
Using Modern Landraces of Wheat to Study the Origins of European Agriculture

Origins of European Agriculture

Agriculture began independently in China, Mesoamerica, and the Fertile Crescent of Southwest Asia, a region comprising the plains of Mesopotamia, parts of Syria and Palestine, and some of the mountainous areas to the east of Anatolia (Diamond, 2002). In Southwest Asia, cereals were among the first plants to be domesticated, with einkorn wheat (*Triticum monococcum* L.), emmer wheat (*T. dicoccum* Schübl.), and barley (*Hordeum vulgare* L.) present at farming sites dating to the 9th millennium BC (Bell, 1987; Kislev, 1992; Zohary and Hopf, 2000). After some 1500 years, cereal cultivation began to expand out of Southwest Asia into Europe, Central Asia, and northeast Africa, with emmer in particular becoming a widespread feature of prehistoric agriculture across much of the Old World and not being substantially replaced by hexaploid bread wheat (*T. aestivum* L.) until 2000 years ago (Zohary and Hopf, 2000). Agriculture first appeared in the Balkans at about 6500 BC and during the next 3000 years spread into Europe by two principal routes, one following the Danube and Rhine valleys through central Europe and into the north European plain, and the second taking a coastal route through Italy and Iberia to northwestern Europe (Barker, 1985; van Zeist et al., 1991; Price, 2000).

Archaeological Questions Concerning the Origins of European Agriculture

There has been much debate about the processes responsible for the origin of agriculture in Southwest Asia and for its subsequent spread into Europe. Blumler (1992) describes two models for agricultural origins: stimulus diffusion, in which agriculture has a very localized start point, and independent invention, in which agriculture has a dispersed geographic origin. When applied to Southwest Asia these models have important implications: Stimulus diffusion at one extreme suggests an almost heroic breakthrough by a small group of humans whose activities resulted in assembly of "a balanced package of domesticates meeting all of humanity's basic needs" (Diamond, 1997:1243), and dispersed origins at the other extreme indicates a transition to agriculture that may have been driven not by human ingenuity but solely or largely by the climatic and other environmental changes occurring across Southwest Asia at the end of the last major glaciation (Sherratt, 1997). Distinguishing between these possibilities has been a goal of archaeologists for the last 20 years, as stated by Harris (1996:6): "If it can be determined that a particular plant . . . was domesticated once only, or several times in different areas, we can gain important insights into the early history of agriculture and pastoralism. . . . This must continue to be a major part of the research agenda for the study of 'agricultural origins.'"

Equally important questions surround the factors responsible for the spread of agriculture into Europe. The application of human genetics to this problem has polarized views between the migrationist and indigenist positions, the former supported by the detailed analysis of nuclear DNA markers (Cavalli-Sforza et al., 1994) and the latter promoted by mitochondrial DNA studies (Richards, 2003). The migrationist view holds that the primary force responsible for agricultural spread into Europe was the immigration of farmers from Southwest Asia, possibly driven by population growth brought about by farming itself, resulting in the displacement of the hunting-gathering communities of preagricultural Europe. The indigenist position is that agriculture spread primarily through contact between frontier populations and subsequent acculturation (Zvelebil, 2000). This debate has now become sterile, with a general consensus that 20–30% of the modern European population arrived on the continent at the same time as farming, so the human dynamic was neither migrationist nor indigenist. In reality, the attention of archaeologists has moved forward and is no longer focused on these simplistic interpretations of agricultural spread. Interest is now centered on the more detailed and complex issues relating to the precise

trajectories followed by agricultural spread within and between localized geographic regions and on the nature of the factors responsible for the initial establishment and subsequent development of agriculture in these regions (Zvelebil, 2000). These factors include not only the contact between the preagricultural foragers and the first farmers but also the ecological pressures placed on the crops and the genetic responses of the crops to these pressures. The issues are exemplified by the debates regarding the stop-go pattern of agricultural spread. Agriculture spread rapidly into Greece and the Balkans but apparently slowed down when it reached southeast Hungary (Halstead, 1989; Zvelebil and Lillie, 2000) before again spreading rapidly through the Danube and Rhine valleys. This and other delays have been ascribed either to human factors, agriculture being an unattractive alternative to a successful hunter-gatherer lifestyle in an environment rich in wild resources or to genetic factors, the delay being the time needed for crops to adapt to alien climatic conditions (Zvelebil and Rowley-Conwy, 1986; Halstead, 1989; Bogucki, 1996; Zvelebil and Lillie, 2000).

