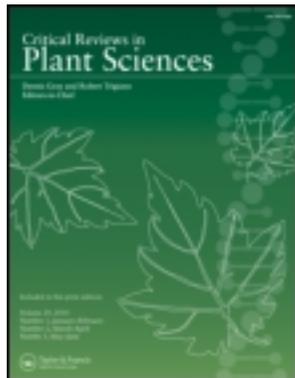


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### Plant Domestication and Crop Evolution in the Near East: On Events and Processes

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# Plant Domestication and Crop Evolution in the Near East: On Events and Processes

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## Table of Contents

I.	INTRODUCTION .....	242
II.	CULTURE, BIOLOGY & ARCHAEOBOTANY: MODELING PLANT DOMESTICATION .....	243
III.	HISTORICAL MODELS OF PLANT DOMESTICATION .....	244
	A. The Emergence of Domesticated Genotypes .....	245
	B. The Proficiency of Our Neolithic Ancestors .....	246
IV.	EVIDENCE FOR PRE-DOMESTICATION CULTIVATION: A CRITICAL CONSIDERATION .....	246
	A. Weeds of Cultivation .....	246
	B. Variation of Crop Plants under Domestication .....	247
	C. Domestication Events or Processes - The Archaeological Record .....	248
V.	DISCUSSION .....	249
	A. The Role of Conscious vs. Unconscious Selection .....	249
	B. The Methodological Implications of the 'Protracted Domestication' Assumption .....	250
VI.	CONCLUDING REMARKS .....	251
	ACKNOWLEDGMENTS .....	253
	REFERENCES .....	253

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Reconstructing the evolutionary history of crop plants is fundamental for understanding their adaptation profile and the genetic basis of yield-limiting factors, which in turn are critical for future

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crop improvement. A major topic in this field is the recent claim for a millennia-long 'protracted' domestication process. Here we evaluate the evidence for the protracted domestication model in light of published archaeobotanical data, experimental evidence and the biology of the Near Eastern crops and their wild progenitors. The crux of our discussion is the differentiation between events or 'domestication episodes' and the later following crop evolutionary processes under domestication (frequently termed 'crop improvement stage'), which are by definition, still ongoing. We argue that by assuming a protracted millennia-long domestication process,

**one needlessly opts to operate within an intellectual framework that does not allow differentiating between the decisive (critical) domestication traits and their respective loci, and those that have evolved later during the crop dissemination and improvement following the episodic domestication event. Therefore, in our view, apart from the lack of experimental evidence to support it, the protracted domestication assumption undermines the resolution power of the study of both plant domestication and crop evolution, from the cultural as well as from the biological perspectives.**

**Keywords** conscious vs. unconscious selection, domestication episode, origin of Near Eastern agriculture

## I. INTRODUCTION

The study of Near Eastern plant domestication has become a highly complex and multidisciplinary research field. The integration of data from various disciplines and sources enable students of the subject to entertain and at times to answer questions concerning the population genetics (e.g., Zohary, 1996; Heun *et al.*, 1997; Özkan *et al.*, 2002, 2005; Allaby and Brown, 2003; Salamini *et al.*, 2004; Honne and Heun, 2009; Haldorsen *et al.*, 2011), the geography (e.g., Ladizinsky, 1999; Lev-Yadun *et al.*, 2000; Nesbitt, 2004; Willcox, 2005; Abbo *et al.*, 2010a; Alo *et al.*, 2011), the ecology (e.g., Harlan and Zohary, 1966; Ladizinsky, 1975; Abbo *et al.*, 2008a, 2008b), the time frame (e.g., Tanno and Willcox, 2006a; Purugganan and Fuller, 2011), the agronomy (Harlan, 1992a; Abbo *et al.*, 2010b, 2011b), the driving forces (e.g., Bar-Yosef and Belfer-Cohen, 1992), the nature of man-plants relations (e.g., Rindos, 1980; Smith, 2007; Laland and O'Brien, 2010), the role of conscious vs. unconscious selection (e.g., Heiser, 1988; Zohary, 2004; Abbo *et al.*, 2005, 2011a), and the molecular genetics (e.g., Doebley *et al.*, 2006) of the underlying domestication traits. Like in all other realms of the human existence, the abovementioned aspects of plant domestication are by definition inter-related and bear on each other. This may explain why at times, answers to seemingly unrelated questions (why? where? and how many times were plants domesticated in the Near East?) coalesce to form models that apparently stem from distinct schools of thought (e.g., Brown *et al.*, 2009 vs. Abbo *et al.*, 2011a). Therefore, it is almost impossible to treat one of the above aspects of plant domestication without resorting to data, interpretations and arguments from the other topics.

