Alternative Modes of Introgression-Mediated Selection Shaped Crop Adaptation to Novel Climates

José Luis Blanco-Pastor 🄳 *

Department of Plant Biology and Ecology, Universidad de Sevilla, Sevilla, Spain

*Corresponding author: E-mail: jblanco2@us.es.

Abstract

Recent plant genomic studies provide fine-grained details on the evolutionary consequences of adaptive introgression during crop domestication. Modern genomic approaches and analytical methods now make it possible to better separate the introgression signal from the demographic signal thus providing a more comprehensive and complex picture of the role of introgression in local adaptation. Adaptive introgression has been fundamental for crop expansion and has involved complex patterns of gene flow. In addition to providing new and more favorable alleles of large effect, introgression during the early stages of domestication also increased allelic diversity at adaptive loci. Previous studies have largely underestimated the effect of such increased diversity following introgression. Recent genomic studies in wheat, potato, maize, grapevine, and ryegrass show that introgression of multiple genes, of as yet unknown effect, increased the effectiveness of purifying selection, and promoted disruptive or fluctuating selection in early cultivars and landraces. Historical selection processes associated with introgression from crop wild relatives provide an instructive analog for adaptation to current climate change and offer new avenues for crop breeding research that are expected to be instrumental for strengthening food security in the coming years.

Key words: crop wild relatives, purifying selection, fluctuating selection, hybridization, polygenic adaptation, climate change.

Significance

Climate change threats on crops are increasing while the genetic base of crops is shrinking. This, coupled with increasing global demand for food, compels us to investigate the genetic diversity associated with adaptation and productivity in unfavorable climates. Results from recent studies show that some crops have benefited from increased genetic diversity following introgression with wild relatives. Such introgression compensated for the effect of unfavorable variants fixed during domestication through various modes of selection on introgressed variants. Characterizing how selection has impacted introgressed genomic variation may show the way forward for adapting current crops to climate change.

The Adaptive Significance of Introgression

The concept of *Introgression* (see Glossary) was originally coined by Anderson and Hubricht (1938). In their seminal paper, introgression was already defined as a pervasive process with a marked adaptive significance. The theoretical framework illustrating the evolutionary significance of introgression was developed 70 years later (Barton 2001).

Since the publication of this theoretical paper, and thereafter in empirical studies, the adaptive significance has been said to be mainly driven by the incorporation of favorable mutations that are rare in the initial stages of introgression. A deeper understanding of its adaptive value led to a consistent increase in publications aiming to identify the adaptive component of introgression in multiple plant groups (Suarez-Gonzalez, Lexer, et al. 2018), a trend that continues today in the genomic era (e.g., Menon et al.

Glossary

- **Disruptive selection**—A mode of natural selection in which extreme values of a trait are favored over intermediate values. Under disruptive selection (also called diversifying selection), the variance of the trait increases and the population splits into two distinct groups.
- **Fluctuating selection**—A mode of natural selection characterized by the fluctuation of the direction of selection on a given phenotype over a relatively brief period of evolutionary time (e.g., across years).
- **Hybridization**—The process of interbreeding between two dissimilar genetic entities (taxa, varieties, or lines) to produce a hybrid with new allele combinations.
- **Incomplete lineage sorting**—A phenomenon in population genetics in which gene copies do not coalesce (looking backwards in time) into a common ancestral copy until beyond previous speciation events. This phenomenon causes discordance between the gene tree and the population or species tree. Incomplete lineage sorting is also termed as deep coalescence or retention of ancestral polymorphisms.
- **Introgression**—The transfer of genetic variation between species through hybridization and repeated backcrossing. The purpose of introgression in crop breeding is to incorporate alleles from one species to the gene pool of another.
- **Linkage drag**—Undesirable effect of nontargeted QTLs in linkage disequilibrium with the QTLs of interest that are being introgressed.
- **Mutation/genetic load**—The decrease in fitness of the average individual in a population relative to the fittest genotype due to the presence of deleterious genes in the gene pool.
- **Purifying selection**—Selection against deleterious alleles.

2021; Morales-Cruz et al. 2021; Rendón-Anaya et al. 2021). Well-designed and very recent genomic studies that use new analytical approaches developed for genome-wide data sets (see Box 1) confirm that introgression provides new and better adapted genetic variants that have been positively selected either by natural selection in crop wild relatives (CWR) or human-mediated selection in cultivars or landraces. However, this is only a small fraction of the diversity of adaptive mechanisms generated after introgression. Introgression can increase the genome-wide genetic diversity which has several adaptive consequences: (1) it can promote new allelic combinations that are favorable for particular environmental conditions, (2) it can improve the efficiency of purifying selection to eliminate deleterious alleles, and (3) it can also promote *disruptive* or *fluctuating selection* in geographical areas with a spatially or temporally highly variable climate.

Introgression from CWR has the potential to increase the adaptive capacity of crops (Dempewolf et al. 2014, 2017). The germplasm of domesticated plants is the product of a continuing history of hybridization to incorporate desired variability and selection on the desired traits while trying to avoid linkage drag (Harlan 1975; Fuentes et al. 2022). Thanks to genetic studies, we know that many crop improvements originated from introgression from close relatives. For example, genes for resistance to grassy stunt virus, brown planthopper, bacterial blight, blast, together with genes related to drought and salt tolerance have been transferred from the wild rice species *Oryza nivara*, *O. longistaminata*, and *O. rufipogon* into the cultivated rice (Brar and Khush 1997; Zhang et al. 2006; Ballini et al. 2007; Quan et al. 2018). Introgression from teosinte (*Zea mays* ssp. *parviglumis*) conferred maize resistance to gray leaf-spot disease (Lennon et al. 2016). Alien introgressions from wild *Triticum* and *Aegilops* species conferred bread wheat resistance to multiple diseases, pests, cold and drought stress (Grama and Gerechter-Amitai 1974; Rong et al. 2000; Zhang et al. 2009; Molnár-Láng et al. 2015; Merchuk-Ovnat et al. 2016; Narang et al. 2020). Also, multiple wild species of tomato (*Solanum* section *Lycopersicon*) have been extensively used for improvement of tomato cultivars (Hanson et al. 2000; Labate and Robertson 2012; Menda et al. 2014). Despite significant advances in the field, there should be far more introgression in crops than those documented in the literature, and there are also more known cases of introgression than those characterized at the genetic or genomic level.

Since the green revolution, modern breeding has used CWR to introduce desirable traits into cultivars, with a historical focus on disease resistance traits, and a more recent focus on adaptation to climate change (Brozynska et al. 2016; Zhang and Batley 2020; Wambugu and Henry 2022), given its evident negative effect on crop productivity and food security (Lobell et al. 2011; Challinor et al. 2014; Rosenzweig et al. 2014). Climate change threats on crops are increasing while the genetic base of crops are shrinking, it is therefore ever more important that we understand how wild, genetically rich species have adapted to past climate changes to improve crop adaptation to future climates (Dempewolf et al. 2017). Recent work using genome-wide

Box 1: Key steps when investigating adaptive introgression

1. Taxonomic sampling: It is essential to have a broad taxonomic sampling that covers phylogenetically close species. Sampling should place special emphasis on those closely related species that are in sympatry with the species under study. However, it should not be reduced exclusively to these as introgression may have occurred in past times when species and genotypes that are geographically distant today did coinhabit in the same areas (e.g., Lovell et al. 2021).

2. Intraspecific diversity: Species have a wide intraspecific diversity that sometimes spans wide geographic regions. It is relatively common to find diverse adaptive introgression events in different parts of the geographic range of the study species (Blanco-Pastor, Manel, et al. 2019; Zhou et al. 2020; Lovell et al. 2021). This means that a broad intraspecific sampling may be required to uncover a complete picture of introgression.

