

Agricultural Origins: Centers and Noncenters; A Near Eastern Reappraisal

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Table of Contents

I. INTRODUCTION	317
II. THE HISTORY OF THE HYPOTHESES	319
III. GENETIC AND CULTURAL EVENTS	319
IV. WAS NEAR EASTERN PLANT DOMESTICATION A “CENTRIC” OR A “NONCENTRIC” PHENOMENON?	322
A. The Population Genetic Perspective	322
B. The Geographic, and Therefore, Eco-Geographic Context	324
C. Biogeographical and Agro-Economic Considerations	324
V. DISCUSSION	325
VI. CONCLUDING REMARKS	325
ACKNOWLEDGEMENT	326
REFERENCES	326

Understanding the evolutionary history of crop plants is fundamental to our understanding of their respective adaptation profiles, which in turn, is a key element in securing future yield and quality improvement. Central topics in this field concern the mono- or polyphyletic origin of crop plants, and our ability to identify the geographic location where certain crop plants have originated. Understanding the geographical pattern of domestication may also assist in reconstructing the cultural processes underlying the Neolithic (agricultural) Revolution. Here we review prevailing views on the geographic pattern of Near Eastern plant domestication, and highlight the distinction between genetic domestication events and independent cultural events. A critical evaluation of the

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wealth of newly published geobotanical, genetic, and archaeological data provides strong support in favor of a specific core area in southeastern Turkey where most, if not all, founder Near Eastern crops were likely domesticated.

Keywords plant domestication, Neolithic Revolution

I. INTRODUCTION

The importance of identifying the geographic origin of crop plants goes far beyond satisfying mere academic curiosity. Unlike the wealth of information on the genetic basis of the domestication syndrome traits (Hammer, 1984), relatively little is known on the genetic basis of crop adaptation traits (Ross-Ibarra *et al.*, 2007). Since geography and associated ecological clines are well reflected in the adaptation profiles of domesticated

TABLE 1
The “founder crops” of the Near Eastern agriculture, after Zohary and Hopf (2000).

Common name	Scientific name	Wild progenitor
Einkorn wheat	<i>Triticum monococcum</i> L.	<i>T. monococcum</i> ssp. <i>boeoticum</i> (Boiss.) A. et D. Löve.
Emmer wheat	<i>Triticum turgidum</i> ssp. <i>dicoccum</i> (Schrank) Thell.	<i>T. turgidum</i> ssp. <i>dicoccoides</i> (Körn.) Thell.
Common barley	<i>Hordeum vulgare</i> L.	<i>H. spontaneum</i> C. Koch
Pea	<i>Pisum sativum</i> L.	<i>P. humile</i> Boiss. et Noë
Lentil	<i>Lens culinaris</i> Medikus	<i>L. orientalis</i> (Boiss.) Handel-Mazzeti
Chickpea	<i>Cicer arietinum</i> L.	<i>C. reticulatum</i> Ladiz.
Bitter vetch	<i>Vicia ervilia</i> (L.) Willd.	<i>V. ervilia</i> (L.) Willd.
Flax	<i>Linum usitatissimum</i> L.	<i>L. usitatissimum</i> ssp. <i>biene</i> Mill.

plants (e.g., Jones *et al.*, 2008) as well as their wild progenitors (Peleg *et al.*, 2008), understanding the geographical context of plant domestication may be valuable for inferring how crop diversity was molded under domestication (Ladizinsky, 1998a). Crop evolution under domestication and the diversity patterns of their progenitors are highly relevant for improving crop adaptation and overcoming yield-limiting factors (Evans, 1993). Such information may help crop breeders to break the ‘yield ceiling’ and with efficient utilization of crop wild relatives germplasm to address the challenges of global climate change. At the same time, understanding the geographical pattern of domestication and especially identifying the core area of crop plants may also assist in reconstructing the cultural processes underlying the Neolithic (agricultural) Revolution (Childe, 1951; Braidwood, 1967; 1975).

Near Eastern agriculture is thought to have started with a group of seven cereal and pulse grain-crops that includes diploid

einkorn wheat (*Triticum monococcum* L.), tetraploid emmer wheat (*T. turgidum* L.), barley (*Hordeum vulgare* L.), lentil (*Lens culinaris* Medikus), pea (*Pisum sativum* L.), chickpea (*Cicer arietinum* L.), and bitter vetch (*Vicia ervilia* (L.) Willd.) (Table 1; Zohary and Hopf, 2000). Flax (*Linum usitatissimum* L.) is considered the first fiber crop of the ancient Near East. The wild progenitors of these crops have been identified based on morphological similarity (botanical criteria) and cytological affinity (genetic criteria) (Zohary and Hopf, 2000). Recently, DNA marker technology has been used to determine the geographic origin of the domesticated stocks (e.g., Heun *et al.*, 1997; Ladizinsky, 1999; Özkan *et al.*, 2002; van Oss *et al.*, 1997; Luo *et al.*, 2007). The Near Eastern ‘Fertile Crescent,’ with its oak-pistachio woodland belt extending from present day Israel, Jordan, Lebanon, into Syria, Turkey, northern Iraq and western Iran, is considered the homeland of the Near Eastern agriculture (Harlan and Zohary, 1966; Zohary and Hopf, 2000; Fig. 1). As

