A critical review of the protracted domestication model for Near-Eastern founder crops: linear regression, long-distance gene flow, archaeological, and archaeobotanical evidence

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Received 28 February 2012; Revised 7 May 2012; Accepted 9 May 2012

Abstract

The recent review by Fuller et al. (2012a) in this journal is part of a series of papers maintaining that plant domestication in the Near East was a slow process lasting circa 4000 years and occurring independently in different locations across the Fertile Crescent. Their protracted domestication scenario is based entirely on linear regression derived from the percentage of domesticated plant remains at specific archaeological sites and the age of these sites themselves. This paper discusses why estimates like haldanes and darwins cannot be applied to the seven founder crops in the Near East (einkorn and emmer wheat, barley, peas, chickpeas, lentils, and bitter vetch). All of these crops are self-fertilizing plants and for this reason they do not fulfil the requirements for performing calculations of this kind. In addition, the percentage of domesticates at any site may be the result of factors other than those that affect the selection for domesticates growing in the surrounding area. These factors are unlikely to have been similar across prehistoric sites of habitation, societies, and millennia. The conclusion here is that single crop analyses are necessary rather than general reviews drawing on regression analyses based on erroneous assumptions. The fact that all seven of these founder crops are self-fertilizers should be incorporated into a comprehensive domestication scenario for the Near East, as self-fertilization naturally isolates domesticates from their wild progenitors.

Key words: Archaeobotany, barley, einkorn and emmer wheat, domestication, genetics, origin of agriculture.

Introduction

The recent review by Fuller et al. (2012a) is part of a series of papers by a group of authors (D.Q. Fuller, R.G. Allaby, and T.A. Brown in co-authorship with, for example, M.D. Purugganan and G. Willecox) maintaining that plant domestication in the Near East was a slow, protracted process lasting circa 4000 years and occurring independently in different locations across the Fertile Crescent. Fuller et al. (2012a) present arguments concerning a variety of crops, while referring to a broad spectrum of topics including the extinct ancestor of modern domesticated cattle, pigs, rice domestication in the Far East and pea in Ethiopia (no wild Pisum has ever been reported from Ethiopia) and also to the vegetative propagation of plants like tubers and fruit trees. These arguments are then combined to counter the core-area hypothesis of plant domestication in the Near East presented by Lev-Yadun et al. (2000) and to promote the protracted Neolithic crop domestication model. Incorporating these diverse arguments into a single review might appear impressive at first glance; however, upon critical review of the evidence and the specific arguments, an entirely different picture emerges.

The approach in the current paper counters the claim put forth by Fuller et al. (2012b) and Purugganan and Fuller (2011) that archaeobotanical evidence indicates that Near Eastern plant...
domestication evolved gradually and slowly (the protracted model). It should be noted here that Purugganan and Fuller (2011) were republished as an ‘original article’ by Fuller et al. (2012b) in Vegetation History and Archaeobotany with an almost identical data set, but the latter was converted into a ‘discussion’ (Fuller et al. 2012c). This current work will mostly refer to Purugganan and Fuller (2011), but the conclusions also apply to Fuller et al. (2012b). Also, the information in Fig. 2 of Fuller et al. (2012a) is derived from Purugganan and Fuller (2011) and Fuller et al. (2012b).

At the core of this paper’s argument is the fact that calculations using linear regression analyses rely on the percentages of wild plant remains at archaeological sites and the proposed age of those sites cannot be interpreted correctly with regard to population genetics and/or evolutionary developments, and thus cannot be used to produce estimates in haldanes and darwins. This is because the founder crops central to the dawn of food production in the Near East do not conform to the genetic criteria necessary for such calculations – all of them are self-fertilizing plants (Zohary and Hopf, 2000). The conclusion is that single crop analyses are required rather than general reviews developed using regression analyses, which are ultimately based on erroneous assumptions.

Can linear regression indicate a slow rate of domestication? What is assumed?

