journal*, 65(3):392–403, dec 2010.
- [61] Myounghai Kwak, Orlando Toro, Daniel G. Debouck, and Paul Gepts. Multiple origins of the determinate growth habit in domesticated common bean (*phaseolus vulgaris*). *Annals of Botany*, 110(8):1573–1580, sep 2012.
- [62] Xianjun Lai, James C. Schnable, Zhengqiao Liao, Jie Xu, Gengyun Zhang, Chuan Li, Erliang Hu, Tingzhao Rong, Yunbi Xu, and Yanli Lu. Genome-wide characterization of non-reference transposable element insertion polymorphisms reveals genetic diversity in tropical and temperate maize. *BMC Genomics*, 18(1), sep 2017.
- [63] Teresa Lenser and Günter Theißen. Molecular mechanisms involved in convergent crop domestication. *Trends in Plant Science*, 18(12):704–714, dec 2013.
- [64] A. A. Levy. The impact of polyploidy on grass genome evolution. *PLANT PHYSIOLOGY*, 130(4):1587–1593, dec 2002.
- [65] Jianrui Li, Yang Dong, Cong Li, Yanlin Pan, and Jingjuan Yu. SiASR4, the target gene of SiARDP from *setaria italica*, improves abiotic stress adaption in plants. *Frontiers in Plant Science*, 7, jan 2017.
- [66] Zhongwei Lin, Xianran Li, Laura M Shannon, Cheng-Ting Yeh, Ming L Wang, Guihua Bai, Zhao Peng, Jiarui Li, Harold N Trick, Thomas E Clemente, John Doebley, Patrick S Schnable, Mitchell R Tuinstra, Tesfaye T Tesso, Frank White, and Jianming Yu. Parallel domestication of the *shattering1* genes in cereals. *Nature Genetics*, 44(6):720–724, may 2012.
- [67] D. R. Lisch. Mutator transposase is widespread in the grasses. *PLANT PHYSIOLOGY*, 125(3):1293–1303, mar 2001.
- [68] Damon Lisch. How important are transposons for plant evolution? *Nature Reviews Genetics*, 14(1):49–61, jan 2013.
- [69] B. Liu, S. Watanabe, T. Uchiyama, F. Kong, A. Kanazawa, Z. Xia, A. Nagamatsu, M. Arai, T. Yamada, K. Kitamura, C. Masuta, K. Harada, and J. Abe. The soybean stem growth habit gene *dt1* is an ortholog of *arabidopsis* *TERMINAL FLOWER1*. *PLANT PHYSIOLOGY*, 153(1):198–210, mar 2010.
- [70] Jun Lyu. Unearthing potato evolution. *Nature Plants*, 3(12):912–912, dec 2017.

- [71] Irina Makarevitch, Amanda J. Waters, Patrick T. West, Michelle Stitzer, Candice N. Hirsch, Jeffrey Ross-Ibarra, and Nathan M. Springer. Transposable elements contribute to activation of maize genes in response to abiotic stress. *PLoS Genetics*, 11(1):e1004915, jan 2015.
- [72] Arnaud Martin and Virginie Orgogozo. THE LOCI OF REPEATED EVOLUTION: A CATALOG OF GENETIC HOTSPOTS OF PHENOTYPIC VARIATION. *Evolution*, pages n/a–n/a, mar 2013.
- [73] Kazuki Matsubara, Eri Ogiso-Tanaka, Kiyosumi Hori, Kaworu Ebana, Tsuyu Ando, and Masahiro Yano. Natural variation in *hd17*, a homolog of *arabidopsis* *ELF3* that is involved in rice photoperiodic flowering. *Plant and Cell Physiology*, 53(4):709–716, mar 2012.
- [74] Wenbin Mei, Markus G. Stetter, Daniel J. Gates, Michelle C. Stitzer, and Jeffrey Ross-Ibarra. Adaptation in plant genomes: Bigger is different. *American Journal of Botany*, 105(1):16–19, jan 2018.
- [75] Allison J. Miller and Briana L. Gross. From forest to field: Perennial fruit crop domestication. *American Journal of Botany*, 98(9):1389–1414, sep 2011.
