

Adapting Crops, Landscapes, and Food Choices: Patterns in the Dispersal of Domesticated Plants across Eurasia

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Abstract

After the domestication of plants and animals, the subsequent spread of agriculture represented a process of adaptation of both species and landscapes. Crop species moved beyond their original ecological limits, and their range expansion, when successful, was generally the result of adaptive post-domestication genetic changes on the part of the plants, human-induced changes in agricultural landscapes, and the dynamics of cultural food choice. This chapter explores the patterns by which agriculture became established as a consequence of the diffusion of domesticated plants (and sometimes people), as well as the ways in which agricultural systems were gradually transformed through the diversification of crop packages. Comparisons from across Eurasia are drawn to identify general patterns in crop dispersal, with three categories playing the largest role in the diffusion of grain-based agriculture. These agricultural systems are discussed and their modes of diffusion, stories of collapse, and examples of new adaptations on the part of the crops and agricultural systems detailed.

Keywords

Agriculture; Neolithic; Domestication, Cuisine; Archaeobotany

Introduction

Agriculture is widely regarded as one of the key changes in ecological and economic systems in the history of *Homo sapiens* (Diamond [2002](#); Bellwood [2005](#); Barker [2006](#); Smith and Zeder [2013](#)). There is no doubt that agriculture set in motion increases in human population density and the transformation of environments, from

biomes to 'anthromes' (sensu Ellis 2011). Over the long-term, land-use intensified primarily through agriculture, supporting denser populations and increasing regional carrying capacity by supporting more people from less land (Ellis et al. 2013). In this regard there should be little surprise that anthropologists and archaeologists have expended considerable effort on the study of agricultural origins, although more often than not this has focused on the search for pristine origins – those relatively few instances in which hunter-gatherers became farmers by domesticating plants and animals that were wild in their environment. As archaeological research and biological studies of wild progenitors have progressed, the number of recognized centres of origins has expanded from half a dozen or less, to close to ten, and perhaps even twenty or more (Fuller 2010; Larson et al. 2014). Nevertheless, it is undeniable that for the majority of the planet, agriculture was introduced from elsewhere and was based on plants and animals introduced as domesticates.

This chapter explores the patterns by which agriculture became established by the diffusion of domesticates (and sometimes people), and how agricultural systems were gradually transformed through the diversification of the choice of domesticates, a process also brought about by the continuing, and intensifying, patterns of interaction between societies over increasing distances (see Boivin, this volume). This is undertaken through a comparative approach that explores instances of agricultural spread and agricultural change across diverse societies of the Old World, mainly in Eurasia, a continent on which we can argue for perhaps nine centres of agricultural origins that emerged variously between 9,500 and 2,500 BC (Figure 12.1). Nevertheless, most of the land area of this region, with the exception of the sub-arctic, eutropical islands and the southern half of Africa, came to be populated by people reliant on food

production, certainly by ca. 500 BC. This supports a rather rapid process for the spread of food producers or the adoption of food production. In more general terms, the dispersal of human-created food-producing environments across this region parallels recurrent processes globally.

Figure 12.1 An updated map of centres of likely independent plant domestication and agricultural origins in the Old World, with the frontier of agricultural dispersal by 500 BC (based on Larson et al. 2014).

This chapter focuses specifically on the spread and adaptation of crop plants. Before a discussion of these processes can be undertaken, what is meant by the domestication process and agriculture, as it unfolded in the regions of origin, must be outlined. *Cultivation*, as discussed here, represents a form of human behaviour that involves the deliberate manipulation of plant lifecycles; *domestication* involves the genetic changes that altered the adaptations of these plants; and *agriculture* is a matter of economic commitment and involves a scale of land-use in which cultivated and managed domesticates dominate human consumption. These definitions are close to those of Harris (1989), and have been further developed elsewhere (Harris and Fuller 2014). From these processes of cultivation, domestication, and the adaptation of agriculture, anthropogenic landscapes were created and species adapted to these landscapes. It was the anthropogenic species and the methods of making landscapes for them that spread, largely during the Neolithic, but also during the Bronze Age to early Iron Age (depending on the region), and that brought food production to most parts of Eurasia. However, as argued here, in some cases the systems of food production and their domesticated species were not well-suited to the varied environments they were brought to. This led to two kinds of processes: collapse and transformation; the former

when agricultural systems were abandoned, and the latter when extensions of the ecological systems of food production dispersed into new environments. Not only was the adoption of crops partly determined by ecological factors, but cultural choice often had a major impact on the dynamics of the dispersal of crop packages.

Domestication: Adapting Crops to a Human Niche

Mounting evidence supports a major shift in thinking about the origins of agriculture, from a chance discovery or rapid revolution to one involving evolution at a slower rate (Zeder [2009](#); Fuller [2010](#)). In the case of the best-studied centre of agricultural origins – the Near East – it has come to be recognized within the past decade that the morphological changes of domestication emerged as part of a protracted process (Tanno and Willcox [2006](#), [2012](#); Fuller et al. [2014](#)). In addition, there has been growing recognition that the anthropogenic ecology of early agriculture created new plant communities, namely weed flora (Hillman et al. [2001](#); Fuller and Qin [2009](#); Willcox [2012](#)). These lines of complementary evidence mean that it is now possible to infer early cultivation behaviours, based on the weed flora, and the resulting changes from those behaviours (i.e. in the domestication traits of the crops), thus helping to unravel the complex feedback between human action and evolutionary change in crops and their associated arable weeds (Fuller et al. [2010](#)). Cultivation pathways are now recognized as prolonged episodes of coevolution, between the genetic adaptations on the part of the plants and the cultural shifts and innovations on the part of people.

While humans had been practising niche construction for some time prior to the advent of cultivation and crop domestication (see Petraglia, this volume), domestication did constitute a fundamental shift (see also Smith, this volume; Denham, this volume), and we may regard this as the third stage of human niche construction. Early forms of

niche construction can be perceived to have focused on nourishing the human body, for example by transforming food through processing and cooking (as discussed in Boivin [2008](#); Wollstonecroft [2011](#); Hillman and Wollstonecroft [2014](#)). This may go back to the very beginnings of fire use, and the origins of the genus *Homo* (as per Wrangham's *Catching Fire* [[2009](#)]). A second level of niche construction, associated with anatomically modern humans in the later Pleistocene, focused on the subsistence landscape, which involved various vegetation management strategies through burning (see Ellis et al. [2013](#)) and adaptations to prey acquisition that archaeologists have recognized as the 'Broad Spectrum Revolution' (e.g., Stiner [2001](#); Weiss et al. [2004](#); Stiner and Kuhn [2006](#)), as well as cases of selective hunting (Rowley-Conwy and Layton [2011](#)). The third level of niche construction, represented by the shift to cultivation, was a change of focus to the microscale – that is, a shift in focus to the lifecycles of one or a few species, and to the manipulation of local microenvironments, especially the soil (Smith [2012](#)). Thus, domestication processes can be conceived as feedback between human harvesting, planting, and soil manipulation practices on the one hand, and the phenotypes of crops on the other ([Figures 12.2 and 12.3](#)). The changed microenvironment that people manipulated came to have plant morphotypes that fit this environment, while human practices, such as crop-processing, adjusted to fit this changed plant environment (see Fuller et al. [2010](#)).

[Figure 12.2](#) Diagrammatic representation of the feedbacks between harvesting and processing wild versus domesticated emmer wheat, with indications of the changes in practices and plant genetics during the domestication process (based on discussions in Fuller et al. [2010](#)).

Figure 12.3 Diagrammatic representation of the feedbacks between harvesting and processing wild versus domesticated rice, with indications of the changes in practices and plant genetics during the domestication process. Note the contrasts between a proto-*indica* non-domestication pathway and a *japonica* domestication pathway (after Fuller 2011a).