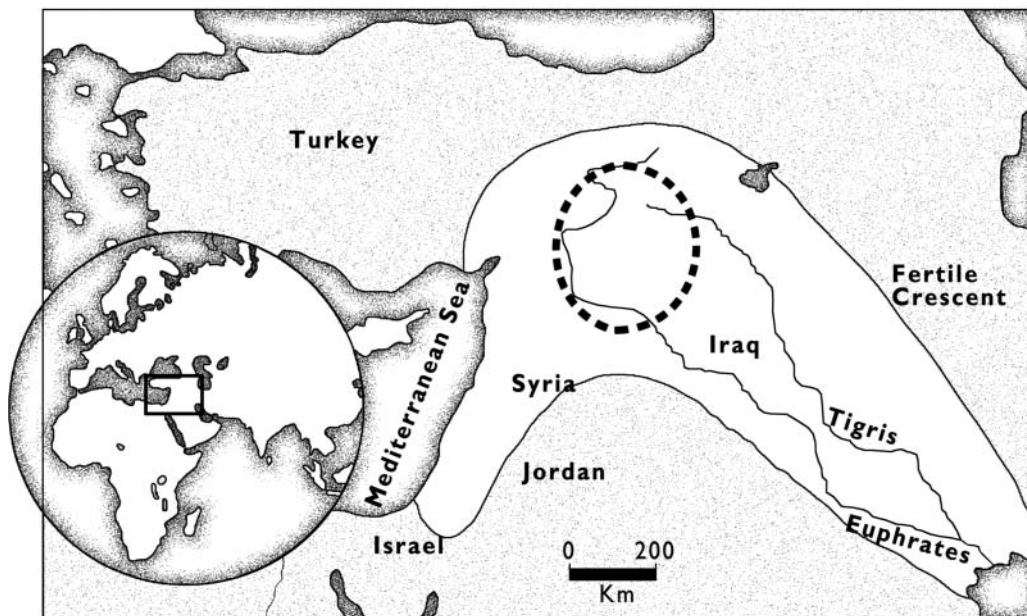


FIG. 1. A map of the east Mediterranean depicting the Fertile Crescent and the presumed core area of Near Eastern plant domestication (*sensu* Lev-Yadun *et al.* 2000) in present-day southeastern Turkey / northern Syria.

the cradle of the ancient Near Eastern civilizations, this region has been extensively studied by archaeologists for more than a century (e.g., Braidwood, 1975; Mellaart, 1975; Redman, 1978; Cauvin, 2000; Simmons, 2007). This long tradition of intensive botanical and archaeobotanical studies across the region makes the modern Near East a natural laboratory for studying the evolutionary, genetic, and agronomic basis of plant domestication (e.g., Ladizinsky, 1998a; Abbo *et al.*, 2005; 2010) as well as the cultural and historical processes captured by the archaeological record (e.g., Bar-Yosef, 2002; Kuijt and Goring-Morris, 2002; Özdoan, 1999; 2002).

This paper deals with the controversy over the geographic origins of Near Eastern founder crops domestication, which is framed in the context of Harlan's (1971) classical paradigm of centers and non-centers. Two alternatives will be evaluated;

Center – The Near Eastern founder crops arose in a distinct “core area” *sensu* Lev-Yadun *et al.* (2000).

NonCenter – Near Eastern plant domestication occurred through a geographically diffused phenomenon in form of “multiple events, multiple centres” *sensu* Willcox (2005).

In this paper we will consider these two geographically based propositions in a cultural context, in the hope of shedding some light on the nature of Near Eastern plant domestication. Our discussion may also have bearing on processes that occurred in other regions of the world where local cultures have adopted a settled agrarian lifestyle.

II. THE HISTORY OF THE HYPOTHESES

The concept of geographical centers of plant domestication is mainly attributed to the pioneering work of the Russian geneticist Vavilov (1951) who conducted plant collection expeditions across five continents between the 1916 and 1940 (Vavilov, 1997). Observing and documenting the geographical pattern of genetic diversity among crop plants around the world, Vavilov (1951, p. 20) proposed “*eight independent centers of origin of the world's most important cultivated plants.*” He defined each of these centers as having the maximal genetic diversity for their respective crop complexes (Vavilov, 1951).

Prior to Vavilov, the Swiss botanist de Candolle (1885) devised a methodology for inferring the possible geographic origins of crop plants from studies of botanical, archaeological, palaeontological, historical, and philological data. He noted an “unequal” geographic distribution of crop origins (de Candolle, 1885; p. 449) with some regions having contributed few crop plants whereas others such as western Asia, China, and India, having given rise to many.

J. R. Harlan's work on crop evolution, which covered over a 50-year period, has been highly influential (partly summarized in: Harlan, 1975; 1992; 1995). Harlan (1971) challenged Vavilov's concept with evidence showing that centers of diversity do not necessarily constitute centers of origin. For example, despite the enormous variation

among Ethiopian tetraploid wheat landraces (Vavilov, 1951; p. 174), no local domestication of this crop in the Ethiopian highlands can be deduced, simply because no wild wheat is native to Ethiopia (Harlan and Zohary, 1966). Harlan (1971) also suggested a global pattern of temperate centers versus tropical non-centers. Describing his methodology for inferring the geographic origin of domesticated plants as “*more in the tradition of de Candolle than Vavilov,*” Harlan (1971, p. 174) proposed that data should be gathered from five sources of evidence:

1. Plants (living): biosystematic analyses, including genetics, cytogenetics, chemotaxonomy, morphology, ecology, geography, and so on, of the crops and their near relatives (essentially the Vavilovian approach).
2. Plants (past): archaeobotany, palynology, Carbon-14 dating.
3. Men (living): linguistics, oral traditions, techniques of use and cultivation, attitudes towards the crop in culture, religion, magic and so on.
4. Men (past): history, art, archaeology (artifacts and refuse left by man).
5. Other sources: geology, hydrology, erosion and siltation patterns, soil analyses, limnology, animal remains, and so on, for supporting evidence of changes in climate, vegetation, and fauna, as well as for circumstantial evidence of agriculture.

For most researchers, the sociocultural nature of plant domestication raises two different sets of either/or questions:

1. Was plant domestication a localized phenomenon occurring within defined ecological, geographical (Fig. 1), and cultural contexts *sensu* Lev-Yadun *et al.* (2000)? Or, was it a geographically diffused development, with each local invention being culturally independent of activities taking place in other sites (e.g., Blumler, 1992) as advocated by Weiss *et al.*'s ‘Autonomous’ model (2006), Ladizinsky (1998b), and the Willcox's “multiple centres” model (2005)?