- [76] D. S. Multani. Loss of an MDR transporter in compact stalks of maize *br2* and sorghum *dw3* mutants. *Science*, 302(5642):81–84, oct 2003.
- [77] Masaya MURAKAMI, Akinori MATSUSHIKA, Motoyuki ASHIKARI, Takafumi YAMASHINO, and Takeshi MIZUNO. Circadian-associated rice pseudo response regulators (OsPRRs): Insight into the control of flowering time. *Bioscience, Biotechnology, and Biochemistry*, 69(2):410–414, jan 2005.
- [78] Rebecca L. Murphy, Daryl T. Morishige, Jeff A. Brady, William L. Rooney, Shanshan Yang, Patricia E. Klein, and John E. Mullet. *1* represses sorghum flowering in long days: Alleles enhance biomass accumulation and grain production. *The Plant Genome*, 7(2):0, 2014.
- [79] Pooja Negi, Archana N. Rai, and Penna Suprasanna. Moving through the stressed genome: Emerging regulatory roles for transposons in plant stress response. *Frontiers in Plant Science*, 7, oct 2016.
- [80] K. Okazaki, K. Sakamoto, R. Kikuchi, A. Saito, E. Togashi, Y. Kuginuki, S. Matsumoto, and M. Hirai. Mapping and characterization of FLC homologs and QTL analysis of flowering time in brassica oleracea. *Theoretical and Applied Genetics*, 114(4):595–608, nov 2006.
- [81] Young-Jun Park, Tomotaro Nishikawa, Norihiko Tomooka, and Kazuhiro Nemoto. The molecular basis of mutations at the waxy locus from *amaranthus caudatus* l.: evolution of the waxy phenotype in three species of grain amaranth. *Molecular Breeding*, 30(1):511–520, sep 2011.
- [82] Rajiv K. Parvathaneni, Vinod Jakkula, Francis K. Padi, Sebastien Faure, Nethra Nagara-jappa, Ana C. Pontaroli, Xiaomei Wu, Jeffrey L. Bennetzen, and Katrien M. Devos. Fine-mapping and identification of a candidate gene underlying the *d2* dwarfing phenotype in pearl millet, *cenchrus americanus* (l.) morrone. *G3: Genes Genomes Genetics*, 3(3):563–572, mar 2013.

- [83] A. H. Paterson, J. E. Bowers, and B. A. Chapman. Ancient polyploidization predating divergence of the cereals, and its consequences for comparative genomics. *Proceedings of the National Academy of Sciences*, 101(26):9903–9908, may 2004.
- [84] M. Pfeifer, K. G. Kugler, S. R. Sandve, B. Zhan, H. Rudi, T. R. Hvidsten, K. F. X. Mayer, and O.-A. Olsen and. Genome interplay in the grain transcriptome of hexaploid bread wheat. *Science*, 345(6194):1250091–1250091, jul 2014.
- [85] B. Pickersgill. Domestication of plants in the americas: Insights from mendelian and molecular genetics. *Annals of Botany*, 100(5):925–940, jul 2007.
- [86] Barbara Pickersgill. Parallel vs. convergent evolution in domestication and diversification of crops in the americas. *Frontiers in Ecology and Evolution*, 6, may 2018.
- [87] Tanja Pyhäjärvi, Matthew B. Hufford, Sofiane Mezmouk, and Jeffrey Ross-Ibarra. Complex patterns of local adaptation in teosinte. *Genome Biology and Evolution*, 5(9):1594–1609, jul 2013.
- [88] Luke Ramsay, Jordi Comadran, Arnis Druka, David F Marshall, William T B Thomas, Malcolm Macaulay, Katrin MacKenzie, Craig Simpson, John Fuller, Nicola Bonar, Patrick M Hayes, Udda Lundqvist, Jerome D Franckowiak, Timothy J Close, Gary J Muehlbauer, and Robbie Waugh. INTERMEDIUM-c, a modifier of lateral spikelet fertility in barley, is an ortholog of the maize domestication gene TEOSINTE BRANCHED 1. *Nature Genetics*, 43(2):169–172, jan 2011.
