

REVIEW PAPER

Early agricultural pathways: moving outside the 'core area' hypothesis in Southwest Asia

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Abstract

The origins of agriculture in the Near East has been associated with a 'core area', located in south-eastern Turkey, in which all major crops were brought into domestication within the same local domestication system operated by a single cultural group. Such an origin leads to a scenario of rapid invention of agriculture by a select cultural group and typically monophyletic origins for most crops. Surprisingly, support for a core area has never been directly tested with archaeological evidence. Over the past decade a large amount of new archaeological and genetic evidence has been discovered which brings new light on the origins of agriculture. In this review, this new evidence was brought together in order to evaluate whether a core region of origin is supported. Evidence shows that origins began earlier than previously assumed, and included 'false starts' and dead ends that involved many more species than the typical eight founder crops associated with the core area. The rates at which domestication syndrome traits became fixed were generally slow, rather than rapid, and occurred over a geographically wide range that included the North and South Levant as well as the core area. Finally, a survey of the estimated ages of archaeological sites and the onset of domestication indicates that the domestication process was ongoing in parallel outside of the core area earlier than within it. Overall, evidence suggests a scenario in which crops were domesticated slowly in different locations around the Near East rather than emanating from a core area.

Key words: Archaeobotany, domestication, genetics, origins of agriculture, paleoethnobotany, protracted transition.

Introduction

Agricultural origins is a topic of continuing interest amongst anthropologists and biologists and the better studied Near Eastern area of crop domestications continues to be at the forefront of debates about the process of plant domestications at the dawn of agriculture (Brown *et al.*, 2009; Honne and Heun, 2009; Purugganan and Fuller, 2009; Allaby *et al.*, 2010; Abbo *et al.*, 2010a, b, 2011; Fuller, 2010). In the present paper, the evidence from both genetics and archaeobotany for a single, rapid origin versus that in favour of a mosaic of slower processes is evaluated and it is concluded that these data increasingly support the latter and undermine the concept of a 'core area' (*sensu* Lev-Yadun *et al.*, 2000).

It is well-established that the wild ancestors of a number of major crops, cereals, pulses, and flax, co-occur in Southwest Asia, in a region that has come to be known as the 'Fertile Crescent', a term coined by the late 19th century archaeologist and orientalist JH Breasted (1906). Through the course of archaeological research and thinking in the 20th century, especially through workers such as Childe (1935) and Braidwood and Howe (1960), this geographical region shifted from being the focus of the earliest civilizations (in Breasted's conception, the western wing extended to Egypt) to being the focus of the development of agriculture which underpinned the civilizations of Egypt, Mesopotamia, and Europe. Botanical research, exemplified

by that of Zohary (1969, 1999) and a tradition continued by Abbo *et al.* (2010a, 2011; Lev-Yadun *et al.*, 2000), served to document the geography and habitats of the closest wild relatives of the crops that originated here and provided the specimens from which genetic work has been able to explore in more detail the interrelationships of existing wild and domesticated populations. Zohary (1996) recognized eight major founder crops, which can be found in cultivation today and in wild form in the region, including einkorn (*Triticum monococcum*), emmer (*Triticum dicocum*), barley (*Hordeum vulgare*), lentil (*Lens culinaris*), pea (*Pisum sativum*), chickpea (*Cicer arietinum*), bitter vetch (*Vicia ervilia*), and flax (*Linum usitatissimum*) (Zohary and Hopf, 2000; Abbo *et al.*, 2010a; Table 1).

Current scholarly opinions are divided between whether agricultural origins in the Near East occurred by a protracted and diffuse process (Nesbitt, 2004; Willcox, 2005; Fuller, 2007; Brown *et al.*, 2009) or a focused, single process (Zohary, 1999; Bar-Yosef, 2003; Kozłowski and Aurenche, 2005; Abbo *et al.*, 2010a, 2011). In some recent reviews on the origins of agriculture in the Near East (Southwest Asia), Abbo *et al.* (2010a, 2011) argue that crop domestication occurred just once in the Near East, in a ‘core area’ (after Lev-Yadun *et al.*, 2000) or ‘golden triangle’ (Kozłowski and Aurenche, 2005), where the whole package of eight ‘founder crops’ were brought into cultivation at essentially the same time. From here, cultivation of these species spread, and if the same wild species was brought into cultivation elsewhere it was under the influence of the earlier traditions of cultivation in this core region. Theirs is an argument in

which agriculture was a great, and rare, invention by a select cultural group in the Near East, and in a few other regions in the world. Their argument implies a rapid domestication process and a simple monophyletic origin for the founder crops (Zohary, 1999). It emphasizes single genes and single traits as markers of domestications, such as non-shattering in cereals (Peleg *et al.*, 2011) and free germination in legumes (Abbo *et al.*, 2010b), whereas the protracted models explore an adaptive syndrome of domestication traits that evolved during the early era of cultivation.

In the present paper, the evidence of genetics, biogeography, and archaeobotany of crop domestication in the Levant region of Southwest Asia which undermines the model of a ‘core area’ (shown in Fig. 1) and rapid domestication (represented by the recent papers of Abbo *et al.*, 2010a, 2011) will be reviewed succinctly. Multiple lines of evidence across several crops point to plant domestication as a protracted evolutionary process that resulted from unintended, as well as intended, consequences of strategic human subsistence behaviours, local ecologies, and processes of population genetics but was not a conscious revolution (Kislev, 2002; Nesbitt, 2004; Willcox, 2005; Weiss *et al.*, 2006; Fuller, 2007; Allaby *et al.*, 2008, 2010; Brown *et al.*, 2009; Purugganan and Fuller, 2009). Beyond arguing for multi-locus and diffuse domestication processes the ‘core area’ hypothesis is tested against current evidence.

Just over a decade ago, the available genetic evidence could be seen to suggest single origins for most Near Eastern crops (Zohary, 1999; Zohary and Hopf, 2000;

Table 1. The additional founder crops of Near Eastern agriculture

These are additional to the eight conventional ‘founder crops’ of Zohary (1996) and Abbo *et al.* (2010a).

Species (wild progenitor)	Early archaeological occurrences	Latest occurrences
<i>Triticum monococcum</i> , two-grained form (wild form could be <i>T. boeoticum</i> ssp. <i>thuaodora</i> or <i>T. urartu</i>)	Latest Pleistocene and earliest Holocene Syria: Abu Hureyra, Mureybit, Tell Abr, Jerf el Ahmar, Djade. Domesticated form from the latest levels at Mureybit, Abu Hureyra El Kowm II, Tell Bouqras, Tell Ramad. Also reported from some PPNB sites in the Southern Levant (e.g. Beidha, Wadi Jilat 7 & 13, Wadi Fidan)	Syria: Chalcolithic, i.e. c. 5000 BC (Van Zeist, 1999) Europe: Late Bronze Age c. 1200 BC (Köhler-Schneider, 2003)
<i>Secale</i> cf. <i>cereale</i> / <i>Secale</i> cf. <i>vavilovii</i>	Syria: Abu Hureyra, Mureybit, Tell Abr, Jerf el Ahmar. Turkey: Cafer Höyük, Çayönü, Nevali Çori. Domesticated: Abu Hureyra 2, El Kowm II and Can Hassan III	Syria and Turkey: Late PPNB, Abu Hureyra and Can Hassan III (i.e. c. 6800–6500 BC). European domesticated rye from of c. 1000 BC
<i>Triticum</i> (4x) <i>turgidum</i> / <i>timopheevi</i> ('striate emmeroid')		Persists to Late Bronze Age in central Europe, i.e. c. 1200 BC (Köhler-Schneider, 2003)
<i>Avena sterilis</i>	Only a localized crop in the Pre-Pottery Neolithic A of the southern Levant (Weiss <i>et al.</i> , 2006)	
<i>Vicia peregrina</i>	Only a localized crop in the Pre-Pottery Neolithic A of the southern Levant (Melamed <i>et al.</i> , 2008)	
<i>Vicia faba</i> (from an unknown/ extinct wild progenitor)	Southern Levant: PPNB Jericho and Iraq ed-Dubb; Domesticated: Extant, a major world crop (broad beans, fava, ful)	
<i>Lathyrus sativus</i>	Tell el-Kherkh, Syria; Yiftahel, Israel	
	Early-Middle PPNB finds from Cafer Höyük, Çayönü, and Nevali Çori; and LPPNB finds from Ras Shamra	Extant: Eastern Mediterranean, Ethiopia and India
<i>Lens nigricans</i>	Not yet recognized archaeologically	Inferred from large-seeded ‘feral’ populations in the Western Mediterranean, genetic origins Turkey (Ladizinsky <i>et al.</i> , 1983)
<i>Ficus carica</i>	PPNA finds of parthenocarpic figs at Gilgal; other PPNA finds at Jericho, Gesher, Mureybit III, Tell Qaramel, Jerf el Ahmar; increased quantities in Early PPNB D’jade (Kislev <i>et al.</i> , 2006; Willcox <i>et al.</i> , 2008). Later phases at Çayönü, Halula	Extant, Mediterranean and world fruit crop: parthenocarpic domesticates vegetatively propagated

