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Adaptation and the Geographic Spread of Crop Species

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Abstract

Crops are plant species that were domesticated starting about 11,000 years
ago from several centers of origin, most prominently the Fertile Crescent,
East Asia, and Mesoamerica. From their domestication centers, these crops
spread across the globe and had to adapt to differing environments as a re-
sult of this dispersal. We discuss broad patterns of crop spread, including
the early diffusion of crops associated with the rise and spread of agricul-
ture, the later movement via ancient trading networks, and the exchange
between the Old and New Worlds over the last ∼550 years after the Eu-
ropean colonization of the Americas. We also examine the various genetic
mechanisms associated with the evolutionary adaptation of crops to their
new environments after dispersal, most prominently seasonal adaptation as-
sociated with movement across latitudes, as well as altitudinal, temperature,
and other environmental factors.

2.1

Contents

1. INTRODUCTION

Domesticated crops are unique species that have arisen in coevolution with humans (146, 147), providing resources and/or services important for human survival. Researchers believe that there are more than 24 regions in the world where plant domestication independently took place, the earliest being in the Fertile Crescent; there, domestication of wheat, barley, and chickpeas, among others, occurred starting ~11,000 years before present (yBP) (147). As domestication proceeded, crops dispersed from their centers of origin and adapted to new environments, moving with human migration, trade, and cultural contact between human societies.

Crop dispersal can be framed in the context of ancient movements and more recent rapid dispersals (11), leading to global expansion in the crop species ranges, even in prehistoric times (99). As these species move across broad geographic regions, they encounter new environments and cultures that necessitate adaptation. Some adaptations may be cultural, as human societies change farming practices to maximize crop productivity in their local environments; other adaptations, however, involve evolutionary genetic changes. Here, we discuss broad patterns of crop dispersals over the last 11,000 years and review genetic mechanisms that allow crops to adapt as they locate to new environments. The study of the patterns and timing of crop movements, as well as past adaptive responses associated with dispersal, provides insights into plant evolutionary biology and helps equip human societies to deal with climate change.

2. MOVEMENT OF CROPS

Fertile Crescent:
region spanning Iraq, southeastern Turkey, and the Levant; believed to be where settled farming and crop domestication first emerged

We focus our discussion on the three most important domesticated food species: wheat, rice, and maize (**Figure 1**). These three major cereals illustrate the main crop dispersal patterns, and the spread of many other crops generally follows similar routes. Crop movement over the last 11,000 years can be roughly divided into several time periods, including (*a*) the ancient spread (diffusion) that occurred early in crop evolution approximately 11,000 to 4,000 yBP, (*b*) long-distance dispersal through trading networks that took place between about 4,000 to 550 yBP, and (*c*) post-Columbian crop exchange between the New and Old World from the end of the fifteenth century.

Crop dispersal during these periods can be reconstructed using various approaches to infer the routes and timing of crop movements. Archaeological records offer direct evidence for the
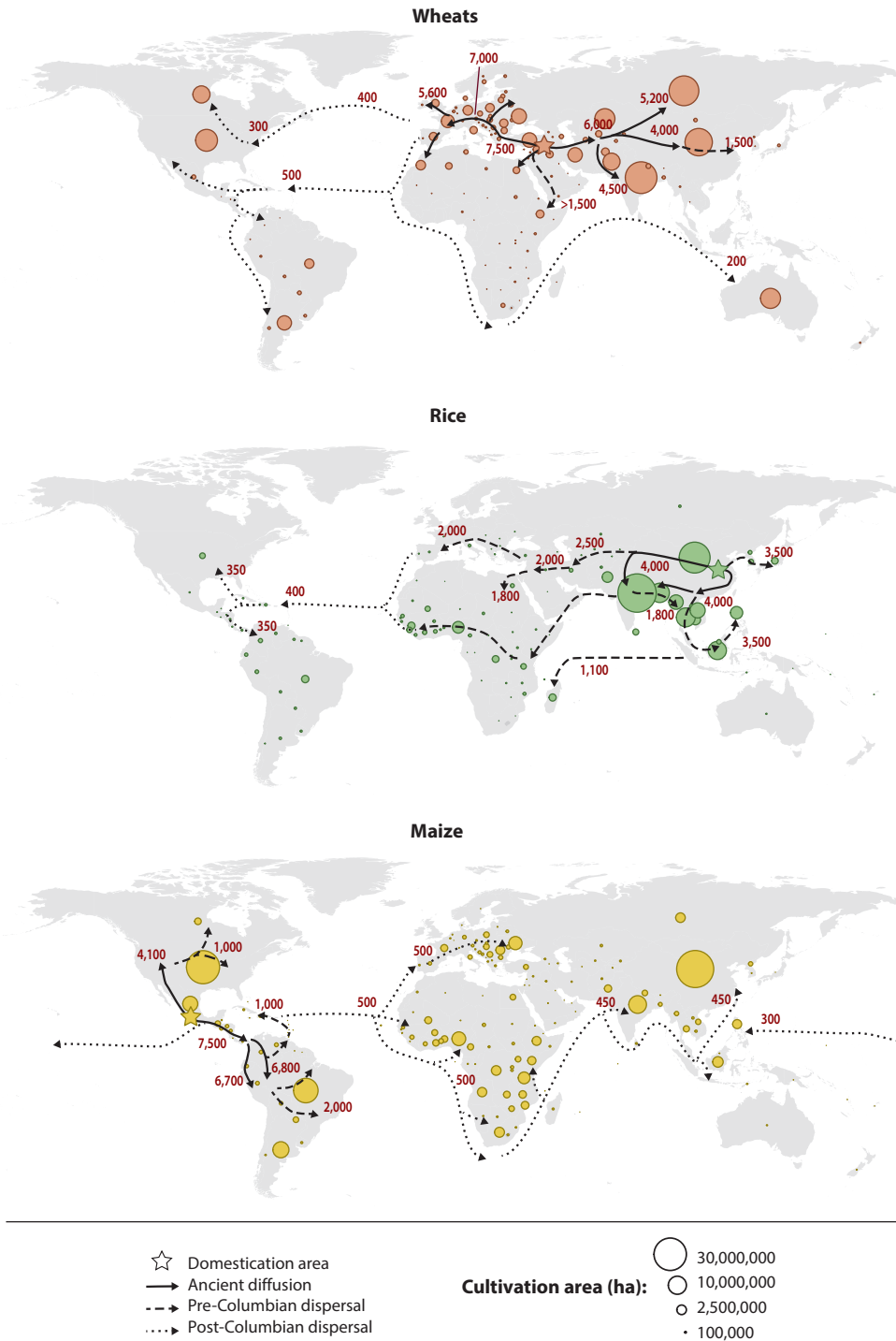
Figure 1

The dispersal of the three main cereal crops around the world. The three most important cereals—wheats, rice, and maize—are used as exemplars of the crop dispersal patterns from the Fertile Crescent and East Asian and Mesoamerican centers of domestication, respectively. Arrows indicate approximate dispersal routes in three epochs: during early crop diffusion, pre-Columbian movement, and post-Columbian exchange. The introduction dates (*red text*, indicating years before the present) represent our current knowledge of the earliest establishment of crop cultivation based on archaeological and historical data sources (see main text for references, e.g., 77, 126, 142). Colored circles represent the cultivation area in hectares (data from the FAOSTAT database for 2021; **https://www.fao.org/faostat/en/#data**).

presence and timing of the appearance of crops in a given area. Historical records often contain nuanced information about the presence and origins of crops, although they are often limited in scope and/or time span (ancient texts are sparse, while more recent documents are limited to the last millennia). Finally, comparative and population genomic analyses allow us to study the source of crop introductions and determine the timing and sequence of dispersals. Combining these approaches, including utilizing genetic information preserved in archaeobotanical samples (i.e., ancient DNA methods) (51, 76), can be a powerful way to reconstruct crop dispersal patterns.

2.1. Ancient Spread and Ongoing Domestication (∼11,000–4,000 yBP)

The practice of plant cultivation and the shift to agriculture took place in different parts of the world from approximately 11,000 to 4,000 yBP, a period which saw the domestication of many of the major food crops. For early cultivated species, various domestication syndrome traits likely evolved over large geographic areas (4, 26) and took ∼2,000–4,000 years to become fixed in the domesticates (148). Many of these early domesticated species subsequently began to spread and were adopted across wide geographic areas, although the timing of movement differs between crop species and regions. These early crop dispersals took place just as humans began the transition to agriculture. The movement of domesticated species from their first centers of origin in the Fertile Crescent, East Asia, and Mesoamerica also signaled the migration of farmer/pastoralist societies (or their ideas) to new regions, displacing local hunter/gatherers. Estimates from archaeological (6) and archaeobotanical remains (159, 166) indicate that this period saw relatively slow rates of crop dispersals linked to this cultural or demic diffusion (55).