Plant Genetics and the Origins of Agriculture

Plant genetics has the potential to play a key role in addressing the questions described in this chapter, but so far this potential has been exploited only with regard to the origin of agriculture in Southwest Asia, not with respect to its spread into Europe. Before 1997, a substantial body of disparate information had been accumulated about the genetics of the founder crops of Southwest Asian agriculture (summarized by Zohary, 1996). The discovery that a key domestication trait in cultivated barley, the nonbrittle phenotype characterized by retention rather than shedding of the grain when the ears become mature, is coded by two different mutations, with some cultivars having one mutation and some having the other (Takahashi, 1964, 1972), led to the view that barley was taken into cultivation at least twice. With einkorn and emmer, however, the absence of evidence to the contrary was taken as indicating that these crops were both taken into cultivation just once (Zohary, 1996).

Since 1997, this area of research has been revolutionized through the acquisition of large amplified fragment length polymorphism (AFLP) data sets that have been analyzed in a phylogeographic manner not only to determine whether a crop is monophyletic or polyphyletic but also, through comparisons with wild populations, to infer the geographic location of the initial cultivations (Salamini et al., 2002). The first analysis, involving

288 AFLP loci in 388 accessions of einkorn, concluded that cultivated einkorn is monophyletic and originates from the Karacadag region of southeast Turkey, the area in which the most similar populations of the wild progenitor, *Triticum boeoticum*, are found today (Heun et al., 1997). Subsequent projects using the same methods assigned monophyletic origins to tetraploid wheats and to barley, the former also originating from southeast Turkey and the latter from the Israel–Jordan area (Badr et al., 2000; Özkan et al., 2002). These studies have been looked on as strong support for the stimulus diffusion model for agricultural origins, but doubts are now being raised about the veracity of the analyses and, if correct, the meaning of the results. One problem is that there is a contradiction between the apparent monophyly of cultivated barley, as shown by the AFLP analysis, and the presence of two separate mutations for the nonbrittle ear phenotype (highlighted by Abbo et al., 2001). A possible explanation is that one of the two mutations arose in the cultivated crop after domestication (Salamini et al., 2004). A second question surrounds the support that the archaeological record provides for the identification of the Karacadag region as a birthplace for agriculture (Jones et al., 1998), but this debate is inconclusive because of the incompleteness of the archaeological record, especially with regard to the identification of domesticated grains at early Southwest Asian sites. Equally difficult to assess, because of a lack of solid evidence, is the possibility that the wild phylogeography has changed in the period since the plants were taken into cultivation. If this has happened then the geographic location of the wild population most related to the crop will not necessarily indicate where that crop was first cultivated. All of these issues raise questions about the interpretations of the AFLP studies, but none provides conclusive evidence against those interpretations. More critical is the demonstration that the method used to analyze the AFLP data sets is not sufficiently robust to enable a monophyletic crop to be distinguished from a diphyletic one under all circumstances. If the markers being studied do not display tight genetic linkage (as may be the case with AFLPs), then the neighbor-joining algorithm that was used in three of the studies previously described (Heun et al., 1997; Badr et al., 2000; Özkan et al., 2002) may combine the members of a diphyletic crop into a single, apparently monophyletic grouping (Allaby and Brown, 2003). The question of whether the AFLPs used in the einkorn, tetraploid wheat, and barley studies display sufficient linkage for neighbor-joining analysis to be valid has not been established (Allaby and Brown, 2003, 2004). Reanalysis of the data using principal coordinate analysis, a more appropriate method, does not contradict

the monophyletic inferences (Salamini et al., 2004) but does not provide conclusive support for them (Allaby and Brown, 2004).