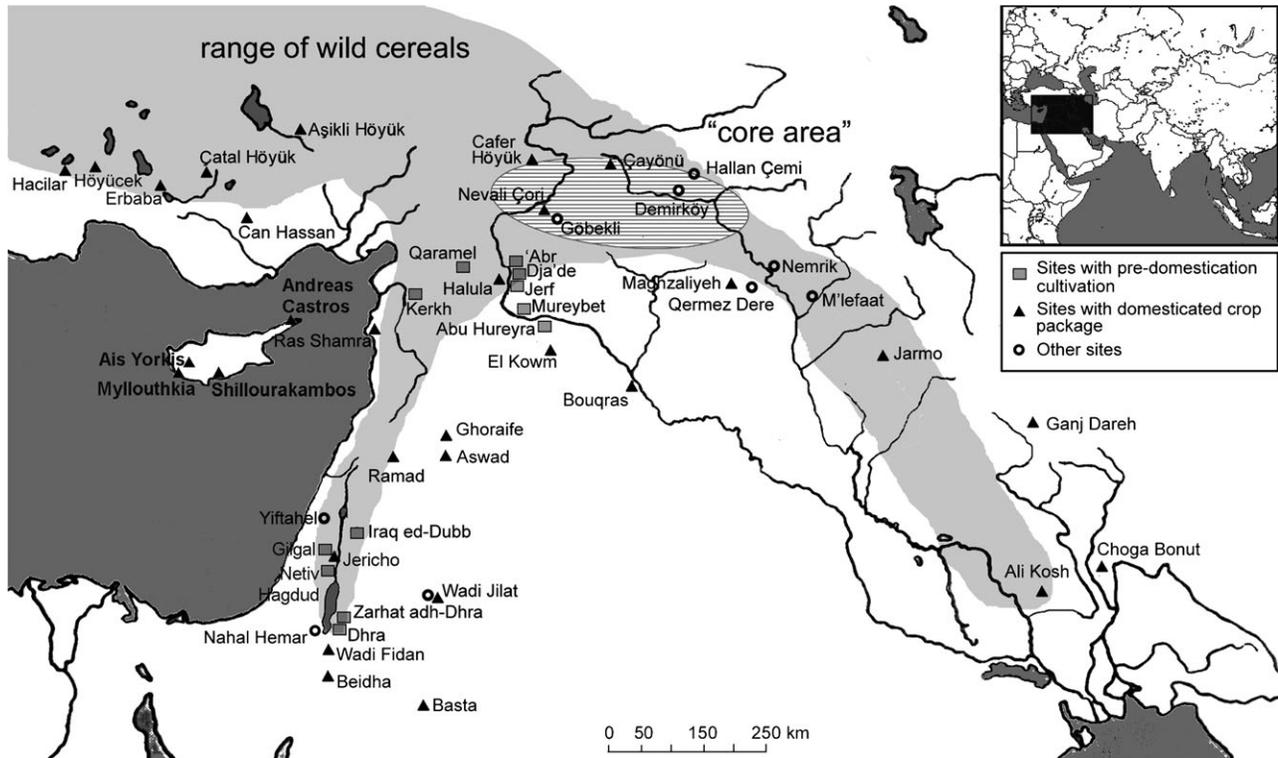


Fig. 1. Map of the Near Eastern early Neolithic sites with archaeobotanical evidence, in relation to the general greater distribution of wild cereals (wheats, barley combined modern distribution) and the hypothetical 'core area', based on the overlap of all progenitors, including *Cicer arietinum*. Sites are differentiated into those with inferred pre-domestication cultivation (Table 2), those with an established package of domesticates (taken as the presence of two confirmed morphological domesticates and at least a third domesticate/semi-domesticated, based on Table 3), and other sites.

Lev-Yadun *et al.*, 2000), and a 'core area' in south-eastern Turkey near the uppermost Tigris and Euphrates rivers was postulated. While this was a reasonable position a decade ago, the accumulation of archaeobotanical evidence—the fossil record of crop domestication—calls this into very serious doubt. Instead, what the archaeobotanical evidence indicates is a more geographically dispersed process, with extended periods of selection for domestication traits, which took millennia (~3000 years), to become fully established in crop populations. In addition, there were numerous 'false starts' and dead-ends, i.e. early cultivars, some fully domesticated and others not, that went extinct before the modern era of crop-breeding and wild progenitor surveys. Genetic evidence has also found the signals of single origins to be increasingly muddled or undermined by more evidence. Experimental growing and harvesting of wild wheat and barley in the South of France for more than a decade by Willcox (2007) has identified reasons why selection for domestication traits might not be as rapid as often assumed, for example, by Hillman and Davis (1990) and Peleg *et al.* (2011). Long-term experiments documenting genetic change in cereals over centuries are not available, but *in silico* experiments, that is, with computer simulation, provides one means of approaching the expected genetic patterns resulting from different domestication scenarios (Olsen and Gross, 2008; Le Thierry D'Ennequin *et al.*, 1999; Allaby *et al.*, 2008, 2010). The

recognition of a protracted transition of 1000s of plant generations means that recurrent processes of gene flow between wild populations and cultivars, and between different cultivated lines, makes trying to pin down a point of origin for most crops from modern genetic studies tenuous and misleading.

Increasing evidence for independent domestications: additional founder crops and multiple lineages

The increase of archaeobotanical data in the Near East over the past 15–20 years has been massive, with more sites and much larger assemblages becoming available (see overviews in Fuller, 2008; Allaby *et al.*, 2010). Even more so there has been an exponential rise in archaeobotanical evidence from Neolithic Europe (Colledge and Connolly, 2007), in which crops of Near Eastern origin played the key role as founder crops. This dataset, consisting of literally many 100 000s of ancient grains, has brought with it the recognition of distinct morphological varieties of cereals, no longer known from cultivation, such as a two-grained form of einkorn (Van Zeist, 1999; Kreuz and Boenke, 2002; Willcox, 2003), a striate emmeroid/timopheevoid wheat unknown in Europe for the last 3000 years or so (Brown *et al.*, 1998, Jones *et al.*, 2000; Kohler-Schneider, 2003). The two-grained form of einkorn can be found both in morphologically wild and domesticated forms on early sites in the Near East. Some of

these finds could be *T. urartu* as opposed to *T. boeoticum* (see next section). The persistence of these crops in European agriculture until perhaps 1000 BC means that they had perhaps 8000–9000 years of history under cultivation, but are not represented in modern crop germplasm. It is impossible to judge how many other lost genetic lines there might have been which are morphologically indistinguishable from modern varieties without gathering ancient DNA evidence (Palmer *et al.*, 2011).