2.1.1. Diffusion from the Fertile Crescent.
The wheats are some of the earliest founder crops of the Fertile Crescent and arguably the most important cereal crop species to emerge from that region. The history of wheat cultivation and early diffusion is complicated, given that there were at least three different wheat species domesticated in the Early Neolithic Fertile Crescent before 10,000 yBP: bread wheat (hexaploid, *Triticum aestivum* L.), emmer wheat (tetraploid *Triticum turgidum* L.), and einkorn wheat (*Triticum monococcum* L.) as well as other species domesticated in the Caucasus (e.g., tetraploid *Triticum timopheevii* Zhuk.) (211). Of these, bread wheat constitutes ∼95% of current global wheat production.

Archaeological studies indicate that bread wheat reached central Asia around 6,000 yBP (81), branching north toward the Altai Mountains by at least 5,200 yBP (209) and to south Asia by 4,500 yBP (119) (see **Figure 1**). Archaeobotanical remains and ancient DNA evidence have identified ∼3,800-year-old grains in Northwest China (188), confirming that by ∼4,000 yBP bread wheat had diffused to China along the Hexi Corridor, an ancient route that connected Central to East Asia (45, 46, 191). This is corroborated by population genomic analysis using whole-genome sequence data from 795 bread wheat accessions, which infers movement of this crop across Eurasia between 7,000-5,000 yBP (204). Genetic analysis of Chinese wheat landraces is also congruent with the early introduction of this crop species, and evolution from early spring to winter growth habit, in eastern and southern parts of China (210).

There are strong indications that during the Early Neolithic the assemblage of crops domesticated in the Fertile Crescent (wheats, barley, peas, lentils, flax, and chickpeas—termed the Neolithic package) diffused to Europe (see **Figure 1**) and was instrumental in the shift to agriculture on that continent (32). The rate of agricultural diffusion in Neolithic Europe was ∼1 km/year (6), leading to the introduction of many crops to central Europe by 7,500 yBP and as far as Ireland by 5,600 yBP (126). Crop spread was modulated by glacial retreat as well as cultural factors (27). The Neolithic package also diffused throughout the Arabian Peninsula to North Africa and eastward to Central Asia (81).

Neolithic: stage of cultural evolution characterized by polished/ground stone tools, settled life, and dependence on domesticated species

Hexi Corridor: a narrow area connecting East and Central Asia that formed part of the northern Silk Road

Barley (*Hordeum vulgare*) is perhaps the most studied of the Neolithic package crops, and, similar to wheat, was cultivated as hulled and free-threshing varieties, the latter replacing the former in Europe at around 7,000 to 6,000 yBP (114). Both wheat and barley contemporaneously reached regions south of Central Asia by 6,000 yBP (81) and South Asia by 4,500 yBP and appeared along the Hexi Corridor ∼4,000 yBP (119). Barley, similar to wheat, has two growth habits—winter and spring—with the latter a genetic novelty originating in the Iranian Plateau that adapted barley to the colder climates of Eurasia and fueled wide adoption in temperate regions (98).

2.1.2. Diffusion from East Asia.

Asian rice (*Oryza sativa* L.) was domesticated in East Asia as subspecies *japonica*, most likely along the Yangtze River Valley (62), beginning about 9,000 yBP (158). Early diffusion of rice cultivation in East Asia was linked with the development of water management practices (61) and took place between 8,000 and 4,000 yBP (64). During this period, it was largely confined to the region between the Yangtze and Yellow Rivers, although rice cultivation eventually accelerated according to a power law distribution and moved by approximately 1 km/year to the northern bounds of Southeast Asia (158) (see **Figure 1**). Climate change occurring ∼4,000 yBP, termed the 4.2-k event, spurred *japonica* rice movement and adaptation (40); analyses of contemporary rice genomes indicate diversification into a tropical lineage that moved throughout Southeast Asia (21) and a temperate lineage that dispersed to colder Northeast Asia (77) soon after (around ∼3,500 yBP) (see **Figure 1**). Rice was also independently cultivated in South Asia by 4,000 yBP, and its domestication as subspecies *indica* was likely a result of hybridization with the East Asian *japonica* rice (25, 63) that arrived in this area through central Asia (159).

Broomcorn (*Panicum miliaceum* L.) and foxtail millet (*Setaria italica* L.) are also key crops domesticated in China in the Yellow River Valley (35, 205) and were staples in colder, drier climates. Millet appears in the archaeological record of the Hexi Corridor by 4,800 yBP (46) and South and West Asia by ∼4,000 yBP (84, 166), in agreement with genetic evidence (93). The climate cooling at ∼4,000 yBP and the retreat of rice agriculture southwards extended millets' importance in East Asia (83). The distribution of broomcorn millet in archaeological records of eastern Europe (94) suggested an ancient connection between Europe and China, although genetic data cannot unambiguously establish the origin of European millet (92). Later archaeobotanical evidence suggests a much later European introduction (132), consistent with global patterns of crop dispersal across Asia. Other species domesticated in the region of contemporary China, such as buckwheats (e.g., *Fagopyrum esculentum*) or soybean (*Glycine max*), diffused locally but did not participate in transcontinental dispersal until much later.

2.1.3. Diffusion across Mesoamerica.

Maize (*Zea mays* ssp. *mays*) was domesticated in the lowlands of Mesoamerica close to the southwestern coast of Mexico (125, 144) and spread rapidly southward with dispersal rates two to three times higher than those of wheat and rice. It diffused through Central America by 7,500 yBP (44) and appeared in southwestern Amazonia by 6,800 yBP (120) and coastal Peru by 6,700 yBP (69) (see **Figure 1**). South American maize has clear genetic origins in Mesoamerica (175), with perhaps a slightly different domestication trajectory (102).

While maize rapidly moved south, it took longer to travel to proximate highland sites. The earliest Mesoamerican archaeological finds at nearly 2,000 m above sea level are dated to 6,200 yBP, approximately 2,000 years after maize domestication in nearby valleys (143). The earliest peri-Andean finds are dated to 4,000 yBP at elevations up to 3,600 m (142), and maize adaptation to Mesoamerican highlands was independent of that in South America (89). Similarly, to slow adaptation along elevation gradients, the spread of maize northward toward the temperate zone was slow. Maize reached the Southwest United States by 4,100 yBP (127), and archaeogenomic data

suggest its introduction was from Mesoamerican highland populations with later gene flow from the lowlands (39); its full establishment in temperate highland conditions took another 2,000 years (168).

Although maize is a key food crop, gourds and squashes in the genus *Cucurbita* are thought to be the earliest domesticated crops in the Americas, originating in the Mexican highlands ~10,000 yBP (161). *Cucurbita pepo* squash was introduced to North America earlier than maize; evidence suggests that it was cultivated in the southeastern (103) and central eastern regions of the continent by 5,000 yBP (162). Other species reached the South American coast, the Andes, and north of Argentina between 4,000 and 3,000 yBP (184). Similar to squashes, beans in the genus *Phaseolus* originated from at least five different species, two of which were domesticated independently in Mesoamerica and South America (155). Chili peppers (also domesticated in Mesoamerica), maize, and other crops of diverse origins were identified from starch grains in Trinidad as early as 7,000 to 6,000 yBP, suggesting that crops that diffused to the Caribbean had multiple origins (140).

2.2. Ancient Trading Networks (4,000–550 yBP)

As agriculture began to mature, long-distance crop dispersal occurred along trade routes in Eurasia that likely originated in ancient seasonal movements associated with pastoralism (67, 171). While the underlying dispersal mechanism by human agency was the same as for early crop diffusions, the forces behind it were likely increasingly different (99). Seed movement became less tightly linked with cultural dominance and more associated with human cultural exchange and trade (11, 164). The distance and environmental change along cross-continental trading routes were more pronounced, often requiring the adoption of agricultural innovations and becoming even more extreme with the development of maritime trading networks (164).