- [89] Marie-Stanislas Remigereau, Ghayas Lakis, Samah Rekima, Magalie Leveugle, Michaël C. Fontaine, Thierry Langin, Aboubakry Sarr, and Thierry Robert. Cereal domestication and evolution of branching: Evidence for soft selection in the tb1 orthologue of pearl millet (*pennisetum glaucum* [L.] r. br.). *PLoS ONE*, 6(7):e22404, jul 2011.
- [90] Simon Renny-Byfield, Eli Rodgers-Melnick, and Jeffrey Ross-Ibarra. Gene fractionation and function in the ancient subgenomes of maize. *Molecular Biology and Evolution*, 34(8):1825–1832, apr 2017.
- [91] S. L. Repinski, M. Kwak, and P. Gepts. The common bean growth habit gene PvTFL1y is a functional homolog of arabidopsis TFL1. *Theoretical and Applied Genetics*, 124(8):1539–1547, feb 2012.
- [92] J. C. Schnable, N. M. Springer, and M. Freeling. Differentiation of the maize subgenomes by genome dominance and both ancient and ongoing gene loss. *Proceedings of the National Academy of Sciences*, 108(10):4069–4074, feb 2011.
- [93] James C. Schnable and Michael Freeling. Genes identified by visible mutant phenotypes show increased bias toward one of two subgenomes of maize. *PLoS ONE*, 6(3):e17855, mar 2011.
- [94] J. Gwen Shlichta, Maximilien A.C. Cuny, Johnattan Hernandez-Cumplido, Juan Traine, and Betty Benrey. Contrasting consequences of plant domestication for the chemical defenses of leaves and seeds in lima bean plants. *Basic and Applied Ecology*, may 2018.

- [95] A. E. Stapleton and V. Walbot. Flavonoids can protect maize DNA from the induction of ultraviolet radiation damage. *Plant Physiol.*, 105(3):881–889, Jul 1994.
- [96] P. L. Steponkus, M. Uemura, R. A. Joseph, S. J. Gilmour, and M. F. Thomashow. Mode of action of the COR15a gene on the freezing tolerance of *Arabidopsis thaliana*. *Proc. Natl. Acad. Sci. U.S.A.*, 95(24):14570–14575, Nov 1998.
- [97] Anthony Studer, Qiong Zhao, Jeffrey Ross-Ibarra, and John Doebley. Identification of a functional transposon insertion in the maize domestication gene *tb1*. *Nature Genetics*, 43(11):1160–1163, sep 2011.
- [98] Y. Takahashi, K. M. Teshima, S. Yokoi, H. Innan, and K. Shimamoto. Variations in *hd1* proteins, *hd3a* promoters, and *ehd1* expression levels contribute to diversity of flowering time in cultivated rice. *Proceedings of the National Academy of Sciences*, 106(11):4555–4560, feb 2009.
- [99] S. Takumi. Cold-specific and light-stimulated expression of a wheat (*triticum aestivum* L.) *cor* gene *wcor15* encoding a chloroplast-targeted protein. *Journal of Experimental Botany*, 54(391):2265–2274, oct 2003.
- [100] Maud I. Tenaillon, Matthew B. Hufford, Brandon S. Gaut, and Jeffrey Ross-Ibarra. Genome size and transposable element content as determined by high-throughput sequencing in maize and *zea luxurians*. *Genome Biology and Evolution*, 3:219–229, jan 2011.
- [101] Z. Tian, X. Wang, R. Lee, Y. Li, J. E. Specht, R. L. Nelson, P. E. McClean, L. Qiu, and J. Ma. Artificial selection for determinate growth habit in soybean. *Proceedings of the National Academy of Sciences*, 107(19):8563–8568, apr 2010.
- [102] S. Tsvetanov, R. Ohno, K. Tsuda, S. Takumi, N. Mori, A. Atanassov, and C. Nakamura. A cold-responsive wheat (*Triticum aestivum* L.) gene *wcor14* identified in a winter-hardy cultivar 'Mironovska 808'. *Genes Genet. Syst.*, 75(1):49–57, Feb 2000.