Purugganan and Fuller (2011) and Fuller et al. (2012b) draw upon linear regression derived from the percentage of domesticated plant remains at particular archaeological sites and the ages of the sites for a variety of crops. It should be noted that implicit to their approach using linear regression analyses is the assumption that once a domesticated crop population emerged (from a wild cereal as a starting point) at one archaeological village site, such as einkorn wheat at Qaramel in Syria, the respective domestication alleles were transferred to another village, for example to Nevali Çori in southeastern Turkey via natural gene flow within the wild populations and thereafter to Tell Ain el Kerkh in Syria and so forth. The authors also postulate that domestication traits like non-brittleness accumulated in the wild einkorn wheat populations throughout the whole species range, which they view as a metapopulation, namely ‘cereals in the Near East as a whole constitute an interacting meta-population’ (Fuller et al., 2012b). They argue, therefore, that the different Neolithic cereal populations at various sites throughout the geographic range of the Fertile Crescent and over the presumed 4000 years of the entire, protracted process (Purugganan and Fuller, 2011) were connected by natural gene flow. Finally, Purugganan and Fuller (2011) conclude that domestication ‘evolved’ at rates similar to those recorded for wild species and was thus completely ‘unconscious’ (sensu Heiser, 1988), i.e. not influenced by any intentional human selection for favourable phenotypes.

The reproductive biology of self-pollinating plants and its bearing on natural gene flow

Self-fertilization is the most extreme type of inbreeding. In self-fertilizing plants, heterozygosity is quickly reduced in just a few generations (Hedrick, 2011, Fig. 8.9; Halliburton, 2004, Fig. 8.7). Similar to the way that plant breeders recognize the distinction between self-pollinating and cross-pollinating species (Allard, 1960), such an approach should be applied to the discussion of the genetic structure of crops and their wild progenitors. The readers’ attention is called to the fact that Purugganan and Fuller (2011) apply their calculations to inbreeding plants, such as barley and einkorn and emmer wheat, but not to maize, which is the most important outcrossing cereal crop and therefore more applicable to their model. They mention several assumptions, but it is sufficient to discuss only two of them here. The erroneous nature of their model is exemplified by the following extracts: ‘an underlying assumption is that material from disparate sites is representative of species-wide evolutionary patterns and not local diversification. This is valid if there is sufficient gene flow between populations, so that selection for observed phenotypes is manifested across the species range (Allaby et al. 2008; Feldman and Kislev, 2007; Allaby, 2010); given that we use data geographically limited to the domestication center of origin, we feel this is a reasonable assumption’ (Purugganan and Fuller, 2011, p 174). In Fuller et al. (2012b), this assumption is given under conclusion in an almost identical way, but with a clear definition of the area: ‘i.e. the Fertile Crescent’.

What is the basis for their assumption? Feldman and Kislev (2007) review archaeological findings and interpret them according to their own view, i.e. that emmer domestication occurred independently at different sites. While Feldman and Kislev (2007) assume transfer of non-brittle genes into the wild via spontaneous hybridization, they provide no empirical or quantitative data concerning gene flow between populations. Feldman and Kislev (2007) also mention gene flow in connection with the work of Luo et al. (2007) on emmer wheat, but Luo et al. (2007) favour a monophyletic origin of domesticated emmer wheat in southeastern Turkey ‘followed by subsequent hybridization and introgression from wild to domesticated emmer in southern Levant’, an argument which does not agree with the one put forth by Feldman and Kislev (2007). Allaby et al. (2008) present a simulation of domestication based on the assumption of 100% outcrossing and largely criticize the results of other authors (e.g. Heun et al., 1997; Salamini et al., 2002) that were based on self-fertilizing plants. Allaby (2010) continues to pursue this line of reasoning, for example by arguing against Zohary and Hopf (2000) that ‘mutants such as the tough rachis mutant are rapidly removed’ with reference to cystic fibrosis in human populations (Allaby, 2010, p 940) and to Ross-Ibarra et al. (2009) discussing Zea. The simple fact that self-pollinating and cross-pollinating species have different population genetics, as outlined briefly by Honne and Heun (2009), is ignored. The argument of Honne and Heun (2009), which serves to challenge the simulations presented by Allaby et al. (2008), will not be repeated here; however, it is worthwhile to point out here that gene flow between populations of self-fertilizing species like barley and einkorn and emmer wheat is very limited and that the assumption mentioned above made by Purugganan and Fuller (2011) is therefore invalid. This is for the simple reason that pollen dispersal in cereals is more common than seed dispersal. Self-pollinating species like barley produce considerably less air-borne pollen compared to outcrossing species like maize. Fertilization in such inbreeders...
Outcrossing rate, pollen and seed dispersal, and gene flow in barley