In addition, within the Near East a number of major food plants appear to have been cultivated in some areas and sites, including additional form(s) of vetch (*Vicia*), oat (*Avena*), and rye (*Secale*), all unrelated to the historical/modern crops of these genera known in European agriculture. Table 1 summarizes these additional founder crops of the Near East. In addition to these, there are other crops which remain important today that also appear on early sites, including possible grasspea (*Lathyrus sativus*), broad bean (*Vicia faba*) which has an unknown/extinct wild progenitor (Tanno and Willcox, 2006b), and fig (*Ficus carica*), which may have been cultivated as early as cereals (Kislev *et al.*, 2006). *Vicia faba*, for example, has early finds in both the southern and northern Levant associated with early cultivation but has not been found on early sites in the core area. These crops are not included in the ‘founder crops’ list of the proposed ‘core area’. These additional or ‘non-core’ crops have two implications: first, that the beginnings of plant cultivation and agriculture in the Near East was about more than just eight founder crops. Indeed, as many as 16 or 17 species were involved in the early cultivation in the Near East and it is unlikely that so many species were linked in cultivation in a small region and short time period. A second implication is that modern botanical surveys and germplasm collections cannot be expected to contain all of the genetic and species diversity that was cultivated in the past. The wild populations that were originally sampled by early cultivators have been subjected to extirpations and range changes caused by 12 000 years of environmental changes, both climatic and, more importantly, environmental degradation due to human impact, over-grazing, deforestation, and fire. The lack of a credible wild ancestor for the broad bean is a likely example, while the extinct ancestor of cattle (*Bos primigenius*) is a well-known case from zoology (Clutton-Brock, 1999). Ancient DNA evidence from archaeological pigs has similarly highlighted how the use of modern genetic patterns only may miss historical distributions of lineages that have been extirpated such as the Neolithic pigs introduced to Europe from the Near East (Larson, 2011).

Several earlier genetic studies suggested that some of the founder crops had single origins. However, it should be noted that such studies invariably relied on a single approach to sampling and analysis, which has been found to be misleading and has been superseded by larger data sets and better analytical techniques that show a more complex picture. Many genetic based studies have relied on phenetic rather than true cladistic analysis, i.e. on fragment length polymorphisms (AFLP) instead of resequencing

data, and on analysis by a clustering technique (Neighbor-Joining Tree, NJT). Such methods *assume* a strongly tree-like, cladistic structure rather inferring one, since they are analysed by clustering; and they have been shown to be inadequate for recognizing reticulation in phylogenies in general (Reeves and Richards, 2007). Problems of reticulate evolution are further confounded by genetic recombination, which is not taken into account in the assumption of a tree-like model. Instead, such analyses must assume that recombination and cross-pollination had a minimal impact on the overall tree structure. Simulations of neutral genetic drift and population extinction have compared the analytical outcome of single versus double domestications when analysed by this method (NJT). This demonstrated that, regardless of how many origins there actually were, this method will tend to find only one of them (Allaby *et al.*, 2008, 2010). More recent studies using such ‘genetic fingerprinting’ data have switched to network analyses (Kilian *et al.*, 2007; Heun *et al.*, 2008; Özkan *et al.*, 2010), which allow for reticulate relationships. Such analyses invariably show a highly reticulate core of ancient cultivated lines and wild populations, whereas only the outer branches, often away from the Near East, have a more tree-like structure. In other words, the base of the ‘tree’ is highly unreliable, whereas the branching signals further up the tree, connected perhaps to major dispersal event bottlenecks, appear more reliable.

As for classical genetic markers, such as genes for domestication traits, it is entirely plausible for these to be transferred between different early cultivated populations through gene flow, even through the bridge of a wild population (Allaby, 2010; Ross-Ibarra *et al.*, 2009). The protracted process of the selection of domestication alleles means that their fixation (domestication *sensu stricto*) could have occurred 1000s of years and 100s of kilometres from where the wild populations were first sampled and brought into cultivation, with recurrent gene flow and resampling being likely. Indeed, in what is arguably the genetically best-studied crop, *Oryza sativa*, it is clear that several selected domestication loci are typically of a single shared origin and often quite recently (Sweeney and McCouch, 2007; Sang and Ge, 2007; Fuller *et al.*, 2010a; Purugganan, 2010), while neutral genetic variation, including non-recombining, maternally inherited chloroplasts are highly diverged with the last common ancestors on the order of 100 000–200 000 years ago (Vitte *et al.*, 2004; He *et al.*, 2011). This means that domestication selected genes have been shared by hybridization between separate early cultivated lines. Even those who favour models of a single main rice domestication posit a large degree of hybridization between domesticated and wild rices in Southern Asia (Molina *et al.*, 2011), although human cultivation would probably have been necessary to account for local (wild) chloroplasts (maternal plants) with domestication mutations deleterious in the wild.

Another facet of the protracted process is that if parallel mutants were to occur at domestication loci, independently giving rise to the same phenotype in separate populations, it

would be expected that one or the other would be rapidly lost through drift when populations met (Allaby, 2010). Consequently, single mutations associated with domestication traits are also an expectation of a protracted process, but parallelisms may still exist at low frequencies if they are in the latter stages of removal by drift. Interestingly, both the waxy (*Wx*) and red pericarp (*Rc*) mutations in rice have independently arisen in *O. sativa indica* and *O. sativa japonica*, but the mutations associated with the *indica* subspecies are now present only at very low frequencies (Yamanaka *et al.*, 2004; Sweeney *et al.*, 2007). Such mobility of domestication trait loci between populations also suggests that the domesticated crop that emerges from the milieu may be expected to have different domestication traits originated from different geographic regions, even if all regions produced all traits (Allaby, 2010). Again, evidence emerging from rice indicates that this appears to be the case where mutant traits for waxy, shattering, and seed width are all associated with different geographic regions (Shomura *et al.*, 2008).

A more reliable source of phylogenetic evidence than either the presence of selected domestication alleles or genome-wide neutral variation may be in the resequencing of variation in and around conserved genes from wild ancestry. Several genes in barley, for example, have polymorphisms suggesting distinct eastern and western Eurasian barley (Saisho and Purugganan, 2007). This is congruent with genetic differences reported from populations in wild barley of the Western and Eastern Fertile Crescent (Morrell and Clegg, 2007; Kilian *et al.*, 2009), and the existence of two alternative non-shattering domestication mutations (Azhaguvel and Komatsuda, 2007). Recently, the recognition that photoperiod-insensitive barleys, which are better adapted to northern latitudes, share a *ppd1* mutation that derives uniquely from wild barleys of the mountains of Iran and not from post-domestication mutations of either of the photoperiod-sensitive Eastern or Western domesticated barley lines suggests the possibility of at least three wild derivations of barley (Jones *et al.*, 2008). Extant emmer landraces (i.e. excluding the extinct emmeroid wheat recognized archaeologically), also have at least two genetic derivations indicated in variants of the gluten gene sequence (Brown *et al.*, 2006). Further evidence, as reviewed in Özkan *et al.* (2010) suggests that emmer wheat was derived from two source populations.