2.2.1. Routes between Europe, Africa, and Asia.
The movement of wheat to East Asia was somewhat complicated (see **Figure 1**). It was present in the Hexi Corridor by ~4,000 yBP and introduced from northern China (210) to western Sichuan and the northeastern Tibetan Plateau by ~3,500 yBP (41), likely associated with the pressures of climate change and a long process of altitudinal adaptation (42); it was, however, notably absent on the eastern coast. By 2,000 yBP, the Silk Road became a regulated trading network, and the blossoming exchange between West and East Asia significantly accelerated crop dispersal and dissemination of agricultural technologies and further pushed the establishment of wheat to the East Asian coast (210). Wheat became a key rotation crop, which increased agricultural yields and led to the formation of the first East Asian empires (164).

On the western end of Asia, wheat (possibly emmer wheat) migrated to western Africa, and linguistic and cultural evidence points to its introduction even before the arrival of Islam. This migration was most likely through the maritime part of the Sabean Lane from the Arabian Peninsula and across the Red Sea (50) and suggests the emerging role of pre-Columbian seafaring in the dispersal of crops between continents. Barley adapted to harsh winters in the Tibetan Plateau and became established there ~3,500 yBP (41), whereas evidence suggests that it was introduced in Ethiopia later, in pre-Islamic times (50). Archaeological dates for both cereals strongly indicate that barley and wheat dispersed around the world contemporaneously.

Chickpeas (*Cicer arietinum*) were cultivated during the Neolithic in West Asia (85), but their dispersal and establishment were delayed with respect to cereals. Historical and archaeological data suggest that chickpeas were introduced to northern Africa by 3,500 yBP and South Asia around 2,300 yBP (177), and the genetics of chickpea dispersal among and within five centers of diversity—the Fertile Crescent, Ethiopia, Morocco, and Central and South Asia—showcases

global as well as regional dispersals (95). Sorghum and pulses, domesticated in Africa, were introduced to South Asia in a staggered fashion starting around 3,500 yBP (59), again most likely through the Sabean Lane.

Rice had reached large swathes of Asia by 4,000 yBP. Even with the Silk Road facilitating crop movement, rice agriculture could not be sustained in Central and West Asia without the development of improved irrigation (165) (see **Figure 1**). Historical evidence (164) suggests that rice may have arrived in West Asia by 2,500 yBP, but its adoption was delayed to 2,000 yBP, the time of the earliest archaeological evidence for its presence (129). Short- and long-range seafaring furthered rice movement beyond Eurasia, reaching Africa most likely through the Arabian Peninsula and across the Red Sea (10). Rice is also found in North Africa by 1,800 yBP, although it likely arrived via a different route (182). On the opposite side of the continent, rice reached Korea and Japan between 3,500 and 3,000 yBP through seafaring (2, 33, 34) (see **Figure 1**), a move that required strong adaptation to temperate conditions, which is reflected in the early split of temperate and tropical *japonica* rice (77). Similarly, rice dispersed through the seas to the Malay Archipelago at a remarkable rate and was established on many islands by 3,500 yBP. The genetics of rice migration in that region, coupled with archaeological jade and bronzeware finds, suggest the existence a complex maritime Austronesian trading sphere (3). Rice also reached Madagascar, most likely with Indonesian seafarers (1), at around 1,100 yBP (37), independently from other Southeast Asian crops introduced to Africa (68).

The blossoming of the Silk and Spice Roads, as well as the expansion of irrigation techniques, facilitated the dispersal of other crops from East to West Asia and thence to Europe and Africa. This period saw a second wave of millet cultivation that spread into the summer-dry regions of southern Central Asia (130), and historical evidence suggests the enhanced movement of fruit crops from Central Asia (164). This period also highlights the importance of the spice routes, which had their origins ∼3,000 yBP and had accelerated the exchange between regions by 2,000 yBP through maritime trade, with many spices originating from Malacca (contemporary Indonesia). By 4,000 yBP, Austronesians independently moved the so-called canoe plants—yams, taro, banana, jackfruit, mulberry, and many others—through the Malay archipelago, Polynesia, and all the way to Hawaii by around 1,000 yBP (100). Austronesians also dispersed sweet potatoes (*Ipomoea batatas*), a crop of South American origin, around 1,000 yBP; genetic and linguistic evidence indicates that Polynesian sweet potatoes are indeed of South American origin, providing evidence for pre-Columbian contact between South America and Oceania (151).

2.2.2. Pan-American routes. In pre-Columbian times, maize was established across the Americas, adapting to diametrically different environments (see **Figure 1**). On its spread north, maize was introduced to the temperate Colorado Plateau by 4,000 yBP, although it took another 2,000 years to become established (30). Archaeogenomic analyses suggest that by ∼2,000 yBP, maize was already temperate-adapted and was an ancestor of lineages that dispersed further north (168), likely replacing now extinct eastern North American crops and reducing the importance of sunflower-based agriculture by ∼1,000 yBP (160).

Maize introduction to the Caribbean is obscured by scarce macrobotanical records and can be convincingly dated only to 1,000 yBP (136). Genetic data of contemporary Caribbean landraces support origins from lowland tropical maize, likely through Trinidad (180). Although there is not much evidence for organized trade between Mesoamerica and South America, archaeogenomic data indicate multiple waves of southern migration of maize (102), with some backflow to Mesoamerica (104). Maize appears early on both sides of the Andes and moved eastward through the Amazon, with evidence of its presence by 4,300 yBP (123) and intensification by ∼2,000 yBP (65, 104).

Austronesian: a group of peoples in Taiwan, the coast and islands in Southeast Asia, Oceania, and Madagascar that speak Austronesian languages

Other crops also moved within South America, forming complex multi-origin assemblages in the eastern Amazon; aside from maize, we see sweet potato by 3,200 yBP, cassava by 2,200 yBP, and squash by 600 yBP (123). Interestingly, there seems to be less dispersal from South America to Mesoamerica. On one hand, cocoa was possibly domesticated in western South America by at least 5,600 yBP, as evidenced by the analysis of microremains (198), and appeared in Mesoamerica only by 3,800 yBP (145). On the other hand, potatoes, a cornerstone of the Andean Tiwanaku civilization ∼2,000 yBP (150), spread to the temperate coast of Chile but had not reached Mesoamerica in pre-Columbian times (107), possibly because they were critically maladapted or the focus of trade for this crop was elsewhere.

Columbian Exchange: the global transfer of biological material and culture between the New and Old Worlds after the late fifteenth century

2.3. Post-Columbian Crop Dispersals (<550 yBP)

The arrival of Europeans to the Americas led to transoceanic cultural and biological contact known as the Columbian Exchange (36). Early post-Columbian crop dispersals were motivated by the introduction of European staples to new colonies (e.g., wheat and barley) (see **Figure 1**), import of exotic goods to the Old World (e.g., potato and tomato), and establishment of cash crop plantations across the globe (cotton, tobacco, sugarcane, cocoa, coffee, tea, bananas, fever tree, and spices). Some sustenance crops were also moved at the initiative of enslaved people who were tragically and inhumanely traded between hemispheres.

Wheat was introduced from Europe to the West Indies during Columbus's second voyage in 1494, although it never took root in the Caribbean. It moved to Mexico and in the beginning of the sixteenth century was adopted in many regions of New Spain (183), spurred by the development of wheat varieties for hot, dry climates in many regions of central and southern North America (7). On the East Coast of North America, wheat was introduced in the sixteenth century with mixed success but was well established by the eighteenth century (14) and subsequently widely cultivated.

Both Asian rice and African rice (*Oryza glaberrima* Steud.), which was independently domesticated in sub-Saharan Africa and cultivated only regionally, were purchased by enslavers in West Africa during the transatlantic slave trade. The role of enslaved Africans in the introduction of rice, as well as key agricultural practices, to the Americas was remarkable (19) (see **Figure 1**). Based on historical records, Asian rice was well established in South Carolina by the second half of the seventeenth century (154) and became a major crop for the region. Meanwhile formerly enslaved people (e.g., Maroons), who between the seventeenth and nineteenth centuries settled in the Caribbean, Mesoamerica, and South America, introduced African rice to those regions. Isolated communities cultivating African rice were noted in the Guyanas (174) and Suriname (176). Genomic analysis of Suriname traditional varieties cultivated by modern Maroon communities identified their sister genotypes in the Ivory Coast (177). Other crops of African origin, such as yams, millets, sorghum, and oil palm, are also found on ship registers that crossed the Atlantic (19), but few were as successful as rice.