Cultivation can also be conceived of in terms of trophic levels, and a shift in the trophic focus of human niche construction. Early *Homo* niche construction focused on the immediacy of what was eaten, and modified it through processing such as cooking. Late Pleistocene niche construction by *Homo sapiens* focused on prey and gathered plants, by broadening the range and techniques needed to acquire resources. Environments were modified in non-targeted ways through burning. Selective hunting, such as that described by Rowley-Conwy and Layton (2011), suggests a subtle but important shift towards manipulating aspects of the reproduction and demographics of other animal species. Cultivation represents a further shift in this direction that starts to impact multiple trophic levels; that is, not just the species that is eaten by humans, but also the sources of nutrients consumed by that species. In the case of plant cultivation, cultivation practices focus on managing the soil and water, the nutrients that edible plants need to reproduce and grow. In the case of herded animals the shift involved humans managing the diet and mating patterns of fauna.

A subsequent fourth stage in niche construction is when the artificial environments created through human actions were transported out of their native regions. Thus, cultivated fields, including their domesticated species and associated arable weeds, were introduced to regions with different native flora and differing climates. This transportation of agricultural landscapes has been the most important

process, in quantitative terms, for transforming the world from one of hunter-gatherers occupying biomes to one of mainly food producers living in anthromes.

In many cases, cultivated niches seem to have focused obsessively on single species. For example, in the Lower Yangtze it is rice and only rice that is cultivated (and ultimately domesticated) for millennia (Fuller and Qin 2009). For some northern Chinese early Neolithic communities, it may have been only broomcorn millet (Lu et al. 2009; Bettinger et al. 2010). Similarly, only pearl millet appears to have been involved in early cultivation in West Africa (Manning et al. 2011; Fuller and Hildebrand 2013). While, ultimately, crop packages came together everywhere, Western Asia is exceptional in having such a diverse range of founder crops (classically there were eight, including wheat and barley, but see Fuller et al. 2012 for a longer list of more than a dozen), and several domesticated animals (see Zeder, this volume). In North China, for example, soybeans were not added to the two-millet agricultural system until perhaps 3,500–2,500 BC, just as cowpea, fonio, or rice appear to be late additions in the West African savannahs. The rapidity of the spread and the adaptability of particular agricultural packages and landscapes may have had something to do with how diverse and complementary their crop packages were, as suggested by Harris (2003). Contrary to the latitudinal versus longitudinal explanations suggested by Jared Diamond (1997), it was probably the higher level of redundancy within the agricultural package (multiple wheats, barleys, and pulses) that made the West Asian agricultural systems so dispersible. One possible reason for this is that as agricultural landscapes dispersed into a wider range of climatic environments, species and varieties were extirpated, leading to local collapse. The higher diversity in the West Asian package meant that it was more

resilient to such collapse, although even in this case, Neolithic farming failures did occur.

The Nature of Early Agricultural Niches: Three Eurasian Types

Although there are a variety of agricultural systems, within Eurasia three major categories have played the largest role in the diffusion of grain-based agriculture. These agricultural systems will be outlined briefly, before a discussion of the issues of diffusion, collapse, and adaptation of these types into new areas. The first of these types is the Mediterranean winter cereal system of wheat and barley winter-cropping from Western Asia, which formed the basis of most agricultural systems of the Neolithic, Bronze Age, or Iron Age from the Indus Valley to Western Europe (e.g. Colledge et al. 2005; Fuller 2006). The second system is based on rice, a domesticated freshwater wetland species of East Asia, which has promoted the creation of vast areas of anthropogenic wetlands (see Fuller et al. 2011). Third are a number of small millet systems, including those of northern China or southern India (and comparable to those of Africa), which have lent themselves to more mobile societies – hunters, pastoralists, or shifting cultivators (e.g. Bettinger et al. 2010; Fuller 2011b; Kingwell-Banham and Fuller 2012).

In the case of Mediterranean systems, these largely supported, and perhaps encouraged, the emergence of sedentary cultural systems and intensive cultivation. Bogaard (2005; see also Bogaard et al. 2013) has drawn together evidence from arable weed flora and stable isotopes to suggest that the earliest farming, in central Europe as well as that in the later Pre-Pottery Neolithic of the Near East, was focused on small-scale intensive cultivation – cereal and pulse gardens rather than what we visualize as extensive field systems today. Those more extensive fields, associated with cattle-drawn

ard tillage and fallow cycles, are more likely developments of the end of the Neolithic or the Bronze Age. The earlier intensive systems had inbuilt redundancy and were complementary with a number of cereals and pulses, making them quite versatile, with great potential for geographic expansion (Harris 2003). It is plausible that small-scale intensive cultivation goes back to the very beginnings of pre-domestication cultivation, but it is clearly the case that the rise of domestication traits, mainly during the middle Pre-Pottery Neolithic B, correlates with the appearance of dung-producing livestock, and likely a period that saw greater commitment towards agriculture and integration of cultivation with herding as a source of manure (Bogaard 2005).

Early rice cultivation systems have similarly been reconstructed as small-scale and intensive (Fuller and Qin 2009; Fuller et al. 2011). This was, in part, necessary because the wild progenitor of East Asian rice is a wetland perennial (*Oryza rufipogon*), which is a poor grain producer except when under water stress. Thus, part of the early evolution of this crop was a genetic shift towards annuality – although many rice varieties are still perennial if left in the field (Hill 2010). Early intensive wet-rice agriculture is evident from preserved field systems, found at two sites in the Lower Yangtze river valley at 4,200–3,800 BC, Chuodun and Caoxieshan, and one site in the Middle Yangtze, Chengtoushan, at ca. 4,500 BC (Fuller and Qin 2009; Nasu et al. 2012), but these systems were actually made artificially dry by contrast to wild rice ecology in order to produce higher grain productivity and annuality (Weisskopf et al 2015). The domestication pathway for rice in China was a labour-intensive one, in contrast to a hypothesized ‘non-domestication cultivation’ pathway in India (Figure 12.3; Fuller 2011a). Because early rice systems of the Yangtze were labour-intensive and lacked complementarity or redundancy (i.e. there were no other crops), their dispersal

was limited. Furthermore, there is some 1,500–2,000 years delay between the domestication of rice and its spread to southern China, Southeast Asia, or Taiwan, and it has been suggested that this is because less intensive rain-fed rice systems (and rice strains) needed to evolve before many groups were willing to try their hand at rice cultivation (Fuller and Qin 2009). When wet rice did spread, it required significant labour investment, but it was also highly productive and the spread of wet rice paddy-field systems in most of tropical Asia is associated with the emergence of urbanism and states, especially during the Iron Age in India, Sri Lanka, and mainland Southeast Asia (Fuller 2011a). The Yayoi Bronze Age in Japan can be seen in a similar light.

The third type of Eurasian grain system was the extensive, drought-tolerant millet system of semi-arid summer rainfall zones. This is the system that dominated, for example, in the loess plateau of northern China, as well as the savannahs of India. These systems lent themselves to mobility, which means that the earliest phases of cultivation remain poorly preserved in the archaeological record and are rather hazy. Only once more committed millet agriculturalists became sedentary does archaeological evidence become clear, such as during the Yangshao period in China (Liu and Chen 2012) or the second phase of the Neolithic in southern India (Fuller 2006). One thing that these societies had in common was a strong interest in adopting new crops to supplement millet agriculture, even on a small-scale, as high-status crops, including rice and later wheat in northern China, and wheat, barley, and African millets in India. There was a tendency for the adoption of millets by cultivators of other systems as a means of risk buffering through cultivation of a crop that could easily be grown in a season complementary to the main crops.

