

Convergence in adaptation after domestication in the grasses

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Abstract

The selection of desirable traits in crops during domestication has been well studied. In this review, the authors explore the current research to determine to what extent domestication in grass cereal crops has shaped environmental adaptation, and whether it is possible to predict which loci in a cereal might confer adaptive properties.

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 <http://www.fao.org> **will need to include this as a citation in the bib file**. Over the last $\approx 10,000$ years, crops have been continually selected by humans for traits including nutrition, yield, and other attractive features with overall crop physiology changing dramatically. As such, domesticated crops are often radically different from their wild relatives. Notably, there are certain traits that often distinguish domesticated crops from their wild progenitors [18], distinctions that are 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, larger fruits or grains, and loss of shattering or seed dispersal (Table 1). This suite of shared traits is known as the domestication syndrome [39].

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 sometimes known as parallelism; parallelism is more likely to occur in closely related species [82]. Conversely, it is possible for unrelated genes in different enzymatic pathways to give rise to alleles which happen to code for similar traits, particularly when species experience similar selection pressures (either human or environmental). **thoughts on a citation here?** This phenomenon, known as convergence, is more likely to occur in substantially diverged species since there are fewer orthologous loci. **citation would be good here as well**

Table 1: Prevalence of Domestication Syndrome Traits

Domestication Trait	In Grass Crops	In non-Grass Crops	References
Compact plant growth	yes	yes	[33, 62]
Reduced axillary branching	yes	yes	[62]
Reduced seed dormancy	yes	yes	[33, 26]
Changes in flowering time	yes	yes	[62]
Uniform flowering or maturation time	yes	yes	[62]
Vernalization	yes	yes	[8]
Increased resource allocation to harvested organ/larger organ (fruit, grain, root)	yes	yes	[72]
Compact inflorescence	yes	yes	[33, 37]
Non-shattering/indehiscent fruit or grain	yes	yes	[62, 19]
Changes in pigmentation	yes	yes	[62]
Self-fertilizing	yes	yes	[33]
Perennial to annual lifecycle	yes	yes	[33, 72]
Sexual to vegetative reproduction	no	yes	[68]
Reduced defensive structures (spines, thorns)	no	yes	[72, 81]
Reduced toxicity	no	yes	[72, 90]
Soft or naked kernel or seed	yes	no	[100]
Increased spikelets	yes	no	[33]
Increased number of kernel rows	yes	no	[62]

After the initial wave of crop domestication yielded many of the aforementioned domestication syndrome traits, another level of domestication ensued—the adaptation of crop species to varied environmental conditions during global expansion. A cultivar of maize bred to thrive 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 due to the loss of diversity during genetic bottlenecks associated with both initial domestication and subsequent crop expansion [101].

Inclusion of a subset of wild relative diversity and selection on particular alleles that code for desirable traits (such as those in the domestication syndrome) have caused a diversity of alleles to be lost during domestication and crop expansion, particularly when breeding populations have been small. Loss of genetic diversity through these genetic bottlenecks can have consequences for adaptation. For example, a dramatic genetic bottleneck in the "lumper" variety of potato led to the infamous Potato Famine in Ireland in the 1840s. *perhaps mention *Phytophthora infestans* with a citation here?* 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.

The ways in which domestication has shaped the potential for adaptation in crops is the topic of this review. We will focus mainly on grass crops, since the major grass crop species—maize, rice, sorghum, wheat, barley, and millet—include a range of divergence times conducive to evolution of domestication syndrome traits through both parallelism and convergence. In addition, grasses share a certain amount of genomic dynamism, including polyploidization and transposable element activity, that can give rise to new alleles which can contribute to both domestication and adaptation. *not sure I quite understand the link here to convergence, but perhaps more clear further on* In this review we will discuss the extent to which the same genes that played a role in domestication syndrome in grass crops also play a potential role in adaptation, which adaptive traits are expected to be convergent or parallel, and if it is possible to predict with any certainty which loci are likely to yield adaptive alleles. *Let's briefly talk this through...I think we need to tweak*