A growing body of recent work points to more than one origin in some founder crops and single origins in others. In addition to the multiple origins now inferred for the cereals, recent work on *Pisum* genetics suggest distinct northern and southern *Pisum sativum* domestications, with the southern lines mostly preserved in Egyptian landraces, while a third pea domestication was the distinct Ethiopian pea (*P. abyssinicum*) (Kosterin and Bogdanova, 2008). Of note in the Ethiopian pea domestication, is that experimental data show that germination rates of these cultivars are low, with little over 50% of planted seed germinating (Weeden, 2007). This suggests that complete elimination of germination inhibition, was not necessarily a first step in legume

domestication. For *Vicia ervilia*, genetic evidence is very limited, but classical genetics indicates two alternative recessive mutations for non-dehiscence (Ladizinsky and Van Oss, 1984), which tends to favour at least two areas of domestication. This species is widespread on early archaeological sites but it is difficult to determine whether it was present as a crop or a weed. Early chloroplast genetics raised the possibility of two distinct lineages in domesticated *Lens culinaris*, one of which is very rare (Mayer and Soltis, 1994), but more recent studies on lentil genetics, especially based on resequenced data are not available. In addition, Ladizinsky *et al.* (1983) inferred that large-seeded free-growing black lentils in secondary habitats of the Western Mediterranean are feral derivatives of a lost domestication of *Lens nigricans*; this forms a single genetic subgroup of diversity of wild *L. nigricans* in western Turkey (Ferguson *et al.*, 1998). Although unconfirmed archaeobotanically, such a lost lineage of lentil would parallel what is known for wheats. Until recently, the only two crops which did appear to be candidates for a clean, single domestication were flax (Allaby *et al.*, 2005; Fu and Allaby, 2010) and chickpea (Shan *et al.*, 2005). However, evidence is emerging that there may have been an earlier separate domestication of flax for non-dehiscent capsules rather than oil or fibre use (Fu, 2011). Chickpea may also be a single origin, although available data are only of the more problematic AFLP variety (Shan *et al.*, 2005).

In the end, the main argument for the ‘core area’ is that all of the eight ‘founder crops’ co-occur there (Abbo *et al.*, 2010a, b). Abbo *et al.* (2010a) offer an anecdotal description of encountering many of these species in near proximity. This is indeed indicative of the subsistence potential of this environment, whether exploited by collectors or cultivators, but these species are not restricted to this core zone. All of the species, with the exception of chickpea, occur wild in the Southern Levant (Southern Syria, Jordan, Israel, Palestine), and some occur well outside the core area through parts of Anatolia and the eastern fertile crescent (the Zagros foothills in Iran). In addition, most of these species occur archaeologically early in the Southern Levant, as early as they do in the northern Levant or the core area. So in the end the ‘core area’ hypothesis rests primarily on the wild distribution of the chickpea (*Cicer arietinum* ssp. *reticulatum*) and where it overlaps other species (Fig. 1). The best documented and earliest finds of this crop, however, come from outside the ‘core area’ (Tanno and Willcox, 2006b). Thus it can be questioned how central it was to the beginnings of agriculture and, indeed it is the cereals that typically dominate ancient samples and would be regarded as the staples. More than one origin has been suggested for each of the extant cereals, added to which are the several overlooked crops of Table 1.

Whether agricultural origins happened just once or more than once in the Near East also raises the issue of how one defines ‘independent’ origins. One must be explicit as to whether one’s emphasis is on specifying the genetic derivation of a cultigen or the cultural tradition cultivation. Abbo *et al.* (2010a) suggest that even if there might be cultivation

deriving from geographically distinct populations of the same species, these would not have been culturally independent. In other words, if there were local domestications in the southern Levant, they would have been influenced by groups already cultivating the Northern Levant: cultivation in one region was learned from another. If this is so, then one would expect there to be clear evidence that cultivation or domesticated plant remains were earlier in one region than another showing a clear chronological pattern. But this is not the case and evidence for cultivation is actually later in this 'core region' than elsewhere in the Near East (see below). Abbo *et al.* (2010a) imply that evidence for 'trade', that is movement of rare materials, which certainly exists for the movement of obsidian, means that knowledge of cultivation could have also spread. Indeed this knowledge probably did. However, Abbo *et al.* (2010a) infer that there was 'trade' in seed corn. Cultivation, however, is unlike a traded commodity. Cultivation (including tending, harvesting, crop-processing, storage) is an integrated series of practices and knowledge which cannot be so easily passed along through brief encounters but is more likely learned through participation and experimentation. As such, casual contacts may have been insufficient on their own to inspire a rapid uptake of cultivation. In addition, 'trade' in crops across climatic boundaries, such as exist in the Near East, would probably be difficult. Wild cereals from Karçadag situated in the cool moist eastern Anatolian uplands would not be adapted to the hot dry lowlands of the southern Levant, for example, in the area around Jericho or Aswad. Thus early cultivators probably had no choice but to take into cultivation local wild progenitors that were well-adapted to local conditions. Only after a long period of slow adaptation would crops become successful in new climatic zones. Yet, as we shall see below, there is no evidence that there was long period of acclimatization through adaptive selection when domesticated crops gradually spread out from the 'core area' as would be expected from the core area hypothesis.

Evidence for early cultivation and domestication in Near Eastern crops

In studying the origins of agriculture, it is important to be clear about causes in human action and consequences in plant genomes. Terms such as agriculture, cultivation, and domestication should be carefully distinguished. The distinctions between these terms, which hinge on the issues of human behaviours, genetic change, and economic dependence have occupied scholars for many years (for overviews see Harris, 1989, 2007; Harlan, 1995; Fuller, 2007). For most archaeobotanists, a key distinction is between *cultivation*, which is something that people do (preparing the soil, planting plants, tending these plants, harvesting) and *domestication*, which is a property of the plant, i.e. the genetic and morphological changes which enhance its adaptation to cultivation. As has been recognized by botanists, there is a recurrent syndrome of traits that characterizes most domesticated grain crops, not just those

of the Near East, but globally (Harlan *et al.*, 1973; Hammer, 1984; Smith, 2006; Fuller, 2007). These traits include loss of wild-type seed dispersal (non-shattering), reduction of wild-type dispersal aids like awns and spines, reduction of germination inhibition, increasing seed size, and increasing apical dominance with reduced lateral branching or tillering. These domestication syndrome traits indicate that recurrent selection pressures were at work on cultivated plants (Purugganan and Fuller, 2009; Fuller and Allaby, 2009). Convergent evolution of crops is to be expected, making it all the more challenging to tease apart parallel trajectories from the same wild species. Agriculture, as suggested by Harris (1989), can be taken to be the resulting form of land-use that results from both of these changes. In other words, agriculture *is a change in the landscape and economy*, as people regularly cultivate, and focus more predominantly on cultivation (also see Smith, 2001); agriculture in this sense could equally precede morphological domestication as follow it. What these considerations highlight is that cultivation–domestication–agriculture, is not a single invention, but represents a spectrum of changes that could have, and usually did, evolve over an extended period. Archaeobotanical evidence provides a fossil record from which we can infer aspects of human behaviour, i.e. cultivation, independently of documenting the domestication traits that were consequences of cultivation.