- [103] A. Turner. The pseudo-response regulator *ppd-h1* provides adaptation to photoperiod in barley. *Science*, 310(5750):1031–1034, nov 2005.
- [104] Huai Wang, Tina Nussbaum-Wagler, Bailin Li, Qiong Zhao, Yves Vigouroux, Marianna Faller, Kirsten Bomblies, Lewis Lukens, and John F. Doebley. The origin of the naked grains of maize. *Nature*, 436(7051):714–719, aug 2005.
- [105] Li Wang, Timothy M. Beissinger, Anne Lorant, Claudia Ross-Ibarra, Jeffrey Ross-Ibarra, and Matthew B. Hufford. The interplay of demography and selection during maize domestication and expansion. *Genome Biology*, 18(1), nov 2017.
- [106] Xianglan Wang, Hongwei Wang, Shengxue Liu, Ali Ferjani, Jiansheng Li, Jianbing Yan, Xiaohong Yang, and Feng Qin. Genetic variation in *ZmVPP1* contributes to drought tolerance in maize seedlings. *Nature Genetics*, 48(10):1233–1241, aug 2016.

- [107] Jacob D. Washburn, Kevin A. Bird, Gavin C. Conant, and J. Chris Pires. Convergent evolution and the origin of complex phenotypes in the age of systems biology. *International Journal of Plant Sciences*, 177(4):305–318, may 2016.
- [108] C. A. Webb, T. E. Richter, N. C. Collins, M. Nicolas, H. N. Trick, T. Pryor, and S. H. Hulbert. Genetic and molecular characterization of the maize rp3 rust resistance locus. *Genetics*, 162(1):381–394, Sep 2002.
- [109] J. L. Weller, L. C. Liew, V. F. G. Hecht, V. Rajandran, R. E. Laurie, S. Ridge, B. Wenden, J. K. Vander Schoor, O. Jaminon, C. Blassiau, M. Dalmais, C. Rameau, A. Bendahmane, R. C. Macknight, and I. Lejeune-Henaut. A conserved molecular basis for photoperiod adaptation in two temperate legumes. *Proceedings of the National Academy of Sciences*, 109(51):21158–21163, dec 2012.
- [110] Thomas Wicker, Yeisoo Yu, Georg Haberer, Klaus F. X. Mayer, Pradeep Reddy Marri, Steve Rounsley, Mingsheng Chen, Andrea Zuccolo, Olivier Panaud, Rod A. Wing, and Stefan Roffler. DNA transposon activity is associated with increased mutation rates in genes of rice and other grasses. *Nature Communications*, 7:12790, sep 2016.
- [111] Edward P. Wilhelm, Adrian S. Turner, and David A. Laurie. Photoperiod insensitive ppd-*ala* mutations in tetraploid wheat (*triticum durum* desf.). *Theoretical and Applied Genetics*, 118(2):285–294, oct 2008.
- [112] M. R. Woodhouse, H. Tang, and M. Freeling. Different gene families in *arabidopsis thaliana* transposed in different epochs and at different frequencies throughout the rosids. *The Plant Cell*, 23(12):4241–4253, dec 2011.
- [113] Margaret R. Woodhouse, James C. Schnable, Brent S. Pedersen, Eric Lyons, Damon Lisch, Shabarimuth Subramaniam, and Michael Freeling. Following tetraploidy in maize, a short deletion mechanism removed genes preferentially from one of the two homeologs. *PLoS Biology*, 8(6):e1000409, jun 2010.
- [114] Jian Wu, Keyun Wei, Feng Cheng, Shikai Li, Qian Wang, Jianjun Zhao, Guusje Bonnema, and Xiaowu Wang. A naturally occurring InDel variation in *BraA.FLC.b* (*BrFLC2*) associated with flowering time variation in *brassica rapa*. *BMC Plant Biology*, 12(1):151, 2012.
- [115] Weiya Xue, Yongzhong Xing, Xiaoyu Weng, Yu Zhao, Weijiang Tang, Lei Wang, Hongju Zhou, Sibin Yu, Caiguo Xu, Xianghua Li, and Qifa Zhang. Natural variation in *ghd7* is an important regulator of heading date and yield potential in rice. *Nature Genetics*, 40(6):761–767, may 2008.