3. Genetic structure analyses and genome-wide introgressions: Genetic clusters should be used as operational units to identify gene flow at the intraspecific level, but neutral and putative adaptive genetic structure usually differ. These differences can be observed at the chromosome level with different signature of selection in different individuals from the same gene pool or genetic cluster (e.g., Freitas et al. 2021; Lovell et al. 2021). Local ancestry blocks across the different chromosomes can be inferred using sophisticated probabilistic hidden Markov models such as those implemented in HAPMIX (Price et al. 2009) or Ancestry_HMM (Corbett-Detig and Nielsen 2017).

4. Confounding signals:

    The adaptive hybridization/introgression signal can be easily confounded with *incomplete lineage* sorting (ILS; Pamilo and Nei 1988; Doyle 1992; Maddison 1997; Rosenberg and Nordborg 2002; Blanco-Pastor et al. 2011; Tang et al. 2022). Analyses that distinguish both patterns (such as the four taxon f_4 [Patterson et al. 2012] or f_d [Martin et al. 2015] statistics or the five-taxon D_{FOIL} [Pease and Hahn 2015] statistic, which are all related to the genome-wide summary ABBA-BABA test [Green et al. 2010]) are essential tools for detecting introgression. Like the local ancestry block identification mentioned above, we could also perform these introgression analyses across the genome in sliding windows to detect the origin of the introgressed genomic blocks. With f_4 or f_d values across the genome, it is also possible to
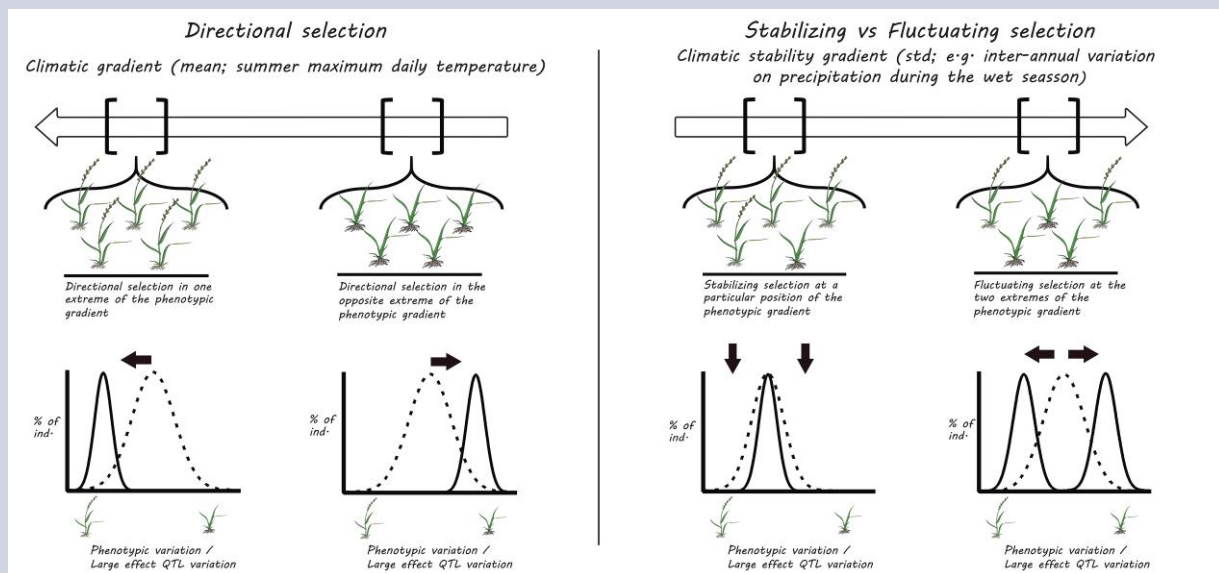
calculate, for each introgressed individual, the genome-wide proportion of genomic introgression coming from each of the potential donor species (Zhou et al. 2020).

5. Investigating the timing of introgression: The temporal pattern of introgression among potential donors can be calculated by the size of the introgression tracts also using hidden Markov models (Guan 2014). This can be achieved under the expectation that tract size negatively correlates with the age of introgression assuming that recombination events keep breaking off donor haplotypes after the initial hybridization (Zhou et al. 2020). Recent extensions to the hidden Markov model of Corbett-Detig and Nielsen (Ancestry_HMM) (Corbett-Detig and Nielsen 2017; Medina et al. 2018) allow to directly infer the timing of the introgression events.

6. Identifying the selective value of introgressed regions: Putative selection signals can be identified in introgressed regions through the use of F_{st} and d_{XY} scans, the XP-CLR statistic (Chen et al. 2010) or more sophisticated models (Günther and Coop 2013) in sliding windows (e.g., He et al. 2019). Other possibilities include checking the overlap between introgressed regions and significant GWAS loci (e.g., Cheng et al. 2019). To check for the effect of introgressed regions on polygenic traits one option is to partition the phenotypic variation for a trait into components explained by introgressed and nonintrogressed regions using, for example, the GCTA-GREML method (Yang et al. 2011). It is also possible to investigate if introgression has influenced nucleotide diversity patterns, this can be done by calculating nucleotide diversity values in the same sliding windows that were previously associated with introgression by f_d-type statistics. Higher allelic diversity in introgressed regions could point to an effect of either disruptive or fluctuating selection on adaptive alleles (see also Box 2).

data have associated signatures of directional selection with signatures of introgression in model herbaceous plants and trees (e.g., Arnold et al. 2016; Suarez-Gonzalez, Hefer, et al. 2018; Mostert-O'Neill et al. 2021). Here I focus on signatures of adaptive introgression in five crop-CWR genetic systems with recently published genomic data and enlarge the vision of adaptive introgression to cover other modes of selection, namely purifying, divergent, or fluctuating selection. It is known from previous studies that introgression from CWR to crops has occurred since the earliest stages

Box 2: Effect of (1) mean climate across years and (2) interannual variability (std) of climate on natural selection processes

Theoretically, under climate-driven directional selection, the allelic diversity in adaptive genes (HeA) is lowest at the two extremes of the climatic gradient. This is because the selective pressure on a particular allele is greatest at the climatic extremes. On the other hand, under fluctuating selection, the HeA reaches the lowest values at the end of the gradient representing the lowest climatic variability and reaches the highest value at the end of the gradient representing the highest climatic variability. This is because high adaptive diversity is required to cope with changing climatic conditions. In the latter case, the selective pressure alternates between the two different alleles over a short period of evolutionary time (see figure). Introgression can play an important role for selection processes occurring across gradients of average climate by introducing newly adaptive alleles previously nonexistent in the population. Such beneficial alleles will increase in frequency in the population by means of selective sweeps or shifts, thus reducing their heterozygosity levels. These climatic gradients have been mainly associated with mean values of climatic parameters (e.g., latitudinal, longitudinal, or altitudinal gradients of mean [daily, monthly, seasonal, yearly, and cross-years] temperature and/or precipitation values), for which numerous examples exist in the literature (e.g., Lasky et al. 2017; Exposito-Alonso et al. 2018; Blanco-Pastor et al. 2021). Another type of climatic gradients is associated with the temporal variability of the climate. Climatic conditions at a given site can fluctuate over different time scales, that is, interseasonal variations or relatively stochastic interannual variations. In this case, the probability of fixation of adaptive alleles will be lower as high heterozygosity would be preferred under such conditions. A good example that associates the diversity of adaptive alleles for a particular trait with the two types of gradients can be found in Keep, Rouet et al. (2021). These authors showed that investment in sexual reproduction during the first year (heading first year, HFY) in perennial ryegrass was partially associated with a gradient of mean summer maximum daily temperature values (SMDT), but the diversity of HFY-associated adaptive loci (which was highest in a geographic region with a signature of introgression, see Fig. 2) was better predicted by a linear combination of both mean SMDT values and the interannual variation on precipitation during the wet season, the latter being the most significant environmental predictor in the model. Perennial ryegrass does not usually flower during the first year and invest in vegetative tissues only, which is an adaptive advantage in optimal rainfall conditions. But first-year flowering is an adaptive strategy in years of low rainfall, given that greater investment in seed formation provides greater fitness under a drought scape strategy (Volaire 2018; Blanco-Pastor et al. 2021), a pattern that was also found at the continental level (Keep, Sampoux et al. 2021).