Gene flow in annual plants with no vegetative reproduction – the case for all seven of the Neolithic founder crops discussed here – occurs via the movement of gametes or zygotes from one population to another and must be followed by subsequent cross-pollination to genetically impact the recipient population (Halliburton, 2004, p 331). Hedrick (2011, p 366) also clarifies that the term gene flow indicates ‘movement between groups that results in genetic exchange’ and that this term should be distinguished from migration and dispersal. Simply multiplying a longer-distance barley pollen migration of some 10 m per year (generation) – an extremely rare occurrence (as will be discussed) – by the proposed 4000 years in order to argue for rapid long-distance gene flow over hundreds of kilometres is misleading. It should also be noted here that, in strict inbreeders, occasional events of gene flow are typically followed by many generations of selfing.

The reproductive biology of wild and domesticated barley, which are both self-fertilizing, has been studied in depth. The general conclusions about barley also hold true for einkorn and emmer wheat. Abdel-Ghani et al. (2004) report a mean outcrossing rate of 0.34% in both traditional landraces and wild barley from Jordan. Given the frequency of drought and heat stress in this environment, the authors conclude that ‘heterozygosity has not been a major force in the course of evolution and domestication of barley’. Cleistogamy (self-pollination in a closed flower) is understood as a way to guarantee fertilization even in drought-stunted plants. When barley genotypes with enhanced anther extrusion were studied, no significant change in the outcrossing rate was observed (Parzies et al., 2008). Artificial selection repeated over many generations was applied to increase outcrossing in barley, and yet the resulting outcrossing rate only changed from 1.4 to 2.8% (Nandety 2010). ‘Gene flow was also detected from transgenic barley at a frequency of 0.005%, over normal levels of 0.0003% (Hermanns et al., 2010), who conclude that isolation at a sufficient distance would result in no hybridization and specify distance in their discussion as follows: ‘A common finding is that the rate of gene flow decreases rapidly at distances beyond a few metres ... although cross-fertilization in barley has been recorded at a distance of 50 metres with similar distances being reported for wild barley’. The infrequent outcrossing in barley occurs mostly between neighbouring plants, with 60 m being a notable exception (Wagner and Allard, 1991). Volis et al. (2010) show in wild barley that the majority of seed dispersal transpired within 1.2 m of the mother plant and that pollen flow was spatially limited to a similar extent. They both tended to be overestimated when measured at spatial scales exceeding that of fine-scale spatial genetic structure. Volis et al. (2010) conclude that, among other things, the combination of selfing, occasional outcrossing, and very limited seed dispersal creates a very fine spatial genetic structure in natural wild barley stands. Hübner et al. (2012) report a higher level of recent introgression from domesticated barley (12 out of 215) into wild barley and identify a wild contaminant among the cultivars maintained by the Israeli gene bank collection. Hübner et al. (2012) use the program MIGRATE to estimate historical gene flow, a program which builds on the Wright-Fisher model (Beerli and Felsenstein, 1999, 2001) assuming random mating; but for self-fertilizing species, parameter changes need to be made (Nordborg, 2000). Hübner et al. (2012), like Morrell et al. (2003), argue for long-distance seed distribution and assume, for example, that a northern ecotype was carried by humans or animals and established itself in unpopulated regions (which is not gene flow, but dispersal, as already discussed). Russell et al. (2011), who base their study on more than 1000 single nucleotide polymorphisms in 448 barley landraces and wild accessions from Jordan and Syria, show a ‘limited degree of secondary contact’ for only eight accessions. The latter two articles might indicate that recent sampling of wild populations are likely to have been affected by habitat destruction and seed dispersal, especially within the past 50 years, making the assumption that today’s wild cereal distribution is equivalent to that of the last 10,000 years less probable. Thus, older collections distinguishing between primary and segetal collection sites (Harlan and Zohary, 1966) are enormously important.