- [116] L. Yan, D. Fu, C. Li, A. Blechl, G. Tranquilli, M. Bonafede, A. Sanchez, M. Valarik, S. Yasuda, and J. Dubcovsky. The wheat and barley vernalization gene *VRN3* is an orthologue of *FT*. *Proceedings of the National Academy of Sciences*, 103(51):19581–19586, dec 2006.
- [117] Yu-Xiang Yuan, Jian Wu, Ri-Fei Sun, Xiao-Wei Zhang, Dong-Hui Xu, Guusje Bonnema, and Xiao-Wu Wang. A naturally occurring splicing site mutation in the *brassica rapa* *FLC1* gene is associated with variation in flowering time. *Journal of Experimental Botany*, 60(4):1299–1308, feb 2009.

- [118] S. Zakhrabekova, S. P. Gough, I. Braumann, A. H. Muller, J. Lundqvist, K. Ahmann, C. Dockter, I. Matyszcak, M. Kurowska, A. Druka, R. Waugh, A. Graner, N. Stein, B. Steuernagel, U. Lundqvist, and M. Hansson. Induced mutations in circadian clock regulator *mat-a* facilitated short-season adaptation and range extension in cultivated barley. *Proceedings of the National Academy of Sciences*, 109(11):4326–4331, feb 2012.
- [119] Yongfei Zhang, Shuping Cheng, Darlene De Jong, Helen Griffiths, Rayko Halitschke, and Walter De Jong. The potato *r* locus codes for dihydroflavonol 4-reductase. *Theoretical and Applied Genetics*, 119(5):931–937, jul 2009.
- [120] Liguozhou, Zaochang Liu, Yunhua Liu, Deyan Kong, Tianfei Li, Shunwu Yu, Hanwei Mei, Xiaoyan Xu, Hongyan Liu, Liang Chen, and Lijun Luo. A novel gene *OsAHL1* improves both drought avoidance and drought tolerance in rice. *Scientific Reports*, 6(1), jul 2016.
- [121] B.-F. Zhu, L. Si, Z. Wang, Y. Z. Jingjie Zhu, Y. Shangguan, D. Lu, D. Fan, C. Li, H. Lin, Q. Qian, T. Sang, B. Zhou, Y. Minobe, and B. Han. Genetic control of a transition from black to straw-white seed hull in rice domestication. *PLANT PHYSIOLOGY*, 155(3):1301–1311, jan 2011.
- [122] Chuanfeng Zhu, Daniela Schraut, Wolfram Hartung, and Anton R. Schäffner. Differential responses of maize MIP genes to salt stress and ABA. *Journal of Experimental Botany*, 56(421):2971–2981, oct 2005.
- [123] Q. Zhu, X. Zheng, J. Luo, B. S. Gaut, and S. Ge. Multilocus analysis of nucleotide variation of *Oryza sativa* and its wild relatives: severe bottleneck during domestication of rice. *Mol. Biol. Evol.*, 24(3):875–888, Mar 2007.