Evidence for cultivation without morphological domestication traits has now been reported from ten archaeological sites dating from >10 000 BC up to *c.* 8500 BC (Table 2). Cultivation can be inferred from the assemblages of non-crop and non-food plants which represent the probable early weeds in arable fields. It has long been recognized by archaeobotanists working in later periods, in Europe, for example, that archaeobotanical evidence consists mainly of crop grains, crop-processing by-products like chaff and straw fragments and weeds seeds, which are also a by-product of crop-processing (Hillman, 1984; Jones, 1985) and, as a result, the weed assemblage provides evidence for past agricultural ecology. This should be equally true of early cultivators, in that weed seeds would be inadvertently harvested with crops and deposited as crop-processing residues. The study of non-crop wild seeds in order to identify a signature of early cultivation independent of morphological evidence of cultivation, and potentially of 'pre-domestication cultivation' has received increasing research in the past 15 years (Hillman *et al.*, 2001; Colledge, 1998, 2002; Willcox and Fornite, 1999; Willcox *et al.*, 2008). In order to control the possibility that wild seeds were collected as food in themselves, Willcox *et al.* (2008) proposed a minimal list of arable weeds (Willcox, 2011). These species have no documented ethnographic food uses, are often toxic, and are reported today primarily as obligate weeds. The inference is that these species were amongst the first to invade and adapt to early cultivated fields and would not have entered the archaeological deposits through other human gathering activities. Pre-domestication has also been inferred in cases where large quantities and stores of seeds

Table 2. Archaeological sites where pre-domestic cultivation has been proposed

Notes: PPNA, Pre-Pottery Neolithic A; EPPNB, Early Pre-Pottery Neolithic B. Natufian is the period that precedes the Pre-Pottery Neolithic A. Dates are in calendar years based on sum of the calibrated ages of radiocarbon dates from each site (Purugganan and Fuller, 2011; see Supplementary Table S1 at JXB online).

Site	Region	Period	References
Mureybet	Upper Euphrates plains, Syria	PPNA (9700–8500 BC)	Van Zeist and Bakker-Heeres, 1986
Çayönü	Upper Euphrates, South-east Turkey ('core area')	EPPNB (8600–8200 BC)	Van Zeist and de Roller, 1994
Netiv Hagdud	Southern Levant: Jordan valley	PPNA (9300–8850 BC)	Kislev, 1997
Abu Hureyra	Upper Euphrates plains, Syria	Late Natufian (11 150–10 450 BC)	Hillman <i>et al.</i> , 2001
'Iraq ed-Dubb	Southern Levant: Jordan valley	PPNA (9700–8800 BC)	Colledge, 2001
Jerf el Ahmar	Upper Euphrates plains, Syria	PPNA (9450–8500 BC)	Willcox <i>et al.</i> , 2008
Dja'de	Upper Euphrates plains, Syria	EPPNB (8700–8250 BC)	Willcox <i>et al.</i> , 2008
Tell Abr	Upper Euphrates plains, Syria	PPNA (9500–9200 BC)	Willcox <i>et al.</i> , 2008
Zahrat adh-Dhra	Southern Levant: Jordan valley	PPNA (9150–8850 BC)	Edwards <i>et al.</i> , 2004
Gilgal	Southern Levant: Jordan valley	PPNA (9400–9100 BC)	Weiss <i>et al.</i> , 2006
Dhra	Southern Levant: Jordan valley	PPNA (9650–9250 BC)	Kuijt and Finlayson, 2009

are available in the absence of morphological domestication indicators (Weiss *et al.*, 2006).

In recent years, with the accumulation of a larger body of archaeobotanical evidence, it has become possible to document morphological domestication traits in ancient populations, in particular, grain size and non-shattering. Such data are not available for all species. In the case of the chickpea, for example, early cultivation is inferred when this species appears outside its wild range, such as find at Tell el-Kerkh (Syria), *c.* 8400 BC, or at Beidha (Jordan), *c.* 7900 BC. Other domestication traits are not directly recoverable in archaeobotanical material. Nevertheless, if those traits are taken which can be found 'fossilized' in archaeological material, then changes over time can be documented and it can be observed that changes were most dramatic during the early millennia of cultivation. While evolution has been continuous, the evolution of domestication syndrome traits appears to have been intensive early on after the start of cultivation and not in more recent millennia. For example, no further change in ear shattering and no significant directional change in average grain size in wheat and barley has been seen for the past 8000 years. This points to a key domestication period before 8000 years ago in the Near East.

Starting with non-shattering, the evolution of domesticated cereals is documented directly on the rachis remains of barley and spikelet fork remains of einkorn or emmer wheat, which can be quantified to assess the proportion of wild-type shattering and domestic-type non-shattering plants in assemblages of particular sites and periods. It is

worth noting that it was in the late 1990s that several sites and several specialists made such data available over a larger time period in the Near East. It is only in the past few years that studies have used such evidence to examine the time gap between the beginnings of cultivation, and the initial appearance of non-shattering or semi-shattering cereal ears, and the establishment of domesticated populations marked by the predominance of domestic-type non-shattering cereals which, in genetic terms, represents the fixation of the non-shattering mutant (Tanno and Willcox, 2006a, 2011; Fuller, 2007). These data suggest that the increase in non-shattering was slow, taking something on the order of 3000 years (Fig. 2, upper left). It should be noted that this trend is seen in combined data both from the northern and Southern Levant and is not a process restricted to a single site or the sites in the proposed 'core area'. For example, barley rachis from the Southern Levant site of Zahrat adh-Dhra are too large a non-shattering minority (between 8% and 28%) to be attributed to wild gathering, and it is earlier than any evidence for a move away from pure wild types in the northern Levant and core area (Edwards *et al.*, 2004). Within the current resolution of the record it appears that more than one part of the Fertile Crescent was taking part in the protracted process of domestication. At Aswad in southern Syria, mixtures of wild and domesticated barley and emmer have been identified in early EPPNB levels dating to 8500 cal BC (Stordeur *et al.*, 2010) which is as early as identifications in or near the 'core area'. Similarly dated domestic einkorn was identified on the island of Cyprus (Peltenburg *et al.*, 2001). Further east at Ganj Dareh