Directional selection

Climatic gradient (mean; summer maximum daily temperature)

Directional selection in one extreme of the phenotypic gradient

Directional selection in the opposite extreme of the phenotypic gradient

% of ind·

Phenotypic variation / Large effect QTL variation

Stabilizing vs Fluctuating selection

Climatic stability gradient (std; e.g. inter-annual variation on precipitation during the wet seasson)

Stabilizing selection at a particular position of the phenotypic gradient

Fluctuating selection at the two extremes of the phenotypic gradient

% of ind·

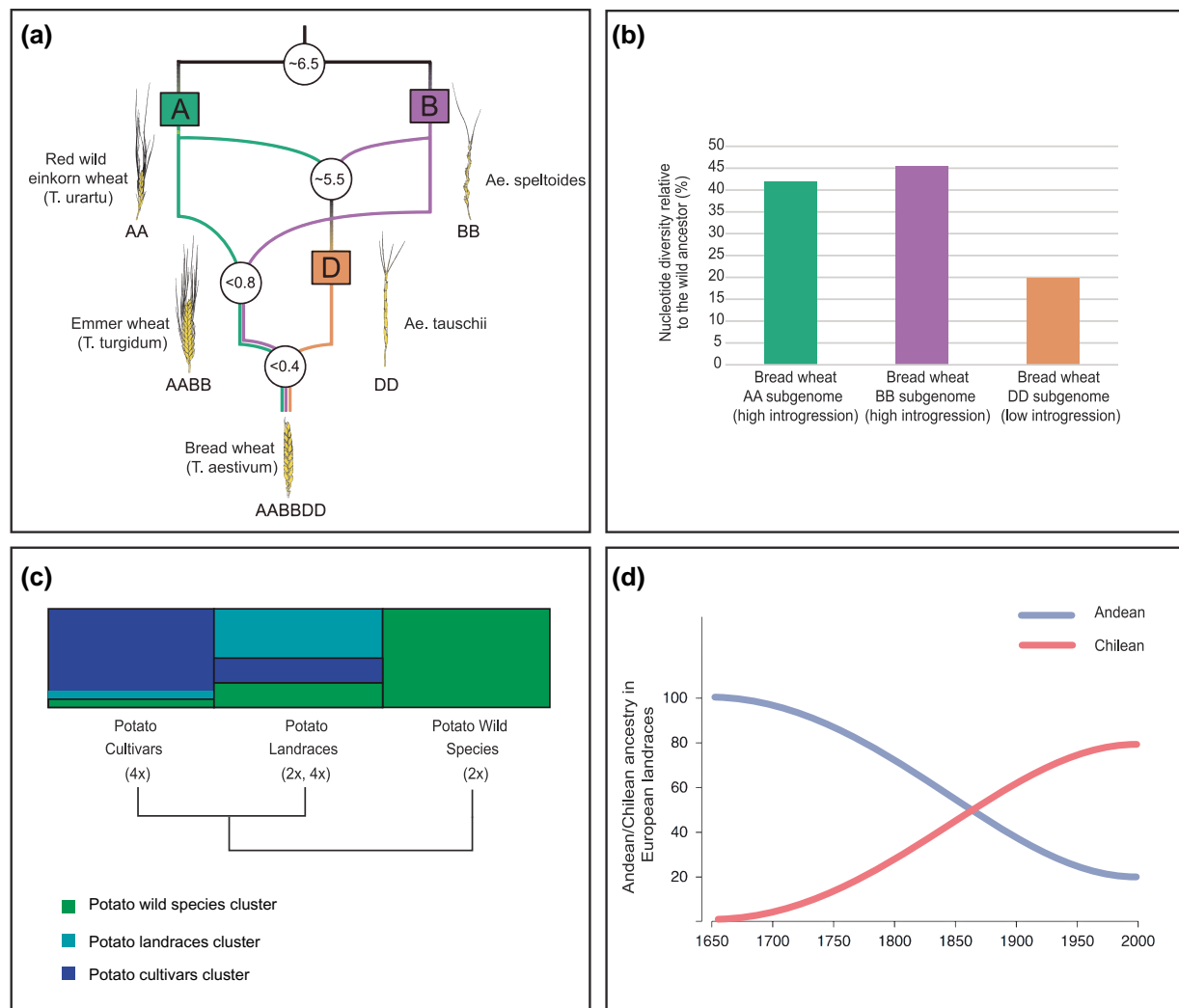Phenotypic variation / Large effect QTL variation

Fig. 1.—Domestication and introgression history in wheat and potato. (a) Phylogenetic history of bread wheat (*Triticum aestivum*; AABBDD) "modified from Marcussen et al. (2014), used with permission from the American Association for the Advancement of Science". (b) Percentage of bread wheat nucleotide diversity ($\pi \times 10^{3}$) in the A, B, and D subgenomes relative to the wild progenitors, from Cheng et al. (2019). (c) Schematic representation of retained wild species ancestry across potato landraces and cultivars, from Hardigan et al. (2017). (d) Reduction in Andean genome ancestry in favor of Chilean ancestry in European potato samples over time, from Gutaker et al. (2019).

of domestication and that this introgression facilitated adaptation to novel conditions, particularly during their geographic expansion. The latest genomic studies now provide further details about the evolutionary consequences of adaptive introgression, revealing its pervasiveness, the number of donor species, its geographical scale, the mode of selection that prevails, as well as the genes or set of genes that are subject to selection. Below I present a summary of findings in wheat, maize, potato, grapevine, and forage grasses. In conjunction, these studies reveal a more complex picture of the evolutionary dynamics during crop domestication and highlight the role of introgression in local adaptation through a variety of selection processes beyond directional selection on certain introgressed alleles.