These examples pertaining to barley are more than enough to conclude that outcrossing in strict self-fertilizing species is possible, yet seldom and spatially limited; hence gene flow between populations is slow and rare. Even if a few authors determine that they have observed higher outcrossing rates, the statement of Purugganan and Fuller (2011) ‘given that we use data geographically limited to the domestication center of origin, we feel this is a reasonable assumption’ is simply improbable. One needs to keep in mind that the occurrence of wild barley throughout the Fertile Crescent covers an area from the southern Levant, through Syria and the Taurus-Zagros mountains, about 2000 km from D’hra in Jordan to Ali Kosh in Iran (measured along the Fertile Crescent arc, Fuller et al., 2012a, Fig. 1). The area in which wild einkorn and emmer wheat occur is smaller (‘Taurus-Zagros arc, this time with Palestine omitted’ in the words of Harlan and Zohary, 1966) but of significant size when compared to rare allele advances on the order of metres per year. Fuller et al. (2012b) even extend the area of distribution for wild einkorn into central Turkey – referred to as the ‘range of wild cereals’ in Fuller et al. (2012a, Fig. 1) but specified as ‘Wild einkorn (mainly one-grained)’ in Fuller (2007, Fig. 2) – ignoring the distinction that Harlan and Zohary (1966, Fig. 3) make between largely primary habitats and habitats that are definitely segetal. This approach is very useful for separating wild, weedy, and feral forms. This excellent publication by Harlan and Zohary (1966) properly defines the natural distribution of wild wheats and barley and seems to have been forgotten. A similar extension of the natural distribution has been done for barley: Morrell and Clegg (2011) write about a natural barley distribution running east to west approximately 3500 km, and by this they mean the Fertile Crescent plus the area across the Zagros Mountains into southwest Asia (which Fuller et al., 2012b do not include) although Harlan and Zohary (1966, Fig. 1) distinguish between massive wild barley stands in fairly primary habitats (the Fertile
Crescent) and barley on disturbed habitats starting in Libya (not considered by Morrell and Clegg, 2011) towards Afghanistan and beyond. The current paper refers to the primary habitats of wild barley and wheat as defined by Harlan and Zohary (1966, see also Haldorsen et al., 2011). Even over a very long time, these infrequent einkorn outcrossing events would not have advanced from Cafer Höyük to Catalhöyük, for example, because these two sites are separated by approximately 1000 years (Purugganan and Fuller, 2011, supporting information) and about 500 km (Fuller et al., 2012a, map; see also below for more details and Fig. 1 and 2). In short, the purported extreme long-distance gene flow (Purugganan and Fuller, 2011) between distant allopatric populations is not supported by the evidence.

**Spread of non-brittleness**

A second statement made by Fuller et al. (2012a, p 620) is also problematic: ‘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 inconsistencies in the argument put forth by Allaby (2010) have been already mentioned. Ross-Ibarra et al. (2009), on which Allaby (2010) is based, in fact write about Zea and make reference to outcrossing plants. Here again, not only do Purugganan and Fuller (2011) not address the distinction between inbreeding versus outbreeding but maintain that a domestication trait like non-brittleness can be transferred quickly over hundreds of kilometres via wild population bridges. While this might be true for outcrossing species, since the Hardy-Weinberg equilibrium would allow such recessive domestication alleles to escape natural selection (i.e. the recessive alleles survive in the heterozygotes), self-fertilizing species would separate very quickly into brittle and non-brittle homozygote lines (shown in general terms in Hedrick, 2011, Fig. 8.9). Given the fact that brittleness is an essential survival mechanism in the wild, non-brittle barley, einkorn and emmer wheat would have been replaced by their wild neighbours very quickly while ‘traveling’ from one ‘domestication’ site to another distant Neolithic village. Indeed, Purugganan and Fuller (2011, p 172) accept that the fixation of non-brittleness ‘reduces the ability for natural seed dispersal and is thus deleterious in wild populations and makes the cultivated species dependent on human intervention for continued reproduction’, and yet they overlook the fact
that self-fertilization leads to homozygotes in wild barley and wheat (and thereby fixation) within a few generations. It is upon those homozygotes that natural selection acts.