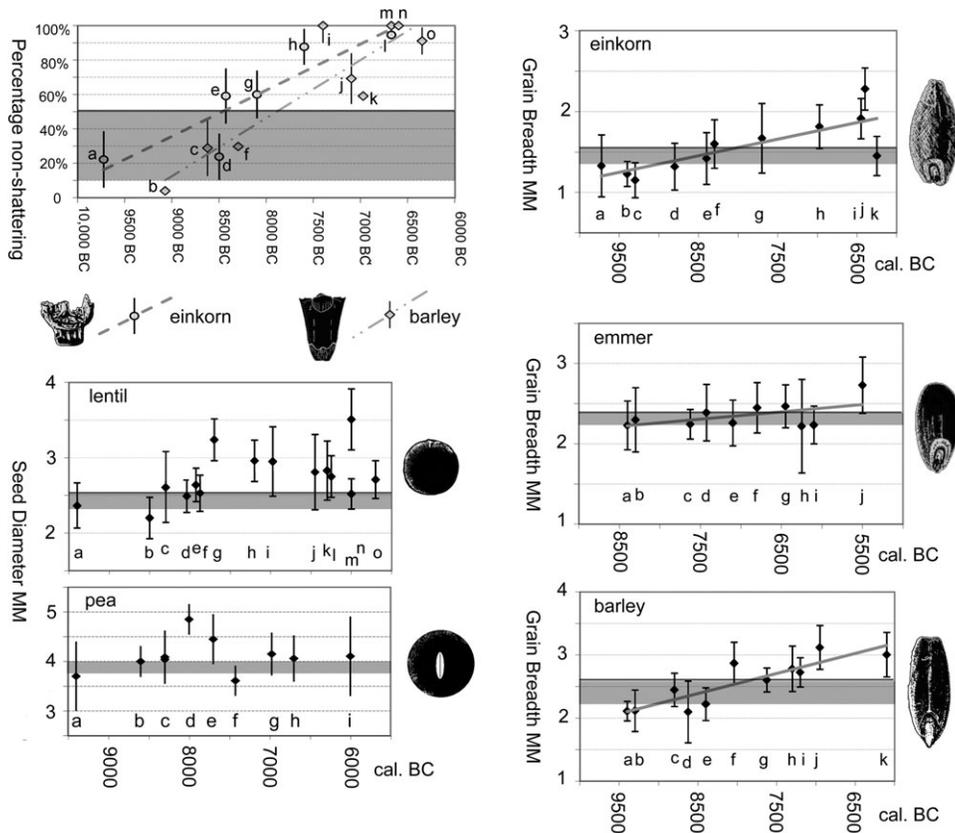


Fig. 2. Graphs showing the gradual evolution of morphological domestication traits based on archaeobotanical evidence, in which a semi-domesticated zone, of some change from the original wild form is shaded. Population averages falling above this grey area are taken to be domesticated (in this trait). Data includes non-shattering in einkorn wheat and barley (top left), in which the mean value represents the proportion of non-shattering (domesticated-type) types, calculated only for the sums of items that were positively identified, and error bars represent a standard deviation estimated from maxima and minima percentages that include indeterminate rachis based on an assumed normal distribution (StDev factors from Pearson and Hartley, 1976). Other graphs show an increase in seed size (breadth) based on measured populations from each site, mean and standard deviation estimates, for lentil, pea, einkorn (which may include some rye grains), emmer, and barley. Time is estimated as a modal/median age based on the summed probability of calibrated dates. Data are compiled in Purugganan and Fuller (2011; see Supplementary Table S1 at *JXB* online). Sites are indicated by lower case letters across the base of each chart. Non-shattering data: a. Tell Qaramel, b. Netiv Hagdud, c. ZAD-2, d. Nevalı Çori, e. Tell el-Kerkh, f. Aswad, g. Cafer Höyük (XIII-IX), h. Cafer Höyük (VIII-III), i. Abu HUeyra 2, j. Wadi Fidan A, k. Ramad, l. m. Çatal Höyük East, n. El Kowm II, o. Wadi Fidan C; Grain size: *Einkorn wheat*: a. Tell Qaramel, b. Mureybet I-III, c. Jerf el Ahmar (early), d. Jerf el Ahmar (late), e. Dja'de, f. Çayönü, g. Wadi Jilat 7, h. Tell Ramad, i. Höyücek, j. Erbaba, i. C. Andreas-Kastros. *Emmer wheat*: a. Dja'de, b. Çayönü, c. Tell Aswad West, d. Ghoraife, e. Tell Ramad I, f. Tell Ramad II, g. Erbaba, h. Höyücek, i. Yarim Tepe, j. Kosak Shamali. *Barley*: a. Mureybet, b. Jerf el Ahmar (early), c. Jerf el Ahmar (late), d. ZAD 2, e. Dja'de, f. Ganj Dareh, g. Tell Aswad West, h. Tell Ramad 1, i. Ras Shamra, j. Tell Bouqras, k. Yarim Tepe. *Lentil*: a. Mureybet I-III, b. Nevalı Çori, c. Tell Aswad, d. Ganj Dareh, e. Beidha, f. Yiftahel, g. Jericho (PPNB), h. Ras Shamra (PPNB), i. Tell Ramad 2, j. Erbaba, k. Ras Shamra (Pottery Neolithic), l. Höyücek, m. Jericho (PN), n. Tepe Sabz, o. Çayönü (PN). *Pea*: a. Mureybet, b. Jericho (early), c. çayönü, d. Aswad, e. Jericho (later), f. Ghoraife, g. Ramad I, h. Ramad II, i. Erbaba.

domestication has been identified at about 8250 cal BC (van Zeist *et al.*, 1986).

Similar data are now available for Chinese rice domestication as well (Fuller *et al.*, 2009, 2010a). Such data allow rates of morphological evolution to be calculated (e.g. in Darwin or Haldane units) and suggest that evolution of domestication traits was within the regular range encountered in microevolutionary studies of natural selection and in the fossil record (Purugganan and Fuller, 2011). If anything, it is slightly on the slower rather than faster side of evolutionary rates. This means that contrary to the

assumption that domestication should be fast (Hillman and Davies, 1990; Innan and Kim, 2004; Abbo *et al.*, 2010b; Haldersen *et al.*, 2011), the actual remains of the plants undergoing domestication indicate slow rates of change. This then represents a very significant contrast from evolution under directed plant-breeding and artificial selection documented in recent times.

While non-shattering is selected for by human harvesting practices, grain size is thought to evolve due to different pressures (Harlan *et al.*, 1973; Fuller, 2007; Fuller and Allaby, 2009; Fuller *et al.*, 2010a). Recent work has

identified important genes involved in increasing grain breadth in domesticated rice (Shomura *et al.*, 2008) and wheat (Gegas *et al.*, 2010). While a review of numerous studies suggests a strongly heritable element in grain size (Sadras, 2007). The archaeobotanical evidence provides an opportunity to document grain size changes over time and to assess these in relation to non-shattering and arable weed indicators of cultivation. Recent studies by us (Willcox, 2004; Fuller, 2007; Fuller and Allaby, 2009; Fuller *et al.*, 2010b; Purugganan and Fuller, 2011) indicate that some increases in grain breadth began prior to the development of non-shattering and that a trend towards increasing grain size continued for 3000–4000 years over the course of the Neolithic, and after the Neolithic grain sizes in general changed little. The extent to which earlier changes might have been, in part, a phenotypic response, the improved conditions of early fields, and the extent of selected genetic change, is unknown, but a gradual evolutionary process is apparent. Similar rates are found in crops from other regions such as rice, sunflower, mungbean, and pearl millet (Purugganan and Fuller, 2011).

Abbo *et al.* (2010a, b) presume that domestication traits would be obvious improvements consciously recognized and selected by early cultivators, but we would emphasize that such a view is an anachronism, from the point of view of modern farmers and plant breeders. Early foragers focused on increasing the populations of food plants and reducing competition, while yield factors like larger grains, apical dominance, and non-shattering are better understood as unintended consequences selected slowly by some early cultivation practices. Farmers who cultivate plants with vegetative reproduction, such as tubers or fruit trees produce cloned crops. They may consciously choose a variety or trait which will appear in the following generation. But this is not the case for annual grain crops such as the founder crops of the Near East. One reason is that domestic traits are not readily visible to the naked eye. During the early stages of domestication, given the high diversity of the cultivated wild populations, mutants with a tough rachis would not be easily recognized because harvests would occur before ears start to disperse. Indeed, even today, barley, emmer, and einkorn are remarkably similar to their wild forms by comparison with some other crops such as maize, sorghum, or pearl millet. A second reason is the technical problems of selecting. The only effective way to select consciously is to build up a single line population from a single seed. This would require keeping the descendants isolated from other plants, which would have been difficult. This single line population would have the disadvantage of reducing genetic diversity which was necessary to create healthy crops with stable year-to-year yields. As noted by Kislev (2002), grains from a truly monophyletic origin are unlikely to produce a viable landrace in barley and emmer because it would drastically reduce genetic diversity, resulting in a population more susceptible to natural catastrophes and with poor yield stability from year to year compared with wild populations with their high diversity.

The implications of protracted transitions are manifold. For one thing, it means that, over the course of a domestication process of 3000 years, social and environmental circumstances are likely to have changed (Fuller *et al.*, 2010b). Thus, whatever motivations might have been there at the beginning of domestication may no longer have played a role later in the process or at the end of the domestication process; selection pressures may have shifted. It also means that early cultivators with their morphologically wild plants or ‘semi-domesticates’ may have moved around, interacted, exchanged germplasm. In this context trying to posit a single core point of origin becomes problematic. Genetic patterns, driven by selection and bottlenecks, are likely to relate to ends rather than the beginnings of domestication episodes.