Genomics of Introgressed Crops

Wheat

Bread wheat (*Triticum aestivum*; AABBDD) accounts for 17% of the world's total cultivated area and is one of the most indispensable staple crops for humans. It originated from hybridization between cultivated tetraploid emmer wheat (*T. turgidum*, AABB) and wild diploid *Aegilops tauschii* (DD) (Marcussen et al. 2014; fig. 1a). The origin of the domestication of bread wheat goes back 10,000 years (Tanno and Willcox 2006). Recent studies have analyzed the role of introgression with wild relatives in shaping the current genetic diversity of the bread wheat genomes (Cheng et al. 2019; He et al. 2019; Zhou et al. 2020). These studies show that cultivated bread wheat had a
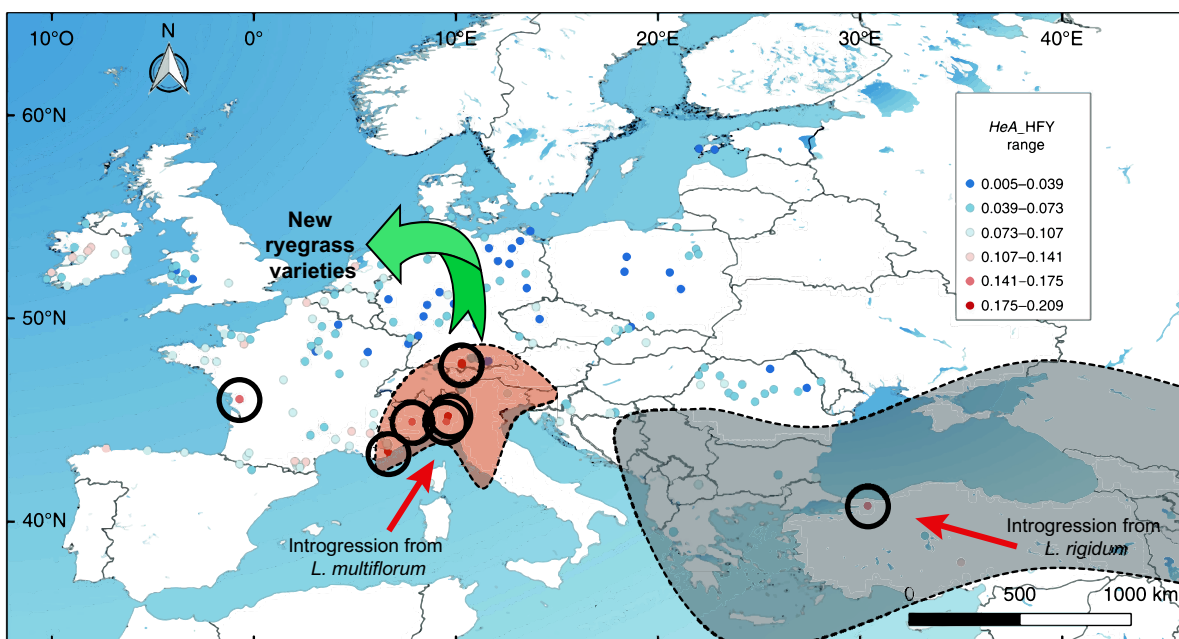
FIG. 2.—Spatial distribution of within-population allelic diversity associated with the trait "heading first year" (a surrogate of reproductive investment during first year, HeA_HFY) shows the highest diversity in regions with a signal of introgression that have been later used as genetic resources for the development of new ryegrass varieties. Circles indicate HeA_HFY > 0.150 (top 33.3%). Adapted from Keep, Rouet et al. (2021), with permission from Oxford University Press.

single domestication event (Cheng et al. 2019). A polyploidization-related bottleneck caused a substantial loss of genetic diversity in the A, B, and D subgenomes of hexaploid wheat compared with its diploid ancestor, with the loss being much more pronounced in the D subgenome (fig. 1b; Cheng et al. 2019). One explanation for the lack of a similar reduction in diversity in the A and B genomes, with respect to the D genome, is gene flow from different tetraploid wild wheat taxa since the earliest stages of domestication (He et al. 2019; Zhou et al. 2020).

Introgression from bread wheat close relatives contributes to a substantial portion (4–32%) of its genome (Zhou et al. 2020). Initially, this introgression (which explained the relatively high diversity of A and B subgenomes in bread wheat) was thought to come only from wild emmer wheat (Cheng et al. 2019; He et al. 2019). However, introgression from wild emmer wheat constitute only a small proportion of the whole history of gene flow, drawing a much more complex picture of introgression that involves several taxonomic complexes within the genus *Triticum* (Zhou et al. 2020). Free-threshing *Triticum* tetraploids (including durum wheat and close relatives) constituted the most important donor group, accounting for 64.78% of the introgressed genomic regions, with a second donor associated with hulled domesticated emmer wheat (*T. turgidum*, AB subgenomes progenitor). These introgression signals have remained in wheat genomes as valuable genetic resources for productivity and adaptation to different environments across continents (Zhou et al. 2020). He et al. (2019) showed that gene flow

from bread wheat close relatives was associated with an increase in effective population size that improved the efficiency of *purifying selection* in the AABB subgenome and contributed to a reduced *mutation load*.

Highly recombining regions also showed signatures of directional selection in this polyploid subgenome, with 8% of locally adaptive alleles introduced by introgression. Rare alleles (derived allele frequency, DAF < 0.1) introduced from the third donor, the wild emmer wheat, explained a substantial proportion of the phenotypic variance for the traits crop weight (up to 30.9%), drought susceptibility (up to 22.5%), and plant height (up to 35%). These rare alleles promoted adaptation in specific geographically restricted habitats (He et al. 2019) following a geographical pattern of introgression and adaptation that can largely be explained by the sympatric distribution of landraces with their donors. Emmer wheat and related tetraploids (donors of the AB subgenomes) are native to the Eastern Mediterranean and West Asia, and *A. tauschii* ssp. *strangulata* (introgression donor of the D subgenome) is native to the southwestern Caspian Sea, both places with high constraints in relation to summer drought and where the introgression signal is strongest for the AB and D subgenomes, respectively.

Potato

The potato (*Solanum tuberosum* L.) was domesticated 8,000–10,000 years ago from its wild progenitor native to the Peruvian Andes. Autopolyploidization of early diploid

ancestral *S. tuberosum* cultivars (Stenotomum and Phureja groups) produced tetraploids cultivated in the Andes (*S. tuberosum* Andigena group). The potato was subsequently cultivated in equatorial high altitude, and later on in southern latitudes with longer summer days (Spooner et al. 2005). Migration from the Andes to coastal Chile resulted in a subspecific group adapted to long-day conditions (*S. tuberosum* Chilotanum group) that has provided much of the genetic background for commercial cultivars of *S. tuberosum* worldwide (Spooner et al. 2005; Hardigan et al. 2017). The genetic diversity of diploid and tetraploid *S. tuberosum* is extremely high, due to the wild introgressions following autopolyploidy and range expansion that captured alleles outside their geographical origin (fig. 1*c*; Hardigan et al. 2017). A recent study on the potato pan-genome shows that both ILS and hybridization/introgression have contributed to blurring evolutionary relationships between wild potato species and landraces (Tang et al. 2022).

Several wild *Solanum* species (most notably the Andean *S. microdontum*) had a role in the spread of cultivated potatoes across the globe by providing tolerance to long-day conditions (Hardigan et al. 2017). The first European potatoes collected during the period 1650–1750 were closely related to Andean landraces and probably not sufficiently adapted to European conditions. These genotypes were crossed with Chilean genotypes preadapted to long-day requirements like those in Europe. The European varieties became progressively more similar to the Chilean genotypes as they became increasingly distant from their Andean counterparts which paved their adaptation to European climatic conditions (fig. 1*d*; Gutaker et al. 2019). Analysis of gene functions in introgressed regions supports their adaptive role with enrichment in multiple abiotic stress-associated genes with unknown specific functions and retention of wild alleles in most (70%) tetraploids (Hardigan et al. 2017).

Maize

Maize (*Z. mays* ssp. *mays*) was domesticated in southwestern Mexico approximately 9,000 years ago from the wild teosinte *Z. mays* ssp. *parviglumis* (Piperno et al. 2009). Gene flow among multiple teosinte species has occurred during *Zea* diversification (Ross-Ibarra et al. 2009). Introgression from the wild teosinte taxon *Z. mays* ssp. *mexicana* (hereafter mexicana) has generated a particular interest due to its adaptive significance to highland areas (Hufford et al. 2013; Wang et al. 2017; Gonzalez-Segovia et al. 2019; Calfee et al. 2021). The subspecies mexicana is endemic to the highland regions of Mexico (1,300–300 m a.s.l.) and diverged from the subspecies parviglumis about 60,000 years ago (Ross-Ibarra et al. 2009). Highland regions of central America present several environmental challenges, including a cooler, drier climate

with higher UV intensity and a shorter growing season requiring earlier flowering. The ancestry of mexicana subspecies in upland maize comes from an ancestral introgression that has maintained much of its diversity in the various upland maize populations of Mexico (Calfee et al. 2021). After the introgression from mexicana, introduction of introgressed maize has been documented in Guatemala and the southwestern USA (Wang et al. 2017).