Domestication in the grasses

Grasses as a whole have been viewed by some researchers as a single genetic system [7, 29], and there are many reasons why this point of view is useful for studying crop domestication. The grass clade is thought to have arisen around 75 MYA [10, 54] with rice, wheat, barley, millet, maize, and sorghum arising sequentially afterward (Figure 1). Prior to the radiation of the grasses, however, there was a genome duplication event approximately 70 MYA [79], which is shared among all grass crops (Figure 1), and both maize and wheat have undergone later polyploidy events after their respective species divergence (Figure 1) [63]. 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) [105, 66], makes the grasses more susceptible to a higher rate of functional mutation compared with

other crop species. Additionally, most grass crops were domesticated within the latitudinal boundaries of the equator and 35 N [45, 33], featuring both wet and dry seasons [45], which means that domesticated grasses shared similar environmental pressures such as temperature and day length; yet each grass cereal has been cultivated separately in separate geographic locations, including maize (Americas), sorghum (Africa), rice (Asia), millet (Eurasia), and wheat and barley (Middle East) [35], representing approaches to domestication that take into account culturally distinct selection of favorable traits. Taken together, these features make domesticated grass species especially conducive to a meaningful study of convergence vs parallelism in both domestication and adaptation of crops, and therefore, the six major domesticated grass crops—maize, rice, sorghum, wheat, barley, and millet—will be the focus of this review.

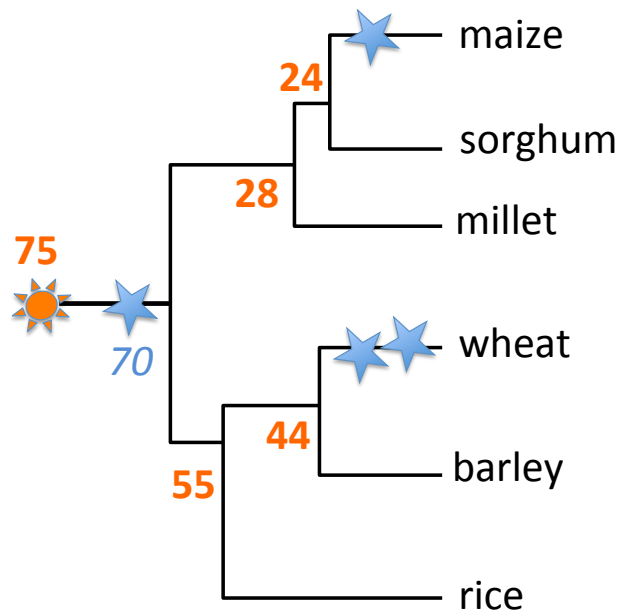


Figure 1: Simple cladogram of major cereal speciation. Numbers are in MYA (millions of years ago). Orange sun: grass speciation event 75 MYA. Blue stars: polyploidy events; the major grass polyploidy event immediately after the grass speciation event occurred approximately 70 MYA. The Ehrhartoideae clade, 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 Panicoideae, which include maize and sorghum, arose approximately 24MYA. The branch length is not proportional to the number of substitutions per site.

Grass crops share a number of domestication syndrome traits observed in other non-grass crop species; these traits are summarized in the introduction and in Table 1. However, there are a few domestication syndrome traits that are not observed in grass crops, such as reduced toxicity,

reduced defensive structures like spines and thorns—by and large the wild relatives of grass crops did not have these defense mechanisms to begin with—or vegetative reproduction. Alternately, there are some domestication syndrome traits in the grasses that are not observed in non-grass crops, such as increased spikelet number and increased number of kernel rows, because these traits occur on structures that do not exist in non-grass crop species.