2. Was plant domestication a protracted evolutionary process (*sensu* Tanno and Willcox, 2006; Allaby *et al.*, 2008a; Brown *et al.*, 2009)? Or, was it a relatively fast revolutionary change as implied by Hillman and Davies (1990) and Ladizinsky (1998b)?

To address these questions, it is first necessary to clarify what “cultural independence” of Neolithic communities means with respect to plant domestication as a discrete phenomenon. For example, in the Near East, there is a wealth of archaeological data indicating extensive interrelationships and exchanges throughout the Neolithic interaction spheres (e.g., Bar-Yosef and Belfer-Cohen, 1989; Gopher, 1989; 1999). We think that deciding between the center versus noncenter alternatives is highly important because it may assist in answering the question regarding the protracted versus contracted domestication process question.

III. GENETIC AND CULTURAL EVENTS

There are two phylogenetic paths by which a crop species can evolve: A crop species of monophyletic origin is the product

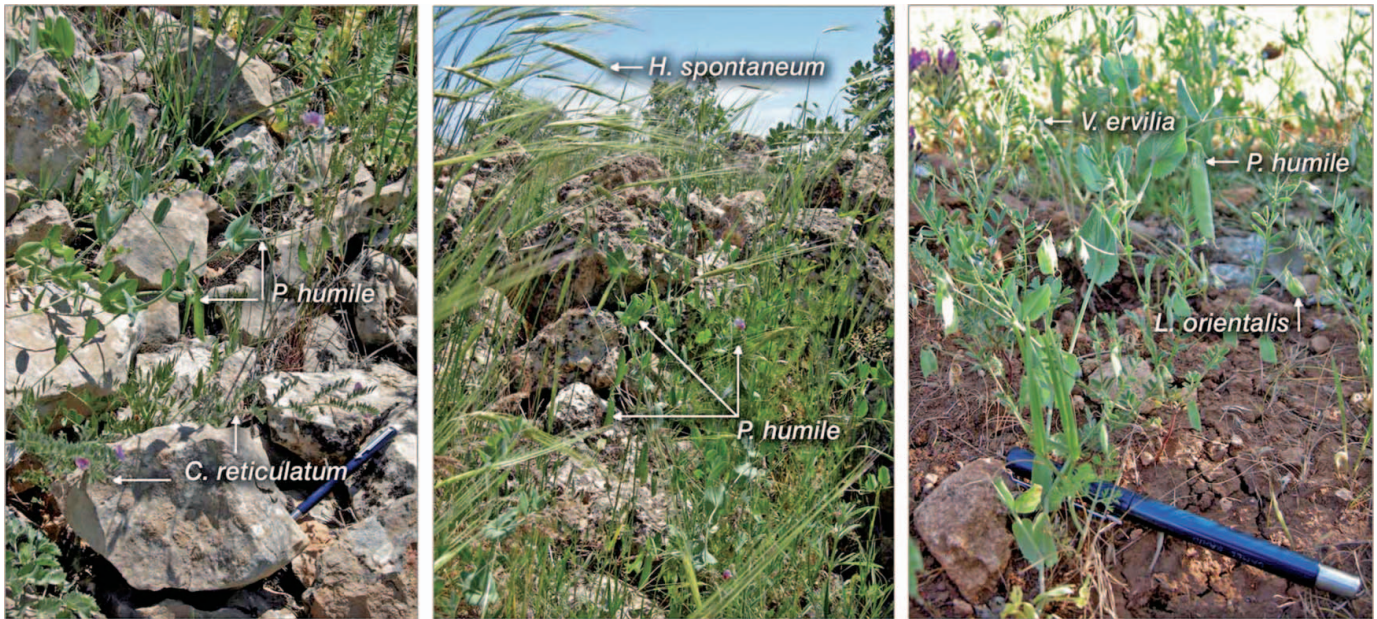


FIG. 2. Three panels showing the sympatric distribution of the wild progenitors of the Near Eastern grain legumes. All three photographs were taken in Mardin province, southeastern Turkey.

of a single genetic event that gave rise to a lineage of related domesticated forms (Zohary, 1996). Chickpea with the limited distribution of its wild progenitor, and the narrow genetic diversity of the cultigen is usually considered a crop of a monophyletic origin (Abbo *et al.*, 2003). A crop species of polyphyletic origin is the product of several *genetically* independent domestication events. As a hypothetical example to illustrate the difference, consider the following scenario for the domestication of a cereal species: Neolithic communities, who are geographically separated in the southern and northern Levant, each select a different population of the same wild cereal species. Over time, individual(s) among the two different populations undergo mutations for a non-brittle rachis at different chromosomal loci, thereby giving rise to two genetically distinct domesticated lineages of this crop species. Takahashi (1955) proposed that domesticated barley (*Hordeum vulgare*) illustrates a polyphyletic origin. It has two independent non-brittle rachis loci (*bt1* and *bt2*) and a differential geographic distribution of domesticated genotypes with *bt1bt1Bt2Bt2* found mostly in Europe, West Asia, and India and *Bt1Bt1bt2bt2* mostly in China and East Asia.