An archaeological test of the of the ‘core area’ hypothesis

Given the postulation of a ‘core area’, it is surprising that the archaeobotanical evidence was not examined for support. In this section, the state of the evidence will be reviewed briefly. The presence/absence of members of the ‘founder crops’, including some of the additional crops that were found on Near Eastern sites, have been tabulated and it is indicated where it can be determined whether morphological domestication traits are present at the site. Domesticated crops are taken to include cereals in which non-shattering rachises are in the majority, or where seed size (in cereals, pea, lentil) of the measured population is significantly larger than wild populations or measured populations at the earliest sites (especially early Mureybet which provides a baseline for archaeological wild-size legumes). Mixed wild/domestic ‘semi-domesticate’ status is given to assemblages in which non-shattering cereal rachises account for 10–50% (a minority, but more than can be expected in the wild for this deleterious mutation) or in which grain size shows some increase in average over the earliest assemblages but is not as large or significantly different as later assemblages. The cut-offs for these criteria are indicated in the graphs in Fig. 2. Because not all assemblages have been documented and published to the same detail, these criteria will tend to err on the side of assuming that early finds are morphologically wild, i.e. wild until proven domesticated.

On this basis, it is possible to count up both the number of founder crops that occur on sites in the core area versus other parts of the Fertile Crescent, and the number of these that are positively domesticated in morphological terms. In Early PPNB sites (between 8800 and 8200 BC) in the core area, for example, early levels at Cafer Höyük, Çayönü, Nevali Çori, a large number of the founder species do co-occur (from six to eight) as do all four of the ‘additional founder crops’, and thus sites in this region have the richest early cultivar assemblages. However, the few earlier sites with data do not indicate this region to be any richer in cultivar diversity than other parts of the Near East and early sites, such as Hallan Çemi and Demerkoy, have evidence for fewer wild progenitors than are found on

Table 3. Tally of crops/ potential cultivars

x=Present; no superscript means wild/ presumed wild; superscript d=domesticated, wd='semi-domesticated', some change from wild form but predominantly still wild morphology. Tally indicates numbers of potential crops present with confirmed domesticated crop counts in parentheses. Compiled based on primary sources (see Supplementary Table S1 at JXB online).

		Triticum monococcum 2-gr	Secale sp.	Triticum monococcum, 1-gr	Triticum dicoccum/ dicoccoides	Hordeum vulgare/ spontaneum	Linum usitatissimum	Lens culinaris/ orientalis	Pisum sativum	Cicer arietinum	Vicia ervilia	Vicia faba	tally
Southern Levant	cal. BCmode (range)												
Iraq ed-Dubb	9300 (9700-8800)	?		?	x?	x						x?	3
Gilgal I	9300 (9400-9100)				x?	x							2
Netiv Hagdud	9200 (9300-8850)				x	x		x			x		4
Zahrat adh-Dhra' 2	8800 (9150-8650)				x ^{wd}	x ^{wd}		x	?				3
Jericho I ('PPNA')	8700 (9150-8350)			x ^{wd}	x ^{wd}	x ^{wd}	x	x ^{wd}	x ^{wd}	?		x	6
Tell Aswad	8400 (8700-8200)				x ^{wd}	x ^{wd}		x ^D			x		4 (1)
Beidha	7900 (8300-7550)	x			x ^{wd}	x ^{wd}		x ^D		x ^D	x		5 (2)
Wadi Jilat 7	7800 (8200-7500)	x ^{wd}		x ^{wd}	x ^{wd}	x ^{wd}				?			4
Yiftahel	7800 (8200-7650)							x ^D				x	1 (1)
Jericho II ('PPNB')	7700 (8200-7500)			x ^D	x ^D	x ^D	x	x ^D	x ^D	?		x	7 (5)
Nahal Hemar	7700 (8000-7050)				x ^{wd}	x ^D							2 (1)
Ghoraife	7500 (7800-7050)			x ^D	x ^D	x ^D	x	x ^D	x ^D		x		7 (5)
Basta	7400 (7550-7050)	x ^D		x ^D	x ^D	x ^D		x ^D	x ^D		x		7 (6)
Ain Ghazal	7200 (8300-6600)				x ^D	x ^D	x	x ^D	x ^D	x ^D		x	7 (5)
Tell Ramad	7100 (7300-6650)	x?		x ^D	x ^D	x ^D	x	x ^D	x ^D	x ^D			8 (6)
Wadi Fidan A	7100 (7300-6750)	x ^D		?	x ^D	x ^D							3 (3)
Wadi Jilat 13	6700 (7050-6600)	x ^D		x ^D	x ^D	x ^{wd}							4 (3)
"Core Area"													
Hallan Çemi	9500 (9700-9300)	X				x		x	?		X		4

Table 3. Continued

		Triticum monococcum 2-gr	Secale sp.	Triticum monococcum, 1-gr	Triticum dicoccum/ dicoccoides	Hordeum vulgare/ spontaneum	Linum usitatissimum	Lens culinaris/ orientalis	Pisum sativum	Cicer arietinum	Vicia ervilia	Vicia faba	
Demirköy	9350 (9450-9300)				x	x		x					3
Göbekli Tepe	8800 (9200-8600)	x	?			x							2
Çayönü (RP,GP,Ch.H)	8300 (8700-8000)	x ^{wd}		x ^{wd}	x ^{wd}	x	x	x	x	x	x	x	10
Nevalı Çori	8300 (8600-7950)	x ^{wd}		x ^{wd}	x	x		x ^D	?		x	x	8 (1)
Cafer Höyük IX-XIII	8100 (8300-7800)	x	x ^D	x ^D	x ^D	x		x ^D	x		x	x	9 (4)
Cafer Höyük III-VIII	7600 (8300-7450)			x ^D	x ^D	x ^D		x ^D					4 (4)
Northern Levant/ Anatolia													
Abu Hureyra I	10,600(11,150-10,450)	x	x ^{wd}				x	x			x		5
Tell Qaramel	9700 (10,300-8850)			x	x	x		x			x		5
Mureybet I-III	9400 (9700-8500))	x	x			x	x	x			x		6
Tell 'Abr 3	9350 (9500-9200)	x	x			x		x					4
Jerf el Ahmar	9300 (9450-8700)	x ^{wd}	x	x		x ^{wd}		x			x		7
Dja'de	8500 (8700-8250)	x ^{wd}	x	x	x	x ^{wd}		x			x	x	9
Mureybet IV	8400 (8750-7950)	x ^D	x			x		x			?		5
Tell el-Kerkh	8400 (8550-8300)	?		x ^{wd?}	x	x		x	x ^D		x	x	7 (1)
Hacılar	7800 (8200-7550)			x ^D	x ^D	x ^D		x ^D					4 (4)
Tell Halula	7650 (7800-7300)	x			x ^D	x ^D		x ^D	x		x	x	6 (3)
Aşıklı Höyük	7600 (7800-7500)			x ^D	x ^D	x ^D		x	x ^D	?	x		6 (4)
Can Hasan III	7600 (7800-6500)		x ^D	x ^D	x ^D	x ^D		x ^D	x ^D		x		7 (5)
Abu Hureyra 2A-C	7400 (7800-7000)	x ^D	x ^D		x ^D	x ^D	x	x ^D	?	x ^D	?	x	8 (6)
Ras Shamra	7200 (7600-6000)	?		x ^D	x ^D	x ^D	x	x ^D	x ^D				6 (5)