The focus of the present review is the protracted domestication model (e.g., Allaby *et al.*, 2008a; Brown *et al.*, 2009; Fuller *et al.*, 2010a; 2010b; Gross and Olsen, 2010; Purugganan and Fuller, 2011), which is a relatively new development in the field. According to this new model, plant domestication is thought to have started with prolonged pre-domestication cultivation, and has gradually culminated in the emergence of domesticated stocks eventually dominating the 'cultivators' fields (e.g., Weiss *et al.*, 2006; Willcox *et al.*, 2008, 2009; Allaby, 2010). According to the proponents of this view, plant domestication arose by way of slow agro-evolutionary processes (e.g., Kislev,

**Foraging** accounts for a state of collecting wild plants reflecting the hunters-gatherers life-way.

**Cultivation** is the mechanism, the set of activities by which the active person treats plants. This may include, but is not limited to threshing, cleaning, sorting, selecting and stocking seeds, soil preparation, sowing, tending and harvesting. Cultivation is thus a chain of husbandry operations, defining the 'agronomic' arena. Cultivation is a human intervention in the life of wild or domesticated plants, a manipulation of plants in a new setting reflecting a new perception of land and plants, a change in the relations between culture and nature.

**Domestication** in biological terms, refers to the major genetically-based phenotypic features that characterize the plants selected by man (e.g., non-brittle rachis, free germination, changes in bio-rhythms, etc.). Domestication, in cultural terms, is an event/episode based on a decision and follow-up action by which the active person selects certain species and particular stocks within species for growing. Thus, domestication involves obtaining desirable plants with distinct phenotypes by educated and conscious human choice-making.

**Plant agriculture** is an economic system based on the cultivation of crops regardless of their phenotype and may be supplemented by gathering from the wild.

BOX 1. Definitions of terms used in the discussion on plant domestication and the evolution of Near Eastern grain crops throughout the paper.

2002; Zeder, 2009). Thereby, other paradigms claiming that a domesticated crop could be established within decades or a couple of centuries of cultivation (e.g., Oka and Morishima, 1971; Ladizinsky, 1987, 1993, 1998a; Hillman and Davies, 1990) were deemed obsolete (Fuller, 2010). As stated above, a comprehensive and critical treatment of the protracted domestication model will necessitate compilation of data and interpretations from almost all other aspects of plant domestication.

Prior to the critical treatment of the subject, we present (Box 1) a set of definitions for several key terms extensively used in the literature as well as in this paper (e.g., Harris, 1989, 2007; Fuller, 2007; Allaby, 2010).

Evidence and arguments from different fields have been advanced to support a protracted Near Eastern plant domestication model including (but not limited to):

- The understanding that "there is necessarily a stage of production (cultivation) that precedes morphological domestication" (Fuller, 2007, p. 904), and see Wilke *et al.* (1972) and Gepts (2004).
- Documenting 'weeds of cultivation' in the very late Natufian and in Early Neolithic archaeobotanical assemblages of Near Eastern sites like the ca. 13,000 years Cal. BP Tell Abu-Hureyra (Hillman, 2000), and a series of other sites (Willcox *et al.*, 2008, Tables 3, 4).
- The assumption that annual sowing of barley fields took place already during the PPNA period, from 10,300-9,500 non calibrated BP (ca. 12,000 – 10,500 Cal BP) (Kislev, 2002), which allegedly led by

agro-evolution to the gradual increase in the frequency of non-brittle genotypes in cultivated fields (therein).

- Observations that mean grain size of wheat and barley from a range of Near Eastern sites gradually increase over a period of several thousand years, starting in the PPNA (Willcox, 2004; Purugganan and Fuller, 2011).
- The observation that the frequency of non-brittle (domesticated) wheat ear remains from Near Eastern sites gradually increase over a period of some 3-4 millennia starting in the PPNA (Tanno and Willcox, 2006a).
- Assuming a 'meta-stable equilibrium' in cultivated fields, which resulted from either shifting or fallowing of cultivated plots that gave selective advantage to wild-type dispersal adaptations, i.e., brittle barley or wheat spikes (Fuller *et al.*, 2010b).
- Assuming a weak selection for non-brittle ear types (under cultivation) due to bolstering of cultivated yields by harvest from neighboring wild cereal populations, or by collection of fallen spikelets from the ground (Kislev *et al.*, 2004; Allaby, 2010), thereby significantly diluting any emerging non-brittle mutants occurring within the 'cultivated populations' (Tanno and Willcox, 2006a; Willcox *et al.*, 2008).
- Archaeological finds of 11,000 years old 'predomestication granaries' in the Jordan Valley (Kuijt and Finlayson, 2009).

Interestingly, both the proponents of the protracted domestication model, as well as the 'Old Guard orthodoxy' who viewed domestication as a fast revolutionary development attribute a major role in the process to unconscious selection (e.g., Harlan *et al.*, 1973; Heiser, 1988; Zohary, 2004; Fuller *et al.*, 2010a). Some authors compare man's field operations (cultivation activities such as land clearing, working the soil, weeding, etc.) with niche construction activities of various wild animals (e.g., Barker, 2006, p. 393; Smith, 2007; Laland and O'Brien, 2010), while others consider plant domestication as a private case of specialized mutualism (Purugganan and Fuller, 2011), which in a way, are 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 (i.e., man-plants and ants/beetles-fungi alike). This approach is conceptually linked with another long literary tradition that attributes plant domestication to the 'fortuitous accumulation of a series of chance discoveries' (Lévi-Strauss 1962, pp. 13–14). A good example to this approach is the so-called 'dump-heap hypothesis' (e.g., Hawkes, 1970). By definition, such models must rely on "automatic" dynamics driven by selection pressures unconsciously exerted by cultivators/man (e.g., Harlan *et al.*, 1973; Heiser, 1988; Harlan, 1992a; Zohary, 2004; Fuller *et al.*, 2010a, 2010b). For criticism of this approach, see Chapman (1992) and Abbo *et al.* (2005, 2011a, 2011b) and references therein.