Based on allozyme polymorphisms data, Ladizinsky and Genizi (2001) suggested a polyphyletic origin of barley. In addition, Ladizinsky (1998b) has argued that the allozyme genetic diversity in domesticated barley is best explained by the emergence of non-brittle spike mutants in approximately 100 independent genetic backgrounds. According to Ladizinsky's (1998) calculations, the cultivated land area required to give rise to such a number of domesticated mutants is rather small. Thus, assum-

ing a sowing rate of 50 plants per square meter and a mutation rate of 10^{-6} , 100 non-brittle rachis mutants would be expected to occur within an area of 200 hectares during a single growing season. Alternatively, a smaller area of 10 hectares annually sown with wild barley over a period of 20 years can yield similar allozyme diversity results. Applying the allozymic diversity data in the context of these hypothetical sowing rates and mutation frequencies, Ladizinsky (1998b) proposed that early barley cultivation was not a common activity, engaging only a small number of 'communities' (families) and occurring on both a small temporal and spatial scale, e.g., over a 20-year period on small area of ca. 10 hectares. However, a major drawback of Ladizinsky's (1998b) model is the requirement for a certain degree of isolation to prevent any seed distribution or trade among the respective communities. Otherwise, following emergence of a domesticated type in one farmer's field, it would rapidly have been distributed to others (Ladizinsky, 1998b; p. 414).

Based on their findings with computer simulations, Allaby and Brown (2003; 2004) and Allaby *et al.* (2008a; 2008b; 2010) offer another view of the domestication model. They posit that domesticated genotypes are genetically distinct from their wild progenitors to the degree that they show a monophyletic origin although their evolutionary history may include multiple domestication events. Regardless of the debate over the genetic marker system of choice for such phylogenetic analyses (Allaby and Brown, 2003; 2004; Salamini *et al.*, 2004), or the validity of the population genetic models and their underlying assumptions (Ross-Ibarra and Gaut, 2008; Allaby *et al.*,

2008a, b; 2010; Honne and Heun, 2009), the possibility of convergent evolutionary processes acting under domestication has a sound theoretical and factual basis (Donald and Hamblin, 1983). For example, selection in a plant populations (wild and or domesticated) for a suit of traits such as a non-brittle rachis, free and uniform germination, reduced tillering and synchronized flowering, free-threshing grains, or nutritional qualities has proven very effective under domestication across a range of crop species (Donald and Hamblin, 1983; Harlan *et al.*, 1973; Paterson *et al.*, 1995). Therefore, the distinctness (in terms of DNA profiles) of domesticated taxa of either genuine mono- or poly-phyletic origins relative to their wild counterparts *sensu* Allaby *et al.* (2008a; 2008b; 2010) is rather trivial and does not help to clarify the geographic context of the domestication process. However, if distinct crop lineages can be affiliated with certain wild progenitor source populations of a known geographic origins, like Kilian *et al.*'s (2007) data on wild einkorn, such a finding can form a basis for considering centric *versus* non-centric domestication process for the crop species in question.

Given the limitation of reconstructing prehistoric domestication events with computer simulations and genetic inferences from studies of current germplasm collections, it would be useful to draw upon archaeological and archaeobotanical evidence to reconstruct the temporal and spatial aspects of plant domestication (e.g., Garrard, 1999; Lev-Yadun *et al.*, 2000; Gopher *et al.* 2001; Nesbitt, 2002; Savard *et al.*, 2006; Tanno and Willcox, 2006). Archaeology and anthropology can shed light on the cultural processes involved since plant domestication was primarily a cultural move, taking place within a distinct cultural context. For example, the domestication of emmer wheat (*T. turgidum* ssp. *dicoccum*) in the Near East and common millet (*Panicum miliaceum* L.) in East Asia, that both occurred contemporaneously circa 10,000 years ago (wheat: Nesbitt, 2002; millet: Lu *et al.*, 2009). Because no evidence for cultural contact between the two respective regions during the relevant period (by means of trade, migration or else) was ever presented, these two domestication events are both culturally and genetically independent of each other.

Returning to the barley example discussed above, two barley lineages — one originating in the Fertile Crescent and the other 1,500 to 3,000 km to the east according to Morrell and Clegg (2007) — may represent two genetically independent domestication events, thereby creating the distinct pattern of the so-called Occidental and Oriental barley cultivar groups discussed by Takahashi (1955). The possible correspondence of the two presumed domestication centers suggested by Morrell and Clegg (2007) to the Oriental and Occidental domesticated barley gene pools notwithstanding, their geographic definition of these domestication centers is quite vague and therefore problematic. Had these two presumed barley domestication events occurred in two non-interacting sociocultural spheres, it would truly represent independent events (Blumler, 1992). Indeed, Morrell and Clegg's (2007) barley domestication centers were not discussed

in the context of dated archaeobotanical remains to support genuine cultural independence.

Despite initial claims for monophyletic origin of domesticated einkorn (*T. monococcum*) by Heun *et al.* (1997), a recent study suggests multiple domestication events occurring within a relatively small geographic area with well-documented prehistoric trade networks and cross-cultural influences (Kilian *et al.*, 2007). Moreover, Kilian *et al.* (2007) state that the domesticated lines could have emerged by means of “*spread through common technology*” from the Karacadağ region throughout a 200–300 km arc extending from the north-northwest to the east-southeast. This region corresponds to the core area (Fig. 1) we have proposed for the origin of the Near Eastern founder crops (Lev-Yadun *et al.*, 2000). Archaeological remains recovered from sites located in this area (e.g., Çayönü, Cafer Hüyük, Nevali Çori, Göbekli Tepe, and other sites) reflect aspects of interacting communities sharing technologies (e.g., flint knapping technologies and tools), private and public architectural designs, burial customs, iconography, and more (e.g., Özdoan and Basgelen, 1999). This evidence dates to the end of the PPN A and the beginning of the PPN B (10,600–10,500 calibrated years BP), which further supports the conclusion that einkorn domestication did not occur by several independent, isolated cultural events.