From the Americas to Europe, maize was introduced as early as the beginning of the sixteenth century (172) (see **Figure 1**). This likely reflected the introduction of tropical varieties from the Caribbean, with later dispersal of temperate varieties from North America and subsequent admixture in Europe (13). Maize was also among the early crops brought from the Americas to Africa (19). Based on historical accounts, maize and a few other American crops (e.g., peanuts) were also brought by Europeans to China by the sixteenth century as part of the Catholic Jesuit influence in the region (87). Maize was also being cultivated in the island of Cebu in the Spanish colony of the Philippines by the early 1700s as a result of the Galleon trade from Mexico. Sweet potato was a novelty in China during the same period, reflected in genetic and linguistic data that suggest introduction by Spaniards from Mesoamerica via the Philippines rather than from Polynesia (151).

No other crop of American origin had a higher impact on the Eurasian continent than potatoes (*Solanum tuberosum*). Historical accounts credit the Spanish for introducing the first potato to Europe in the late sixteenth century (82), although they were initially ornamental plants. The potatoes that were adopted as crops in Europe in the early nineteenth century (5) had a hybrid genetic origin between potatoes from the South American Andes and those from the Chilean coast (78). The key to the potato's adaptation to European growth was a change in its response to daylength that allowed tuber setting in the summer (106). Interestingly, the introduction of potatoes to North America was via European colonists rather than directly from South America, possibly due to its environmental unsuitability in the Mesoamerican environment.

3. GENETIC ADAPTATIONS TO NEW ENVIRONMENTS

As crops moved around the globe over the last 11,000 years, they have also genetically adapted to new geographic locations, evolving in response to new environments and cultural practices and tastes. Understanding the genetic bases of crop dispersal and geographic adaptation is critical in an agricultural context, as the ability to grow crops in new environments has implications for food security. Here, we review some examples of the genetics underlying crop adaptation to new environments postdispersal, including for stress avoidance and tolerance traits, and we highlight some general patterns illuminated by these studies.

3.1. Seasonality and the Geographic Spread of Crops

As crops disperse to new geographical locations, they encounter seasonal variations in temperature, precipitation, and daylength (**Figure 2**); remaining competitive in the new location necessitates the evolution of adaptations to optimize their growing seasons to new environments (60, 118, 139). These are particularly acute in crop movements across latitudes, in which dispersal of tropical crops to temperate regions (or vice versa) led to changes in optimal seasons for crop productivity.

Flowering time regulation is a key stress escape mechanism to deal with environmental challenges (135). Crop species can adapt their flowering time to new seasonal environments by modulating their response to seasonal cues such as photoperiod (139) and vernalization (135), ensuring both survival and high yield. Evolution in this life history trait is the most widely studied adaptive mechanism and is associated with the geographic movement of crops (135).

3.1.1. Flowering time adaptation across latitudes: the case of rice. Rice has been a focus of the study of geographical adaptation in flowering time. This Asian cereal, domesticated in the Yangtze River Valley beginning ~9,000 yBP (158), is considered a short-day tropical/subtropical plant in which flowering is promoted at critical daylengths of less than 13.5 h (179). As rice moves northward to temperate latitudes, new landraces have evolved to flower during longer days and allow harvesting before the autumn frost arrives.

Over the last two decades, more than 70 rice genes have been identified that control flowering time, but 4 key loci—*Hd1*, *Ghd7*, *OsPRR37/Ghd7.1*, and *GHD8/DTH8*—appear to be the most critical in seasonal adaptation (57, 58, 96, 115, 116, 199, 200, 206) (see **Figure 3**). Loss-of-function (LOF) or hypomorphic alleles of these 4 genes have been identified in rice (**Figure 3b**), which lead to reduced photoperiod sensitivity and allow for adaptation and geographic expansion of this crop (57, 58, 96, 185, 199, 200, 202, 206) (**Figure 3**). The *Hd1* gene is homologous to the *Arabidopsis* gene *CO*, encoding a transcription factor that positively regulates *Hd3a* expression and induces flowering in short days (197). This gene can modulate long-day flowering depending in part on the allelic status of *Ghd7*, which encodes a CCT domain protein that interacts with *OsGI*, *DTH8*, and *Hd1* to repress flowering under long days (193). *Ghd7.1* (also known as *DTH7* and *OsPRR37*)
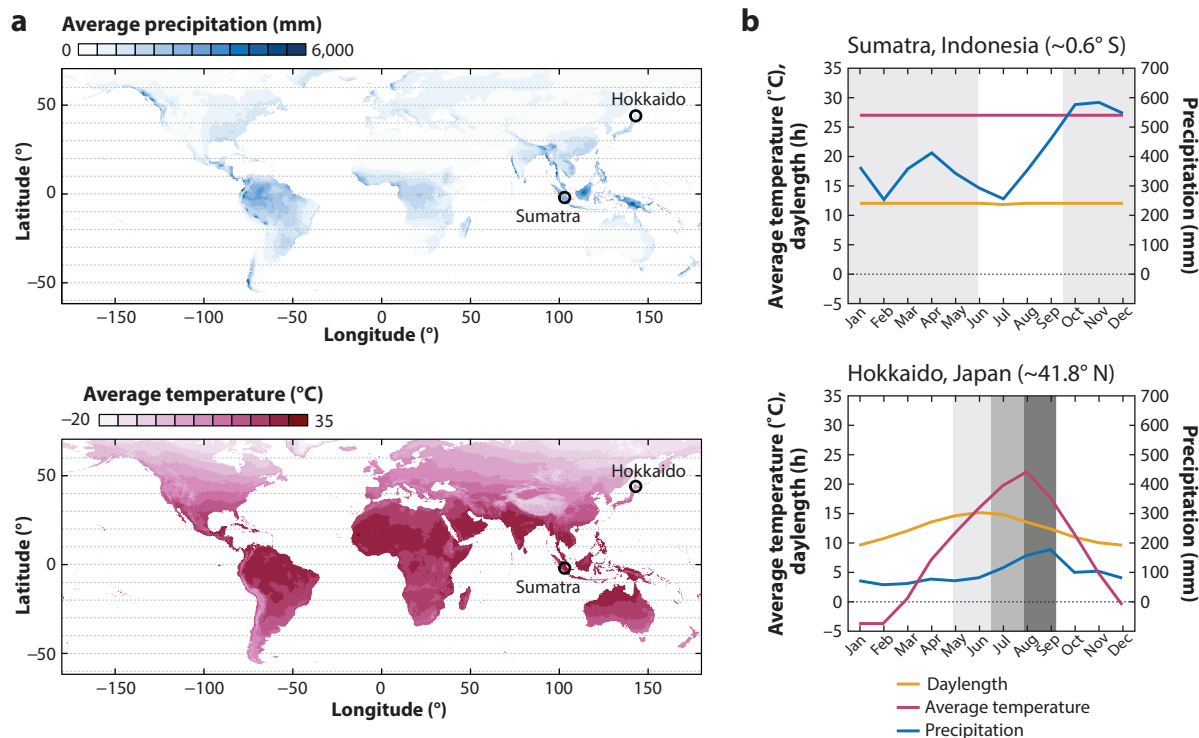
Figure 2

Environmental differences across crop distributions. (*a*) Geographic gradients based on two environmental variables, annual precipitation (*top*) and average annual temperatures (*bottom*), highlight differences across the global cultivation areas. Circles represent two distinct rice growing regions, the equatorial tropical area of Sumatra, Indonesia and the temperate southern areas of Hokkaido, Japan. Data from WorldClim version 2.1 (**https://www.worldclim.org/data/bioclim.html**). (*b*) Annual changes in the daylength, temperature, and precipitation in Sumatra and Hokkaido necessitate adaptation. Shaded gray areas indicate the rice growing season. In Sumatra, the long season depends on midyear precipitation and can accommodate two flexible plantings in a year. In Hokkaido, the season is much shorter to escape winter frosts. The rice growing season in Hokkaido begins when the temperatures are appropriate (*light gray*). In this northern area, rice starts heading during warm and wet long daylengths (*mid-gray*), and ripening occurs during falling temperatures, necessitating cold tolerance adaptation (*dark gray*). Data from **http://www.hakodate.climatemps.com** and **https://www.sumatra.climatemps.com**.

encodes a pseudoresponse regulator protein and delays long-day flowering (108), while *DTH8* encodes the HAP3 subunit of a CCAAT-box-binding transcription factor (48).