Large genomic regions (at megabase scale) introgressed from mexicana and associated with directional selection have been recently identified on chromosomes 3, 4, and 9 (Hufford et al. 2013; Wang et al. 2017; Gonzalez-Segovia et al. 2019). The introgressed region on chromosome 3 corresponds to a chromosomal inversion associated with flowering time. The region on chromosome 4 contains the *Inv4m* region, a large 14 Mb inversion (Calfee et al. 2021) which overlaps with QTLs for leaf pigmentation and macrohairs (Lauter et al. 2004), and is associated with adaptation to cold stress and increased maize yield at high elevations (Crow et al. 2020). The region on chromosome 9 overlaps with the locus macrohairless1 (*mhl1*), a large-effect locus also linked to the production of macrohairs (Lauter et al. 2004; Moose et al. 2004; Gonzalez-Segovia et al. 2019). Despite the documented introduction of introgressed maize into the southwestern USA, these populations have lost the signature of introgression in chromosome 4, a possible signal of geographically restricted local adaptation (Wang et al. 2017).

Introgression-affected genomic regions in upland maize showed higher recombination rates (Calfee et al. 2021), and a significantly lower number of deleterious single nucleotide polymorphisms (Wang et al. 2017). This supports an improved effect of purifying selection driven by introgression in upland maize, similarly as shown for wheat (He et al. 2019; see above). It also needs to be noted that most of the outlier loci with high introgression from mexicana do not show signs of reduced genetic diversity by selective sweeps (Calfee et al. 2021). This can be explained by an effect of either *disruptive* or *fluctuating* selection (see Box 2) over multiple mexicana haplotypes in those introgressed regions. This maintenance of high haplotype diversity is consistent with the selective pressures caused by microhabitat heterogeneity or interannual variability of highland climates (Blanco-Pastor, Fernández-Mazuecos, et al. 2019). However, pronounced allelic clines are observed with elevation such as in the *Inv4m* and *mhl1* loci (Calfee et al. 2021). Altogether, both high haplotype diversity and the presence of specific alleles in key genes under directional selection may be at play in the adaptation of upland maize.

Upland maize from central America flowers earlier than lowland maize. The large introgressed region in upland maize on chromosome 3 corresponds to a chromosomal

inversion associated with flowering time (Wang et al. 2017), but no genes from the core maize flowering time pathway overlap with mexicana introgressed loci (Calfee et al. 2021). This is because not all genes causing flowering time differences in maize are fully annotated, and also because flowering time is a highly polygenic trait in maize (Buckler et al. 2009), which may reduce the strength of selection on most individual genes under detectable levels using standard approaches. These results suggest that many more mexicana genes are beneficial at higher altitudes, but only in conjunction and when present in specific allele combinations.

Grapevine

The cultivated grapevine, *Vitis vinifera* ssp. *vinifera*, was domesticated in the southern Caucasus 8,000 years ago from the dioecious taxon *V. vinifera* ssp. *sylvestris* (This et al. 2006). It was initially thought that grapevine domestication included two separate domestication events, one derived from wild Caucasian grapevines and the other from wild Western European grapevines (Grassi et al. 2003; Arroyo-García et al. 2006). However, recent genomic data have confirmed a single origin in West Asia with a strong introgression signal from the subspecies sylvestris as it moved toward the western Mediterranean (Terral et al. 2010; Myles et al. 2011; Bouby et al. 2013; Freitas et al. 2021), which lead to a reduction in its genetic load (Zhou et al. 2017; Freitas et al. 2021). One of the first and strongest evidence of introgression was the increase in genetic diversity toward the west, contrary to expectations given the east-to-west direction of domestication.

Environmental adaptation played a key role in both the evolution of wild genotypes and the outcome of introgression with cultivated varieties. Freitas et al. (2021) found significantly enriched climate- and pathogenesis-associated loci in introgressed genomic regions of Iberian cultivated grapevines. The proportion of introgressed regions ranged from 25% to 50% of the grapevine genome, in a set of related Iberian varieties. These introgressed genomic regions were significantly enriched in genes under directional selection in both Iberian cultivars and Iberian wild populations and were enriched in genes associated with abiotic and biotic stress stimuli, including genes associated with flowering time and light perception, hormone signaling, abiotic stress responses to cold and drought, sugar content regulation, and pathogen perception (Freitas et al. 2021). Also including some large-effect genes such as abscisic acid (*ABA*) signaling genes, a key hormone in plant adaptation to abiotic stress stimuli (Kuromori et al. 2018), and pathogenesis-related proteins (Fernandes et al. 2013). This reveals a scenario in which introgression from the wild grapevine genome into cultivated Iberian grapevine varieties favored their local adaptation.

Genomic data of archaeological samples further support gene flow from wild to cultivated grapevines in the western Mediterranean occurring in the early stages of viticulture during the Iron Age (510–475 BC; c.a. 2,500 years ago; Ramos-Madrigal et al. 2019). This coincides with the earliest evidence of vine cultivation in the Iberian Peninsula 2,900 years ago under Phoenician influence (Iriarte-Chiapusso et al. 2017), making it the earliest tentative time of a human-mediated grapevine introgression event in this region.

Ryegrass

Perennial ryegrass (*Lolium perenne*) is among the most used grasses for cover crops and forage crops in temperate regions of the world and the most prevalent species in European grasslands grazed by cattle. This species has been recently adopted as a model species for the genetics of temperate forage grasses (Byrne et al. 2015; Blanco-Pastor, Manel, et al. 2019; Blanco-Pastor et al. 2021). *L. perenne* received alleles from the close relatives *L. rigidum* and *L. multiflorum* since >380 kya after initial divergence (Blanco-Pastor, Manel, et al. 2019). Introgression from *L. rigidum* to *L. perenne* has taken place in a genetic cluster located in southeastern Europe and Near East regions where the two species coexist. In this region, 15% of alleles present in *L. perenne* originated in *L. rigidum*. Gene flow from *L. multiflorum* to *L. perenne* has taken place in northern Italy. In this region, 5% of alleles present in *L. perenne* originated in *L. multiflorum* (fig. 2; Blanco-Pastor, Manel, et al. 2019). Interestingly, North Italian populations have been recently used as a source for the generation of new ryegrass varieties with increased productivity and water-soluble carbohydrate content (Faville et al. 2004).

In these two regions, Keep, Rouet et al. (2021) found significant relationships between the genetic diversity at major QTLs (adaptive loci) (HeA, sensu Keep, Rouet et al. 2021) and both the mean values of the local climate and its temporal variability (Box 2). Keep, Rouet et al. (2021) modelled the HeA index for several adaptive traits from mean climate and climate variability indicators. For several traits such as heading in the first year (HeA_HFY), spring canopy height (HeA_SPH), and heading date (HeA_HDT), the most significant explanatory variable was a climate variability indicator (standard deviation, std). The region with the highest heterozygosity of genes associated with reproductive investment during the first year (HeA_HFY) was found precisely in northern Italy, a region with high variability in spring rainfall and with strong genomic signature of introgression from the relative *L. multiflorum*, suggesting that fluctuating selection has favored maintenance of introgressed genetic variation in this geographical region (fig. 2, see also Box 2).