Two aspects of Ladizinsky's (1998) model — the rarity of barley cultivation and the requirement for sociocultural isolation to prevent seed exchange between different communities — make sense if one accepts the possible role of isolated (‘autonomous’) domestication pockets. However, it is difficult to explain Ladizinsky's theory for barley in a region where Near Eastern Neolithic trade and other sociocultural interactions are so well documented. Moreover, as Jet (1973, p. 225) appropriately noted:

Even if genetic independence of cultivated plant populations is demonstrated, this does not demonstrate cultural independence, since ideas and techniques of the cultivation of a plant may be introduced but with a local plant substituting for the plant grown in the idea-donating area. Local environmental differences would favor use of local rather than foreign plant types.

A recent study on common bean (*Phaseolus vulgaris* L.) traced the geographical origin of common bean to the Lerma-Santiago basin of Mexico (Kwak *et al.*, 2009), which is several hundred kilometers away from the central Balsas River drainage where maize is presumed to have originated (Matsuoka *et al.*, 2002). This discovery in Mesoamerica points out the universality of the interrelationships between genetic and sociocultural events at the heart of the domestication processes. Just as there are questions of the possible cultural independence of common bean domestication from that of maize, and similarly for barley, emmer and einkorn in the Near East, it is prudent to question the economic, agronomic and nutritional viability of a single crop economy (Abbo *et al.*, 2010). More specifically, we wonder whether there was a period in which common bean farming

TABLE 2
A list of literature in support of a core area of Near Eastern plant domestication.

Authors	Crops	Type of evidence
Garrard 1999	All founder crops	Archaeobotany
Lev-Yadun <i>et al.</i> 2000, Gopher <i>et al.</i> 2001	All founder crops	Compilation of genetic, botanic, archaeobotanic and archaeological data
Heun <i>et al.</i> 1997	Einkorn wheat	DNA polymorphism
Özkan <i>et al.</i> 2002, Luo <i>et al.</i> 2007	Emmer wheat	DNA polymorphism
Salamini <i>et al.</i> 2002	Einkorn and emmer wheat	Review of genetic archaeological data
Abbo <i>et al.</i> 2006	Emmer wheat	DNA polymorphism (re-interpretation of published data)
Ladizinsky 1999	Lentil	Chromosome linear order, chloroplast DNA polymorphism, crossability relations
Abbo <i>et al.</i> 2001	Lentil, barley	Allozyme and DNA polymorphism (discussion of published data)
Honne and Heun 2009	Cereals	Genetic consideration and floral biology

occurred in isolation with no cultural contact whatsoever with maize growing cultures in prehistoric Mexico? In our view, only a positive answer to this question can support a noncentric domestication pattern for that region.

IV. WAS NEAR EASTERN PLANT DOMESTICATION A “CENTRIC” OR A “NONCENTRIC” PHENOMENON?

Accumulation of genetic and archaeological (mainly archaeobotanical) data over the past five decades has inspired two contrasting views concerning the origin of domesticated crop plants in the Near East (Table 2). Our view as proposed by Lev-Yadun *et al.* (2000) claims that Near Eastern plant domestication took place in a relatively small core area (Fig. 1), and radiated thereof to surrounding world regions as reflected in the gradients of ^{14}C dates of archaeobotanical remains and other cultural markers (e.g., Braidwood, 1967, 1975; Ammerman and Cavalli-Sforza, 1971; Abbo *et al.*, 2006; Pinhasi *et al.*, 2005; Weininger *et al.*, 2006). This reconstruction is based on archaeology, archaeobotany, biogeographical evidence, and phylogenetic analyses of wild and domesticated forms (Lev-Yadun *et al.*, 2000). Central to this view are sociocultural considerations and the conscious selection of candidates (and most likely of specific desirable phenotypes) for domestication (see for example, Kerem *et al.*, 2007; Abbo *et al.*, 2009, pp. 39–42) within the background of unconscious selection pressures taking place in cultivated fields. According to this reconstruction, which agrees with Zohary (1996), all (or most) founder crops of the Levantine Neolithic region were domesticated in an evolutionary process that involved very few or possibly one genetic event for each crop species. In a way, this core area concept is akin to Braidwood’s (1967; 1975) nuclear zone concept. Both the core area and nuclear zone ideas share a similar view of the role of sociocultural influences in guiding an interdependent

evolutionary process of domestication of a complex of companion crop species. In this respect, the core area reconstruction of Lev-Yadun *et al.* (2000) and Gopher *et al.* (2001) encompasses both a genetic and sociocultural ‘centric’ phenomenon.

The alternative view describes Near Eastern plant domestication as a geographically diffused phenomenon (Table 3). Quite a number of researchers, among them Willcox (2005), Weiss *et al.* (2006), Allaby *et al.* (2008a; 2008b; 2010), and Brown *et al.* (2009), proposed a non-centric model for plant domestication in the Near East. Willcox (2005) for example, suggests that each cereal species was domesticated in a different place by virtue of its varying ecological preferences. Additional arguments are building on studies of individual crop species — for example, multiple, independent domestication events proposed for einkorn in the Karacada region, Turkey (Kilian *et al.*, 2007); and for barley in the Near East (Ladizinsky, 1998b; Morrell and Clegg, 2007), Central Asia (Takahashi, 1955; Morrell and Clegg, 2007), Ethiopia (Bekele, 1983; Orabi *et al.*, 2007), and Morocco (Molina-Cano *et al.*, 1987; 1999; 2005).

What kind of considerations and evidence may assist in deciding between the two alternative views?

A. The Population Genetic Perspective

The seminal paper by Heun *et al.* (1997) and later studies by Salamini and colleagues (reviewed in Salamini *et al.*, 2002) have reignited the old debate concerning the mono- or polyphyletic origins of Near Eastern crop plants (Allaby and Brown, 2003; 2004; Salamini *et al.*, 2004). Apparently this debate is far from being resolved (Allaby *et al.*, 2008a; 2008b; 2010; Ross-Ibarra and Gaut, 2008; Brown *et al.*, 2009; Honne and Heun, 2009). The inherent uncertainty associated with some of the assumptions underlying Allaby *et al.*’s (2008a) simulation model makes it difficult to obtain definite answers. Given the difficulties in reconstructing prehistoric events, we offer an

TABLE 3
A list of literature supporting a diffused, multiple centers reconstruction of plant domestication in the Near East.