Allelic combinations of these genes lead to a continuous distribution of flowering time and act either additively or epistatically to be adaptive across different latitudes and environments. *Japonica* rice, for example, can be differentiated into temperate and tropical *japonica*, and the functionalities of *Hd1* appear to differ between these two groups (58, 73, 96). There are at least 10 LOF alleles of this gene, some of which have allowed the northward movement of rice to the island of Hokkaido in Japan (the northern limit of rice cultivation), while others have been selected in tropical and subtropical populations further south (58, 73, 96). A LOF allele in *Ghd7* has also been associated with rice in Hokkaido and is presumed to allow for early flowering to escape possible autumn frost (200, 206). Functionally deficient alleles of *OsPRR37* and *Ghd8* are also known in high-latitude cultivation areas, where the typical growing season is shorter. Different combinations are also associated with different cultivation zones in China (205). Under long-day conditions, nonfunctional *Hd1*

Pseudoresponse regulator: a member of a group of genes that regulate the plant circadian oscillator
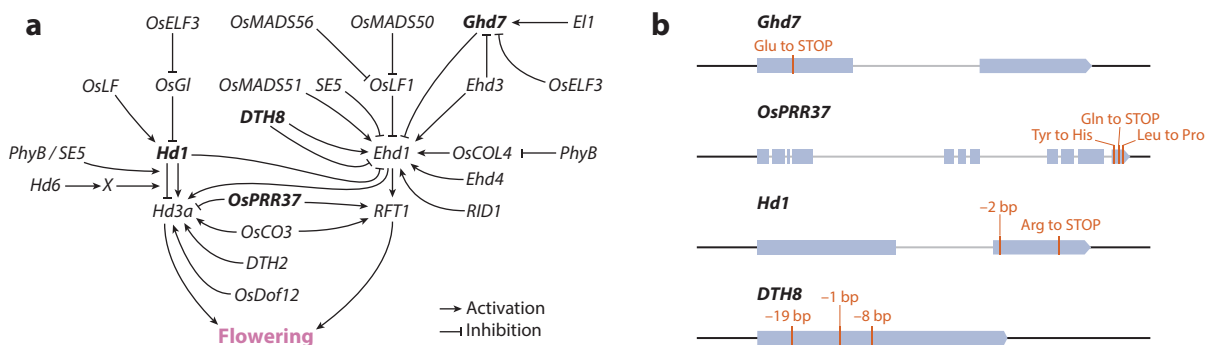
Figure 3

Flowering time gene network in rice. (*a*) Exemplified by rice, changes in flowering time can be achieved through mutations in multiple genes of the gene network, although the genes in bold are the key loci that display the variation associated with rice dispersal in Asia. Panel adapted from Reference 167 (CC BY 4.0). (*b*) Structure of four genes associated with flowering time variation in rice. The mutational lesions in each of the genes are indicated, including nonsense mutations for *GHD7*, *OsPRR37*, and *Hd1*, and frameshift mutations for *DTH8*. Data from Reference 96.

and *OsPRR37* determine flowering time for all varieties, while *Ghd8* regulates regional varieties in East China and *Ghd7* in North China, Korea, and Japan (206).

Aside from these four genes, variation at other loci may contribute to local adaptation of rice flowering time and seasonality. For example, the gene *DTH2* also activates *Hd3a* and *RFT1*, and the A4 allele at this locus promotes flowering in long-day conditions and is associated with northern expansion of rice; moreover, there is evidence of a selective sweep in this gene (187). The gene *Hd6* also regulates *Hd1*, and functional haplotypes of this gene are geographically structured (73). It is indeed likely that other flowering time loci may have other (possibly rare) functional variants that help different rice populations adapt to different latitudes.

Finally, an interesting correlation has been observed in rice (as well as maize), in which telomere length is negatively correlated with flowering time variation (23). This is accompanied by a latitudinal distribution in which rice and maize populations in more temperate regions had a significantly higher telomere repeat copy number (23), suggesting that the movement of crops to higher latitudes may be associated with telomere length variation.

3.1.2. The movement of maize from tropical to temperate zones.   Maize is a cereal crop species that originated in the lowland tropics (Mexico) and subsequently dispersed over a region spanning 90° of latitude; the same set of genes involved in the adaptation of other cereal crops appear to underlie latitudinal adaptation in this species. For example, *ZCN8* is an *FT* family member, and a promoter single-nucleotide polymorphism (SNP) shows a strong association with the flowering time and differential binding of the flowering inducer *ZmMADS1* (72). This SNP appears to have been selected for early flowering and to have increased in frequency throughout the Americas, while the late-flowering allele is restricted to low latitudes.

Other genes involved in flowering time adaptation include the *Ghd7*-like genes *ZmCCT9* (90) and *ZmCCT10* (196) and the *AP2*-like gene *Vgt1* (15, 20, 49) (**Figure 4a**). *Vgt1* was identified as a flowering time quantitative trait locus (QTL), and the insertion of a miniature transposon located ∼70 kb upstream of *ZmRap2.7* was shown to be the causal variant and is strongly correlated with latitude (15, 20, 49) (**Figure 4a**). A transposon insertion ∼57 kb upstream of *ZmCCT9* (90) and a transposon insertion within the *ZmCCT10* promoter (196) repress the expression of these two genes (**Figure 4a**). These two mutations allow for long-day flowering and appear to have arisen sequentially; molecular evolutionary analyses suggest that the insertion at *ZmCCT10* came

Selective sweep: the process where an advantageous mutation together with adjacent mutations increases in frequency in a population

Haplotype: closely linked DNA variants along a chromosome that tend to be inherited together
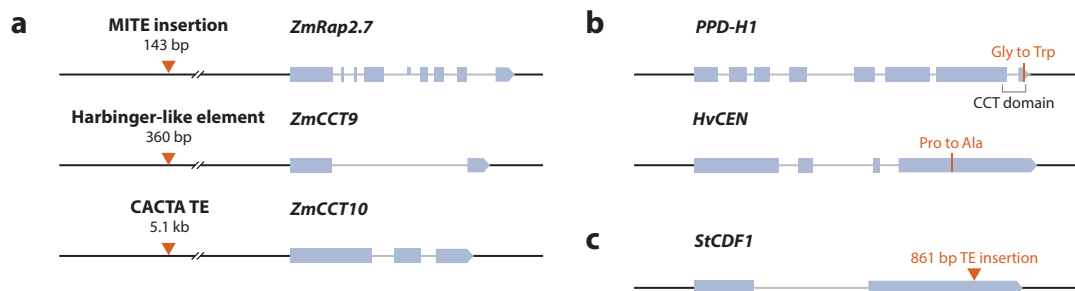
Figure 4

Key genes for crop dispersal in different species. (*a*) The structures of three genes associated with flowering time variation in maize. These three genes have transposable element (TE) insertions in their *cis*-regulatory regions that are associated with maize dispersal to temperate regions or highland areas. (*b*) The structures of *PPD-H1* and *HvCEN* genes associated with flowering time variation in barley. Amino acid missense mutations associated with hypomorphic alleles are shown. Data from Reference 28 and 173. (*c*) The structure of *StCDF1* that controls tuberization in potato. A transposon insertion in the second exon leads to truncated proteins and the adaptation of potato tuberization to northern temperate latitudes. Introns in all gene structures are indicated by horizontal gray lines. Data from Reference 78.

first in tropical maize, and the transposable element (TE) insertion in *ZmCCT9* subsequently occurred, allowing maize to move toward high-latitude regions (90). Unlike the *ZCN8* SNP widely distributed in the Americas (72), the mutations in *ZmCCT9*, *ZmCCT10*, and *Vgt1* occur at high frequency in North America and are associated with maize's northward expansion. Interestingly, a *ZmCCT10* allele that contains a distinct 4.2-kb TE intron insertion leads to a contrasting allelic response to photoperiods between low- and high-latitude regions compared to the *CACTA*-like insertion allele (208), suggesting the ability of multiple insertions to lead to modulated phenotypes. These and other studies suggest that maize adaptation to northern latitudes is complicated and likely had a polygenic basis (168).