Transported Landscapes: Remaking a Homeland

Much of today's vegetation is anthropogenic, having been altered through human-mediated species introductions and dispersals as well as by the obvious manipulation of species communities through agriculture. While the spread of agriculture has been a staple topic of archaeological discourse, this has tended to focus on anthropological issues, with botanical data used to demonstrate the presence of species of crops and to infer practices of cultivation. Less attention has been paid to the biogeographic aspects of the spread of agriculture, in particular how the historical process of humans transplanting agricultural systems restructured plant communities. The accumulation of archaeobotanical data has elucidated patterns in the origins and spread of agriculture in many world regions. Especially within the context of Near Eastern and European studies, evidence for the crops present has been complemented by increasing attention to wild species, many of which were probably field weeds.

As crops spread, weeds went with them. Weeds were transported with the crops, contaminating seed corn, whether carried by migrating farming populations or by the trade in grain. While we would expect the initial Neolithization based on introduced crops to involve a significant component of such dispersals, it is equally reasonable to expect later episodes of weed dispersal, in the context of trade that could have included grain, or in the diffusion of new crops or crop varieties (see Boivin, this volume). In addition to those species that are dispersed as contaminants, other weed species may represent local recruitments, species that are endemic to a region which come to thrive in the ecological niche offered by the fields of farmers. The ecology of the new regions, together with competition from locally recruited species, has the potential to exclude some weeds. We therefore expect the weed floras of any particular time and place to represent some combination of dispersal and local recruitment ([Figure 12.4](#)). The

statistical study of weeds in a Europe-wide Neolithic archaeobotanical database indicates eight key changes in the composition of common weeds between Anatolia and the Balkans (Colledge et al. 2004; Coward et al. 2008), including both species loss and new recruitment of weed flora, even though the dispersal between these regions was relatively minor in biogeographic terms. The changes were even greater the further agriculture spread across Europe. For instance, in Britain and Ireland, there is a clear increase in weeds originating from the wetlands and moors of the British Isles and a decline in the weeds deriving from Eurasian steppic grasslands (McClatchie et al. 2012).

Figure 12.4 A schematic, quantitative diagram of the geographical evolution of weed flora as agriculture disperses and the weed assemblage shifts by recruitment and extirpation.

What is true of weeds, in terms of the reduction in species with dispersal, is equally true of crops, especially if one takes into account genetic strains which may not be morphologically recognizable. It is increasingly clear that there were several lost crops, especially varieties of wheat (Fuller et al. 2012), in the Near East, which never made it past central Europe. The more the spread of agriculture is examined in detail, the more apparent it is that crop species and varieties dropped out along the way (Colledge et al. 2005), and those which did make it probably become less genetically diverse. A recent analysis of Neolithic Ireland illustrates the pattern of crop diversity at the extreme western edge of Neolithic dispersal from Western Asia (McClatchie et al. 2012), demonstrating the quantitative reduction in most crops in Neolithic Ireland compared with elsewhere in Europe (Figure 12.5). Emmer wheat, naked barley, and a bit of flax essentially sums up the crop assemblage of Neolithic Ireland. This is in stark contrast to the eight 'founder crops' that are suggested to have characterized the start of

agricultural dispersal from the Near East. A similar package of barley and wheat (with a dash of flax) characterizes the British early Neolithic, which, like Ireland, saw the dramatic introduction of cereal farming shortly after 4,000 BC (Stevens 2007; Jones and Rowley-Conwy 2007).

Figure 12.5 The attrition of crop diversity during Neolithic dispersal across Europe, as indicated by the frequency of occurrence of crops in regional archaeobotanical evidence. Quantitative data from McClatchie et al. (2012).

This pattern parallels what we see in the East, as crops spread eastwards across the Iranian Plateau and eventually on to India and China. Sites in north-eastern Iran and Turkmenistan, including Sang-i-Chakhmaq (Iran) and Djeitun (Turkmenistan), have produced a diverse assemblage of wheat species (emmer, striate emmeroid, two-grain einkorn, and one-grain einkorn) and barley but lack evidence for flax or the pulse assemblage commonly found in the Fertile Crescent (Charles 2007; Charles and Bogaard 2010; Sang-i-Chakhmaq: authors' unpublished data). Similarly, current evidence from Mehrgarh in Pakistan does not include pulses, only various varieties of wheat and barley (Costantini 2008). This indicates a reduced crop package in the initial eastward spread of agriculture, although pulses did eventually diffuse to the Indus region by ca. 3,000–2,500 BC (Fuller 2006). Subsequently, dispersal further eastward shows a pattern of attrition in the West Asian crops in regions of India where native crops were prominent (Figure 12.6). Thus, while wheats (including emmer and free-threshing), barley, several pulses, and flax seem to be important in the Indus Valley, this 'package' becomes less frequent and less stable as one moves into 'inner' India (Fuller 2005; Boivin et al. 2012). Wheat and barley make it both eastwards to Bihar and south to Karnataka, but generally with a strong preference for barley and few, or none,

of the winter-grown pulses that originated in southwest Asia. In China, only select wheat, and rarely barley, make any showing at all, and the wheat is initially quantitatively negligible (Boivin et al. 2012; Dodson et al. 2013; Betts et al. 2013). Contrary to the conclusion of Dodson et al. (2013), the transition from millet to wheat at 2,000 BC, which they attribute to climate change, seems unlikely. Wheat did not become significant agriculturally until perhaps the Han Dynasty, which is clearly indicated in quantitative archaeobotanical evidence (e.g. Lee et al. 2007; Boivin et al. 2012), as well as textual sources (Bray 1984). Given aridification, at around ~2,000 BC, millets would have been far better, drought-tolerant crops to focus on. The adoption of wheat, instead, needs to be seen in terms of social drivers for the adoption of the exotic (Boivin et al. 2012).

Figure 12.6. The attrition of West Asian crop diversity during the dispersal of agriculture eastwards and southwards towards India and Arabia, as indicated by the frequency of occurrence of crops in regional archaeobotanical datasets. Note also the increasing importance of local South Asian domesticates. Quantitative data from Fuller 2011b; Boivin and Fuller 2009; Charles 2007.

Factors in Crop Package Persistence

As the last comment suggests, the dispersal of cultivated plants was not just motivated by practical but also by social factors. In some cases, the caloric and subsistence needs were not the primary motivation for the adoption of a crop introduced from the Near East. Previously, Fuller (2005) argued that wheat and barley in southern India might have been adopted as status crops, used perhaps for beer, rather than as staples. To some extent, this could also be the case with the westernmost spread of cereals in Europe. Their presence may be more about food preferences than

subsistence necessity, especially given that wild sources such as hazelnuts were still so readily used and available. Thus, the adoption of a reduced crop package in Western Europe may reflect the adoption of only certain crops for social reasons, as well as the likelihood that the Western Asian and Mediterranean package was not so well-adapted to environments distal from their point of origin. This, in turn, raises the likelihood that such agricultural packages were increasingly fragile and prone to failure as they moved outside the original biogeographical context from which they originated.