Authors	Crops	Type of evidence
Weiss <i>et al.</i> 2006	Barley, oats, lentil	Archaeobotany
Willcox 2005	Einkorn and emmer wheat, barley	Distribution of the wild progenitors
Allaby <i>et al.</i> 2003, 2004, 2008a, 2008b	Not specified	Population genetics based on computer based modeling
Brown <i>et al.</i> 2009	Barley, einkorn wheat	Review of DNA polymorphism and archaeobotanical data
Tanno and Willcox 2006	Einkorn and emmer wheat	Archaeobotany
Nesbitt 2002, 2004	Cereals	Archaeobotany
Morrell and Clegg 2007, Badr <i>et al.</i> 2000	Barley	DNA polymorphism
Ladizinsky 1998, Ladizinsky and Genizi 2001	Barley	Allozyme polymorphism (interpretation of published data)
Kilian <i>et al.</i> 2007	Einkorn wheat	DNA polymorphism
Molina-Cano <i>et al.</i> 1987, 1999, 2005, Orabi <i>et al.</i> 2007	Barley	Allozyme, and DNA polymorphism

* See section III for our interpretation of Kilian *et al.*'s data, which grants support of a 'core area.'

alternative approach for dealing with the two conflicting views of centric versus noncentric crop origins in the Near East using the following assumptions:

1. By definition, each genetic analysis of a given founder crop species is independent from other analyses. For example, Ladizinsky's (1999) work on wild and domesticated lentils is unrelated to Heun *et al.*'s (1997) study of wild and domesticated einkorn. Likewise, their data are independent of those for wild and domesticated emmer produced by Özkan *et al.* (2002; 2005) and Luo *et al.* (2007), and similarly for pea or chickpea.
2. Each founder crop species is polyphyletic.
3. Allaby *et al.*'s (2008a; 2008b; 2010) view that in each of these cases the phylogenetic analyses resulted with an erroneous monophyletic origin (Özkan *et al.*, 2002; Luo *et al.*, 2007; Heun *et al.*, 1997) is acceptable.

Given these assumptions, we then ask the following questions:

1. Is it likely that each of these independent analyses would point to monophyletic origin from wild stocks from the same geographic region in southeastern Turkey?
2. Is it likely that two independent genetic analyses for einkorn and emmer wheat would point to the environs of the Karacadağ mountain range, in southeastern Turkey?
3. Is it mere chance that the earliest dated archaeobotanical remains of domesticated cereals were unearthed from sites with close proximity to the geographic location of the wild stocks with the closest affinity to the cultigens?

We think that neither question can be answered in the positive. We find it highly unlikely that the so called "erroneous"

monophyletic origin of both einkorn and emmer wheat would be located near the same mountain range in southeast Turkey. And we find it even more unlikely that the origin of the lentil domesticated stock would also be found close to that region (Ladizinsky, 1999).

Moreover, given the fact that the wild progenitor of chickpea is known only from the very same area in southeastern Turkey (Ladizinsky, 1995; van der Maesen *et al.*, 2006), we find no other simple explanation but to assume that our core area reconstruction is true to life rather than an artifact produced by the algorithms used to calculate the genetic similarity parameters, or caused by a biased sampling of living plant material. Interestingly enough, R. Allaby, who challenged Salamini and co-workers monophyletic domestication claims (Allaby and Brown, 2003; 2004; Allaby *et al.*, 2008a; 2008b; 2010), does support a monophyletic origin for domesticated flax (Allaby *et al.*, 2005; Fu and Allaby, 2010), yet with an uncertain geographic origin. The monophyletic origin of domesticated flax was inferred based on a sample of six wild pale flax (*Linum angustifolium* synonym, *L. bienne*) lines and additional 25 domesticated genotypes by Allaby *et al.* (2005), and by four accessions of the wild progenitor *L. bienne* and 11 domesticated stocks (Fu and Allaby, 2010), while the work of Salamini's group on einkorn and emmer wheat employed hundreds of samples in both cases (Heun *et al.*, 1997; Özkan *et al.*, 2002; 2005). Quite surprisingly, none of the theoretical considerations contesting the monophyletic origin of the Near Eastern cereals (Allaby and Brown, 2003; 2004; Allaby *et al.*, 2008a; 2008b; 2010), were discussed by the same author while arguing for a monophyletic origin of domesticated flax (Allaby *et al.*, 2005; Fu and Allaby, 2010).

Even if one accepts our core area idea, the barley domestication case remains unresolved (Lev-Yadun *et al.*, 2000). Given

the immense literature on the subject (e.g., Takahashi, 1955; Komatsuda *et al.*, 2004, Azhaguvel and Komatsuda, 2007; Ladizinsky, 1998b; Ladizinsky and Genizi, 2001; Badr *et al.*, 2000; Bekele, 1983; Morrell and Clegg, 2007; Orabi *et al.*, 2007; Kilian *et al.*, 2006; Neale *et al.*, 1988; Abbo *et al.*, 2001; Li *et al.*, 2004; Molina-Cano *et al.*, 1987; 1999; 2005; Tanno *et al.*, 2002; von Bothmer, 2003; and Murphy *et al.*, 1982; to mention just few, and numerous citations therein), this issue requires a comprehensive treatment under a separate title. The fact that none of the modern phylogenetic studies points to southeastern Turkey as the origin of domesticated barley is indeed a weakness inherent to the core area reconstruction. It is worth noting, however, that based on morphology and disease and pest response data, Turkish domesticated barley germplasm encompass the widest genetic diversity compared with cultivars from other world regions (Table 5 of Takahashi, 1955). Hence, at least from a Vavilovian perspective, Turkey may well have played a certain role in barley domestication after all. We are reluctant to use Blumler's (1992) suggestion that due to its weedy tendencies, barley was in fact a secondary domesticate, that evolved on multiple occasions and locations in human-made habitats. Such a polyphyletic weedy origin offers too easy a solution that can never be experimentally supported or refuted. Still we argue that the fact that the geographic origin of the majority of the Near Eastern crops was identified in southeastern Turkey tips the balance in favor of our core area hypothesis (Lev-Yadun *et al.*, 2000; Gopher *et al.*, 2001).