Rapid spread of a cultural innovation is expected to significantly reduce the likelihood of an independent development of a similar synchronic (or nearly so) development within the boundaries of the respective cultural interaction sphere, a phenomenon termed 'pre-emptive domestication' by Diamond (1997). Contrary to the above, slow unfolding of the abovementioned pre-domestication cultivation processes as suggested by Allaby *et al.* (2008a), Fuller *et al.* (2010b), and Purugganan and Fuller (2011) may accord with the idea of multiple (autonomous) cultivation foci across the Near East (e.g., Willcox, 2005; Weiss *et al.*, 2006). Under such scenario it does make some sense that each of the candidate plant species may have been adopted more than once (Allaby *et al.*, 2008a; Allaby, 2010; Gross and Olsen, 2010) and probably in several independent locations (e.g., Ladizinsky, 1998a; Ladizinsky and Genizi, 2001; Willcox, 2005; Weiss *et al.*, 2006; Morrell and Clegg, 2007; Allaby *et al.*, 2010).

Indeed, when taken together, the abovementioned literature corpus offers a comprehensive view of a highly complex long-term pattern of a long domestication process (Brown *et al.*, 2009; Zeder, 2009) occurring over vast tracts of the Near East over millennia (Willcox, 2005; Tanno and Willcox, 2006a; Fuller and Allaby, 2010; Fuller *et al.*, 2010b), with successes and (alleged) failures [e.g., Weiss *et al.*, 2006 (oats); Melamed *et al.*, 2008 (*Vicia peregrina*); Willcox *et al.*, 2009 (rye)], driven by a combination of environmental (e.g., Hillman *et al.*, 2001; Bar-Yosef, 2004, 2009; Gepts, 2004; Allaby *et al.*, 2008a; Laland and O'Brien, 2010), and cultural factors, mediated by human activities like fallowing, deep or shallow sowing, harvesting techniques, seed stocking and taste preferences, etc. (Harlan, 1992b; Zohary *et al.*, 1998; Zohary, 2004; Allaby, 2010; Fuller *et al.*, 2010b). It is this, apparently harmonic and appealing reconstruction of Near Eastern plant domestication that we wish to challenge herein.

## II. CULTURE, BIOLOGY & ARCHAEOBOTANY: MODELING PLANT DOMESTICATION

In seeking deep understanding of plant (and animal) domestication, several students of the subject have attempted a multidisciplinary approach combining archaeology, botany, zoology and genetics (e.g., Zohary *et al.*, 1998; Zohary and Hopf, 2000; Lev-Yadun *et al.*, 2000; Gopher *et al.*, 2001; Willcox, 2005; Zeder *et al.*, 2006; Brown *et al.*, 2009; Gross and Olsen, 2010). One of the most important contributions to modeling plant domestication was made by combining insights gained through decades of field work and a wide literature corpus encompassing anthropological, ecological, socioeconomic, botanic, and evolutionary aspects by Harris (1989, and citations therein). Harris' (1989) classical (multi-stage) model is structured as an evolutionary continuum of people-plants interaction which gave rise to plant domestication. This model (and variations of it) can be summarized in the form of the following four stages: (1) foraging, or wild food gathering and hunting, (2) cultivation of wild plants, or pre-domestication cultivation,

(3) systematic cultivation of wild plants and eventually, and (4) agriculture based on domesticated forms (*sensu* Fuller, 2007; and see Allaby, 2010). Implicit in Harris' (1989) model is that the commencement of stage 4 is mediated by the selective propagation of domesticated genotypic and phenotypic variants (see Figure 1.1 of Harris, 1989). While Harris expanded his model (adding animals) and fine-tuned it over the years (e.g., Harris, 1996, 1998, 2002), his basic evolutionary continuum remained unchanged (Fig. 2.1 in Harris, 2007). A republication of the Harris' (1989) paper in Denham and White (2007) was accompanied by a short update by Denham (2007) pointing out some refinements and a generalization that simplified the model. Denham (2007) pointed out Harris' growing emphasis on 'transitional' (in between 'hunting and gathering' and agriculture) life ways and their flexibility – to either develop into agriculture or not. Another aspect in Harris' approach is the decoupling or at least the partial decoupling of agriculture from domestication and the blurring of the conceptual boundary between these two terms. Harris (2007) revised his 1989 model and depicted three (rather than four) modes of food procurement and production. These are: wild-food procurement (foraging), wild food production (pre-domestication cultivation) and agriculture (based mainly on domesticated crops). Indeed, Harris (2007) stressed that the distinction between the above three modes of subsistence is made for analytic purposes, while the reality they represent is made of mixed subsistence systems, in which gradual decrease in the dependence on wild foods occurred in parallel to the gradual increase in the dependence on domesticated crops (legend to Figure 2.1, therein).