Even if the conclusions of the AFLP projects are correct, it is not reasonable to extrapolate from the demonstration of monophyly for a crop to the assumption that the crop was taken into cultivation just once. Part of the problem is that concepts such as monophyly, which have clear meanings and implications when the evolution of several species is studied, become much less determinative when applied to populations of a single species. A modern crop could appear to be monophyletic because it originated from a single domestication event, but monophyly could equally well result from events occurring after the initial cultivations. Salamini et al. (2002) point out that there are inconsistencies between the apparent monophyly displayed by the key founder crops of Southwest Asian agriculture and the gradual transition from gathering to cultivation to domestication that is apparent in the archaeological record for at least some of these crops. They suggest that genetic monophyly might arise after multiple domestications have taken place if for each crop a superior landrace emerges from the variety of forms generated by the initial cultivations, and this superior landrace subsequently spreads and becomes the progenitor of all the modern landraces and cultivars sampled. Considerations such as this show that there is difficulty in linking studies of the genetics of modern crops to archaeological questions regarding agricultural origins. In this particular example, it cannot be assumed that the superior landrace is descended from the first wild plants to be cultivated, and it may not even be the first cultivated population to become domesticated. The geographic origin of this superior landrace therefore cannot identify the location of the farming communities that first took the wild plants into cultivation, nor can it identify the location of the possibly different communities whose cultivated forms first became transformed into domesticated varieties.

Wheat Glutenin Loci

Large data sets have a seductive charm simply because of their size: After all, it must be better to study many loci rather than just one. However, each marker in an AFLP or similar data set is, in effect, a point mutation, and therefore a similar amount of information can be obtained by studying a single locus with many polymorphic sites. The single locus has the added, major advantage that the tight linkage between the informative sites enables evolutionary models to be constructed, tested, and applied to broader questions regarding the evolution of the organism in which the locus is found. Even when the

number of polymorphic sites at a locus is few, the potential information that can be obtained is arguably greater than is possible with data sets of dispersed markers, which can be analyzed only by methods based on similarity matrices. The potential of single-locus studies is illustrated by work that we have carried out with the high-molecular weight (HMW) glutenin loci of wheat.

The HMW glutenins are a complex group of seed storage proteins coded by a pair of tightly linked multiallelic loci, *Glu-1-1* and *Glu-1-2*, on homologous chromosome 1 (Payne et al., 1982). We have carried out an extensive phylogenetic analysis of the *Glu* genes in order to understand the long-term evolution of these genes and of the A, B, D, and G genomes of wild and cultivated wheats (Allaby et al., 1999). One observation arising from this work is that cultivated emmers and their descendants can be divided into two genetic lineages according to the allele type present at the *Glu-B1-1* locus (the x-type *Glu* gene on the B chromosome set). We refer to these two lineages as α and β (figure 9.1) and have dated their divergence to

1.4–2.0 million years ago by application of the appropriate molecular clock (Wolfe et al., 1989). The date is clearly many millennia before the origins of emmer cultivation, which could indicate that this crop was domesticated twice, once from a population of wild plants belonging to the α lineage and once from plants belonging to the β lineage. The heterogeneity could also have arisen from a single domestication of a mixed population of α and β plants or by introgression of α (or β) alleles into a crop domesticated on a single occasion from a wild population of β (or α) plants. The data are also consistent with many domestications of emmer (rather than just two) because if different assumptions are made about the earlier evolution of the *Glu* loci, the phylogenetic analysis that results in identification of the α and β lineages could be interpreted as indicating the presence in cultivated emmers of ancient lineages additional to α and β . As we state in Allaby et al. (1999), the data do not enable a distinction to be made between different scenarios for emmer domestication.

Phylogeography of Glutenin Alleles

To gain further information on the α and β subclades, we determined the lineage affiliation for a total of 185 cultivated emmers (table 9.1), spanning the full range of the expansion of emmer cultivation from Southwest Asia into Europe, Asia, and Africa. Alpha alleles were more common than β alleles among these cultivated wheats (78% α , 22% β), and the geographic distributions of the two *Glu-B1-1* allele types among cultivated emmers were different (figure 9.2). The more common α alleles were present in all areas from which accessions were obtained, whereas β alleles were found only in cultivated emmers from Turkey, the Balkans, southeastern and central Europe, and Italy.

We also examined *Glu-B1-1* alleles in 59 wild emmer wheats (*T. dicoccoides* (Korn) Schweinf.) (table 9.1). Most of the wild emmers came from the two regions of the Fertile Crescent in Southwest Asia that have been highlighted as possible locations for crop domestication: the southern Levant and the border between southeast Turkey and northern Syria (Jones et al., 1998; Nesbitt and Samuel, 1998). The 36 southern accessions came from Jordan, Israel, Lebanon, and the D'ara region of south Syria, and the 20 northern specimens were from the north Syrian borderlands and the Gaziantep region of southeastern Turkey. The collection also included two accessions from Iran and one from Iraq, within the eastern arm of the Fertile Crescent, outside the postulated domestication centers. The α and β allele frequencies were