A critical test for our hypothesis would be a detailed phylogenetic analysis of wild and domesticated pea, and bitter vetch, and a geographic resolution of the flax case. A geographic origin for these latter crops in southeastern Turkey would strongly corroborate our centric core area reconstruction, while pointing elsewhere would not.

B. The Geographic, and Therefore, Eco-Geographic Context

Although not always cited, Harlan's (1971) "centers and non-centers" paper has set the theoretical grounds for treating crop domestication as a diffused phenomenon. Therefore, it is appropriate to now reexamine the underlying rationale for Harlan's domestication centers and noncenters. The fundamentals of Harlan's (1971) thesis lie in his comparison between the so-called "Near Eastern center" and the "African noncenter" (Harlan, 1971; Fig. 6). In Table 1 of his article, Harlan (1971) specified a list of African crops each with their presumed area of domestication (determined by his above listed criteria), and in Figure 5 he depicted the respective areas of origin on a map of the African continent.

An immediate question that arises is to what extent is this comparison between the Near Eastern Fertile Crescent and sub-Saharan Africa valid? Can we treat the whole region from the Ethiopian highlands to the Niger River basin and beyond as a single eco-geographic unit? Indeed, compared with the vast and

diverse environs of sub-Saharan Africa, the east Mediterranean oak-pistachio belt of Harlan's Near Eastern center, which supports wild forms of barley, wheat, lentils, pea, and bitter vetch, can be seen as a single geobotanical unit. Moreover, when depicted on a map using the same scale (e.g., Fig. 6 of Harlan, 1971), the Near Eastern Fertile Crescent is similar in physical size to the Ethiopian highlands area. Therefore, given its unique ecology, there is no difficulty in accepting the Ethiopian highlands as a center of domestication for the endemic Ethiopian crops tef (*Eragrostis tef* [Zucc.] Trotter; Ketema, 1997) and noog (niger, *Guizotia abyssinica* [L. f.] Cass.; Murthy *et al.*, 1993) both in the sociocultural context and in the genetic and agronomic Vavilovian sense.

But what about crop domestication in West Africa? What can we say about the cultural isolation, or contacts between the Ethiopian highlands and the Niger basin? There is no question of the genetic independence of tef domestication in Ethiopia from the domestication of African rice (*Oryza glaberrima* Steud.) in West Africa because these are two different genera native to two different ecogeographic zones. Sorghum (*Sorghum bicolor* [L.] Moench) and pearl millet (*Pennisetum glaucum* [L.] R. Br.) are two major examples used by Harlan (1971) in arguing for a noncentric origin of sub-Saharan crops. Aside from Harlan's unmatched experience with these African crops given the extent of gene flow between these two crops and their wild progenitors (e.g., Doggett and Majisu, 1968; Miura and Terauchi, 2005; Tesso *et al.*, 2008), such a conclusion on diffused origin becomes questionable. This is because the extensive crop-wild gene flow in these two crops would have created local foci of crop-wild similarity. Based on morphology alone, such crop-wild similarity foci were apparently interpreted by Harlan (1971) as reflecting a mosaic of noncentric domestication pattern. Recently however, Oumar *et al.* (2008) used a collection of 355 domesticated and 84 wild pearl millet accessions to study DNA microsatellite diversity and demonstrated the existence of wild accessions that carry introgressed sequences typical to domesticated germplasm. Based on phylogenetic analysis employing domesticated germplasm and wild accessions not showing such evidence for introgression, Oumar *et al.*, (2008) found that a monophyletic origin of pearl millet in the region between eastern Mali and northwestern Niger is the most likely scenario, thereby ruling out Harlan's (1971) non-centric reconstruction of a pearl millet domestication belt extending from the Sudan to Senegal.

C. Biogeographical and Agro-Economic Considerations

The different ecological preferences, with special emphasis on adaptation to different soil types, of the different wild progenitors of the Near Eastern cereals is a major argument used by Willcox (2005) in proposing multiple domestication events and multiple centers (Willcox, 2005). However, our own observations in Mardin province (southeastern Turkey) may support a different reconstruction. For example, during a one day

trip (20 May 2009) along the Mardin - Midyat - Gercus, and Savur - Midyat - Dargecit roads, we observed numerous mixed stands of wild barley (*H. spontaneum*), wild pea (*P. humile*), wild lentil (*L. orientalis*), wild chickpea (*C. reticulatum*), and wild biter vetch (*V. ervilia*) (Fig. 2). Wild einkorn (*T. boeoticum*) is also common throughout southeastern Turkey (Harlan and Zohary, 1966), and wild rye can also be seen along the Savur - Midyat road, and near Ömerli, Mardin province (Abbo, unpublished field diaries). Indeed rich stands of wild emmer were not reported from this region, but rather some 60 km to the northwest in the Karacada range west of Diyarbakir. This current sympatric occurrence (growing in the same soils, Fig. 2) of six out of the seven wild progenitors of the Near Eastern founder grain crops (*sensu* Zohary and Hopf, 2000; Table 1) in the heart of our proposed core area challenges Willcox's (2005) multiple domestication centers hypothesis for wild cereals, and in fact turns this argument on its head, lending support to our core area of Near Eastern plant domestication (*sensu* Lev-Yadun *et al.*, 2000).