Although there are broad similarities in the westward and eastward spread of the Near Eastern crop assemblage with regards to a reduction in the number of species as crops moved further from their point of origin, there are differences in the dynamics of their spread, including mode of dispersal, environmental circumstances, and cultural preferences. While in India and China the easterly spread of wheat and barley is seen largely in terms of the adoption of crops by local populations that were already farmers, in Western Europe there is evidence for a greater role for migration of farmers into lands already occupied by foragers (Rowley-Conwy 2009). In India we tend to attribute the lack of acceptance of the West Asian crops to the local importance of *Brachiaria ramosa* and mungbean in the south or rice in the Ganges (Fuller 2006; 2011), whereas a prior presence of crops was clearly not the case in Ireland. The evidence, therefore, suggests that crop packages weakened more the further they moved from their point of origin. This was not as a result of their mode of dispersal as it occurs in cases of both migration and adoption. We therefore conclude that a key factor was that crops crossed ecological and cultural frontiers where they were less suited to pre-existing conditions, either environmental or in terms of culinary culture. In the case of ecological frontiers, agriculture may have expanded quicker than some crops could adapt to new

environments, or beyond which some crops were not able to adapt. Northern Europe certainly presented great challenges to agriculture, highlighted in its extreme margins such as Norway, but also in Britain, by the apparent abandonment of cereals in the later Neolithic (discussed in the next section). Further, Monsoon Asia was not ideally suited to Near Eastern crops either; so, the drivers in the dispersal of continued importance of these crops to this region must then be attributed to social preferences beyond caloric needs.

Were Early Neolithic Cultivated Landscapes Fragile? Cases of Collapse

We usually think about the spread of Neolithic agriculture as an inevitable, progressive march, as well-adapted cereal systems – for example, wheat and barley from the Near East – were extended along favoured soils and river valleys, such as Europe's Danube valley. While this is the standard wave-of-advance model (popularized by Diamond [1997](#)), and while it may have much going for it in the middle latitudes, researchers fail to consider both the limits of agriculture and past attempts to push those limits. A recent study of the introduction of agriculture to northern Norway provides an example of the challenge of climatic limits to a crop package. Sjogren and Arntzen ([2013](#)) report the limited botanical macro-remains, pollen, and settlement data relating to the earliest agriculture on Kveoy Island, at nearly 69 degrees north, and reveal an environment in which agriculture was rather more marginal than in the Mediterranean region where these crops had originated. Evidence for agriculture before about 1,000 BC is lacking, with fields established only in the Late Bronze Age. The archaeobotanical assemblage from this site is comprised mainly of barley, with limited evidence for wheat. The wheat is probably emmer wheat, which, like the early Neolithic emmer wheat of Britain (including Scotland), suggests the presence of cold-adapted

landraces in early prehistory that we would be hard-pressed to find in the relict emmer populations of today, which are found in hot Mediterranean climates, Ethiopia, and South India. This early Norwegian agriculture, however, may well have failed and there is a suggested hiatus in the late centuries BC/early centuries AD, before a Late Roman-Iron Age re-establishment of farming. This may be an extreme example, but as we investigate further we will likely find more regions in which farming was abandoned due to local climatic oscillations in areas where farming productivity would have been marginal at best.

There is also significant evidence that cereal agriculture and population declined in the later Neolithic of Britain. A recently published database of radiocarbon dates from Britain, considering only direct AMS dates on cereals and wild plant foods (mainly hazelnuts), clearly shows an increase in crops and population during the earlier fourth millennium BC. This is followed by marked declines in both, and the subsequent absence of radiocarbon dates from cereal remains, despite continuity in radiocarbon dates for wild nuts (Stevens and Fuller [2012](#); [2015](#)). This suggests that within five centuries of the first crops arriving in Britain, large parts of England and mainland Scotland abandoned cereal agriculture for close to two millennia, until a reintroduction of agriculture and new population growth took place in the Middle and Late Bronze Age ([Figure 12.7](#)). This archaeological study has support from the analysis of pollen data, which suggests that while the initial Neolithic transformation of landscapes in Britain was rapid and widespread, the process was subsequently reversed, with reforestation a few centuries later, until clearance began again in the middle Bronze Age (Woodbridge et al. [2012](#)). One likelihood is that the Mediterranean crop package that was introduced to the island was both poorly adapted to the British environment, especially as it cooled

after 3,600 BC, and had limited redundancy on arrival – it basically consisted of emmer wheat, barley, and flax. When agriculture was introduced a second time, in the Middle Bronze Age, a much more complete and northerly adapted crop package seems to have been adopted: this probably included cold-adapted spelt and summer varieties of wheat and barley, as well as nitrogen-fixing legumes such as pea and broad bean.

Figure 12.7. Evidence for arrival, abandonment, and reintroduction of crops to prehistoric Britain, based on the summed radiocarbon age distribution of directly dated crops (in black) and wild foods (in grey). Key events in the interpretation of this sequence are indicated by arrows. Based on Stevens and Fuller (2012).

Other cases of Neolithic agricultural abandonment can be suggested, and it ought to be explored to what extent these also represent crop packages that had limited resilience in the face of changing environments or the crossing of biogeographic zones. The apparent abandonment of millet cultivation between the end of the Dadiwan culture and the Yangshao period in Gansu (Northwest China) may be one such case (Bettinger et al. 2010). In another parallel with distant Britain, the agriculture and sedentism in parts of the Deccan, most clearly in Western Maharashtra, where wheat and barley were quite prominent, appear to have collapsed and possibly been abandoned over a wide area, in this case around 1,200–1,000 BC, at the end of the Jorwe period (Dhavalikar 1988). In this region, the heavy reliance on winter crops, such as wheat and barley, in a summer rainfall area may have made this system especially vulnerable to climatic oscillations, which appear to have been pronounced at the end of the second millennium BC (Prasad et al. 2014: figure 4; Roberts et al. 2015). What these examples suggest is that the initial spread of crops may have been fairly fragile and lacked the resilience of agricultural packages that were introduced later.

Moving Beyond Limits Through Post-domestication Enhancements and Secondary Crops

In retrospect, the history of the Holocene has been dominated by the conversion of wild landscapes to managed lands of productive agriculture, with related growth in human populations wherever agriculture was possible (Ellis et al. 2013). But the historical spread of agriculture, as we have seen, was not inexorable. Avoiding failure was key to agriculture's successful dispersal. There are a number of ways in which agricultural packages were made more stable and resilient in the past, including through genetic changes to crops themselves, changes to crop packages involving the addition of new crops from other regions, and the labour-intensive modification of landscapes. One of the major ways in which crops became genetically adapted to new environments was through alterations in genetic controls on seasonality, especially for flowering and length of growing season. Adaptations through seasonality changes are likely to have had a dramatic effect, as recognized in general by Sherratt (1980). Many species, including domesticated crops and wild progenitors, are either short-day plants, flowering as days shorten at the end of summer, or long-day plants, flowering as days lengthen running up to summer. This, of course, has implications for when crops must be planted. One of the best-documented historical instances of a new crop variety transforming agricultural production was the 'champa' rices that were introduced to China from Southeast Asia in the twelfth/thirteenth centuries (Ho 1956; Barker 2011). These rice varieties had a shorter growing season, tolerated poor water conditions, and were not controlled by day length for flowering. This allowed crops to be grown on land that had not previously produced rice, and it allowed rotations of two rice crops a year

in some areas. China underwent a major demographic expansion as result of this agricultural adoption.

Another example is that of the *japonica* rice varieties. Recent genetic research on rice has identified the DTH gene, which is linked to day-length-controlled flowering (or the lack thereof), and underwent a post-domestication selection event in temperate *japonica* rice (Wu et al. 2013). This suggests important adaptations as rice first spread north, for example, from the Yangtze basin to the Yangshao culture zone. In the north, rice would have been restricted to wetter soils, such as are found in alluvial settings. However, cooler springs and autumns would have reduced photosynthesis and productivity, requiring longer growth seasons and earlier planting. But this can be prevented by strong seasonality controls over grain production tied to day-length. Thus, genetic changes that altered or relaxed these seasonal constraints on flowering and grain production were important. The DTH gene variants found in temperate *japonica* allowed greater grain production under naturally long-day conditions, as found in the summers of the northern latitudes, while southerly DTH variants were suited to planting only during the monsoon, a pattern found in the wild rices of Southern Asia and Southeast Asia (Figure 12.8). The northern DTH variants in rice appear to have evolved after domestication and dispersal.