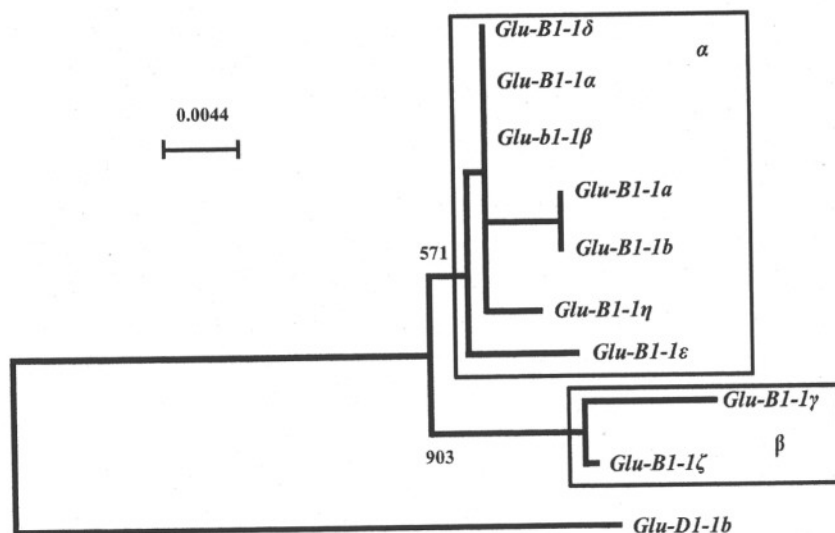


FIGURE 9.1 Neighbor-joining tree of the nine known *Glu-B1-1* alleles, all of which are present in cultivated emmers or emmer descendants (e.g., *T. aestivum* L.), based on multiple-sequence alignment of a 241- to 243-bp region immediately upstream of the open reading frame (Allaby et al., 1999). The *Glu-D1-1b* allele was used as the outgroup, and the robustness of the branching order was tested by creating 1000 bootstrap replicate trees using the CLUSTAL W program. The bootstrap values are the numbers above the branches of the tree. The α and β allele groups within the *Glu-B1-1* clade are highlighted.

Table 9.1 *Glu-B1-1* Allele Types in Wild and Cultivated Emmer Wheats

Wheat and Country of Origin	Number of Accessions Containing	
	α Alleles	β Alleles
<i>Cultivated Emmer</i>		
Armenia	6	0
Bulgaria	1	1
Czech Republic	12	20
Ethiopia	20	0
Georgia	3	0
Germany	15	1
Greece	1	1
Hungary	1	0
India	3	0
Iran	6	0
Israel	1	0
Italy, north and central	21	12
Italy, south	24	1
Kuwait	1	0
Montenegro	2	0
Morocco	2	0
Romania	1	0
Serbia	3	2
Slovenia	1	0
Spain	8	0
Switzerland	5	2
Turkey	3	1
USSR	4	0
All cultivated emmers	144	41
<i>Wild Emmer</i>		
Iran	0	2
Iraq	1	0
Israel	13	3
Jordan	3	4
Lebanon	3	3
Syria (north)	2	2
Syria (south)	4	3
Turkey	4	12
All wild emmers	30	29