Table 3. Continued

		Triticum monococcum 2-gr	Secale sp.	Triticum monococcum, 1-gr	Triticum dicoccum/ dicoccoides	Hordeum vulgare/ spontaneum	Linum usitatissimum	Lens culinaris/ orientalis	Pisum sativum	Cicer arietinum	Vicia ervilia	Vicia faba	
Tell Bouqras	7100 (7500-6300)			x ^D	x ^D	x ^D	x	x ^D	x ^D				6 (5)
Çatalhöyük East	6900 (7100-6400)	?		x ^D	x ^D	x ^D		x ^D	x ^D	x ^D	x		7 (6)
El Kowm II	6600 (7100-6350)	x ^D	x ^D		x ^D	x ^D					x		5 (4)
Eastern Fertile Crescent													
Qermez Dere	9200 (10,100-8800)					x		x			x		3
M'lefaat	9200 (9500-8800)	?		?		x		x			x		3
Nemrik	8400 (10,200-8200)							x	x				2
Ganj Dareh	8100 (8250-7850)					x ^D		x ^{wd}	x				3 (1)
Tepe Abdul Hosein	8000 (8300-7800)				x ^D	x ^D		x ^D					3 (3)
Jarmo	7700 (8000-7400)			x ^{wd}	x ^{wd}	x ^{wd}		x ^D	x ^D				5 (2)
Ali Kosh (B M ph.)	7300 (7650-6800)			x ^D	x ^{wd}	x ^D	x						4 (2)
Chogha Bonut	7250 (7600-6900)			x ^D	x ^D	x ^D		x ^D					4 (4)
Tell Maghzaliyeh	6700 (7100-6300)			x ^D	x ^D	x ^D	x	x ^D					5 (4)

equally early sites elsewhere in the Near East. Furthermore, the number of species that have domesticated morphology or even intermediate 'semi-domesticate' status are few, semi-domesticated einkorn and emmer at Çayönü, and semi-domesticated einkorn and domestic-size peas at Nevali Çori. By contrast, peas remain in the wild size range at Cafer Höyük, while lentils appear domesticated, as do cereals, based on rising frequencies (but not dominance) of non-shattering rachises. By contrast, at Mureybet IV, peas and lentils indeed appear enlarged. It is only later, mainly after 8000 BC when sites such as Abu Hureyra 2 and later Cafer Höyük, does one find consistently morphologically domesticated assemblages of founder crops. While these data do support the idea that the Near Eastern crop package came together as a whole in this region, it does not appear to be domesticated rapidly or simultaneously. It is also worth noting that *Cicer*, so important in determining the geography of the core area, features on very few of these sites (although this species is prone to preservation difficulties).

A comparison of evidence from sites in other parts of the Near East does not indicate that domesticates arrived any later or occurred in less of a package (Table 3). In the southern Levant, for example, at least six of the founder crops are reported as domesticated by the Mid-Late PPNB levels of Jericho, (Hopf, 1983) while all occur in earlier levels of the site in an unclear morphological state, and four of these are even earlier found morphologically wild at Netiv Hagdud (Kislev, 1997). The site of 'Zahrat adh-Dhra' (9150–8800 BC) provides evidence for cultivation associated with barley (and some fragmentary wheat), and the grain size data and barley rachises suggest selection for domestication traits was under way (Edwards *et al.*, 2004). Other sites in the Northern Levant, but outside the core area, have domesticates occurring in the mid Ninth Millennium BC, such as Tell el-Kerkh. In the Eastern Fertile crescent at Ganj Dareh, domesticated barley and semi-domesticated lentil is recorded as early as that from Nevali Çori in the core area. The 'fossil' record of archaeobotany as it stands points to equal antiquity of cultivation and early domesticates in more than one part of the Fertile Crescent, and that in the 'core area' even appears somewhat delayed. Early domesticates occur as one or two species alongside morphologically wild species and the combinations of species varied across sites. This points to a diffuse mosaic and not a single, rapid package of domestication. It could perhaps be suggested that the overall crop package is more diverse in this core region than elsewhere, based on the range of taxa at Çayönü, Nevali Çori, and Cafer Höyük. Perhaps this was the region where all of the crops were first combined, but this would appear to have happened before all were morphologically domesticated and after some domesticated forms had already appeared elsewhere.

Conclusion

In summary, eight reasons are listed why up-to-date evidence points to a protracted and geographically diffuse process of

plant domestication in the Near East. (i) Adherents of the 'core area' hypothesis ignore the evidence that pre-domestic cultivation during the PPNB was occurring over a wide area at sites south and possibly east of the 'core area' and these sites pre-date key sites in the core area such as Göbekli Tepe and Çayönü. (ii) They also ignore finds of mixed wild and domestic populations which occur simultaneously across most of the Fertile Crescent (within and far beyond the core area) demonstrating that the evolutionary process of domestication was occurring independently in different areas (e.g. see Asikli Höyük in Table 3). (iii) The 'core area' hypothesis suggests that crops were traded across climatic boundaries into areas where they would have been poorly adapted compared with local ecotypes. (iv) They do not consider that monophyletic rapid domestication would lead to a genetically weakened crop. (v) They ignore that several genetic studies point to crops having been domesticated more than once. (vi) At present, molecular studies which suggest south-east Turkey as the core area are limited to two species (one-grained einkorn and chickpea), and methods which have been questioned. Only two crops, chickpea and flax, lack evidence for more than one domestication event. (vii) Present-day chickpea distribution may be reduced, as suggested by chickpeas being found at early PPNB sites outside the core area (Tanno and Willcox, 2006b), and modern wild chickpeas may be a poor basis from which to map a 'core area'. (viii) Beyond the genetic evidence for more than one origin of current crops, archaeobotanical evidence indicates a number of lost crops, which were cultivated and even morphologically domesticated but are no longer extant in cultivation, and therefore modern germplasm sampling in itself underestimates the diversity of early cultivated lineages.

It is therefore concluded that the hypothesis of a single 'core area' for agricultural origins in the Near East (Levy-Yadun *et al.*, 2000; Kozłowski and Aurenche, 2005) has been tested and shown to not fit the data available at the time of writing. Instead, we are confronted by a mosaic of parallel evolution, both culturally and botanically. Beyond the Near East, the world as a whole is polycentric when it comes to agricultural origins, and whether we only except the nine or ten centres posited by Diamond (2002) or Zeder (2006), or accept that there could be as many as 20 or 24 (Purugganan and Fuller, 2009; Fuller, 2010), it seems clear that agriculture was not invented once and only once. A full review of these origins is beyond the scope the present comments, but it is worth noting that, in many instances, multiple domestications are indicated for some of the better documented species, for example, rice (Sweeney and McCouch, 2007; Fuller *et al.*, 2010a; He *et al.*, 2011), *Phaseolus vulgaris* (Koenig and Gepts, 1989). As with the Near Eastern crops, there remains some ground for debate over whether rice might have had a single origin (cf. Molina *et al.*, 2011), but a range of analyses based on numerous genetic markers and archaeological evidence tends to favour more than one origin of cultivation for the genetic diversity represented in rice (Fuller *et al.*, 2010a), and this has also been indicated to be the case across most of the Near Eastern crops.

It is hypothesized that the reasons domestication happened in parallel numerous times is that human groups drew upon a collective memory and deep cultural traditions of plant tending that developed in the later Palaeolithic/Pleistocene. There is no reason to doubt that all hunter-gatherers understood how plants reproduce and multiply, whether it be by seeds or tubers. Ethnographic evidence strongly indicates this, even in regions which never had prehistoric traditions of agriculture, such as Australia (Harris, 1977, 1989; Steensberg, 1986; Harlan, 1995). Such knowledge could be turned to cultivation when local ecological and social circumstances warranted, and the issue of most interest is what those circumstances were.

Judging by recent trends in the accumulation of more data, further research is likely to lead to increasingly rich evolutionary patterns of domestication, which provide important research opportunities for understanding the evolutionary outcomes of human cultivation activities and the generation and loss of genetic diversity in crops and their wild relatives.

Supplementary data

Supplementary data can be found at JXB online.

Supplementary Table S1. Archaeobotanical primary data sources, used for compiling Table 3 and Figs 1 and 2.

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