In this context it is important to bear in mind that Harris (1989) stressed the importance of accurate definitions of the terms used in describing the people-plants liaison (the evolutionary continuum that gave rise to domesticated plants), such as 'cultivation,' 'domestication,' 'agriculture,' and 'food production.' We wholeheartedly support Harris' (1989) attitude to the subject, and agree that "the meaning attributed to such general concepts can and do directly affect research design and the *interpretation of evidence*" (Harris, 1989, p. 11, *emphasis added*).

In this multidisciplinary spirit, we wish to advance our approach to Near Eastern plant domestication while combining cultural insights and evidence across archaeobotany, plant science, genetics, ecology, and agronomy boundaries.

### III. HISTORICAL MODELS OF PLANT DOMESTICATION

Most or at least a large portion of past cultural phenomena have a history best described in ontogenetic terms and Gaussian (bell shaped) curves, i.e., a birth stage – the invention; the growth (following the adoption of the new invention) stage up to maturity – peak in frequency; stabilization for a while; and finally a decline stage and eventual disappearance from the record (see Figure 1). For the case detailed here, i.e., Neolithic Near Eastern plant domestication, the birth and growth stages are met

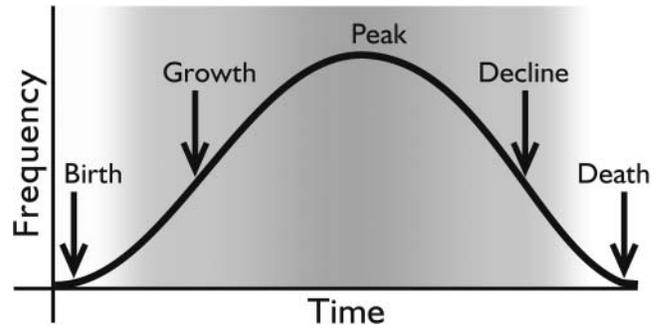


FIG. 1. A bell-shaped curve describing an ontogenetic pattern of historical phenomena.

as well as the stabilization stage (e.g., the current role of barley, pea, chickpea, and lentil in the global economy), while the decay stage of the model (except maybe for bitter vetch, einkorn and emmer wheat) is not. However, since this paper relates to the birth and partly to the growth stages, we may rely on those aspects of the ontogenetic model, at least as a heuristic device.

The necessary and sufficient conditions for the birth event in the case of plant domestication is a suitable accumulation of human knowledge and creativity (man), a natural potential (environment and plants), as well as, and no less crucial, an ideological-perceptual arena enabling such a change in man-world (culture-nature) relationship. After these conditions are met, a positive and/or supporting social milieu is needed for innovations to be made and adopted. Once an innovation (new practice) is made (born), adopted and assimilated, a growth stage (rise in frequency) may follow, which involves a continuous complex array of socio-political negotiations, through which society continuously reaffirms its decisions by way of inspecting the results of the new practices. This is especially true for a very significant change such as plant domestication. As opposed to some technological inventions that may be adopted and assimilated without causing major change in the system, the adoption of domesticated plants and the lifestyle and cultural changes it inspired (a food production way of life) were basically a dramatic disruption of the old (hunter-gatherers food collection) order, i.e., a highly significant socioeconomic change. In the Near Eastern case, the domestication of a plant package (for food and fiber production) and the related changes were successfully adopted, have grown to a peak and became part of a new life way. The identification of species (and certain genotypes), the recognition of the advantage of domesticated plant types, and the beginning of a selection in their favor by Neolithic communities, are/were all elements of the birth stage – i.e., domestication followed by the adoption and assimilation of these species into the economy of these communities. Once domesticated, the following temporal dynamics (rise in frequency of domesticated types/plants out of the total bulk of vegetal food procured, processed and consumed by the relevant communities) and the socio-political developments in these Neolithic communities in the core area represent the abovementioned 'growth

stage'). The later growth relates to the geographic spread of the innovation and its adoption by surrounding communities of Neolithic cultural entities (Colledge, 2004; Colledge and Conolly, 2007; Coward *et al.*, 2008). Thus, an episode<sup>1</sup> of domestication (deciding on the species, and actual choice of types for sowing and, selection in their favor), was followed by long and still ongoing processes of crop evolution under domestication.