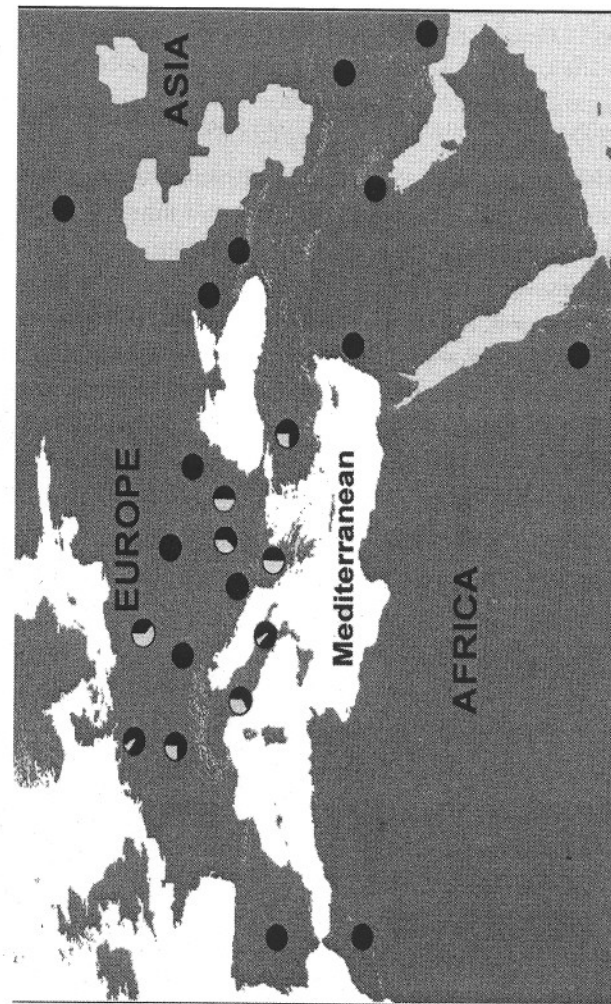


FIGURE 9.2 Geographic distribution of *Glu-B1-1* subclades in cultivated emmers. The pie charts show the proportion of α (black) and β (white) alleles in each geographic region, using the data listed in table 9.1.

Wheats were obtained from the John Innes Centre, Norwich, UK; Institut für Pflanzengenetik und Kulturpflanzenforschung, Gatersleben, Germany; the International Centre for Agricultural Research in the Dry Areas, Aleppo, Syria; and private collections.

similar among the wild emmers as a whole (50.8% α , 49.2% β), but there were distinct geographic biases, with α alleles common in Israel (81.3% α , 18.7% β) and β alleles common in Turkey (25% α , 75% β). Largely as a result of these biases, the allele frequency in the southern domestication region was higher for α than for β (64% α , 36% β) whereas in the northern region β alleles were predominant (30% α , 70% β). These phylogeographic data are illustrated in figure 9.3.

Limitations of a Phylogeographic Approach with Cultivated Wheats

The objective of this analysis was to obtain a broad picture of the geographic distribution of *Glu-B1-1* alleles in wild and cultivated emmers and to see whether these distributions can be related to the expansion of cultivated wheats from Southwest Asia. For cultivated wheats, the current phylogeography of *Glu-B1-1* alleles will reflect the phylogeography established during the expansion phase if there was no significant movement of wheats or alleles

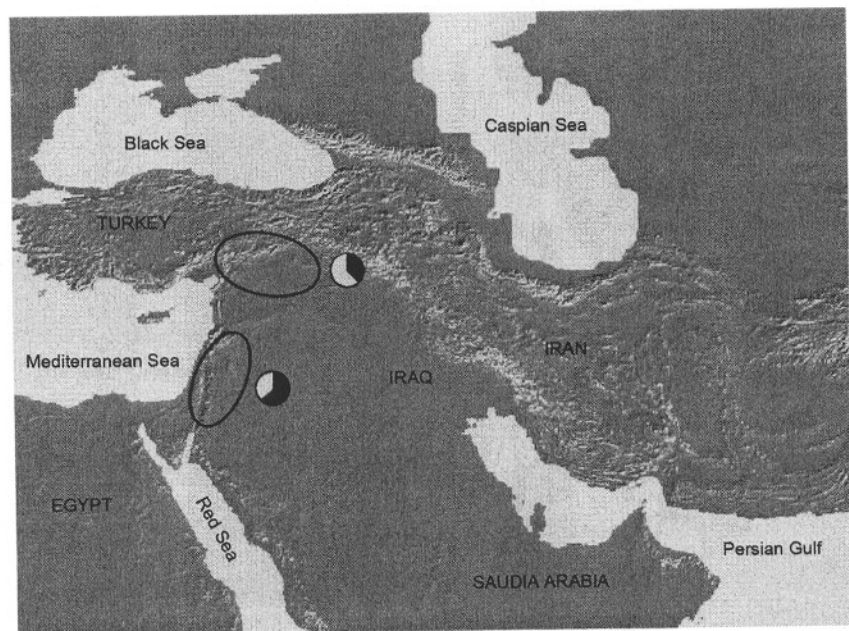


FIGURE 9.3 Map of Southwest Asia showing the northern and southern regions from which most of the 59 wild emmers we studied were collected. The southern region includes part of the Levant, and the northern region is located on the border between southeast Turkey and northern Syria. The pie charts show the proportion of α (black) and β (white) alleles in each geographic region, using the data listed in table 9.1.