Figure 12.8 The geographical distribution of rice genotypes (DTH2 allele variants) relating to season of flowering, and the presence of wild rices, *indica*, temperate, and tropical *japonica* cultivars (after Wu et al. 2012). A2 and A4 types are less sensitive to day length, and A4 are most productive under longer growth-season, summer-flowering regimes. A1 types typically flower as days shorten towards winter.

A1 and A2 type segregate geographically in wild populations based on latitude, while A4 only occurs in northerly domesticates.

Rice contrasts with barley, a crop in which day-length-neutral varieties already existed in the wild, prior to domestication and anthropogenic shaping. It was the secondary dispersal of these day-length neutral varieties that allowed for spring-sown and summer-grown barley in Europe (Jones et al. 2008), and such varieties dominate cultivation in northern Europe in modern and historical times, and have probably done so since later prehistory. The latter can be inferred to have arrived in Europe in the post-Neolithic period, or at least later than the initial dispersal of crops, as the varieties of the western Fertile Crescent and the Mediterranean are genetically distinct and tied to cultivation over the winter (Jones et al. 2012; 2013). Another constraint in barley is the need for a cool period after early growth before flowering is possible (called vernalization). Genetically, most Mediterranean barley landraces require this vernalization by being sown in autumn and growing through a mild winter. Various mutations, likely to have arisen since domestication, have turned off the need for a winter vernalization, and have thus facilitated planting in spring and a long summer period of cultivation at more northerly latitudes (Cockram et al. 2011).

The situation with wheats is similar, although unravelling the genetics has been more complex because of the multiple genomes found in most wheats (hexaploid wheats such as bread wheat have three genomes, while tetraploid wheats such as emmer or durum have two genomes). Nevertheless, it is clear that non-functional mutants of the vernalization gene (especially on the A-genome derived from einkorn wheat) differ geographically across landraces (e.g. Shindo and Sasakuma 2002; Henderson et al. 2003). For example, dominant mutations that remove the need for

vernalization are found among the spring-sown wheats of the Tibetan plateau, while wild recessive genes for vernalization are found in the majority of winter-sown wheat varieties in northern and central China (Zhang et al. 2008). Amongst Iranian and Pakistani wheats, winter and spring genotypes can also be differentiated, and spring-sown types are today in the majority, while the large minority of winter wheats are presumed to represent the more ancient forms (cf. Iqbal et al. 2011; Derakshan et al. 2013). Spring-sown wheats have presumably been facilitated by the development of irrigation since the Bronze Age. Further documentation of seasonality-controlling genotypes in traditional cultivars, together with ancient DNA studies, promises to unravel the complex history of wheat adaptations as the crop was dispersed across Eurasia. Based on current evidence, one might hypothesize that it was sometime in the Bronze Age, perhaps after 3,000 BC, that spring-sown barleys and wheats entered Europe. Their absence from the early Neolithic is likely to have been one of the factors that contributed to agricultural failures along the northern margins of agriculture.

As noted, another way in which agriculture adapted to environments marginal to where it began was through the adoption of new crops, which expanded the ecological tolerance and cropping seasons of agriculture overall. There are two ways in which this occurred: 1) through secondary domestications, and 2) through the adoption of crops from elsewhere. The best-known cases of secondary domestication are those of oats and rye, both of which were present in Europe as weeds throughout the Bronze Age, but originated in the same Western Asian region as wheat and barley. However, the earliest evidence for domesticated forms of these crops comes from the very late Bronze Age and Iron Age onwards, suggesting that they were secondarily domesticated by farmers from existing weeds. These crops tolerate worse soil and climatic conditions than many

forms of wheat and barley. Similarly tolerant of poor soils and having summer seasonality (like PPD-neutral, non-vernalizing barleys) were the Asian millets, *Panicum miliaceum* and *Setaria italica*, which reached Europe from the East and took off in cultivation mainly in the Middle/Late Bronze Age and later. Winter wheat plays a similar role in China, eventually being rotated with rice or millets.

The Filters of Taste: Culinary Frontiers and Non-ecological Adaptations

A final factor that needs to be taken into account in understanding the dispersal of crops and crop varieties is the social drivers involved in the filtering process of broader, regional culinary preferences. One of the most dramatic and long-lasting culinary frontiers in Eurasia is between the western zone of breads, oven, and roasting, and the East Asian zone where the emphasis is on boiling and steaming (Rowlands and Fuller [2009](#); Fuller and Rowlands [2011](#); see also Sakamoto [1996](#); Hosoya et al. [2010](#)). These cooking traditions necessarily made foods that were different in character, with those boiled or steamed in China being more cohesive in texture and sticky, for example. This is reflected in the crops themselves, and also in the post-domestication genetic changes to East Asian crops, which help them to fit increasingly well into cohesive and sticky food traditions. There are different varieties of rice, including some that are inherently sticky. This rice stickiness is only in small part due to cooking; it is mostly due to the structure of the starch in the grain, which in turn comes from a genetic change. Rice is not the only sticky cereal; there are also sticky forms of the Chinese millets and several other cereals. In addition to the texture of the cooked cereal, the pounded or ground form is often used to make sticky foods, such as Japanese *mochi*. Also, sticky rice and sticky millets are sweeter when boiled in water and have often been favoured as the base for alcohol production, as in the rice and millet ‘wines’ of

China and neighbouring countries. Although hard evidence is lacking, one can infer from geographical patterns in modern genetics and later historical documents that it was millets, and probably *Panicum*, that first evolved to be sticky, somewhere in northern China (Fuller and Castillo, 2016). In this case, the evolution of rice towards increasing stickiness took place secondarily, after rice had spread northwards and after the first wave of rice, which was non-sticky, had spread to Southeast Asia.

What is interesting from a cultural point of view is the distribution of sticky types of rice and millets ([Figure 12.9](#)), because it shows the role of cultural preferences for taste and texture in both driving the evolution of cereals, and in filtering which forms spread. Sticky cereals are basically restricted to Eastern Asia and Southeast Asia. These sticky forms have failed to spread westward, even though non-sticky forms of these species have spread substantially in this direction. The case of the Chinese millets *Panicum miliaceum* and *Setaria italica* is particularly clear, since it seems likely that sticky forms had evolved before these species diffused westwards from China (starting ca. 2,500 BC), but the sticky forms nonetheless did not spread. In addition, cereals originating elsewhere which have spread into East Asia have had sticky varieties evolve and persist there, including taxa such as sorghum, barley, and maize, indicating strong selection on cultural grounds. Thus, as cereals dispersed out of China, there was a selection against stickiness, while dispersal into China favoured stickiness. Even in adopted crops that are not truly sticky, particular cooking approaches may have made them more suitable for boiling, such as flour-based noodles made from wheat. The frontier between the sticky and non-sticky cereal traditions is of particular interest as it comes very close to correlation with the milking (Western) versus non-milking

(Eastern) worlds with regard to cattle and other potential milkable livestock (Simoons 1970; see discussion in Fuller and Rowlands 2011).

Figure 12.9. Map summarizing the geographical distribution of sticky (low amylose) and non-sticky forms of cereals in Asia; the limits of these distributions are approximate and have yet to accurately mapped (based on Sakamoto 1996; Fuller and Rowlands 2011; updated with references to with reference to Lu and Dahlberg 2001; Rana et al 2009; Li et al 2010; Li et al 2011; Araki et al. 2012; Hachiken et al 2013).