Some of the genes involved in the domestication syndrome, both within and outside of the grasses, have been identified; these genes are summarized in Table 2 (modified from [62]). These domestication genes are categorized in Column 3 by whether or not they have orthologs strictly within a species, orthologs across the grasses, orthologs within and outside of the grasses, or orthologs entirely outside of the grasses. While there has been much debate regarding the delineation of parallel versus convergent traits **perhaps cite the Arendt and Reznick paper here**, for the purposes of this review we will use the definitions of both as set out in the introduction, where parallelism is defined as similar phenotypes due to mutations in orthologous genes, whereas convergence is due to mutations in genes that are not orthologous. Column 7 in Table 2 indicates whether a domestication gene is expected to be convergent or parallel, based on the phylogeny of orthology; for example, if a domestication gene is found only within a species, it cannot be selected in parallel. For instance, coloration in blood orange due to selection on the Ruby gene and coloration in grapevine due to selection on the *VvMYBA1-3* gene are predicted to be convergent since the alleles for these traits seem to be species-specific. And yet there are other coloration genes, such as *BADH2* and *DFR*, which occur in species as diverse as rice and soybean, or rice and potato, respectively. **have they been implicated as targets of selection during domestication?** It should be noted, however, that coloration is a very generic term, and enters into yet another level of argument regarding convergence or parallelism, associated with the physiological location of a domestication trait. Can a trait that is observed in vastly different organs such as a potato tuber and a rice grain (as with *DFR* coloration) truly be considered parallel, even if the alleles that code for them are on orthologous genes? **perhaps thinking about this as coloration of harvested plant part** For the purposes of this review, we will keep our definitions of convergence and parallelism to within gene families and enzymatic pathways.

What might cause domestication syndrome traits to be parallel (i.e. orthologous) rather than convergent? Lenser and Theissen's 2013 review [62] sets out four examples: (1) Genes occupying a nodal position upstream of genes that effect 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. The first three cases all rely on the retention of the orthologous genes throughout evolution that have not undergone functional divergence. Therefore, loss of certain orthologs prior to widespread crop domestication would ensure that parallel domestication for some traits would be impossible. Some of the genes predicted as convergent in Table 2 could have lost their orthologs in other species over evolutionary time.

Table 2 gives us a starting point to predict which domestication genes are likely to be found in the grasses, which genes in the grasses are likely to be parallel, and which are likely to be convergent. 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 QTLs with orthologs across species by simple comparative genomics. In fact, comparative genomics can

