

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 [28]. Over the last $\approx 10,000$ years, crops have been continually selected by humans for traits including nutrition, yield, and other attractive features a process that has dramatically changed crop physiology. 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 collectively known as the domestication syndrome [42].

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 [85]. 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 [19]). This phenomenon, known as convergence, is more likely to occur in substantially diverged species since there are fewer orthologous loci [106, 85].

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

Table 1: Prevalence of Domestication Syndrome Traits

Domestication Trait	In Grass Crops	In non-Grass Crops	References
Compact plant growth	yes	yes	[35, 65]
Reduced axillary branching	yes	yes	[65]
Reduced seed dormancy	yes	yes	[35, 27]
Changes in flowering time	yes	yes	[65]
Uniform flowering or maturation time	yes	yes	[65]
Vernalization	yes	yes	[8]
Increased resource allocation to harvested organ/larger organ (fruit, grain, root)	yes	yes	[75]
Compact inflorescence	yes	yes	[35, 40]
Non-shattering/indehiscent fruit or grain	yes	yes	[65, 20]
Changes in pigmentation	yes	yes	[65]
Self-fertilizing	yes	yes	[35]
Perennial to annual lifecycle	yes	yes	[35, 75]
Sexual to vegetative reproduction	no	yes	[71]
Reduced defensive structures (spines, thorns)	no	yes	[75, 84]
Reduced toxicity	no	yes	[75, 93]
Soft or naked kernel or seed	yes	no	[103]
Increased spikelets	yes	no	[35]
Increased number of kernel rows	yes	no	[65]

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 [104].

Only a subset of wild relative 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 in 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 the catastrophic outbreak of *Phytophthora infestans*, resulting in the infamous Potato Famine in Ireland in the 1840s [38]. 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/convergence during post-domestication adaptation. 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 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 enable further adaptation.

Domestication in the grasses

Grasses as a whole have often been studied as a cohesive genetic group [7, 31], 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, 57] 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 [82], which is shared among all grass crops (Figure 1). Subsequently, both maize and wheat have undergone additional, lineage-specific polyploidy events (Figure 1) [66]. 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) [109, 69], make 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 [48, 35], featuring both wet and dry seasons [48], which means that many

domesticated grasses shared similar environmental pressures such as temperature and day length; yet 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) [37]. Approaches to domestication in these distinct regions reflected culturally distinct selection of traits. Taken together, these features make domesticated grass species especially conducive to the meaningful study of convergence and parallelism. We argue that the six major domesticated grass crops in particular—maize, rice, sorghum, wheat, barley, and millet—with their shared histories of selection for domestication traits and adaptation during global expansion offer compelling opportunities for basic evolutionary insight regarding the repeatability of evolution.

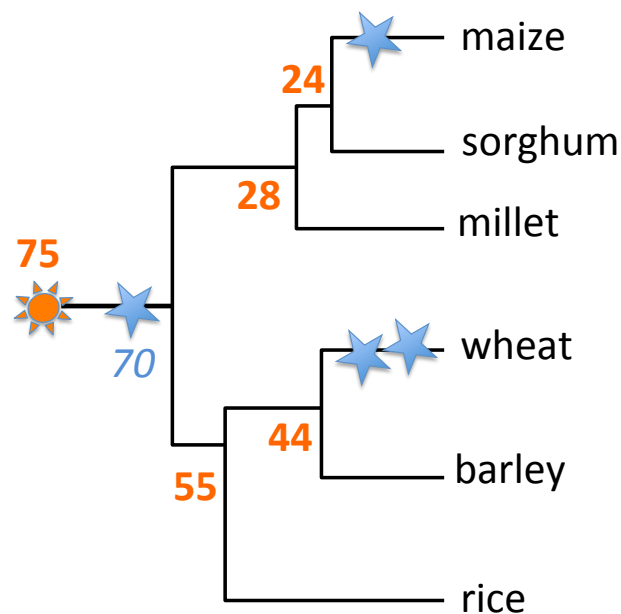


Figure 1: Simple cladogram of major cereal speciation. Numbers are in MYA (millions of years ago). Orange sun: grass speciation event 75 MYA. Blue stars: polyploidy events; the major grass polyploidy event immediately after the grass speciation event occurred approximately 70 MYA. The Ehrhartoideae clade, 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 do share a number of common 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 genes involved in the domestication syndrome are being identified both within and outside of the grasses; these genes are summarized in Table 2 (modified from [65]). Grass domestication genes specifically can be categorized by 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). We have expanded upon examples identified by [65] in Table 2, indicating in column 7 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 species, it cannot be selected in parallel. **check to make sure this is new** For instance, coloration in blood orange through selection on the Ruby gene and coloration in grapevine due to selection on the *VvMYBA1-3* gene is an example of convergence since these respective genes appear to be species-specific. Other coloration genes, such as *BADH2* and *DFR* (Table 2), occur orthologously in species as diverse as rice, soybean, and potato. We should note, however, that coloration is a broad term, and raises an important question 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 occur in orthologous genes? 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? A review by Lenser and Theissen [65] 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 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 QTL with orthologs across species by simple comparative genomics. In fact, comparative genomics can 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?