This distinct cultural frontier between East and West suggests food preferences have strongly filtered and genetically shaped diffusing crops, contributing to the expansion of agricultural repertoires. Similar filters can be suggested to have operated between the Near East and African savannahs (see Haaland 2007), between northern and southern India (see Fuller and Rowlands 2011), and plausibly between Mediterranean Europe, with its bread and oven culture, and northern and Western Europe, with its interest in porridges, gruels, and beers (e.g., Skoglund 1999; Kubiak-Martens et al. 2015). It is certainly the case that there is no evidence for ovens in the Neolithic of Germany or Britain. A shift towards bread may well have occurred largely as a result of Roman influence. It should perhaps come as no surprise, then, that it was the porridge traditions of the north that found oats attractive as a secondary domesticate. In summary, we must consider cultural frontiers alongside ecological barriers in the structuring of the diversification and local adaptations of agricultural packages as they spread.

Concluding Remarks

The development and spread of agriculture has been the key process by which humans have transformed the earth to support ever-growing population densities and

complex societies. This key form of niche construction was underway in some parts of the world by the Early Holocene (Smith and Zeder 2013) and was widespread, occurring on most continents, by sometime in the Middle Holocene (Fuller et al. 2014). This spread represents a process of globalization of agricultural ways of life, and led to some crops becoming widely dispersed, with translocation over very long distances, and transference between different cultural traditions of food and farming starting around 4 ka (Boivin et al. 2012, Boivin, this volume). While the long-term trend over the Holocene was for agriculture to spread and intensify and for human populations to rise, there were local crises, when populations may have declined after the initial boom of early farming (Stevens and Fuller 2012; 2015; Shennan et al. 2013). Crop packages tended to undergo attrition as they spread, and in some cases became less sustainable, leading to crop abandonment or agricultural collapse. Nevertheless, transformations of the production system allowed for new phases of growth and intensification (Ellis et al. 2013). Transformations of the subsistence system were brought about through genetic adaptations of crops, such as through switches in seasonality genes, through cultural adaptations that adjusted the environment to better support the transported landscapes of agriculture, and through multiple waves of agricultural ‘package’ dispersals that brought greater levels of redundancy and therefore resilience.

Agriculture changed the rules of how humans adapted to new landscapes, shifting carrying capacity upwards but at the expense of the flexibility provided by mobility. While we might characterize the long-term story of humanity as one of how people got to be everywhere (Gamble 1993), the second half of the Holocene was about how densely settled populations become established on most continents, aside from deserts and permafrost zones. In other words, the Holocene is characterized by

humans migrating to new lands and peopling continents, while the post-Neolithic world was about people staying put, putting in roots, and supporting ever-larger populations through the intensification enabled by the spread of agriculture. While hunter-gatherers were adaptable, and adjusted to a wide range of environments, farmers carried an environment with them, a lifeboat of domesticates, commensals, and weeds. In some places and cases, this raft of plants and animals failed to stay afloat. The cultural environment of tastes may have filtered out some crops, while climatic constraints made others fail. Genetic changes in some of the crops, together with new crops and new varieties, and to some degree environmental modifications such as through irrigation, allowed the raft to be jerry-rigged to overcome these limits, but often at the cost of resilience, leading to crop failures and local population collapse. As we now depend on a globally connected food system that supports increasingly larger and more dense urban populations, we would do well to heed our Holocene history and be vigilant of the potential fragility of crops, and crop systems, noting historical evidence for the adaptive benefits of diverse, redundant, and locally adapted crop packages.

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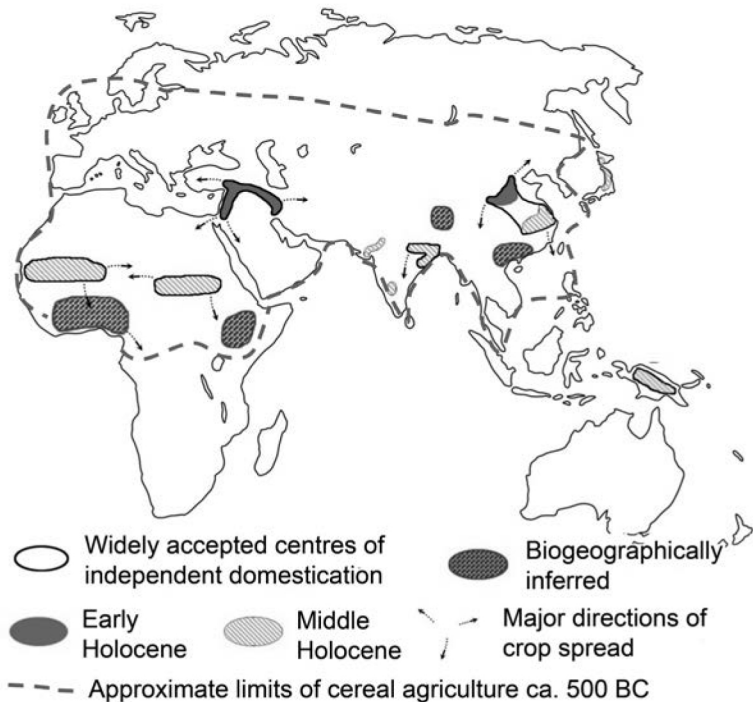


Figure 12.1 An updated map of centres of likely independent plant domestication and agricultural origins in the Old World, with the frontier of agricultural dispersal by 500 BC (based on Larson et al. 2014).

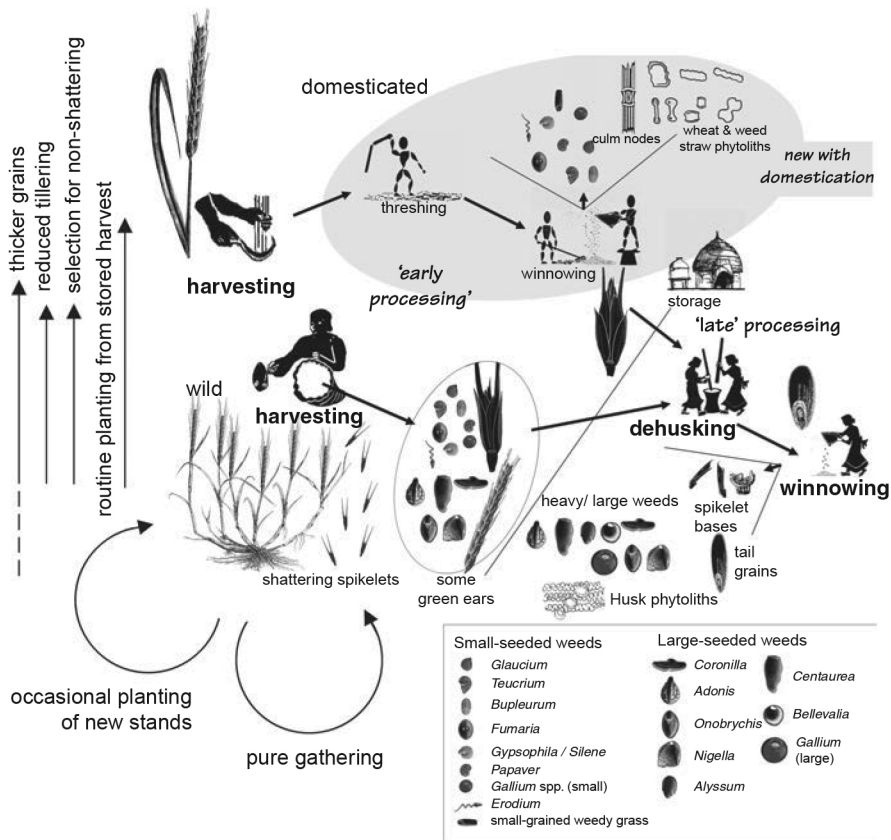


Figure 12.2 Diagrammatic representation of the feedbacks between harvesting and processing wild versus domesticated emmer wheat, with indications of the changes in practices and plant genetics during the domestication process (based on discussions in Fuller et al. 2010).