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, 47]
Wheat	Species	species-specific, grass	Rht-1	SH2-TF	Dwarfism	domestication	convergent	[18]
Sorghum, pearl millet	Family	grass-wide	dw3, d2	Transporter protein	Dwarfism	domestication	parallel	[73, 78]
Tomato, soybean, common bean	Family/above family	outside the grasses	SP, D1, P, TFL1y	Signaling protein	Determinate growth	domestication	parallel	[18, 87, 67, 60, 97]
Barley, pea, strawberry	Above family	grasses and beyond	HvCEN, P, TFL1c, FvTFL1	Signaling protein	Flowering time	both	parallel	[14, 28, 57]
Barley, wheat, ryegrass	Species/family	grass-wide	VRN1, BM5, TmaP1, WAP1, LpVRN1	MADS domain TF	Flowering time	both	parallel	[4]
Barley, wheat, maize	Species/family	grass-wide	VRN2, ZCCT1, ZmZCCT9	Zinc finger-CCT domain TF	Flowering time	both	parallel	[42]
Rice, barley, wheat, sorghum, sugar beet	Species/family/above family	grasses and beyond	OsPRR37, Ppd-H1, Ppd1, ShPRR37, BvBTC1	Circadian clock pathway	Flowering time	both	parallel	[74, 99, 48, 5, 106, 16]
Turnip, Brassica oleracea	Family	outside the grasses	BtFLC2, BoFLC2	MADS domain TF	Flowering time	both	parallel	[109, 111, 76]
Rice, barley, pea, lentil	Family/above family	grasses and beyond	Hd17, EAM8, Mat-a, HR, LcELF3	Circadian clock pathway	Flowering time	both	parallel	[104, 71, 112, 25]
Rice, wheat, sunflower, barley	Family/above family	grasses and beyond	Hd3a(Heading date 3a), VRN3/TaFT, HaFT1, HvFT3a	Signaling protein	Flowering time	both	parallel	[110, 95, 9]
Rice	Species	species-specific, grass	Hd1	Zinc finger TF	Flowering time	both	convergent	[70]
Sorghum, rice, maize	Family	grass-wide	Sh1, OsSh1, ZmSh1	YABBY-like TF	Shatter resistance	domestication	parallel	[65]
Rice, wheat, maize, foxtail millet, barley, amaranth, sorghum, broom	Species/family/above family	grasses and beyond	GBSSI, Waxy	Metabolic enzyme	Glutinous seeds	domestication	parallel	[46, 24, 52, 53, 44, 77]
Rice, soybean	Species/family	grasses and beyond	BADH2, GmBADH2	Metabolic enzyme	Fragrance	domestication	parallel	[58, 50]
Rice, potato	Species/above family	grasses and beyond	Ru/DFR, DFR	Metabolic enzyme	Coloration	both	parallel	[31, 113]
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	[115]
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	[70]
Rice	Species	species-specific, grass	Rc	bHLH-TF	Coloration	both	convergent	[70]
Grapevine	Species	species-specific, outside grasses	VvMYBA1-3	MYB-TF	Coloration	both	convergent	[70]
Maize, pearl millet, barley	Family	grass-wide	tbl, Pgtb1, INT-C	TCP-TF	Plant architecture	both	parallel	[93, 85, 84]
Barley	Species	species-specific, grass	VRs1	Homeodomain-TF	Plant architecture	both	convergent	[70]
Maize	Species	species-specific, grass	Opaque2	bZIP-TF	Grain quality	domestication	convergent	[70]
Wheat, rye	Family	grass-wide	TtaALMT1, ScALMT1	Transporter protein	Metal tolerance	adaptation	parallel	[70]
Sorghum, Maize	Family	grass-wide	SbMATE1, ZmMATE1	Transporter protein	Metal tolerance	adaptation	parallel	[70]
Maize, Arabidopsis	Above family	grasses and beyond	ZmVPP1, AVP1	Vacuolar-type H(+) pyrophosphatase	Drought tolerance	adaptation	parallel	[102]
Rice	Species	species-specific, grass	OsAHL1	AT-hook PPC domain	Drought tolerance	adaptation	convergent	[114]
Barley, wheat	Family	grass-wide	HVA1, Wrab18, Wrab19	LEA protein	Cold tolerance	adaptation	parallel	[41, 22]
Wheat, barley	Family	grass-wide	Wcs19, Wcor14, Wcor15, Bcor14b	Cor protein	Cold tolerance	adaptation	parallel	[96]
Barley, maize, spinach	Above family	grasses and beyond	HvPIP2;1, ZmPIP2-4, PM28A	Aquaporin	Soil salinity	adaptation	parallel	[51, 116, 27]
Rice, foxtail millet, tomato	Above family	grasses and beyond	OsASR1, OsASR3, SiASR1, SiASR1	ABA stress ASR protein	Soil salinity	adaptation	parallel	[64, 56]
Maize	Species	species-specific, grass	Rp3	NBS-LRR	Pathogen resistance	adaptation	convergent	[103]
Wheat, rice, sorghum	Family	grass-wide	LR34	ABC transporter	Pathogen resistance	adaptation	parallel	[59]

easily demonstrate that many of the genes in Table 2 described as convergent do in fact have orthologs in other clades, even if the function of these orthologs have yet to be deduced (Figure 2). But to what extent can this knowledge help us to understand how domestication has impacted a crop's ability to adapt to new environments?

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 shatterproofing would not be considered favorable; therefore, we will narrow down the definition of an adaptive trait in this review 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: The level of carbon dioxide in the air; the level of UV radiation due to altitude; temperature; daylength; humidity; rainfall; wind; soil nutrient load; soil salinity; and pathogen microbiome. By dividing the environment into these discrete elements, we can now address each element individually by asking what sort of adaptive trait we would expect to observe in response to each, and how many of these adaptive traits are expressed in the same genetic pathway as known domestication genes.