during the millennia since the initial phylogeography was set up. Movement of cultivated wheats requires human agency because these plants, lacking a fragile rachis, cannot shed their seeds without human intervention and therefore cannot move from one geographic region to another unless physically transported by humans. Similarly, extensive movement of alleles requires human agency because cultivated wheats are predominantly self-fertilizing, limiting the opportunities for gene flow in the absence of directed cross-fertilization by humans. Modern phylogeographies therefore reflect ancient events only if wheats and alleles have not been moved extensively by human activity during the millennia since the initial expansion of agriculture from Southwest Asia. Extensive movement of both wheats (by trade and exchange of seed corn) and alleles (through breeding programs) has occurred in the last 150 years, but we made particular efforts to use accessions thought by the suppliers to be genuine landraces associated with a specified geographic region so that the results would be affected as little as possible by these recent events.

The question of whether the resulting phylogeographies have been significantly affected by human activities in premodern agricultural periods therefore is an open one. However, studies we have made of microsatellite genotypes in emmer accessions from Italy suggest that at least some landraces retain a Neolithic phylogeography. Isaac et al. (submitted) genotyped five microsatellite loci in 52 landraces of Italian emmer wheat. Each of the five loci was polymorphic, with 43 allele combinations identified in the 52 accessions. The allele combinations fell into two evolutionarily distinct groups, the larger of these comprising 27 genotypes found in 42 accessions, with a significant correlation between geographic and genetic distance matrices ($r = .393$, $p = .003$). Using a model that predicts the point of origin of crop cultivation within a geographic region by comparing the genetic and geographic distances between accessions, we identified a point on the coastline of northern Puglia as the most likely origin for this group of wheats. This phylogeographically determined origin corresponds closely with the location of the earliest agricultural sites in Italy; radiocarbon dating shows that they occur at 6100–5900 BC in northern Puglia and eastern Basilicata, in a geographically distinct region known as the Tavoliere. The coincidence between the origin predicted by the genetic analysis and the actual origin as revealed by archaeology lends strong support to the hypothesis that at least some emmer landraces have remained geographically static since their original introduction into Europe, so phylogeographic analysis of these modern plants can provide information on events occurring as agriculture spread into Europe.

Implications of the Glutenin Phylogeographies

Two Expansions of Cultivated Emmer into Europe

Among cultivated emmers, the phylogeographic distributions of the α and β alleles are markedly different: α alleles are ubiquitous, but β alleles are restricted mainly to central and southern Europe. A possible explanation of the dissimilar distributions is that α alleles have a selective advantage over β alleles throughout the greater part of the geographic range of cultivated emmers. It is difficult to imagine what the nature of this selective advantage might be because the nucleotide differences between the α and β alleles appear to be neutral: They lie upstream of the *Glu-B1-1* open reading frame, and the variations between the α and β sequences do not affect motifs thought to be involved in transcription or translation initiation (Allaby et al., 1999). In the absence of selection it is unlikely that the two allele subclades achieved their modern distributions via a single agricultural expansion. Therefore the data suggest that there have been at least two independent expansions of emmer cultivation into Europe, one involving plants carrying α alleles and the other involving plants with β alleles.

The possibility that there were two independent expansions of emmer cultivation correlates with evidence from other sources. The archaeological record contains direct evidence of two trajectories of spread of agriculture into Europe, one following the Mediterranean coast to Western Europe and the other following the major river valleys through the Balkans to northern Europe (reviewed by Bell, 1987). Similarly, the expansion of Indo-European languages into Europe, thought to be associated with the expansion of agriculture, involves two language groups: the Slavo-Germanic branch, which gave rise to the Slavic and Germanic languages of central and eastern Europe, and the Greco-Italic-Celtic branch, from which the Romance and Celtic languages of Western Europe are derived (Renfrew, 1989). One explanation of the glutenin phylogeography is that β alleles were underrepresented or even absent among plants that followed the Mediterranean trajectory.

The archaeological evidence appears to indicate that the two expansions of agriculture occurred at different times. The geographical ubiquity of the α subclade, not only in Europe but also in Asia and northern Africa, could be taken as evidence that it was associated with the primary expansion of wheat farming out of Southwest Asia and that expansion of plants with the β subclade was a secondary phenomenon. The archaeological record can also accommodate a more localized expansion of β plants during the early Neolithic, covered over by a later α expansion with a global impact. Although

our current data do not allow us to distinguish between these alternatives, it should be possible to address the question by examining ancient DNA from charred wheats, using techniques that are now well established for genetic analysis of this type of material (Brown, 1999). Whichever scenario is correct, the implication is that the human events that led to the initial expansion of agriculture from Southwest Asia during the period 6500–3500 BC were not unique and recurred on at least one occasion.