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, 50]
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	[76, 81]
Tomato, soybean, common bean	Family/above family	outside the grasses	SP, Dt1, PvTFL1y	Signaling protein	Determinate growth	domestication	parallel	[18, 90, 70, 63, 100]
Barley, pea, strawberry	Above family	grasses and beyond	HvCEN, PsTFL1c, FvTFL1	Signaling protein	Flowering time	both	parallel	[14, 30, 60]
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	[45]
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, 102, 51, 5, 110, 16]
Turnip, Brassica oleracea	Family	outside the grasses	BFLC2, BoFLC2	MADS domain TF	Flowering time	both	parallel	[113, 115, 79]
Rice, barley, pea, lentil	Family/above family	grasses and beyond	Hd17, EAM8, Mat-a, HR, LeELF3	Circadian clock pathway	Flowering time	both	parallel	[108, 74, 116, 26]
Rice, wheat, sunflower, barley	Family/above family	grasses and beyond	Hd3a (Heading date 3a), VRN3/TaFT, HaFT1, HvFT	Signaling protein	Flowering time	both	parallel	[114, 98, 9]
Rice	Species	species-specific, grass	Hd1	Zinc finger TF	Flowering time	both	convergent	[73]
Sorghum, rice, maize	Family	grass-wide	Sh1, OsSh1, ZmSh1	YABBY-like TF	Shatter resistance	domestication	parallel	[68]
Rice, wheat, maize, foxtail millet, barley, amaranth, sorghum, broomMaize millet	Species/family/above family	grasses and beyond	GBSS1, Waxy	Metabolic enzyme	Glutinous seeds	domestication	parallel	[49, 25, 55, 56, 47, 80]
Rice, soybean	Species/family	grasses and beyond	BADH2, GmBADH2	Metabolic enzyme	Fragrance	domestication	parallel	[61, 53]
Rice, potato	Species/above family	grasses and beyond	RuDFR, DFR	Metabolic enzyme	Coloration	both	parallel	[33, 117]
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	[119]
Soybean	Species	species-specific, outside grasses	R	MYB-TF	Coloration	both	convergent	[36]
Pea, potato	Above family	outside the grasses	flavonoid 3',5'-hydroxylase	Metabolic enzyme	Coloration	both	parallel	[73]
Rice	Species	species-specific, grass	Rc	bHLH-TF	Coloration	both	convergent	[73]
Grapevine	Species	species-specific, outside grasses	VvMYBA1-3	MYB-TF	Coloration	both	convergent	[73]
Maize, pearl millet, barley	Family	grass-wide	tb1, Pgrb1, INT-C	TCP-TF	Plant architecture	both	parallel	[96, 88, 87]
Barley	Species	species-specific, grass	VR51	Homeodomain-TF	Plant architecture	both	convergent	[73]
Maize	Species	species-specific, grass	Opaque2	bZIP-TF	Grain quality	domestication	convergent	[73]
Wheat, rye	Family	grass-wide	TaALMT1, ScALMT1	Transporter protein	Metal tolerance	adaptation	parallel	[73]
Sorghum, Maize	Family	grass-wide	SbMATE1, ZmMATE1	Transporter protein	Metal tolerance	adaptation	parallel	[73]
Maize, Arabidopsis	Above family	grasses and beyond	ZmVPP1, AVP1	Vacuolar-type H(+) pyrophosphatase	Drought tolerance	adaptation	parallel	[105]
Rice	Species	species-specific, grass	OsAHL1	AT-hook PPC domain	Drought tolerance	adaptation	convergent	[118]
Barley, wheat	Family	grass-wide	HVA1, Wrab18, Wrab19	LEA protein	Cold tolerance	adaptation	parallel	[44, 23]
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	[54, 120, 29]
Rice, foxtail millet, tomato	Above family	grasses and beyond	OsASR1, OsASR3, SiASR1, SiASR3	ABA stress ASR protein	Soil salinity	adaptation	parallel	[67, 59]
Maize	Species	species-specific, grass	Rp3	NBS-LRR	Pathogen resistance	adaptation	convergent	[107]
Wheat, rice, sorghum	Family	grass-wide	LR34	ABC transporter	Pathogen resistance	adaptation	parallel	[62]

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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 [45]. 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 [94, 39]. Therefore, a return of coloration could likely lead to a greater tolerance of UV radiation in cereals that were bred at higher elevations [86]. 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 [105]. Since this gene has a drought-tolerant ortholog in Arabidopsis, *AVPI* [34], it suggests that orthologs could exist elsewhere in the cereals as well. However, another drought-tolerance gene in rice, *OsAHL1* [118], 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* [101] and *Bcor14b* [15], all of which encode chloroplast-targeted COR proteins analogous to the Arabidopsis protein *COR15a* [95, 99]. The LEA protein orthologs *HVA1* and *Wrab18/19* in barley and wheat, respectively, are also associated with cold tolerance [44, 23]. 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 [54]. *HvPIP2* has an ortholog in maize, *ZmPIP2-4* [120], and in spinach, *PM28A* [29]. There are also the ASR (abscisic acid, stress, and

ripening-induced) genes that are associated with salinity tolerance in rice [52], *Setaria* (millet) [67], and tomato [59].

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 [21]. 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 [43], maize (with an increase in deleterious alleles) [24, 104], rice [121], Sorghum [41], and barley [58] 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* [96], *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 [56]. However, a comprehensive review of TEs and plant evolution [69] 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 [64].

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 *ZmCCT9*), rather than on the genes that appear unrelated to domestication (such as *ZmVVP1*). 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 home-

ologs is widespread in maize [46], which has undergone a recent tetraploidy event approximately 5-12MYA [97]; 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 [83].

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) [112, 91], and there is evidence that fractionation is biased not only in maize, but in wheat as well [22]. 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 [92]. 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 [89] 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 [92]. Yet about forty percent of the genes on the more fractionated subgenome do exhibit some amount of expression dominance and phenotypic variation [89], 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 [111]; reviewed in [1]. Orphan genes tend to be very dynamic, arising and becoming lost much faster than their basal counterparts [32]. 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 [32, 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, 72] reviewed in [78], 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.

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