Table 1: Prevalence of Domestication Syndrome Traits

Domestication Trait	In Grass Crops	In non-Grass Crops	References
Compact plant growth	yes	yes	[33, 63]
Reduced axillary branching	yes	yes	[63]
Reduced seed dormancy	yes	yes	[33, 25]
Changes in flowering time	yes	yes	[63]
Uniform flowering or maturation time	yes	yes	[63]
Vernalization	yes	yes	[8]
Increased resource allocation to harvested organ/larger organ (fruit, grain, root)	yes	yes	[75]
Compact inflorescence	yes	yes	[33, 38]
Non-shattering/indehiscent fruit or grain	yes	yes	[63, 19]
Changes in pigmentation	yes	yes	[63]
Self-fertilizing	yes	yes	[33]
Perennial to annual lifecycle	yes	yes	[33, 75]
Sexual to vegetative reproduction	no	yes	[70]
Reduced defensive structures (spines, thorns)	no	yes	[75, 85]
Reduced toxicity	no	yes	[75, 94]
Soft or naked kernel or seed	yes	no	[104]
Increased spikelets	yes	no	[33]
Increased number of kernel rows	yes	no	[63]

Table 2: Parallel or Convergent Orthologies

Crop species	Ortholog phylogeny	Phylogeny of domestication trait	Orthologous gene(s)	Gene product	Phenotypic trait	Trait type	Convergence	References
Rice, barley	Family	grass-wide	OsGA20ox-2, HvGA20ox-2	Metabolic enzyme	Dwarfism	domestication	parallel	[3, 2, 48]
Wheat	Species	species-specific, grass	Rht-1	SH2-TF	Dwarfism	domestication	convergent	[17]
Sorghum, pearl millet	Family	grass-wide	dw3, d2	Transporter protein	Dwarfism	domestication	parallel	[76, 82]
Tomato, soybean, common bean	Family/above family	outside the grasses	SP, Dt1, PvTFL1y	Signaling protein	Determinate growth	domestication	parallel	[17, 91, 69, 61, 101]
Sorghum, rice	Family	grass-wide	Ghd7, SbGhd7	CCT-domain protein	Flowering time	both	parallel	[115, 78]
Barley, pea, strawberry	Above family	grasses and beyond	HvCEN, PsTFL1c, FvTFL1	Signaling protein	Flowering time	both	parallel	[14, 28, 58]
Barley, wheat, ryegrass	Species/family	grass-wide	VRN1, BM5, TmAP1, WAP1, LpVRN1	MADS domain TF	Flowering time	both	parallel	[4]
Rice, barley, wheat, sorghum, sugar beet	Species/family/above family	grasses and beyond	OsPRR37, Ppd-H1, Ppd1, SbPRR37, BvBTC1	Circadian clock pathway	Flowering time	both	parallel	[77, 103, 49, 5, 111, 16]
Turnip, Brassica oleracea	Family	outside the grasses	BFLC2, BoFLC2	MADS domain TF	Flowering time	both	parallel	[114, 117, 80]
Rice, barley, pea, lentil	Family/above family	grasses and beyond	Hd17, EAM8, Mat-a, HR, LeELF3	Circadian clock pathway	Flowering time	both	parallel	[109, 73, 118, 24]
Rice, wheat, sunflower, barley	Family/above family	grasses and beyond	Hd3a (Heading date 3a), VRN3/TaFT, HaFT1, HvFT	Signaling protein	Flowering time	both	parallel	[116, 98, 9]
Rice	Species	species-specific, grass	Hd1	Zinc finger TF	Flowering time	both	convergent	[72]
Sorghum, rice, maize	Family	grass-wide	Sh1, OsSh1, ZnSh1	YABBY-like TF	Shatter resistance	domestication	parallel	[66]
Rice, wheat, maize, foxtail millet, barley, amaranth, sorghum, broom/Maize millet	Species/family/above family	grasses and beyond	GBSS1, Waxy	Metabolic enzyme	Glutinous seeds	domestication	parallel	[47, 23, 53, 54, 45, 81]