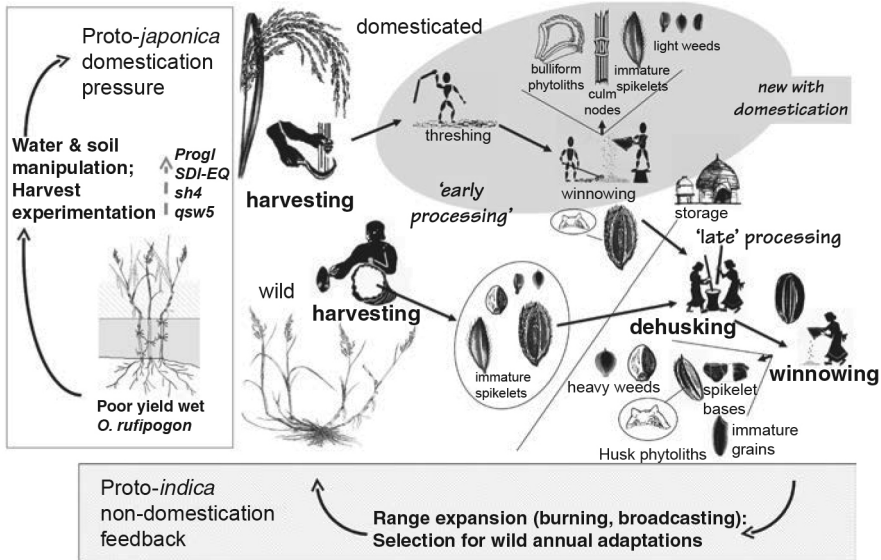


Figure 12.3 Diagrammatic representation of the feedbacks between harvesting and processing wild versus domesticated rice, with indications of the changes in practices and plant genetics during the domestication process. Note the contrasts between a proto-*indica* non-domestication pathway and a *japonica* domestication pathway (after Fuller 2011a).

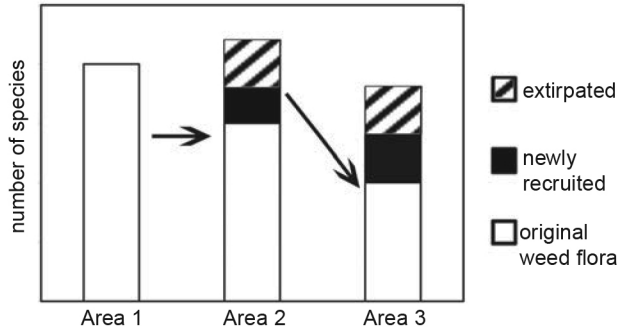


Figure 12.4 A schematic, quantitative diagram of the geographical evolution of weed flora as agriculture disperses and the weed assemblage shifts by recruitment and extirpation.

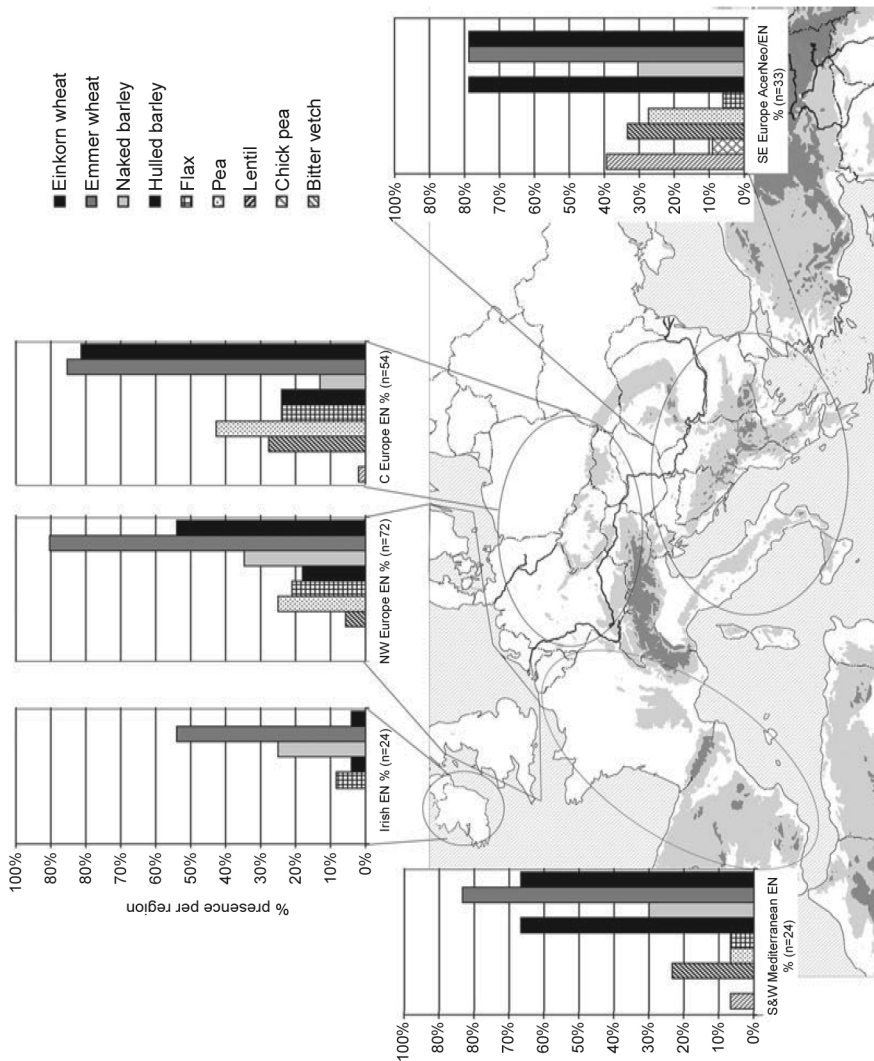


Figure 12.5 The attrition of crop diversity during Neolithic dispersal across Europe, as indicated by the frequency of occurrence of crops in regional archaeobotanical evidence. Quantitative data from McClatchie et al. (2014).