Concluding Remarks

The studies reviewed here show that genomic data broaden our understanding of the history of crop domestication and gene flow with their wild or early domesticated relatives. Previous studies showed that the genetic basis of crops was produced through domestication events followed by adaptive gene flow from relatives encountered during post-domestication expansion processes (Janzen et al. 2019). New genomic data reveal that introgressed loci of large effect that are target of directional selection explain a small proportion of the full phenotypic variance in traits associated with altitudinal, latitudinal, and longitudinal climatic gradients in different crop species (phenotypic variance associated with cold stress [maize; Crow et al. 2020], drought stress [wheat, grapevine, and ryegrass; He et al. 2019; Blanco-Pastor et al. 2021; Freitas et al. 2021] and day length [potato] differences [Hardigan et al. 2017]). These studies also show that the evolutionary consequences of introgression from wild relatives are also far more diverse than previously identified (Martin and Jiggins 2017; Warburton et al. 2017; Suarez-Gonzalez, Lexer, et al. 2018; Janzen et al. 2019). Introgression between populations and species can provide new beneficial alleles or allele combinations but can also increase the intrapopulation/intravariety genome-wide diversity, thereby enhancing the effect of purifying (wheat, maize, and grapevine), and disruptive or fluctuating selection (maize and raygrass).

All cases reviewed here reflect that introgression is local or regional in scope, but that in some cases new introgressed alleles spread more widely (e.g., maize or potato). In all cases, adaptive introgression was clearly linked to specific environmental conditions (eastern Mediterranean and west-central Asia for bread wheat, European region for potato, western Mediterranean for grapevine, and northern Italy for ryegrass). These alleles represent a promising source for further introgressions that could be used for adapting these crops to novel stressful climatic conditions, in these same regions or elsewhere (Dempewolf et al. 2014; Brozynska et al. 2016; Zhang and Batley 2020).

From the earliest stages of crop expansion, farmers moved from place to place, selecting and carrying with them the seeds best adapted to the new local conditions, and eventually crossing these genotypes with local wild species or other varieties. This contributed to the adaptation of crops to new climates and led to the formation of landraces. These landraces, most of which disappeared or have been relegated to germplasm banks, have already contributed to crop improvement in multiple traits, such as increased efficiency in nutrient uptake, protein and mineral content, disease resistance, and abiotic stress tolerance (see Carvalho et al. 2011 for a review), and should be considered for breeding modern varieties with higher priority than wild populations, given their more advanced state of domestication.

Past adaptation to newly colonized areas through introgression in species reviewed here provide an instructive analog for adaptation to current climate change. The genomics of adaptation to climate in the past provides new avenues for adapting crops to future climatic constraints, as well as for improving crop productivity under variable climatic conditions. Although it remains important to focus on identifying the substitution of high-effect alleles for breeding, the way forward in research on adaptive introgression from wild to crop species should also address the more subtle effects of diversity gain following introgression. It is long known that increasing intraspecific diversity is a viable strategy to increase yield and/or yield stability, specially under the effect of biotic or abiotic stressors (Frankel 1939; Allard 1961), but this issue has only recently received especial attention in the context of the agroecological revolution under increasing climate variability (Newton et al. 1997, 2009; Prieto et al. 2015; Reiss and Drinkwater 2018; Litrico and Huyghe 2019).

The recent studies reviewed above raise new outstanding questions, for example: Is purifying selection a common selection mode in crops after introgression with wild relatives? Is it an important element in the elimination of deleterious alleles arising from the mutation load associated with the cost of domestication? Does domestication eliminate alleles that have been subject to fluctuating selection in regions with variable climates, thus favoring phenotypic stability? Can we recover these alleles from wild relatives to favor crop adaptation in regions with increasing climatic instability? How important are traits with polygenic architectures, both additive and nonadditive (epistasis), for climate adaptation in crops? How much of this adaptive genomic variation is present in cultivated varieties and how much in wild populations? What are the best breeding approaches to maximize adaptive diversity while avoiding the negative effects of linkage drag associated with introgression from wild relatives?

We note a general pattern in the studies presented here: that geographic expansion of crops was driven primarily by an increase in genetic diversity following introgression with wild relatives that offset the cost of domestication. To a large extent, the success of certain modern cultivars is due to the interaction between multiple introgressed alleles from wild relatives, rather than the introduction of specific alleles with a large effect. The effect of polygenic architectures could have been significant in relation to increasing the efficiency of balancing and disruptive/fluctuating selection but the detailed effect of increased adaptive diversity on the evolution of polygenic traits, remains to be fully determined. Re-analysis of genomic data using models that account for the small but significantly coordinated variation of multiple small-effect alleles involved in phenotypic determinism under additive (Zhou et al. 2013; Berg and Coop 2014; Barghi et al. 2020) and nonadditive

(Exposito-Alonso et al. 2020) polygenic architectures will show the way forward for the introgression-mediated breeding of new, more diverse, and climate-resilient crops.

Literature Cited

Allard RW. 1961. Relationship between genetic diversity and consistency of performance in different environments. Crop Sci. 1: 127–133.

Anderson E, Hubricht L. 1938. Hybridization in tradescantia. III. The evidence for introgressive hybridization. Am J Bot. 25:396–402.

Arnold BJ, et al. 2016. Borrowed alleles and convergence in serpentine adaptation. PNAS 113:8320–8325.

Arroyo-García R, et al. 2006. Multiple origins of cultivated grapevine (*Vitis vinifera* L. ssp. *sativa*) based on chloroplast DNA polymorphisms. Mol Ecol. 15:3707–3714.

Ballini E, et al. 2007. Modern elite rice varieties of the 'Green Revolution' have retained a large introgression from wild rice around the Pi33 rice blast resistance locus. New Phytol. 175:340–350.

Barghi N, Hermisson J, Schlötterer C. 2020. Polygenic adaptation: a unifying framework to understand positive selection. Nat Rev Genet. 21:769–781.

Barton NH. 2001. The role of hybridization in evolution. Mol Ecol. 10: 551–568.

Berg JJ, Coop G. 2014. A population genetic signal of polygenic adaptation. PLoS Genet. 10:e1004412.

Blanco-Pastor JL, Barre P, et al. 2021. Canonical correlations reveal adaptive loci and phenotypic responses to climate in perennial ryegrass. Mol Ecol Resour. 21:849–870.

Blanco-Pastor JL, Fernández-Mazuecos M, Coello AJ, Pastor J, Vargas P. 2019. Topography explains the distribution of genetic diversity in one of the most fragile European hotspots. Divers Distrib. 25:74–89.

Blanco-Pastor JL, Liberal IM, et al. 2021. Annual and perennial *Medicago* show signatures of parallel adaptation to climate and soil in highly conserved genes. Mol Ecol. 30:4448–4465.

Blanco-Pastor JL, Manel S, et al. 2019. Pleistocene climate changes, and not agricultural spread, accounts for range expansion and admixture in the dominant grassland species *Lolium perenne* L. J Biogeogr. 46:1451–1465.

Blanco-Pastor JL, Vargas P, Pfeil BE. 2011. Coalescent simulations reveal hybridization and incomplete lineage sorting in Mediterranean *Linaria*. PLoS ONE. 7:e39089.

Bouby L, et al. 2013. Bioarchaeological insights into the process of domestication of grapevine (*Vitis vinifera* L.) during roman times in southern France. PLoS ONE. 8:e63195.

Brar DS, Khush GS. 1997. Alien introgression in rice. In: Sasaki T, Moore G, editors. Oryza: from molecule to plant. Dordrecht: Springer Netherlands. p. 35–47.