If we take another look at Table 2, Column F, we find descriptions of domestication phenotypes that seem to also describe traits that would be involved in response to environment. For example, variation in flowering time is known to be a response to photoperiod sensitivity: the gene *ZmCCT9* in maize appears to be involved in flowering under the long days of higher latitudes in the Americas, but a transposon insertion upstream of *ZmCCT9* in domesticated maize cultivars is thought to have led to reduced photoperiod sensitivity, which has allowed domesticated maize to expand its range [42]. This is an excellent example of a domestication-related gene that has an environmentally adaptive component.

Another example of a domestication trait with an adaptive component is coloration. Loss of coloration has been favored in a variety of cereal cultivars, from rice to maize, as a cultural preference (ref?). As it turns out, coloration assists with UV tolerance in cereals and other plant species [91, 36]. Therefore, a return of coloration could likely lead to a greater tolerance of UV radiation in cereals that were bred at higher elevations [83]. Table 2 attempts to match examples of adaptation traits to domestication traits, where possible, using the definition of adaptive as described above.

On the flip side, 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. Table 2 includes some adaptive genes and their orthologs, and whether or not they are associated with domestication traits. Adaptive genes not expected to be associated with domestication include the maize *ZmVPP1* gene, where an upstream insertion is linked to drought tolerance [102]. Since this gene has a drought-tolerant ortholog in Arabidopsis, *AVP1* [32], it suggests that orthologs could exist elsewhere in the cereals as well. However, another drought-tolerance gene in rice, *OsAHL1* [114],

does not appear to have a defined drought-tolerant ortholog in any other species at the time of this writing. Wheat and barley possess a small family of cold-tolerance genes including *Wcs19* [13], *Wcor14* [98] and *Bcor14b* [15], all of which encode chloroplast-targeted COR proteins analogous to the Arabidopsis protein *COR15a* [92, 96]. The LEA protein orthologs *HVA1* and *Wrab 18/19* in barley and wheat, respectively, are also associated with cold tolerance [41, 22]. 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 [51]. *HvPIP2* has an ortholog in maize, *ZmPIP2-4* [116], 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 [49], *Setaria* (millet) [64], and tomato [56].

Of course, finding orthologs for genes known to be adaptive is no guarantee that the function will be similar in different species. Though foxtail millet has a functional ortholog of the maize *tb1* (*teosinte branched1*) gene [17] which restricts branching in domesticated maize, the foxtail millet ortholog only exhibits slight control over branching, which shows that even though two species might share orthology for a gene, it does not mean that the phenotype will be the same in both species [20]. And so far, we have only discussed adaptive phenotypes that are driven by alleles in one locus; this neglects all the other adaptive phenotypes that are due to alleles at multiple loci. Most importantly, however, the extent to which we can expect to find adaptive alleles for existing orthologs is dependent on the severity of the domestication bottleneck within a given cereal species.

Domestication bottlenecks are the result of selection for traits that make for desirable crops but not necessarily for environmental adaptability. Massive nucleotide diversity loss is reported in domesticated bread wheat [40], maize (with an increase in deleterious alleles) [23, 101], rice [117], Sorghum [38], and barley [55] 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 pose a challenge.

Outside of breeding to a wild relative, is it possible for cereal crops to be rescued from a diversity bottleneck? We have seen that grasses tend to have relatively active transposons, and this transposon activity may permit a higher mutation rate in cereals than in other crops, allowing for new alleles to arise in a population. In Table 2, several of the domestication and adaptive phenotypes are due to a transposon insertion somewhere in the functional region of a gene: *tb1* [93], *ZmCCT9*, and *ZmVVP1*, to name just a few. In addition, diversity in waxy foxtail millet crops in southeast Asia was shown to be mediated by multiple transposable element insertions [53]. However, a comprehensive review of TEs and plant evolution [66] 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 [61].