### A. The Emergence of Domesticated Genotypes

A major theme in the plant domestication literature concerns the genetic changes in the constitution of the (would-be crop) plants populations induced by the human action of sowing and reaping (e.g., Harlan and Zohary, 1966; Wilke *et al.*, 1972; Harlan *et al.*, 1973). Namely, the selection in favor of alleles controlling non-brittle spikes (in the case of wheat and barley), over the wild-type (brittle) alleles selected for in nature (therein). The likelihood of the emergence of such maladaptive (in nature) alleles in cultivated fields (e.g., Ladizinsky, 1998a; Hillman and Davies, 1990), which in the early days were rather small compared with the vast tracts of wild cereals across the Near East, suggests that such mutants are (and were) present in the Near Eastern native flora (e.g., Kamm, 1974; Honne and Heun, 2009). It should be noted that in natural populations (even without the assumption of panmixis), effective natural selection acts upon the rare homozygous recessive (non-brittle) individuals by reducing their fitness, while heterozygous individuals may persist (almost) indefinitely or, be maintained in the population at least at the naturally occurring mutation frequency of the respective loci. Therefore it is fair to assume that non-brittle phenotypes (in the case of wheat or barley) or free germinating legumes (*sensu* Ladizinsky, 1987) have re-appeared spontaneously (albeit at very low frequencies) in the native Near Eastern flora (the 'standing genetic variation' discussed by Doebley *et al.*, 2006, p. 1311; Tang *et al.*, 2010; Davies and Hillman, 1992, pp. 212–213). Such natural variants must have been repeatedly encountered by the local hunter-gatherers and (once sowing became a perceptual option) recognized as especially useful resources (by way of their traits) of high potential similar to other surrounding natural resources. Hence, we need not assume that the emergence of a domesticated crop was entirely dependent upon a 'necessary stage' of protracted pre-domestication cultivation, which drove automatic (and unconscious) selection processes (e.g., Wilke *et al.*, 1972; Harlan *et al.*, 1973; Heiser, 1988; Kislev, 2002; Zohary, 2004; Purugganan and Fuller, 2011). Rather, in our view, because 'domesticated' types were an integral part of the surrounding nature (the standing genetic variation *sensu* Doebley *et al.*, 2006), albeit a rare element, they could have been selectively identified (like preferred flint types, water sources, salt deposits, bitumen or else), propagated and utilized by the early farmers, once the perceptual and social background had been ripe for this change.

Here we wish to resort to Harris' (1989) widely accepted multi-stages model (e.g., Fuller, 2007; Allaby, 2010), which was founded on intellectual assumptions regarding the nature of

the long continuum of people-plants interaction (Harris, 1989, pp. 11, 16; and see Gross and Olsen, 2010). In formulating the model, Harris stressed that the different human activities are presented (in his model) as sequential only in the sense of the human energy input, but not in the sense of replacing one another over time (Harris, 1989, p. 18). Harris also suggested that all the specific (human) activities embedded in the term 'cultivation' are still practiced today in both agricultural and non-agricultural contexts and some are assumed to have predated agriculture (Harris, 1989, p. 18).

Passage through wild wheat and/or barley populations few weeks after full ripening can expose natural non-brittle variants (Kamm, 1974), similarly, observations few weeks after the first autumn rains may expose wild legumes populations with high germination rates. Therefore, accepting Harris' (1989) statement that some of the specific activities have pre-dated 'agriculture,' which he defined as the "cultivation of domesticated crops," and adding to his list of such activities the selective stocking of seeds from standing genetic variants with (or without) domesticated phenotypes as suggested by Ladizinsky (1987) and Abbo *et al.* (2011a), may reconcile Harris' (1989, 2007) models with experimental evidence suggesting that Near Eastern legumes domestication is unlikely to have resulted from long term cultivation of wild types (Ladizinsky, 1987, 1993; Abbo *et al.*, 2011b). Stated differently, while placing the selective propagation of desired stocks (e.g., based on taste preferences or with domesticated seed dispersal and seed dormancy phenotypes) at the head of Harris' stage 2 (Harris, 1989, Fig. 1.1, p. 17; 2007) does not change the gradient of human energy input, it does render the assumption regarding the necessity of pre-domestication cultivation (Fuller, 2007, p. 904) redundant.

The crux of our reasoning is the differentiation between historical 'events' and long- (*durée*) term historical processes, namely short 'episodes' as opposed to deep running currents that activate larger scale processes related to deeply ingrained phenomena (Braudel, 1980). Pickersgill (2009) for example, did make a distinction between "early domestication" and "post domestication" but without any delimitation of the respective time frames. Nor did she address the bearing of such a distinction on the discussion of the role of conscious vs. unconscious selection during these two phases (Pickersgill, 2009). While we see the domestication episode as a culmination of a long process of deep perceptual change in culture-nature (man-world) relations (e.g., Cauvin, 2000; Watkins, 2001), the proponents of the protracted domestication model see domesticated crops as an end product of a long unconscious process, which began with no intention to domesticate (e.g., Barker, 2006, p. 392; Fuller *et al.*, 2010b). Admittedly, the long (protracted) processes described by Fuller *et al.* (2010a, 2010b) and Purugganan and Fuller (2011) are long-term historical processes of cultural change but we consider them to have taken place after domestication (under domestication, *sensu* Ladizinsky, 1998b; post-domestication, *sensu* Pickersgill, 2009). In our view, the domestication episode took place in a short time

window that separated two long-term historical processes – namely, the preceding build-up of the perceptual and technological background for cultural change, and later plant evolution under domestication processes (Figure 1). Therefore, it follows that not all Neolithic groups have adopted domesticated plants right away, and that people may have continued to gather from the wild (Barker, 2006, p. 140), like some still do in the Near East some 10 millennia after domestication (e.g., Ertug, 2000). Continued gathering (e.g., of cereals), even at low intensity is expected to leave its mark in the archaeological record creating mixed assemblages of both wild type and domesticated type ear remains. Likewise, this is expected to create a ‘jigsaw puzzle’ pattern of contemporary sites throughout the core area some of which contain domesticated plant remains while others do not. The continued gathering/delayed adoption can easily account for the time span between the domestication episode and the full dominance of domesticated types in the consumed grains/vegetal food, which Fuller (2010) and co-workers consider as the end of the domestication process.