Brozynska M, Furtado A, Henry RJ. 2016. Genomics of crop wild relatives: expanding the gene pool for crop improvement. Plant Biotechnol J. 14:1070–1085.

Buckler ES, et al. 2009. The genetic architecture of maize flowering time. Science 325:714–718.

Byrne SL, et al. 2015. A synteny-based draft genome sequence of the forage grass *Lolium perenne*. Plant J. 84:816–826.

Calfee E, et al. 2021. Selective sorting of ancestral introgression in maize and teosinte along an elevational cline. PLOS Genet. 17: e1009810.

Carvalho NM, Ehsan Dulloo M, Ford-Lloyd BV, Frese L, Iriondo J, de Pinheiro MAA. 2011. Agrobiodiversity conservation securing the diversity of crop wild relatives and landraces. Wallingford, UK: CAB International.

Challinor AJ, et al. 2014. A meta-analysis of crop yield under climate change and adaptation. Nat Clim Change 4:287–291.

Chen H, Patterson N, Reich D. 2010. Population differentiation as a test for selective sweeps. Genome Res. 20:393–402.

Cheng H, et al. 2019. Frequent intra- and inter-species introgression shapes the landscape of genetic variation in bread wheat. Genome Biol. 20:136.

Corbett-Detig R, Nielsen R. 2017. A hidden Markov model approach for simultaneously estimating local ancestry and admixture time using next generation sequence data in samples of arbitrary ploidy. PLoS Genet. 13:e1006529.

Crow T, et al. 2020. Gene regulatory effects of a large chromosomal inversion in highland maize. PLoS Genet. 16:e1009213.

Dempewolf H, et al. 2014. Adapting agriculture to climate change: a global initiative to collect, conserve, and use crop wild relatives. Agroecol Sustain Food Syst. 38:369–377.

Dempewolf H, et al. 2017. Past and future use of wild relatives in crop breeding. Crop Sci. 57:1070–1082.

Doyle JJ. 1992. Gene trees and species trees: molecular systematics as one-character taxonomy. Syst Bot. 17:144–163.

Exposito-Alonso M, et al. 2018. Genomic basis and evolutionary potential for extreme drought adaptation in *Arabidopsis thaliana*. Nat Ecol Evol. 2:352–358.

Exposito-Alonso M, Wilton P, Nielsen R. 2020. Non-additive polygenic models improve predictions of fitness traits in three eukaryote model species. bioRxiv 2020.07.14.194407; doi:10.1101/2020.07.14.194407.

Faville MJ, et al. 2004. Functionally associated molecular genetic marker map construction in perennial ryegrass (*Lolium perenne* L.). Theor Appl Genet. 110:12–32.

Fernandes H, Michalska K, Sikorski M, Jaskolski M. 2013. Structural and functional aspects of PR-10 proteins. FEBS J. 280:1169–1199.

Frankel OH. 1939. Analytical yield investigations on New Zealand wheat: IV. Blending varieties of wheat. J Agric Sci. 29:249–261.

Freitas S, et al. 2021. Pervasive hybridization with local wild relatives in Western European grapevine varieties. Sci Adv. 7:eabi8584.

Fuentes RR, de Ridder D, van Dijk ADJ, Peters SA. 2022. Domestication shapes recombination patterns in tomato. Mol Biol Evol. 39: msab287.

Gonzalez-Segovia E, et al. 2019. Characterization of introgression from the teosinte *Zea mays* ssp. *mexicana* to Mexican highland maize. PeerJ. 7:e6815.

Grama A, Gerechter-Amitai ZK. 1974. Inheritance of resistance to stripe rust (*Puccinia striiformis*) in crosses between wild emmer

(*Triticum dicoccoides*) and cultivated tetraploid and hexaploid wheats. II. *Triticum aestivum*. Euphytica 23:393–398.

Grassi F, et al. 2003. Evidence of a secondary grapevine domestication centre detected by SSR analysis. Theor Appl Genet. 107:1315–1320.

Green RE, et al. 2010. A draft sequence of the neandertal genome. Science 328:710–722.

Guan Y. 2014. Detecting structure of haplotypes and local ancestry. Genetics 196:625–642.

Günther T, Coop G. 2013. Robust identification of local adaptation from allele frequencies. Genetics 195:205–220.

Gutaker RM, et al. 2019. The origins and adaptation of European potatoes reconstructed from historical genomes. Nat Ecol Evol. 3: 1093–1101.

Hanson PM, et al. 2000. Mapping a wild tomato introgression associated with tomato yellow leaf curl virus resistance in a cultivated tomato line. J Am Soc Hortic Sci. 125:15–20.

Hardigan MA, et al. 2017. Genome diversity of tuber-bearing *Solanum* uncovers complex evolutionary history and targets of domestication in the cultivated potato. PNAS 114:E9999–E10008.

Harlan JR. 1975. Crops and man. Madison, WI: American Society of Agronomy.

He F, et al. 2019. Exome sequencing highlights the role of wild-relative introgression in shaping the adaptive landscape of the wheat genome. Nat Genet. 51:896–904.

Hufford MB, et al. 2013. The genomic signature of crop-wild introgression in maize. PLOS Genet. 9:e1003477.

Iriarte-Chiapusso MJ, Ocete-Pérez CA, Hernández-Beloqui B, Ocete-Rubio R. 2017. *Vitis vinifera* in the Iberian Peninsula: a review. Plant Biosyst Int J Dealing Aspects Plant Biol. 151:245–257.

Janzen GM, Wang L, Hufford MB. 2019. The extent of adaptive wild introgression in crops. New Phytol. 221:1279–1288.

Keep T, Rouet S, et al. 2021. Inter-annual and spatial climatic variability have led to a balance between local fluctuating selection and wide-range directional selection in a perennial grass species. Ann Bot. 128:357–369.

Keep T, Sampoux JP, et al. 2021. To grow or survive: which are the strategies of a perennial grass to face severe seasonal stress? Funct Ecol. 35:1145–1158.

Kuromori T, Seo M, Shinozaki K. 2018. ABA transport and plant water stress responses. Trends Plant Sci. 23:513–522.

Labate JA, Robertson LD. 2012. Evidence of cryptic introgression in tomato (*Solanum lycopersicum* L.) based on wild tomato species alleles. BMC Plant Biol. 12:133.

Lasky JR, Forester BR, Reimherr M. 2017. Coherent synthesis of genomic associations with phenotypes and home environments. Mol Ecol Resour. 18:91–106.

Lauter N, Gustus C, Westerbergh A, Doebley J. 2004. The inheritance and evolution of leaf pigmentation and pubescence in teosinte. Genetics 167:1949–1959.

Lennon JR, Krakowsky M, Goodman M, Flint-Garcia S, Balint-Kurti PJ. 2016. Identification of alleles conferring resistance to gray leaf spot in maize derived from its wild progenitor species teosinte. Crop Sci. 56:209–218.

Litrico I, Huyghe C. 2019. Can increased within-field diversity boost ecosystem services and crop adaptability to climatic uncertainty? In: Lemaire G, de Faccio Carvalho PC, Kronberg S, Recous S, editors. Agroecosystem diversity. Academic Press. p. 191–197.

Lobell DB, Schlenker W, Costa-Roberts J. 2011. Climate trends and global crop production since 1980. Science 333:616–620.

Lovell JT, et al. 2021. Genomic mechanisms of climate adaptation in polyploid bioenergy switchgrass. Nature 590:438–444.

Maddison WP. 1997. Gene trees in species trees. Syst Biol. 46:523–536.