Rice, soybean	Species/family	grasses and beyond	BADH2, GmBADH2	Metabolic enzyme	Fragrance	domestication	parallel	[59, 51]
Rice, potato	Species/above family	grasses and beyond	RuDFR, DFR	Metabolic enzyme	Coloration	both	parallel	[31, 119]
Blood orange	Species	species-specific, outside grasses	Ruby	MYB-TF	Coloration	both	convergent	[11]
Rice	Species	species-specific, grass	Bh4	Transporter protein	Coloration	both	convergent	[121]
Soybean	Species	species-specific, outside grasses	R	MYB-TF	Coloration	both	convergent	[34]
Pea, potato	Above family	outside the grasses	flavonoid 3',5'-hydroxylase	Metabolic enzyme	Coloration	both	parallel	[72]
Rice	Species	species-specific, grass	Rc	bHLH-TF	Coloration	both	convergent	[72]
Grapevine	Species	species-specific, outside grasses	VvMYBA1-3	MYB-TF	Coloration	both	convergent	[72]
Maize: pearl millet, barley	Family	grass-wide	tb1, Pgrb1, INT-C	TCP-TF	Plant architecture	both	parallel	[97, 89, 88]
Barley	Species	species-specific, grass	VR51	Homeodomain-TF	Plant architecture	both	convergent	[72]
Maize	Species	species-specific, grass	Opaque2	bZIP-TF	Grain quality	domestication	convergent	[72]
Wheat, rye	Family	grass-wide	TaALMT1, ScALMT1	Transporter protein	Metal tolerance	adaptation	parallel	[72]
Sorghum, Maize	Family	grass-wide	SbMATE1, ZmMATE1	Transporter protein	Metal tolerance	adaptation	parallel	[72]
Barley, wheat, maize	Species/family	grass-wide	VRN2, ZCCT1, ZmCCT9	Zinc finger-CCT domain TF	Flowering time	adaptation	parallel	[43]
Maize, Arabidopsis	Above family	grasses and beyond	ZmVPP1, AVP1	Vacuolar-type H(+) pyrophosphatase	Drought tolerance	adaptation	parallel	[106]
Rice	Species	species-specific, grass	OsAHL1	AT-hook PPC domain	Drought tolerance	adaptation	convergent	[120]
Barley, wheat	Family	grass-wide	HVA1, Wrab18, Wrab19	LEA protein	Cold tolerance	adaptation	parallel	[42, 21]
Wheat, barley	Family	grass-wide	Wcs19, Wcor14, Wcor15, Bcor14b	Cor protein	Cold tolerance	adaptation	parallel	[99]
Barley, maize, spinach	Above family	grasses and beyond	HvPIP2;1, ZmPIP2-4, PM28A	Aquaporin	Soil salinity	adaptation	parallel	[52, 122, 27]
Rice, foxtail millet, tomato	Above family	grasses and beyond	OsASR1, OsASR3, SiASR1, SIASR1	ABA stress ASR protein	Soil salinity	adaptation	parallel	[65, 57]
Maize	Species	species-specific, grass	Rp3	NBS-LRR	Pathogen resistance	adaptation	convergent	[108]
Wheat, rice, sorghum	Family	grass-wide	LR34	ABC transporter	Pathogen resistance	adaptation	parallel	[60]

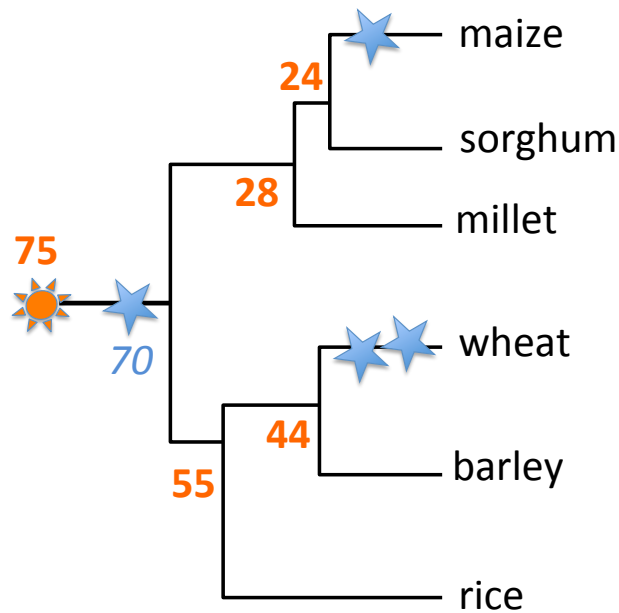


Figure 1: Simple cladogram of major cereal speciation. Numbers are in MYA (millions of years ago). Orange sun: grass speciation event 75 MYA. Blue stars: polyploidy events; the major grass polyploidy event immediately after the grass speciation event occurred approximately 70 MYA. The Ehrhartoideae clade, which includes rice, arose approximately 55MYA. The Pooideae clade, which includes wheat and barley, arose around 44MYA; Chloridoideae which contains foxtail millet 28 MYA, and the Panicoids, which include maize and sorghum, arose approximately 24MYA. The branch length is not proportional to the number of substitutions per site.