**Long-distance spreading**

For einkorn, Purugganan and Fuller (2011, Fig. 2b and supporting information for site names) connect the percentages of non-brittle rachis types (i.e. domesticated plants) at Qaramel in Syria, Nevali Çori in SE Turkey, Tell el Kerkh in Syria and Cafer Höyük (IX–XII) and (III–VIII) in southeast Turkey as well as Çatalhöyük in Central Turkey (Fig. 2) giving an purported gene flow of roughly 1300 km. For barley the purported gene flow (Fig. 1) is roughly 3700 km. As discussed above, crossing the distances between these sites by natural gene flow within the specified time frame is unrealistic for selfers. Are there other mechanisms for spreading these plants? Morrell et al. (2003) speculate that hunter-gatherers may have facilitated long-distance dispersal of wild barley, but they also suggest that wild barley seed might have been spread in the fur of animals. As already mentioned, dispersing seed into unpopulated regions can lead to weedy stands of such plants, but these phenomena shall not become confused here with gene flow, which Purugganan and Fuller (2011) focus on. Therefore, given that these migrants would also have to impact the recipient population by outcrossing to result in gene flow (Halliburton, 2004, p 331; Hedrick 2011, p 366), seed dispersal involving animals seems to be too sporadic to have played much of a role. The current paper would prefer to focus more closely on seed dispersal involving humans and would not rule out the possibility that grains were systematically traded. Indeed, Fuller et al. (2010, p 23) proposed that domesticated forms, which evolved in certain regions, were transferred to other regions through grain exchanges. Interestingly however, Fuller et al. (2012a, p 622) stress the independence of the supposed multiple domestication centres across the Near East and do not accept that human ‘trade’ of seed grain had a role in the spread of the domesticated genotypes. Nevertheless, Fuller et al. (2012a, p 625) portrays this differently again. Here the authors draw on the behaviour of early cultivators much later in time, as they exchanged wild or semi-domesticated species. Practically isolated by very slow natural gene flow (as already shown) and culturally independent (if one accepts the claims of Fuller et al., 2012a), the Neolithic sites under discussion and their nascent crop populations as described by the ‘percentage of domesticated remains’ cannot be seen as a unified evolutionary entity showing a clear trajectory as presented by Tanno and
Willcox (2006) and adopted by Fuller (2007), Purugganan and Fuller (2011), and Fuller et al. (2012b). It is also interesting that Tanno and Willcox (2012), in sharp contrast to their 2006 publication, now show a zigzag curve for domesticated barley (Tanno and Willcox, 2012, Fig. 5) and an up/down curve for wheat (Tanno and Willcox, 2012, Fig. 4), both of which certainly are not neither linear nor in agreement with what Purugganan and Fuller (2011) have suggested. In addition, it should be noted that at a single major Neolithic site (Çayönü, which is ignored by Purugganan and Fuller, 2011 for wheat brittleness), non-brittle emmer (and einkorn) are recorded by van Zeist and de Roller (1994) at the advent of settlement there. At the very beginning, the size of the grain at Çayönü did not correspond exactly to the range for domesticated grain, but it also increased over time (van Zeist and de Roller, 1994). In fact, this trait is still the focus of selection by modern plant breeders and no one would refer to modern plant cultivars as ‘semi-domesticated’, because of the ongoing breeding efforts to improve this trait. Brittleness of the rachis is the first obvious phenotypic, archaeologically relevant descriptor of Neolithic Near Eastern cereals, and thereafter the early farmers kept improving their crops both genetically for a variety of other traits and through better agricultural practices.

Percentages of domesticates in particular archaeological sites

While Tanno and Willcox (2006), Fuller (2007), and Purugganan and Fuller (2011) consider the proportions of wild versus domesticated remains in the archaeobotanical assemblages from several selected Neolithic sites as representing the genotypic composition of the crop populations in Neolithic fields, Haldorsen et al. (2011) point out several inherent problems with this assumption. Three anthropogenic factors, namely continued gathering from wild cereal stands, weedy cereal types in the cultivated fields, and imperfect seed cleaning procedures, are proposed by Haldorsen et al. (2011) as possible reasons for the persistence of morphologically wild cereals alongside domesticated forms in the relevant Near Eastern sites.