3.1.3. The dispersal of the Fertile Crescent cereal crops barley and wheat.

Barley and wheat are two cereal crop species that originated in the Fertile Crescent but subsequently expanded to temperate Europe and East Asia. Barley has winter and spring varieties, the former cultivated in southern areas (e.g., the Fertile Crescent and the Mediterranean) where it can overwinter and flower before a very dry summer, while spring varieties are found further north and sown after winter cold temperatures have passed (28, 153). As in other cereal crops, variation in flowering time genes is crucial in determining spring versus winter barley and the associated geographic distribution of these varieties. In the *HvCen* gene in barley, a proline in position 135 is associated with winter barley, while an Ala substitution is found in spring genotypes (see **Figure 4*b***); this substitution displays a north-south cline (28, 152). Spring barley may also have the dominant allele of *Ppd-H2*, also known as *HvFT3*, while recessive nonfunctional alleles are found in winter varieties (28, 101). The key gene in barley, however, appears to be *Ppd-H1*, which encodes a *PRR37* homolog and in which a Gly-to-Trp replacement in the CCT domain region (see **Figure 4*b***) appears to lead to a differing flowering time (28, 98, 119, 173). At least eight distinct *Ppd-H1* haplotypes show geographic structuring across Eurasia, with one haplotype found largely in Europe, while another is found in Asia and associated with barley dispersal across Central Asia and the Tibetan Plateau (28, 98, 119). Interestingly, an exon 6 SNP that shows a separate amino acid change from the CCT domain SNP also shows latitude-dependent geographical distribution and is found largely in low latitudes in Europe and associated with flowering later under short days; conversely, the SNP associated with a day-neutral

CACTA-like:
an abundant superfamily of class 2 plant DNA transposons

phenotype is found in northern Europe, although it most likely arose in the Iranian Plateau
(98, 119).

Barley adaptation across latitudes also requires changes in three genes that regulate vernaliza-
tion: *VRN-H1* (137), *VRN-H2* (193), and *VRN-H3* (also referred to as *HvFT*) (194). *VRN-H1* is the
key vernalization gene and encodes an *AP1*-like MADS-box gene; dominant/semidominant alleles
of *VRN-H1* are associated with deletions of a *cis*-regulatory element within intron 1 (169). Both
VRN-H2 and *VRN-H3* are downstream of *VRN-H1* and are thus considered part of the vernal-
ization pathway but are also responsive to long-day conditions, making them photoperiod genes
as well (53). *VRN-H2* encodes a CCT-like protein (193) that is activated by long-day conditions
and repressed by *VRN-H1*; this gene acts to repress the floral activator *VRN-H3*. Cold condi-
tions in winter varieties lead to increased *VRN-H1* activity, which reduces *VRN-H2* expression
and in turn derepresses *VRN-H3*, inducing vernalization and leading to flowering (53). Natural
recessive mutations in *VRN-H2* that delete a cluster of up to three genes at this locus are found
largely in spring varieties (28, 169), which concomitantly attenuates the long-day pathway for
floral repression acting through this gene. *VRN-H3* is also activated by long days via *PPD-H1*
(53), and polymorphisms in intron 1 have also been suggested as responsible for some flowering
time variation (194). Studies have shown that *VRN-H1/vrn-h2/VRN-H3* genotypes flower under
long days and are spring varieties, while *vrn-h1/VRN-H2/vrn-h3* are winter barley varieties (153,
170); others suggest an epistatic model involving only *VRN-H1* and *VRN-H2* (169). Interestingly,
the distinct pathways for vernalization in barley and *Arabidopsis* suggest parallel evolution for this
seasonal signaling trait.

Similar to barley, wheat varieties also vary in photoperiod (via the *Ppd* genes encoding PRR37
proteins) and vernalization (via the MADS-box *Vrn* genes) responses (43, 75, 157, 189, 195). There
is the added complication of multiple homoeologous loci associated with the polyploid constitu-
tion of some wheat species. Similar to examples in other cereal crop species, mutations in wheat
genes also involve promoter mutations as well as copy number variants that differentiate spring
versus winter wheat varieties (43).

3.1.4. Seasonal adaptation in flowering time in other crops.

Variation in flowering time
associated with the dispersal of other crops generally involves the same genes underlying seasonal
adaptation over a wide group of species. Sorghum, for example, is a short-day plant related to maize
but with origins in Northeast Africa and has also expanded its range to temperate areas, including
southern Africa, East Asia, and the Americas (17). Multiple loci, including homologs to the rice
genes *DTH7/OsPRR37* (105, 133), *GI*, *Hd3a* [as well as other members of the *FT* family (38)], and
Hd1, as well as phytochrome genes (52), appear to be associated with its geographic expansion.
Aside from cereal crops, soybeans are the best-studied crop species with respect to the genetic basis
of seasonal adaptation (47), and at least 20 genes have been implicated in photoperiod sensitivity
in this legume crop, including homologs of *FT*, *LHY*, and *PRR37* genes and B3 domain proteins
(47, 66, 112, 121, 203). Together, these studies suggest that parallel evolution in seasonal/latitudinal
adaptation involves homologous loci in these as well as other crop species.

3.1.5. The dispersal of potato to Europe and photoperiod control of tuber growth.

Pho-
toperiod sensitivity has also been crucial in the dispersal of another crop species, although not to
coordinate flowering. In potato, photoperiod controls the formation of aboveground shoots from
stolons under long days but forms tubers belowground under short days (97). Potato was do-
mesticated in South America and spread globally with the Columbian Exchange, particularly to
temperate Eurasia. The short-day tuberization of Andean potatoes would happen in late autumn
in Europe, where plants are subsequently exposed to frost. Overcoming short-day dependency for
tuberization was therefore an important adaptation to high-latitude seasons in Europe (78).

The key gene for this adaptation is *StCDF1*, which encodes a cycling DOF factor (106). At least three disrupted *StCDF1* alleles are known, one of which is a TE insertion allele (see **Figure 4c**), and two others have 7-bp frameshift insertions; all lead to truncated *StCDF1* proteins that result in clock deregulation and the long-day maturity of tubers (106) (see **Figure 4**). These alleles are latitudinally distributed and appear to have been introduced into European potatoes in the nineteenth century (78).

3.2. Temperature Adaptation and Crop Dispersals

Environmental tolerance mechanisms (as opposed to stress escape mechanisms that utilize flowering time) are another class of adaptations that facilitate crop colonization in new environments. To grow in new geographic locations, for example, crops may need to tolerate various thermal regimes, particularly colder conditions associated with movement to temperate regions (**Figure 2**). Tolerance to cold is especially necessary to help survive frosts; in barley, for example, an association study identified SNPs in polyamine oxidases and at the *CBF* region associated with frost tolerance (*CBF4*), although the precise physiological mechanism is unclear (29).

Much of the work, however, has focused on rice, where genetic changes are observed in temperate *japonica* planted at northern latitudes. A genome-wide association study (GWAS) identified 156 loci associated with cold tolerance, with several showing evidence of selection (71). Alleles in *CTB4a* and *Ctb1* appear to have arisen in *japonica* rice, allowing expansion to North Korea, the Yunnan province, and parts of Northeast China (111). Other studies identified an amino acid polymorphism (I408V) in *CTB2* that is associated with cold adaptation (111). It has been suggested that there is selection for a joint *CTB2/CTB4a* haplotype in temperate *japonica* in the Yunnan province in China, with the I408V polymorphism in *CTB2* selected first, followed by selection at *CTB4a*, which then spread to higher altitudes in Yunnan and temperate areas of Northeast China, Korea, and Japan (111). Another key gene for chilling tolerance in temperate *japonica* rice, *COLD1*, encodes a regulator of G protein signaling associated with low-temperature sensing and accelerated G protein GTPase activity (71, 122, 207). Another gene, *HAN1*, encodes an oxidase that inactivates a form of jasmonic acid; temperate *japonica HAN1* alleles appear to have gained a putative *MYB cis*-element, leading to enhanced chilling tolerance (124).

Unlike genes for cold tolerance, less is known about crop loci for high-temperature adaptation. *TT1* was identified in African rice *O. glaberrima* (113), a species that shows greater heat stress tolerance than Asian rice. This gene encodes an a2 subunit of the 26S proteasome, which may protect from heat stress by the elimination of denatured proteins (113). There are at least two haplotypes of *TT1* in Asian rice associated with differences in heat stress response that may be important in rice dispersal to geographic regions with high temperatures (113). Another gene, *SLG1*, encodes the rice cytosolic transfer RNA 2-thiolation protein 2 (RCTU2) and also plays a role in the response to high-temperature stress and possibly in the geographic dispersal of *indica* rice across the tropics (192)

An adaptation to different temperature regimes with a unique genetic trade-off is observed with the *Tannin1* locus in sorghum, which encodes a WD40 protein that controls tannin biosynthesis (110). Variation in *Tannin1* is geographically structured, with the functional allele occurring at high frequency in cool, wet conditions where tannins help suppress mold growth and preharvest sprouting. In warmer, drier environments, however, mold growth and preharvest sprouting are limited, so a null allele containing a 1-bp deletion is found at higher frequencies in geographic regions with greater mean temperatures (>32°C) (110). At these higher temperatures, without the need to control for molds, humans select for less astringent grains that have reduced tannins.