### B. The Proficiency of Our Neolithic Ancestors

A major argument in favor of a long (protracted) domestication process concerns the proficiency of our Neolithic ancestors. Stated differently, attributing a major role to unconscious (automatic) selection in plant domestication (Harlan *et al.*, 1973; Heiser, 1988; Zohary, 2004), as well as to unintended human action (Barker, 2006, pp. 392–393; Fuller *et al.*, 2010b), by definition, includes an implicit assumption regarding the ineptness of the early Neolithic farmers to identify useful types of plants among the surrounding wild flora or to detect subtle changes in the composition of the plant populations they were managing. Namely, that the domesticators (early farmers) were unable to recognize superior types of plants in order to propagate them selectively (Abbo *et al.*, 2011a). Recently, this implicit assumption became a bold part of the argumentation;

... for non-shattering, both forms (wild type and non-brittle ear types, our addition) are present in the crop and are so similar that the early Neolithic farmers may have simply considered them the same crop and could not consciously differentiate cultivated from wild forms in the field. (Purugganan and Fuller, 2011)

While studying wild bean populations in Latin American Gepts (personal communication) encountered farmers who are very knowledgeable about the existence of wild beans, their location in the landscape and their year-to-year variation. These farmers often integrate wild beans into their crops, which lead to a significant increase of genetic diversity in fields (Payro *et al.*, 2005; Zizumbo-Villarreal *et al.*, 2005). Hence, we offer an alternative approach based on the recognition of the immense floristic knowledge of recent hunter-gatherers and our Neolithic ancestors alike (e.g., Lévi-Strauss, 1962; Kelly, 1995; and see Abbo *et al.*, 2011a). We claim that the first Neolithic farmers were capable of recognizing unique types in their sur-

rounding flora and nascent fields and propagate them selectively (Abbo *et al.*, 2011a). Therefore, we argue for an episodic domestication and consider the proposed protracted (weak and unconscious) selection phase stretching over millennia, redundant.

A wealth of ethnographic data documenting the floristic knowledge of hunters-gatherers is available (e.g., Lévi-Strauss, 1962). For a detailed case, one amongst many, see an account on the Ituri forest foragers (Terashima, 2005; and references therein). Therefore, we doubt whether the portrait of the ‘protracted Neolithic cultivator’ does make justice to our Neolithic ancestors who developed one of the best crop assemblages on Earth (see Abbo *et al.*, 2010b, 2011a). The advancements and innovations in Neolithic times as expressed in a plethora of aspects; e.g., the ‘domestication’ of energy – like the transformative pyrotechnology for limeplaster (e.g., Kingery *et al.*, 1988) and later for pottery production; the ‘domestication’ of water (the EPPNB wells of Cyprus, Peltenburg *et al.*, 2001; and later in the Levant Galili *et al.*, 1993; Garfinkel *et al.*, 2006); wood domestication as seen through tree felling and sophisticated carpentry (Barkai, 2005); or if one wishes the “domestication of Symbols” [and God(s)] (Cauvin, 2000; Stordeur, 2010), need be considered before accepting the assumption that the Neolithic ‘cultivators’ were unable to differentiate between *wild-type* wheat or barley and non-brittle (domesticated) stocks growing in their own fields.

## IV. EVIDENCE FOR PRE-DOMESTICATION CULTIVATION: A CRITICAL CONSIDERATION

Of the arguments in favor of a protracted plant domestication process via a prolonged pre-domestication cultivation period listed above in our introduction we wish to elaborate on the following to illustrate our case.

### A. Weeds of Cultivation

The presence of ‘weeds of cultivation’ is apparently a strong argument attesting for pre-domestication cultivation. However, can one really distinguish in the archaeobotanical data of the relevant periods between species identified as weeds of cultivation and naturally occurring species typical of disturbed and natural habitats regardless of human activity, or ruderal taxa naturally thriving along human (or animal) tracks and trails around the sites, where they may simply have enjoyed some advantages? Does the limited archaeobotanical record of taxa considered as weeds, allow for a statement on the presence of field weeds? And how can such remains be separated from non-food or non-target plants brought into the sites (e.g., Nadel *et al.*, 2004; Abbo *et al.*, 2008b)?

As an example let us consider Tell Abu Hureyra, with its detailed archaeobotanical report (de Moulins, 2000; Hillman, 2000). The Natufian (Layer 1) lists of plants claimed to accompany the cultivated fields are in most cases generally classified to the family and genus levels and rarely to the species level.

In many cases such families or genera include a large number of species of which only one or a few are genuine field weeds and thus the lack of species definitions undermines a reliable statement on their weedy nature. Hillman writes about the plants considered as weeds of cultivation in Natufian Layer 1 that they can be “eventually also weeds of dry land cultivation,” or “plants of wadis, wadi banks, valley bottoms and N-enriched ruderal habitats also eventually weeds of irrigated cultivation (*our addition: weeds on condition the fields were irrigated*) mostly edible” (Hillman, 2000, pp. 343–344, 346), leaving their weediness as indicators of agricultural operations an open question.