Marcussen T, et al. 2014. Ancient hybridizations among the ancestral genomes of bread wheat. Science 345:1250092.

Martin SH, Davey JW, Jiggins CD. 2015. Evaluating the use of ABBA-BABA statistics to locate introgressed loci. Mol Biol Evol. 32:244–257.

Martin SH, Jiggins CD. 2017. Interpreting the genomic landscape of introgression. Curr Opin Genet Dev. 47:69–74.

Medina P, Thornlow B, Nielsen R, Corbett-Detig R. 2018. Estimating the timing of multiple admixture pulses during local ancestry inference. Genetics 210:1089–1107.

Menda N, et al. 2014. Analysis of wild-species introgressions in tomato inbreds uncovers ancestral origins. BMC Plant Biol. 14:287.

Menon M, et al. 2021. Adaptive evolution in a conifer hybrid zone is driven by a mosaic of recently introgressed and background genetic variants. Commun Biol. 4:1–14.

Merchuk-Ovnat L, et al. 2016. Ancestral QTL alleles from wild emmer wheat improve drought resistance and productivity in modern wheat cultivars. Front Plant Sci. 7:452.

Molnár-Láng M, Ceoloni C, Doležel J, editors. 2015. Alien introgression in wheat. Cham: Springer International Publishing.

Moose SP, Lauter N, Carlson SR. 2004. The maize macrohairless1 locus specifically promotes leaf blade macrohair initiation and responds to factors regulating leaf identity. Genetics 166:1451–1461.

Morales-Cruz A, et al. 2021. Introgression among North American wild grapes (*Vitis*) fuels biotic and abiotic adaptation. Genome Biol. 22:254.

Mostert-O'Neill MM, et al. 2021. Genomic evidence of introgression and adaptation in a model subtropical tree species, *Eucalyptus grandis*. Mol Ecol. 30:625–638.

Myles S, et al. 2011. Genetic structure and domestication history of the grape. PNAS 108:3530–3535.

Narang D, et al. 2020. Discovery and characterisation of a new leaf rust resistance gene introgressed in wheat from wild wheat *Aegilops peregrina*. Sci Rep. 10:7573.

Newton AC, Begg GS, Swanston JS. 2009. Deployment of diversity for enhanced crop function. Ann Appl Biol. 154:309–322.

Newton AC, Ellis RP, Hackett CA, Guy DC. 1997. The effect of component number on *Rhynchosporium secalis* infection and yield in mixtures of winter barley cultivars. Plant Pathol. 46:930–938.

Pamilo P, Nei M. 1988. Relationships between gene trees and species trees. Mol Biol Evol. 5:568–583.

Patterson N, et al. 2012. Ancient admixture in human history. Genetics 192:1065–1093.

Pease JB, Hahn MW. 2015. Detection and polarization of introgression in a five-taxon phylogeny. Syst Biol. 64:651–662.

Piperno DR, Ranere AJ, Holst I, Iriarte J, Dickau R. 2009. Starch grain and phytolith evidence for early ninth millennium BP maize from the Central Balsas River Valley. Mexico. PNAS 106:5019–5024.

Price AL, et al. 2009. Sensitive detection of chromosomal segments of distinct ancestry in admixed populations. PLOS Genet. 5:e1000519.

Prieto I, et al. 2015. Complementary effects of species and genetic diversity on productivity and stability of sown grasslands. Nat Plants 1:15033.

Quan R, et al. 2018. Improvement of salt tolerance using wild rice genes. Front Plant Sci. 8:2269.

Ramos-Madrigal J, et al. 2019. Palaeogenomic insights into the origins of French grapevine diversity. Nat Plants 5:595–603.

Reiss ER, Drinkwater LE. 2018. Cultivar mixtures: a meta-analysis of the effect of intraspecific diversity on crop yield. Ecol Appl. 28:62–77.

Rendón-Anaya M, et al. 2021. Adaptive introgression facilitates adaptation to high latitudes in European aspen (*Populus tremula* L.). Mol Biol Evol. 38:5034–5050.

Rong JK, Millet E, Manisterski J, Feldman M. 2000. A new powdery mildew resistance gene: introgression from wild emmer into common wheat and RFLP-based mapping. Euphytica 115:121–126.

Rosenberg NA, Nordborg M. 2002. Genealogical trees, coalescent theory and the analysis of genetic polymorphisms. Nat Rev Genet. 3: 380–390.

Rosenzweig C, et al. 2014. Assessing agricultural risks of climate change in the 21st century in a global gridded crop model inter-comparison. PNAS 111:3268–3273.

Ross-Ibarra J, Tenaillon M, Gaut BS. 2009. Historical divergence and gene flow in the genus *Zea*. Genetics 181:1399–1413.

Spooner DM, McLean K, Ramsay G, Waugh R, Bryan GJ. 2005. A single domestication for potato based on multilocus amplified fragment length polymorphism genotyping. PNAS 102:14694–14699.

Suarez-Gonzalez A, Hefer CA, Lexer C, Cronk QCB, Douglas CJ. 2018. Scale and direction of adaptive introgression between black cottonwood (*Populus trichocarpa*) and balsam poplar (*P. balsamifera*). Mol Ecol. 27:1667–1680.

Suarez-Gonzalez A, Lexer C, Cronk QCB. 2018. Adaptive introgression: a plant perspective. Biol Lett. 14:20170688.

Tang D, et al. 2022. Genome evolution and diversity of wild and culti-vated potatoes. Nature 606:535–541.

Tanno K, Willcox G. 2006. How fast was wild wheat domesticated? Science 311:1886–1886.

Terral J-F, et al. 2010. Evolution and history of grapevine (*Vitis vinifera*) under domestication: new morphometric perspectives to under-stand seed domestication syndrome and reveal origins of ancient European cultivars. Ann Bot. 105:443–455.

This P, Lacombe T, Thomas MR. 2006. Historical origins and genetic di-versity of wine grapes. Trends Genet. 22:511–519.

Volaire F. 2018. A unified framework of plant adaptive strategies to drought: crossing scales and disciplines. Global Change Biol. 24: 2929–2938.

Wambugu PW, Henry R. 2022. Supporting in situ conservation of the genetic diversity of crop wild relatives using genomic technologies. Mol Ecol. 31:2207–2222.

Wang L, et al. 2017. The interplay of demography and selection during maize domestication and expansion. Genome Biol. 18:215.

Warburton ML, et al. 2017. The use of crop wild relatives in maize and sunflower breeding. Crop Sci. 57:1227–1240.

Yang J, et al. 2011. Genome partitioning of genetic variation for com-plex traits using common SNPs. Nat Genet. 43:519–525.

Zhang X, et al. 2006. Identification of a drought tolerant introgression line derived from dongxiang common wild rice (*O. rufipogon* Griff.). Plant Mol Biol. 62:247–259.

Zhang F, Batley J. 2020. Exploring the application of wild species for crop improvement in a changing climate. Curr Opin Plant Biol. 56:218–222.

Zhang Z, Lin Z, Xin Z. 2009. Research progress in BYDV resistance genes derived from wheat and its wild relatives. J Genet Genomics 36:567–573.

Zhou Y, et al. 2020. *Triticum* population sequencing provides insights into wheat adaptation. Nat Genet. 52:1412–1422.

Zhou X, Carbonetto P, Stephens M. 2013. Polygenic modeling with Bayesian sparse linear mixed models. PLoS Genet. 9:e1003264.

Zhou Y, Massonnet M, Sanjak JS, Cantu D, Gaut BS. 2017. Evolutionary genomics of grape (*Vitis vinifera* ssp. *vinifera*) domes-tication. PNAS 114:11715–11720.

Associate editor: Tanja Slotte