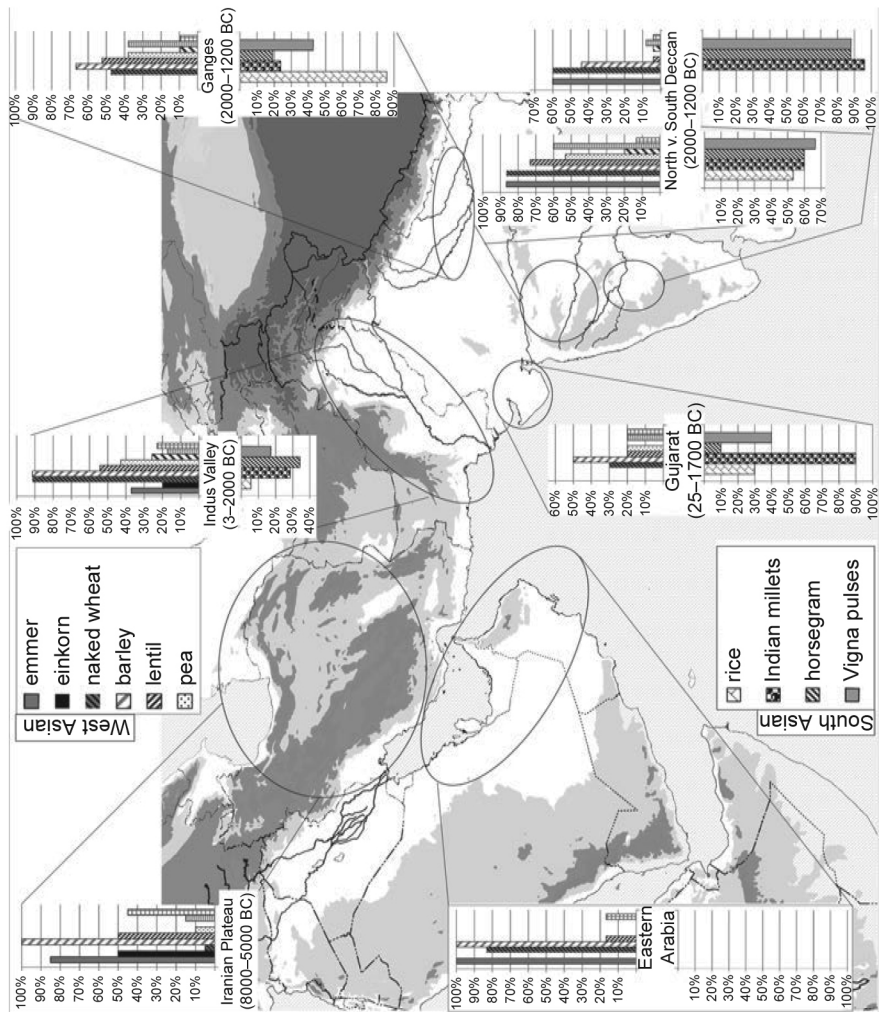


Figure 12.6 The attrition of West Asian crop diversity during the dispersal of agriculture eastwards and southwards towards India and Arabia, as indicated by the frequency of occurrence of crops in regional archaeobotanical datasets. Note also the increasing importance of local South Asian domesticates. Quantitative data from Fuller (2011b); Boivin and Fuller (2009); Charles (2007).

A. Cereal farming introduced

B. Farming decline, wild foods persist

C. Cereal farming abandoned

D. Farming reintroduced

E. Wild foods abandoned

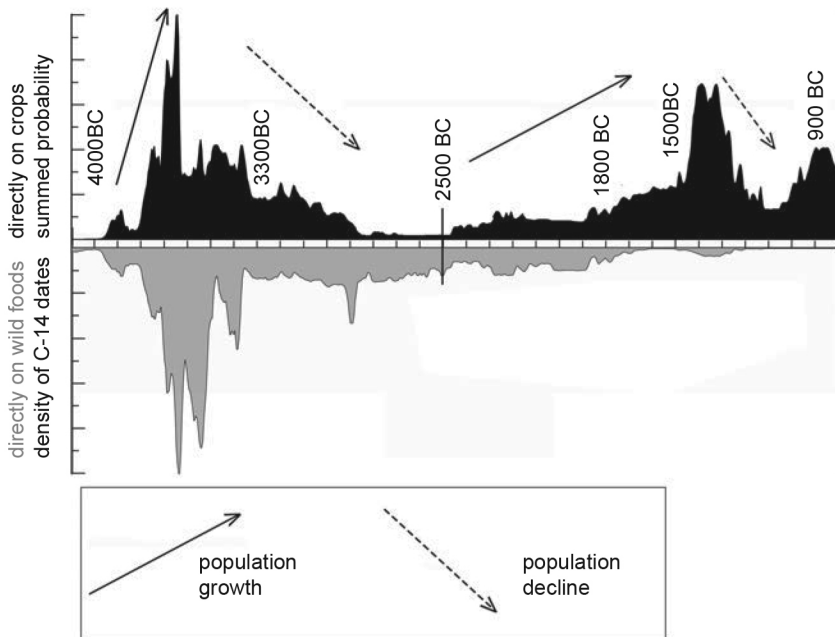


Figure 12.7 Evidence for arrival, abandonment, and reintroduction of crops to prehistoric Britain, based on the summed radiocarbon age distribution of directly dated crops (in black) and wild foods (in grey). Key events in the interpretation of this sequence are indicated by arrows. Based on Stevens and Fuller (2012).

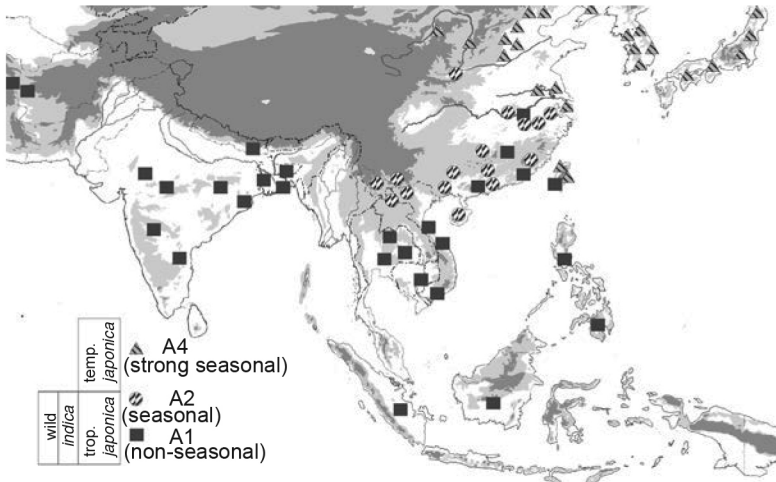


Figure 12.8 The geographical distribution of rice genotypes (DTH2 allele variants) relating to season of flowering, and the presence of wild rices, *indica*, temperate, and tropical *japonica* cultivars (after Wu et al. 2012). A2 and A4 types are less sensitive to day length, and A4 are most productive under longer growth-season, summer-flowering regimes. A1 types typically flower as days shorten towards winter. A1 and A2 type segregate geographically in wild populations based on latitude, while A4 only occurs in northerly domesticates.

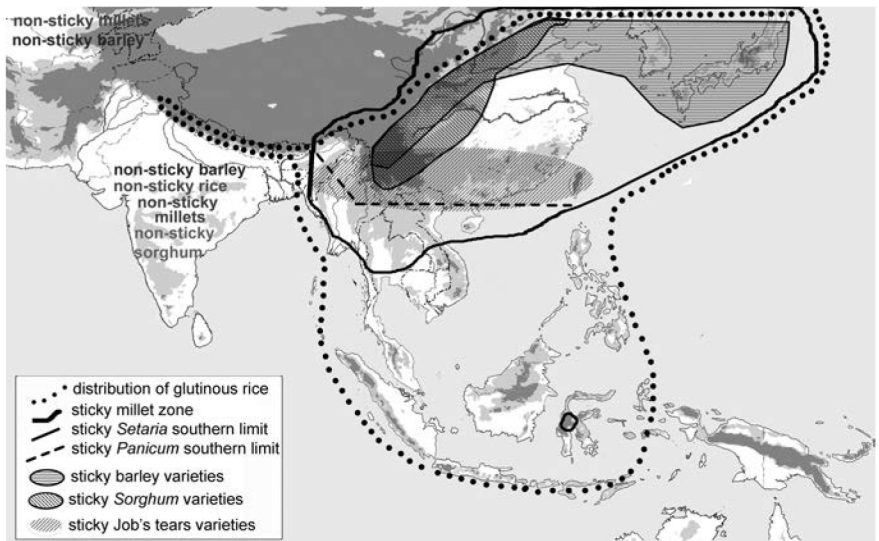


Figure 12.9 Map summarizing the geographical distribution of sticky (low amylose) and non-sticky forms of cereals in Asia; the limits of these distributions are approximate and have yet to accurately mapped (based on Sakamoto 1996; Fuller and Rowlands 2011; updated with reference to Lu and Dahlberg 2001; Rana et al. 2009; Li et al. 2010; Li et al. 2011; Araki et al. 2012; Hachiken et al. 2013).