Another example is the finds from Natufian Mureybet (Stratum I) (Van Zeist and Bakker-Heers, 1984; and see also Willcox *et al.*, 2008), which is similarly problematic. The botanical identification is again in many cases only to the family and genus level and even if there are finds of possible weeds of cultivation these are very scant – like the three *Gallium* sp. seeds reported by Van Zeist (1970) for the old Mureybet excavation (see also Willcox and Fornite, 1999). We should note that in the Levant the genus *Gallium* includes dozens of species and only one of them (*G. tricornutum*) is a weed of cultivation. Moreover, some *Gallium* seeds appear already in Paleolithic (60–50 KA) Kebara Cave (Lev *et al.*, 2005).

The interpretation of the archaeobotanical remains from Tell Abu Hureyra was a major supporting set of data for claiming pre-domestication cultivation, and for determining the time span of such activities (see summaries in Hillman, 2000; Hillman *et al.*, 2001). Therefore it is important to note that in a recent reassessment of the evidence for cultivation of wild plants at Tell Abu Hureyra, Colledge and Conolly (2010) state as follows: “cultivation is not needed to explain the changes in proportion of plant taxa” (p. 136, therein), and they conclude by stating that a model which does not include cultivation of cereals and legumes in the Late Epipalaeolithic is “more parsimonious” (p. 137, therein).

Finally, we wish to point out two problems with the logic of the ‘weeds of cultivation’ argumentation. First, when one assumes that there was “necessarily a stage of production (cultivation) that precedes morphological domestication” (Fuller, 2007, p. 904), such (presumed weeds) seeds may be interpreted as ‘weeds of cultivation’ (e.g., Willcox *et al.*, 2008; and citations). However, to use the presence of such (presumed weeds) seeds, after making the above assumption (regarding the necessity of the pre-domestication cultivation) as a proof of pre-domestication cultivation, and as a testimony for the protracted nature of the domestication episode is, in our view, a circular argument. Second, if one accepts Willcox’s (2007, p. 33) statement regarding the possibility that cultivation would not have left any “detectable sign in the archaeobotanical record,” how can remains of certain seeds serve as a reliable indication for cultivation? And we wonder, what are the ecological settings that allow cultivation to take place with or without traces?

## B. Variation of Crop Plants under Domestication

The concept of extending plant domestication over millennia of cultivation, made necessary by the presumed inability of the incipient farmers to distinguish useful phenotypes in their crops (Purugganan and Fuller, 2011), is not in accord with the immense body of observations made by ethnographers, agronomists and botanists who studied traditional farming systems (e.g., Elazari-Volcani, 1930; Johannessen *et al.*, 1970; Johannessen, 1982; Harlan, 1995; Ladizinsky, 1998b). The fact that under traditional farming systems crop plants are dynamic populations harboring genetic variation in many agronomic, physiological and nutritional traits is well documented (e.g., Johannessen, 1982; Evans, 1993; Harlan, 1995; Butler and D’Andrea, 2000; Woldeamlak *et al.*, 2008; and see also Abbo *et al.*, 2010b). In such traditional systems, farmers invest time and efforts to select specific types as seed stocks for the coming seasons (e.g., Butler, 2009; Doggett and Majisu, 1968, p. 12 and appendix; Harlan, 1995). This happened (and still happens) to this very day. Despite the evolutionary bottlenecks associated with plant domestication (e.g., Ladizinsky, 1985; Abbo *et al.*, 2003a), the result of such selection and other crop evolutionary processes under domestication is the immense morphological, adaptive, and nutritional profile variants in traditional landraces worldwide (e.g., Johannessen, 1982; Evans, 1993; Harlan, 1995; Ladizinsky, 1998b). Under domestication, many physiological and morphological parameters in traditional crop populations change over time as a result of environmental factors and husbandry operations. These selection processes mediated by the biotic and abiotic factors as well as by man’s conscious selection and husbandry are the main engines of crop evolution (and diversification) under domestication (Evans, 1993; Ladizinsky, 1998b).

As an example, let us consider the argumentation concerning grain size. In chickpea, numerous cultivars (mostly desi) have seeds with indistinguishable size (and some are even smaller) from those of the wild progenitor *Cicer reticulatum* (Figure 1 in Abbo *et al.*, 2009). Therefore, archaeological evidence for increase in seed size over millennia (Purugganan and Fuller, 2011) does not necessarily attest for changes that took place in association with the domestication episode. Willcox (2004) has stated the difficulty to make progress by phenotypic selection for cereals grain size, and stressed the key role of highly conscious selection (of large grained types) from standing variation in the wild. Because Willcox’s data sets were used by Fuller (2007, Fig. 4) and Fuller *et al.* (2010a, Fig. 7.9) to claim for evolutionary trends mediated by unconscious selection, it would have been fair to give the two options (regarding the role of conscious vs. unconscious selection) a similar weight in the discussion.