It should be stressed that very little is known about the nature of cultivated fields in the early parts of the Neolithic period or, for that matter, about threshing areas. To begin with, where were the fields? Did the farmers use the same plots repeatedly or did they rotate the fields every year or after several years? Did they weed their plots manually, and if so, did they do it on a regular basis? Did they use the harvested fields as grazing plots for their livestock once animals became part of the system? Were the fields sown with a single crop or mixtures of crops? After all, the archaeobotanical assemblages used in the regression analysis by Purugganan and Fuller (2011) were not obtained directly from the excavation of Neolithic einkorn, barley, or emmer fields. Purugganan and Fuller (2011) use, as is always the case, archaeobotanical samples extracted from the archaeological strata of certain sites (most likely in occupational contexts), which they assume to be representative of plant domestication. Of course, there is variability in the scale of excavation and the reliability of the archaeological contexts, which yielded the archaeobotanical assemblages. The site formation processes (including the deposition of the archaeobotanical record) at Neolithic sites as well as postdepositional processes (disturbances, erosion, and preservation rate) are both site specific and context specific. It is likely that most are not only highly complex but in some cases cannot be fully reconstructed. The archaeobotanical assemblages studied from the different sites may thus represent a complicated array of sources, prone to ‘contamination’ by various elements vis-à-vis plant domestication. Here, the above distinction between the as-yet unknown Neolithic fields and the excavated sites is considered as more than enough to cast doubt on the use of the ratio between wild and domesticated remains as a demographic descriptor of Neolithic crops. However, further elaboration and several points pertaining to assumptions made by Purugganan and Fuller (2011) are required.

Wild einkorn and wild rye are not only genuine elements of the southeastern Turkish flora but are also commonly considered weeds in cultivated fields across Turkey to this very day. Similarly, wild barley invades cereal fields across the southern Levant (e.g. Abbo et al., 2005). The persistence of these weedy forms of einkorn, rye, and barley on arable land across the Near East long after the introduction of herbicides, modern seed sanitation, and modern agricultural procedures leaves little doubt that these wild forms were also an integral part of the early Neolithic environment. As such, it was probably inevitable that these wild types would have been harvested along with the domesticated crops and hence taken to the threshing grounds, where they would eventually end up at the subsequently excavated site. In addition, Nadel et al. (2004) document the use of Puccinellia convoluta straw for bedding at Ohalo II, while Weiss et al. (2004) suggest the use of this species at the same site as a staple grain. Is it possible that wild cereals had this kind of dual use at sites discussed by Purugganan and Fuller (2011)? Indeed, for Catalhöyük, phytoliths (siliceous plant remains) indicate that wheat and other wild plants were used for basket making (Ryan, 2011). Abbo et al. (2008) document the occurrence of both target and non-target plant species in experimental gathering of wild legumes. Cleaning the target grains and discarding the non-target ones significantly increases the likelihood of the preservation of non-target grains in the archaeobotanical strata at the expense of the target grains, the majority of which would have been consumed as food (Abbo et al., 2008). Is it possible that a similar mechanism artificially inflated the fraction of the morphologically wild cereals at certain sites?

Speculating about introgression between the surrounding wild populations and early crops could be continued, for example using spikelet material gathered from the ground, as suggested by Kislev et al. (2004). There are other possible factors that may have affected the ratios of wild and domesticated archaeobotanical remains at the sites discussed by Purugganan and Fuller (2011). Therefore, this current work can only remind the researcher who sees a systematic relationship between the demographic composition of the cultivated Neolithic fields and the archaeobotanical record at any archaeological site that this is a problematic supposition at the very least. Moreover, one cannot assume that similar factors have exercised an influence equally across the various sites referenced by Purugganan and Fuller (2011) within the relevant time period. Therefore, using such
calculated ratios of the archaeobotanical samples as the basis for a quantitative argument is not reliable.