Loss of allelic diversity due to domestication bottlenecks may have a more significant impact on those adaptive phenotypes that are controlled by the same genes that control domestication phenotypes (such as *ZmZCCT9*), rather than on the genes that appear unrelated to domestication (such as *ZmVPP1*). So it is not a foregone conclusion that a bottleneck in a flowering time allele, for

instance, would necessarily lead to a bottleneck in an allele related to drought tolerance, unless loss of diversity in a population were severe and genome-wide, or unless drought tolerance and flowering time were phenotypically or genetically linked. Therefore, one might predict that selection for transposable element insertion would be greater for domestication-syndrome adaptation alleles than in adaptation alleles unrelated to domestication syndrome.

But another way an adaptation trait could escape a domestication bottleneck is if the domestication-syndrome allele were on a gene with a retained homeolog, allowing for subfunctionalization or neofunctionalization of the other homeolog to an adaptive allele. Neofunctionalization of homeologs is widespread in maize [43], which has undergone a recent tetraploidy event approximately 5-12MYA [94]; and in bread wheat, subfunctionalization of homeologs as a result of wheat's hexaploidy event appear to have given rise to alleles associated with baking quality [80].

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) [108, 88], and there is evidence that fractionation is biased not only in maize, but in wheat as well [21]. Schnable and Freeling found that of the "classical" maize genes, or characterized genes that have a known mutant phenotype, the majority are on the less fractionated subgenome [89]. 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 [86] because they are under greater purifying selection. If genes associated with domestication tend to be on the less fractionated subgenome, and greater phenotypic variation is observed in the less fractionated subgenome, then adaptive traits should more likely be associated with the homeolog on the less fractionated subgenome. 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 [89]. Yet about forty percent of the genes on the more fractionated subgenome do exhibit some amount of expression dominance and phenotypic variation [86], and genome dominance alone is not a guarantee that adaptive alleles could not arise on the more fractionated genome as well.

Finally, there are some adaptive traits that are less likely to have orthologs in even closely related species. These include pathogen resistance and stress response. While there are examples of pathogen defense and stress response genes in the grasses that are orthologous to other species (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 [107]; reviewed in [1]. Orphan genes tend to be very dynamic, arising and becoming lost much faster than their basal counterparts [30]. 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 convergence 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 uniquely to its niche. 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, 69] reviewed in [75], and this is one way that crop species might be able to

escape domestication bottlenecks in adaptation.

Conclusions

This review set out to explore how domestication has influenced the potential for adaptation in the grasses. Factors of domestication that have influenced adaptation include the selection for domestication traits that also have adaptive qualities, and to what extent diversity of a locus has undergone a domestication bottleneck. We discussed the possible ways that a crop might escape a domestication bottleneck, including homeolog sub- or neofunctionalization, transposable element activity, and trans duplication or fast-evolvability of lineage-specific adaptive genes. We also set out to see whether it is possible to predict the likelihood of adaptability of any given trait, irrespective of domestication syndrome effects. How realistically we can predict this in any given cereal crop is dependent upon (1) the existence of an ortholog to a known adaptive gene in another species; (2) the retention of functionality in the ortholog; (3) which subgenome a putatively adaptive gene is on within a species that had undergone a recent polyploidy; and (4) the propensity of an adaptive gene or gene family to be orthologous. Table 2 attempts to summarize these findings by correlating adaptivity with domestication traits as well as orthology in other species.

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 *loium 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. Poverino 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] J. Doebley, A. Stec, and L. Hubbard. The evolution of apical dominance in maize. *Nature*, 386(6624):485–488, Apr 1997.
- [18] John F. Doebley, Brandon S. Gaut, and Bruce D. Smith. The molecular genetics of crop domestication. *Cell*, 127(7):1309–1321, dec 2006.