The Near Eastern founder crop package with its three cereals and three food legumes is considered a 'natural choice' due to the complementary amino acid composition that provides balanced dietary proteins (Zohary and Hopf, 2000, p. 92). No less important is the inherent agro-ecological balance, which this crop package provides as a naturally occurring maturity gradient that offers 'insurance' against the adverse effects of drought and erratic seasonal precipitation typical to the Near East (Abbo *et al.*, 2010). Moreover, the determinate (relatively synchronous flowering and grain maturation) growth habit of the cereals and the indeterminate (extended) growth habit of the legumes provide a compensating pattern of grain yield in response to the natural year-to-year fluctuations typical to the east Mediterranean basin (Fig. 2 of Abbo *et al.*, 2009; Halstead, 1989, p. 73). Given the inability of the farmer to predict the seasonal rain profile when sowing the winter crops and the differences in grain production in a given year between these crops, reliance on a single crop would be too risky a strategy. Only with a diverse crop assemblage, with different developmental patterns (i.e., legumes and cereals) can the farmer ensure a minimal level of yield stability (Abbo *et al.*, 2009; 2010). Hence, the simplest of agronomic reasoning is in favor of crop diversification rather than reliance on a single crop plant, as implied in Willcox's (2005) multiple events, multiple centers hypothesis.

Nesbitt (2004) who has advocated noncentric plant domestication in the Near East, and similarly, Willcox (2005) do not specify whether they are referring to genetic or sociocultural independence. More specifically, Willcox (2005) does not provide an explanation for the agronomic viability of the presumed cropping systems based on a single locally adapted cereal at any one such location. Nor does the archaeobotanical record support a reliance on a single crop (Garrard, 1999; Nesbitt, 2002; Savard *et al.*, 2006). We find the typical Mediterranean year-to-year seasonal rain fluctuations and their agronomic implications (Abbo *et al.*, 2010) as posing a major obstacle for

accepting such noncentric (single crop) reconstructions of the Near Eastern domestication process.

V. DISCUSSION

Smith (2007a; 2007b) and Zeder (2009, p. 45) portray plant domestication as a stage along a continuum extending from foraging to "true agriculture." Smith (2007a) even compares niche construction activities of various animals (e.g., tree-cutting and dam building by beavers) with man's controlled burning and cultivation activities (Smith, 2007a). This is akin to Rindos' (1980) approach to plant domestication in terms of an evolutionary outcome of a predator/prey relationship resulting in mutualism between genetically unrelated organisms (man-plants). We prefer to view Near Eastern plant domestication (and the Near Eastern Neolithic Revolution as a whole) as a fully conscious sociocultural move based on a well-educated choice of specific food sources (e.g., Kerem *et al.*, 2007; Abbo *et al.*, 2005; 2009) with an almost perfect yield compensation ability to suit the east Mediterranean environments (Abbo *et al.*, 2009; 2010).

As stated above, we see the embarkation on agriculture in the Neolithic Levant as a move within a culturally interacting sphere involving all (or most) founder crops together. Accordingly, we find Willcox's (2005) "multiple event, multiple centres" and Weiss' *et al.* (2006) autonomous models lacking in another major aspect. Accepting these two latter reconstructions assumes that independent communities engaged in growing just one or very few crop species. Also implicit in this assumption is that such practice lasted long enough to allow the emergence of genetically independent domesticated mutant(s), i.e., several non-brittle ear types for each of the different cereals. Following Willcox (2005), Willcox and Tano (2006), Weiss *et al.* (2006), or Allaby (2008a), this would mean cultural isolation for hundreds of years or even millennia.

Accepting such a scenario of a number of independent, culturally isolated domestication foci across the Neolithic Levant, one wonders how, in cultural terms, did the eventual formation of the "harmonic founder crop package" come about? Namely, how did the founder crop package coalesce? Arguing for independent domestication centers, one would require a fine well-dated sequence of archaeobotanical remains and gradients of ^{14}C dates to demonstrate the presumed cultural cross-flow from the different foci showing how each individual crop radiated from its putative independent center. At present, the archaeobotanical record (e.g., Garrard, 1999; Nesbitt, 2002; Savard *et al.*, 2006) does not support such a reconstruction for the Near East. On the contrary, it points to a single core area in southeastern Turkey, fitting a centric model. The Near Eastern archaeological record too does not lend itself to assumptions of cultural isolation/independence of the various suggested domestication foci.

VI. CONCLUDING REMARKS

We have made our view about the agro-ecological, genetic and sociocultural "centric" characteristics of Near Eastern plant

domestication quite clear. However, the actual sequence of events in other regions may have been different. Since we are unfamiliar with the archaeological and/or the phytogeographic contexts of plant domestication outside the Near East, regrettably, we have only questions rather than answers concerning the biological and cultural processes underlying plant domestication in other world regions. Therefore, unlike Harlan (1971) or Blumler (1992), we refrain from making cross continental comparisons and depicting possible global scenarios. Still we would cautiously suggest that every presumed noncentric crop should be treated like the Levantine, African and Mesoamerican crops (e.g., Salamini *et al.*, 2002; Matsuoka *et al.*, 2002; Oumar *et al.*, 2008; Kwak *et al.*, 2009). Only detailed phylogenetic studies of representative collections of wild and domesticated forms can determine the place of origin and their phylogeny. However, it should always be borne in mind that the resolution power of such analyses is rather limited in discriminating between possible scenarios ranging from (1) a monophyletic adoption of a single mutant (in a specific genetic background) to (2) ‘variety domestication’— an episode by which several mutants (a few genetic backgrounds) have been extracted from the adopted population. Therefore, such analyses will only answer genetic questions concerning the number and geographic location of events involved in the origin of the respective crops. They are unlikely to provide answers to questions of sociocultural influence, or independent inventionism (Jett, 1973).

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