3.3. Moving to New Altitudes

In many cases, adaptation to higher altitudes poses the same challenges as adaptation to higher latitudes: Seasonal growth needs to adapt to a different onset of cold seasons. Thus, many flowering time variation genes involved in latitudinal dispersal, which provide the evolutionary basis for stress escape, are also deployed in altitudinal movement. In rice, for example, the *Hd1*, *Ghd7*, *OsPRR37*, and *DTH8* genes are employed in both latitudinal and altitudinal adaptation in Chinese varieties (198, 200). In barley, variation in *Ppd-H1* is associated with movement to higher elevations of Central Asia and the Tibetan Plateau (119), while in maize, diversity at *vgt1*, *ZCN8*, and *ZMM4* is important in highland agriculture (181). In the case of maize, there is also evidence for selection at *CONZ1*, *LUX*, *ZmPRR59*, *ZEITLUPE*, *RVE2*, *PRR5*, *PHYA1*, and *ZmCCT* genes in some highland populations (181). Finally, an interesting pattern has also been observed in maize: In both Mesoamerica and South America, there is a negative correlation between genome size and altitude, possibly associated with changes in cell division rate and flowering time (9). This suggests that selection may have an impact on genome size that accompanies the movement of maize to higher altitudes.

Altitudinal adaptation, like latitudinal adaptation, also involves the evolution of stress tolerance. Cold tolerance genes are also associated with altitudinal dispersal, including *CTB1*, *CTB2*, and *CTB4a* in rice (111) and *CBF4* in barley (29). Other genes in Tibetan wheat, which grows at fairly high altitudes, include a TaHY5-like regulation hub that is advantageous at altitude. This regulates not only *TaERF4* for cold tolerance but also other genes associated with the ability to withstand other environmental challenges at high altitude, including *TaPCO1* (hypoxia), *TaCHLH* (high light), and *TaTDP1* [ultraviolet light (UV) levels] (74); this is consistent with previous studies that suggest greater stress tolerance and DNA repair in high-altitude plants (74). Finally, in maize, transcriptome analysis indicates that phenylpropanoid and flavonoid biosynthetic genes associated with UV-B protection may be relevant to highland adaptation (109), while analysis of highland populations of Taiwan rice suggests selection in a region spanning the *OsUGT706D1* gene that has been shown to contribute to UV tolerance (3).

3.4. Other Adaptations

Other genetic adaptations to new environments have been identified, although to a more limited extent. One trait that shows strong environmental association with humidity/aridity is pod dehiscence in legumes. In soybean, indehiscent alleles at *Pdh1* and *NST1A* are required to ensure nonshattering in Northeast China, while only *Pdh1* is needed in the more southerly Huang-Huai-Hai region/North China Plain (201). Pod dehiscence is enhanced by low humidity in arid regions, and there is a strong correlation between humidity and indehiscent *Pdh1* allele frequency. This pattern is also observed in the common bean *Phaseolus vulgaris*, where the pod indehiscent allele of *PvPdh1* (which has a Thr162Asn replacement) is prevalent in the northern, semiarid highlands of Mexico and at low frequency in humid Mesoamerican populations (141).

Another interesting set of adaptations are traits that lead to greater cultural acceptance in specific societies, which could facilitate crop dispersal to new areas. Aspects of taste, cooking quality, and visual appeal are some features prized in specific cultures, and crop varieties that exhibit these traits could lead to greater acceptance. In rice, for example, glutinousness (or stickiness) is a trait governed by amylose/amylopectin levels as determined by the *waxy* gene (86, 138). This is preferred in the culinary traditions of Japan and Korea, and mutations in *waxy* appear to have originated in mainland Southeast Asia but subsequently migrated to Northeast Asia (138). Similarly, in maize, the amylopectin levels controlled by the *su1* gene determine whether corn is suitable for

popcorn (its original use) or may be ground into a more pasty flour to make tortillas and porridge, and this gene was possibly under heavy selection after 2,000 yBP (39)

Gene–environment association (GEA): statistical associations between allele frequency and the environment of origin of a genotype

3.5. Genome-Wide Scans of Adaptive Regions

The previous sections have focused attention on specific genes that have been isolated and identified by molecular genetic analysis, usually via genetic mapping and functional validation. Other approaches to examine the genetics of crop dispersal genes have scanned the genome to identify possible selected regions that (*a*) harbor genes for local adaptation, (*b*) are associated with environmental/climatic variables, (*c*) possess alleles with geographic distributions linked to selection, and (*d*) exhibit transcriptional differences between environments. Although these latter approaches generally cannot resolve specific loci that underlie geographical adaptation, they can identify multiple genes or genomic regions containing the signatures of local adaptation necessary for crop dispersal. Unfortunately, they lack the molecular genetic characterization that would provide strong functional validation; nevertheless, these approaches establish hypotheses for further molecular genetic and evolutionary analyses.

Geographically structured selective sweeps have been identified in pearl millet (18), maize (181), apricot (70), pear (186), and potato (78, 106). In potato, for example, genome-wide analysis suggests that a genomic region that encompasses eight photoperiod response genes has been selected in Europe; there is also evidence of selection in the clock-associated genes *REVEILLE6* and *ELF4*, as well as in gibberellic acid genes that appear to be involved in tuber formation (78, 106). Selective sweeps have also been used in conjunction with GWASs to identify traits involved in local environmental adaptation, such as salinity tolerance in African rice (128).

Gene–environment associations (GEAs) have also identified SNPs or genomic regions associated with specific environments, including in rice (77, 207) (see **Figure 5**), sorghum (110), flax (156), bean (8), and wild barley (22); these studies have identified SNPs that correlate with temperature, precipitation, or soil characteristics. Furthermore, local adaptation has been inferred by examining geographic patterns of allele distribution and applied to examining lowland versus upland adaptation in rice (190), temperature adaptation and other traits in sorghum (131),
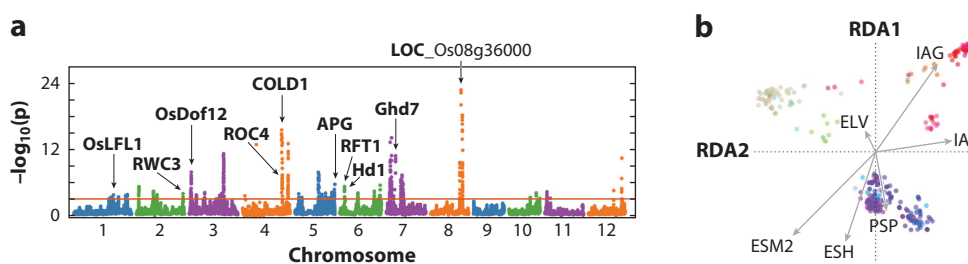
Figure 5

Gene–environment associations in rice. (*a*) Manhattan plots for a genome-wide scan of associations between SNPs and the temperature and daylength of the geographic locations for which specific rice varieties are grown. The names of significant loci are included. The horizontal line indicates the empirical probability threshold (10^{-3}). Panel adapted with permission from Reference 207 (CC BY-NC 4.0). (*b*) *Japonica* rice genotypes (*colored dots*) projected on RDA1 and RDA2 axes in a redundancy analysis. Arrows are environmental predictors that strongly correlate with the proportion of variation in linear combinations of SNPs. Panel adapted from Reference 77. Abbreviations: ELV, elevation; ESH, end of growing season heat; ESM2, early growing season minimum temperature 2; IAG, interannual coefficient of growing degree days variation; IAP, interannual coefficient of precipitation variation; PSP, pregrowing season precipitation; SNP, single-nucleotide polymorphism.

and genomic regions associated with highland adaptation in maize (181). Finally, transcriptional changes across geographic environments identify gene expression differences associated with the adaptation of maize to altitude and UV levels (89, 109).

3.6. The Genetic Architecture of Crop Dispersal Adaptations

The identification of genes associated with crop dispersal provides the foundation for examining aspects of the molecular genetic architecture of adaptations. Since flowering time genes associated with seasonal adaptation have been the most comprehensively studied, they serve as a starting point in examining the nature of the evolutionary genetics of crop dispersal traits.