- [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] Andrew N. Doust, Katrien M. Devos, Michael D. Gadberry, Mike D. Gale, and Elizabeth A. Kellogg. Genetic control of branching in foxtail millet. *Proceedings of the National Academy of Sciences*, 101(24):9045–9050, jun 2004.
- [21] N. A. Eckardt. Genome dominance and interaction at the gene expression level in allohexaploid wheat. *The Plant Cell*, 26(5):1834–1834, may 2014.
- [22] 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.
- [23] 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.
- [24] 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.
- [25] 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.
- [26] 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.
- [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] 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.
- [37] 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.
- [38] M. T. Hamblin. Challenges of detecting directional selection after a bottleneck: Lessons from sorghum bicolor. *Genetics*, 173(2):953–964, apr 2006.
- [39] Karl Hammer. Das domestikationssyndrom. *Die Kulturpflanze*, 32(1):11–34, jun 1984.
- [40] 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.
- [41] 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.
- [42] 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.
- [43] 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.

- [44] 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.
- [45] 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.
- [46] 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.
- [47] 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.
- [48] 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.
- [49] Joungsu 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.
- [50] 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.
- [51] 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.
- [52] 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.
- [53] 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.
- [54] E. A. Kellogg. Evolutionary history of the grasses. *PLANT PHYSIOLOGY*, 125(3):1198–1205, mar 2001.

- [55] 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.
- [56] 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.
- [57] 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.
- [58] 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.
- [59] 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.
- [60] 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.
- [61] Xianjun Lai, James C. Schnable, Zhengqiao Liao, Jie Xu, Gengyun Zhang, Chuan Li, Er-liang 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.
- [62] Teresa Lenser and Günter Theißen. Molecular mechanisms involved in convergent crop domestication. *Trends in Plant Science*, 18(12):704–714, dec 2013.
- [63] A. A. Levy. The impact of polyploidy on grass genome evolution. *PLANT PHYSIOLOGY*, 130(4):1587–1593, dec 2002.
- [64] 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.
- [65] 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.

- [66] D. R. Lisch. Mutator transposase is widespread in the grasses. *PLANT PHYSIOLOGY*, 125(3):1293–1303, mar 2001.
- [67] 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.
- [68] Jun Lyu. Unearthing potato evolution. *Nature Plants*, 3(12):912–912, dec 2017.
- [69] 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.
- [70] 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.
- [71] 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.
- [72] 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.
- [73] 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.
- [74] 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.
- [75] 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.
- [76] 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.
- [77] 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.
- [78] 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.

- [79] 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.
- [80] 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.
- [81] B. Pickersgill. Domestication of plants in the americas: Insights from mendelian and molecular genetics. *Annals of Botany*, 100(5):925–940, jul 2007.
- [82] Barbara Pickersgill. Parallel vs. convergent evolution in domestication and diversification of crops in the americas. *Frontiers in Ecology and Evolution*, 6, may 2018.
- [83] 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.
- [84] 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.
- [85] 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.
- [86] 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.
- [87] 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.
- [88] 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.
- [89] 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.

- [90] 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.
- [91] 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.
- [92] 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.
- [93] 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.
- [94] Z. Swigonova. Close split of sorghum and maize genome progenitors. *Genome Research*, 14(10a):1916–1923, sep 2004.
- [95] 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.
- [96] 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.
- [97] 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.
- [98] 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.
- [99] A. Turner. The pseudo-response regulator *ppd-h1* provides adaptation to photoperiod in barley. *Science*, 310(5750):1031–1034, nov 2005.
- [100] 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.
- [101] 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.
- [102] 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.

- [103] 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.
- [104] 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.
- [105] 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.
- [106] Edward P. Wilhelm, Adrian S. Turner, and David A. Laurie. Photoperiod insensitive ppd-a1a mutations in tetraploid wheat (triticum durum desf.). *Theoretical and Applied Genetics*, 118(2):285–294, oct 2008.
- [107] 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.
- [108] Margaret R. Woodhouse, James C. Schnable, Brent S. Pedersen, Eric Lyons, Damon Lisch, Shabarinath 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.
- [109] 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.
- [110] 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.
- [111] 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.
- [112] 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.

- [113] 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.
- [114] 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.
- [115] 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.
- [116] 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.
- [117] 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.