Origins of the *Glu-B1-1* Allele Subclades

The presence of the α and β allele subclades in cultivated wheats can be explained by multiple domestication of emmer, single domestication of a highly divergent wild population, or introgression of novel alleles after domestication (Allaby et al., 1999). The second of these possibilities is unlikely because single domestication of a population of wheats containing both α and β alleles would be expected, after expansion, to give a phylogeography in which α and β alleles are fairly equally distributed, presuming that, as argued earlier, there is no differential selection between alleles of the two subclades. The distributions of α and β alleles in wild emmers do not preclude multiple domestication; a possible scenario is that the α subclade entered the cultivated gene pool via domestication of an emmer population from Israel, where α alleles are common, and the β subclade originates from a domestication in the Gaziantep region of southeastern Turkey, where β alleles predominate. Both areas contain some of the earliest farming villages and therefore are possible locations for crop domestication according to the archaeological record (Jones et al., 1998; Nesbitt and Samuel, 1998). However, the *Glu-B1-1* phylogeographies are equally consistent with a single domestication of emmer, in either the south or north of the western arm of the Fertile Crescent, followed by acquisition of the other allele subclade by introgression from nonancestral wild wheats. Introgression could have been by direct cross-hybridization between wild and cultivated emmers or by hybridization between a wild emmer and a cultivated hexaploid, the latter resulting in a pentaploid intermediate whose segregation products could include a tetraploid with domestication traits inherited from the hexaploid parent and *Glu-B1-1* alleles from the wild emmer. Introgression of one form or another is supported by other results, based on 5S rDNA comparisons, that suggest that wild emmers from several parts of the western Fertile Crescent have contributed to the gene pool of domesticated wheat (Allaby and Brown, unpublished results).

Conclusions

Both the origins of agriculture in Southwest Asia and its spread into Europe are accessible to examination by genetic analysis. Although to date the large AFLP data sets obtained for einkorn, emmer, and barley have not been analyzed in a convincing manner, these data sets and others like them have the potential to provide extensive information on the development of early crops in Southwest Asia. Genetic studies of crops throughout Europe are beginning to show that some landraces have remained geographically static since their first introduction into the continent, and more detailed phylogeographic analysis of these will tell us much about the trajectories followed by the spread of agriculture. Through examination of selective markers, it may be possible to assess the impact of environmental factors on the spread of cereal cultivation from the Fertile Crescent into the less hospitable regions of northern Europe. The great challenge for the next decade is to link the findings of plant genetics with archaeological evidence so that the former can contribute to the debates about the human dynamics underlying the transition from hunting-gathering to agriculture in Southwest Asia and across Europe.

Acknowledgments

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CHAPTER 10

Breadfruit Origins, Diversity, and Human-Facilitated Distribution

I received the seeds of the bread tree. . . . One service of this kind rendered to a nation, is worth more to them than all the victories of the most splendid pages of their history, and becomes a source of exalted pleasure to those who have been instrumental in it.

—Letter from Thomas Jefferson to M. Giraud (1797)

Background

Breadfruit (*Artocarpus altilis* (Parkinson) Fosberg, Moraceae) is a staple crop in Oceania, where it was originally domesticated. It is a versatile tree crop with many uses including construction, medicine, animal feed, and insect repellent. However, it is principally grown as a source of carbohydrates and is an important component of agroforestry systems. Unlike many herbaceous starch crops harvested for their vegetative storage tissues, breadfruit is a large tree grown for its fruit (technically an infructescence, as the breadfruit is a syncarp made up of many small fruitlets fused together) (figure 10.1). Many cultivars have no seeds, just tiny aborted ovules (these will be called seedless cultivars), whereas others may have few to many seeds. Breadfruit typically is harvested when it is slightly immature and still firm, and seedless cultivars are prepared in much the same way as potatoes: baked, boiled, steamed, roasted, or fried. Ripe fruits are sweet and used in desserts. In seeded cultivars, seeds are chestnut-like in both size and taste and are boiled or roasted.

Although breadfruit yields vary between individual trees and cultivars, productivity typically is quite high. A commonly cited figure for seedless