It is clear, at least from the analysis of seasonal flowering time, that many adaptations have a polygenic basis. Allelic variation at multiple genes, for example, acts additively or epistatically to provide quantitative diversity in crop flowering time, which adapts dispersing populations to new seasonal growing conditions by modifying photoperiod and/or vernalization sensitivity. Interestingly, many polymorphisms associated with seasonal adaptation are LOF mutations, including nonsense, frameshift, and/or insertion/deletion (see **Figures 3b** and **4**) mutations that either delete the gene, reduce its expression, or result in nonfunctional truncated protein products. This is seen in rice, where LOF mutations in *Hd1*, *Ghd7*, *OsPRR37*, and *Ghd8* (**Figure 3b**) are associated with geographic expansion. In soybean, the key gene *E1*, which encodes a legume-specific B3 domain protein and represses *FT* homologs (47, 66), has functionally deficient alleles adapted to shorter growing seasons in high latitudes, including the alleles *e1-fs* (frameshift), *e1-as* (amino acid substitution), *e1-b3a* (B3 domain mutation), *e1-re* (retrotransposon insertion), and *e1-null* (∼130-kb deletion) (117). It appears that, for genes associated with flowering time, disabling parts of the functional regulatory network provides crop plants with the ability to adapt to different latitudes.

Evolution at *cis*-regulatory elements underlies some variation associated with dispersal and crop adaptation. In barley, for example, *VRN-H1* alleles result from deletions of an intron *cis*-regulatory element associated with dispersal to temperate environments (169). Similarly, a *HAN1* allele in temperate *japonica* rice gained a putative MYB *cis*-element, which enhances chilling tolerance and allows rice to adapt to temperate climates (124). Regulatory regions of *ZmCCT9*, *ZmCCT10*, *ZCN8*, and *ZmRap2.7* are also crucial for maize adaptation to temperate climates (15, 49, 72, 90, 196) (see **Figure 4a**), and natural variation in these regulatory regions promotes flowering under long-day conditions at higher latitudes.

Several *cis*-regulatory mutations result from TE insertions in relevant genes. This is most prominent in maize, where the role of TE insertions in upstream regions of *ZmCCT9* (90), *ZmCCT10* (194), and *ZmRap2.7* (15, 49) in latitudinal and/or altitudinal adaptation is observed (see **Figure 4a**). Another TE regulatory insertion has been described in *Brassica napus*, where a *Tourist*-like MITE insertion upstream of the *BnFLC.A10* gene is associated with winter rapeseed (88). The role of TE insertions in crop dispersal adaptation also extends to the evolution of LOF or hypomorphic alleles, such as retrotransposon insertions in *E1* and *E4* soybean genes (117) leading to reduced photoperiod sensitivity to long daylength. Flowering time is further modified by transposon insertion in the first intron of *E9/FT2a* that reduces expression level (203). Another example is transposon-mediated truncations in *StCDF1* (**Figure 4c**) leading to nonsense alleles that result in potato tuberization under long days in higher latitudes (106).

Two other features of the molecular basis for crop dispersal adaptations are noteworthy. The first is how similar genes and pathways are targets of evolution across multiple species. This is evident in flowering time and seasonal adaptations across cereal crops, legumes, and solanaceous species, where the same genes in photoperiod response and/or vernalization are mutated across

multiple crop taxa. This pattern conforms to Vavilov's law of homologous series in variation (178), which states that if one species displays phenotypic variation in a trait, the same variation would be observed in other (even distant) species. This law suggests that the conservation of genes for homologous traits across species, as well as similarities in selective forces, may result in parallel and/or convergent evolution (146). The latter is particularly relevant to dispersing crop species, where distantly related taxa confront the same environmental challenges even as they move to different latitudes, altitudes, or other geographic locations.

Second, introgression—either from distinct populations or wild relatives—plays a role in adapting to new environments as crops move to new locations. It has become clear that numerous crop species, including rice (24), maize (91), apples (31), date palms (54), grapes (56, 134), and beans (8), have experienced introgressive hybridization after domestication, and it has been suggested that introgression provides the ability to adapt as crops disperse from their centers of origin (16). In maize, for example, the colonization of high-altitude environments was facilitated by gene flow from wild *Z. mays* ssp. *mexicana*; nine genomic regions of introgression of *mexicana* into maize landraces are associated with adaptive traits such as leaf macrohair levels and pigmentation intensity (91). Wild alleles of potato *StCDF1* permitted cultivation of *S. tuberosum* in temperate Europe and North America and were likely introduced via introgressive hybridization (80). There are also examples in pearl millet (18), sorghum (163), and grapes (56, 134) where hybridization with wild populations/species may have allowed for local adaptation of crops as they moved to new areas; together, these examples suggest a role of adaptive introgression in the establishment of crop populations outside of their ancestral range.

Interestingly, the introgression of adaptive traits can work with or against cultural preferences. In maize, temperate varieties from the Colorado Plateau passed on a complex polygenic architecture into more recently dispersed landraces that led to the evolution of contemporary temperate maize more suited for tortilla making (168). By contrast, the introgression of adaptive flowering time alleles from wild relatives that enabled flax cultivation in Europe worked against its original cultivation for oil and instead promoted cultivation for fiber (79).

4. PERSPECTIVES

The study of crop dispersals continues to move forward, fueled by multidisciplinary interest encompassing plant biology, genetics and genomics, evolution, ecology, archaeology, anthropology, history, and paleoenvironmental and even cultural studies. There has been interest in reconstructing the dispersal of crops and the genetic basis for adaptation to new environments, and we have only been able to sample some of the studies in this review. Future studies will continue to highlight interdisciplinary work to untangle patterns and processes of crop dispersal, identify evolutionary adaptations associated with crop movement, and harness this knowledge to address agricultural issues across the globe.

We need to continue to trace the timing and direction of crop dispersals, integrating studies from archaeology, history, and genomics. While the dispersal narrative is being fleshed out for major crops, we need to expand the scope of investigations to less well-known cereal crops, legumes, vegetables, and fruit trees. There is also a need to look at regions that are currently understudied by archaeology or undersampled by genetic studies, such as Africa, Oceania, and Southeast Asia. There is an opportunity to harness genomic information coupled with more sophisticated population genomic analytical techniques to reconstruct crop histories (12). Moreover, we now have the ability to use ancient or historical DNA to provide direct genetic windows to the past (51, 76). The resulting reconstruction of individual dispersal trajectories will help identify overarching patterns across the movements of crop species, which could then be compared with movements of human

populations or histories of cultural contacts. Finally, by cross-referencing the location and timing of dispersals with paleoclimatic or historical weather shifts (3, 77), we may examine the interaction between climate change and crop demographies.

Central to studies of crop dispersals is the attempt to advance our understanding of the genetic basis for adaptation associated with the ability of species to thrive in new environments and climates. While there has been substantial progress in examining seasonal/flowering time adaptation in crop dispersals, much less is known about genetic adaptations to other abiotic and biotic environments; more sustained effort may identify key adaptive genes and regulatory networks that allow plants to adapt to local environmental features. Moreover, mounting evidence suggests that many of these adaptations may be polygenic and associated with standing genetic variation (as opposed to new mutations), and further work will need to examine whether these features indeed underlie postcolonization adaptations.

Finally, uncovering patterns of crop dispersals and genes that allow crops to grow outside their original centers of origin can help develop new crops tailored to specific geographies and changing climates. This is relevant to current and looming issues of food security, which necessitate an increase in food production, as well as adapting it to the climate crisis, which promises to transform regional weather patterns. Studies of crop dispersal and adaptation can dovetail with new genomic methods for plant breeding, such as genomic selection, or new genome engineering approaches utilizing CRISPR-Cas9 to advance agricultural productivity (149). By examining the evolutionary histories and genetics of crop populations, we can provide the knowledge necessary for tinkering with genomes and channeling the future evolution of these species that are key to feeding the world population.

SUMMARY POINTS

1. Crop species dispersals began early during the domestication process, with ancient diffusion across the landscape associated with the spread of agriculture ($\sim$11,000–4,000 yBP), followed by later spread through ancient trading networks (4,000–550 yBP) and global spread between Old and New Worlds during the post-Columbian Exchange ($<$550 yBP).

2. A major aspect of crop adaptation postdispersal is a generalized stress escape response associated with seasonal adaptation across different latitudes, which necessitates the evolution of flowering time pathways to adjust photoperiod and vernalization sensitivity.

3. There is marked parallel evolution of flowering time across multiple cereal, legume, and other crop species, associated with genetic changes across homologous genes.

4. A substantial number of mutational changes associated with dispersal adaptation are loss-of-function mutations, sometimes associated with transposable element insertions, as well as *cis*-regulatory mutations.

5. The study of crop dispersal and evolution is a multidisciplinary exercise that brings in data and ideas from genetics, genomics, archaeology, and history.

DISCLOSURE STATEMENT

ACKNOWLEDGMENTS

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