Furthermore, inaccuracies are present in the calculations made by Purugganan and Fuller (2011) and Fuller (2007). Tanno and Wilcox (2006, supporting online material) distinguish between upper and lower spikelet fragments and report the following for einkorn wheat at Nevali Çori: 64 wild, 38 potentially domesticated, and three domesticated for the upper spikelet; and 179 wild, 35 potentially domesticated, and 36 domesticated on the lower spikelet. Purugganan and Fuller (2011, supplementary material) use these data and merge the wild (64 + 179 = 243) and the potentially domesticated (38 + 35 = 73), but do not include the 36 domesticated samples from the lower rachis portion and only mention the three domesticated samples from the upper portion. So, Purugganan and Fuller (2011, supplementary data) provide the following for Nevali Çori: 243 shattering, 73 probably non-shattering, and three non-shattering with a total of 319 (also see Fuller, 2007, Fig. 5B and note the total of 319 for Nevali Çori). Their calculations for the domesticated samples, including possibly domesticated ones, come to 23.824 %, and yet they should be 31.549 % (243, 73, and 39, respectively, giving a total of 355). This would appear to be a minor mistake, but given that Purugganan and Fuller (2011) argue that it was 4000 years before full non-brittleness is fixed, this difference translates into a few centuries.

Conclusions

While commenting on Tanno and Willcox (2006) in a previous paper, Lev-Yadun et al. (2006) note that the sites used as a reference in their model are spread over a time period of some 4000 years from the early Pre-Pottery Neolithic to the Pottery Neolithic, and this is also the case presented by Purugganan and Fuller (2011) and Fuller et al. (2012a, b). Although not explicitly stated, attempting to incorporate such chronologically isolated sets of data can be understood as a way to ‘read backwards’ in time from later periods to earlier ones. However, the late archaeobotanical samples originated from sites where very distinct, complex (almost historical) societies had developed. They would have been fully immersed in an agricultural way of life with a far more complex economy than was the case with the older samples. It is this decontextualization that may cause one to be left with an erroneous impression that it is possible to represent change over time in this case by a continuous (linear) progression. Archaeobotanical assemblages from these much later sites do not necessarily – or perhaps not at all – translate into a justification or support for an argument made for earlier data sets pertaining to domestication. Such late archaeobotanical assemblages/samples only show that, as time passed, domesticated plants were successful enough to become established in the economic systems of the time. Since Near Eastern plant domestication is being discussed here, rather than crop evolution, this represents a major oversight on the part of Purugganan and Fuller (2011). A much more contextual account related solely to plant domestication in a strict sense is required (e.g. Abbo et al., 2012). Proper plant reproductive biology needs to be considered for each case as well, when attempting to bring together the disciplines of archaeology, social anthropology, vegetation history, and genetics to create a scenario for the domestication of individual crop species (Haldorsen et al., 2011). However, due to the interdisciplinary nature of this topic, it must also be approached with the greatest care. Kilian et al. (2007, p 2665) suggest a ‘dispersed-specific’ model of einkorn domestication, because, for example, ‘multiple (Gebel 2004) appearance of domesticate phenotypes’ was demonstrated (in their view). Heun et al. (2008) indicate that Gebel (2004) does not present any original genetic data and therefore this publication cannot be used to argue in favour of a new genetic domestication model. Similarly, the recent review of Özkan et al. (2011), which also suggests this model for emmer wheat with reference to Gebel (2004), must be read carefully. The current paper is in complete agreement with Gebel (2004) when he states: ‘the interdisciplinary competence and readiness of Neolithic research ... needs much to be improved’. Therefore, this critical review of the ‘archaeological evidence’ for a protracted domestication model should be seen as a contribution to a wider discussion that includes other crops as well. The fact that seven of the Near East founder crops of the Neolithic revolution are self-fertilizers should be incorporated into the bigger picture of plant domestication scenarios for this region, since self-fertilization naturally isolates domesticates from their wild progenitors, maintains genetic structure within the population, and favours rapid domestication (Zohary and Hopf, 2000).

Acknowledgements

The authors would like to thank Prof. Bjørn Ivar Honne, Stjørdal, Norway, for constructive comments and suggestions. The English text was proofread for language errors by Christopher and Nancy McGreger Freising, Germany. Thanks to Jens Thaulow, UMB, Norway, for preparing figure 1 and 2. The authors assume responsibility for any errors in the text.

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Near Eastern founder crops