Based on our (above) distinction between the episodic domestication (event) and later evolutionary changes under domestication, we see the gradual seed size changes (if indeed these are true representations of the relevant crop populations), as a reflection of plant evolution under domestication rather than

a testimony to a protracted domestication process. It should be noted that efforts to increase crops' grain size continue to this very day in numerous breeding programs all over the world. Why therefore declare that wheat, barley, lentil, or chickpea domestication have lasted only two, three or four millennia? Taking this argument to its full extent, maybe one should acknowledge that present-day plant breeders are still engaged in lentil, wheat and barley domestication? In a fascinating account of traditional maize farming in Guatemala, Johannessen (1982) claimed that the domestication process of maize continued to the time of his observations, made during the 1960's and 1970's. In doing so he also severely criticized the role attributed to unconscious selection "at the start of the domestication process" (p. 97, therein).

The slow rate of crop evolution as documented by Purugganan and Fuller (2011) is compatible with the 'founder effect,' which severely narrowed the genetic base of the nascent crops (e.g., Ladizinsky, 1985; Hamblin *et al.*, 2011). This Neolithic selective seed stocking out of a wide array of genetic variation present in the wild progenitors' populations resulted in relatively narrow allelic variation under domestication (Ladizinsky, 1985). Given the polygenic nature of seed size in cereals and legumes, and the reduced allelic variation due to the founder effect, it is therefore no surprise to find a very slow change in seed size even under selection (Willcox, 2004).

### C. Domestication Events or Processes - The Archaeological Record

The evidence for the earliest domesticated plant remains may enable us to show that domestication itself has been quite rapid and the spread of the domesticated plants started immediately upon domestication. Let us discuss two examples, namely wheat and chickpea. For wheat, the earliest archaeobotanical evidence for domestication (non-brittle rachis) was found at EPPNB (spanning most of the second half of the 11th millennium cal. BP) Çayönü (Van Zeist and de Roller, 1991/2); Nevali Çori (Pasternak, 1998); and Cafer Hüyük (following de Moulins, 1993 for both the archaeobotany and the chronology; and see also de Moulins, 1997), all within the proposed core area in south-eastern Turkey (Lev-Yadun *et al.*, 2000). And note wheat finds from Tell Ain el-Kerkh as early as the EPPNB (Tsuneki *et al.*, 2006).

Genetic studies and phytogeographic data lend strong support to this view (see Abbo *et al.*, 2010a) while seemingly opposing views such as Kilian *et al.*'s (2007) or Özkan *et al.*'s (2011) suggesting (pseudo) autonomous multi-domestication events of wheat (einkorn and emmer) are inconclusive. These 'multi-domestication foci' within the proposed southeastern Turkey core area, or bordering it (Mori *et al.*, 2003; Alo *et al.*, 2011) can be seen as the signatures of the early spread of domesticated stocks from the core area (Abbo *et al.*, 2006). This spread continues and shows a clear gradient into Eastern Europe and further west (e.g., Zohary and Hopf, 2000; Colledge *et al.*, 2004, 2005; Pinhasi *et al.*, 2005; Coward *et al.*, 2008; and one may

also refer to the very similar 'old' reconstruction by Braidwood, 1967, 1975).

As for chickpea, the earliest evidence for the domesticated type is meager and originates from just a handful of sites such as Çayönü (Van Zeist and de Roller, 1991/2); Nevali Çori (Pasternak, 1998); and possibly Djade too (note in Tanno and Willcox, 2006b), all within the core area (Lev-Yadun *et al.*, 2000). An interesting case for chickpea is Tell Ain el-Kerkh, 300 km west-southwest of the core area where domesticated types were found in the EPPNB (Tanno and Willcox, 2006b; Tsuneki *et al.*, 2006) together with other legumes and cereals. Chickpea, like wheat (above) may be seen as an illustration for the fast domestication of this crop and its spread from the core area westwards, because Tell Ain el-Kerkh is outside the present-day distribution of the wild progenitor. The study of the archaeobotanical finds from Tell Ain el-Kerkh promoted some questions concerning the accepted chickpea domestication model. No doubt was cast on whether the progenitor of domesticated chickpea is indeed *Cicer reticulatum*. Questions were, however, raised (based on the relatively meager dataset on the distribution of the progenitor) on whether its present geographical distribution is relevant to the time of domestication and whether the suggested monophyletic model still holds in light of claims made by Allaby and Brown (2003, 2004; and see Tsuneki *et al.*, 2006; Tanno and Willcox, 2006b; Allaby, 2010). We believe that both these questions find good answers. The distribution aspect was dealt by Willcox (2005) who concluded that present day distribution of the Near Eastern cereals is similar to the early Holocene situation. Therefore, we see no *a priori* reason to assume that the range of the wild legumes have changed significantly over the same time span. The other question was dealt with by Salamini *et al.* (2004), Ross-Ibarra and Gaut (2008), Heun *et al.* (2008), Honne and Heun (2009), and Haldorsen *et al.* (2011) who casted severe doubt on the model and conclusions of Allaby and Brown (2003) and Allaby *et al.* (2008a), and see also review by Abbo *et al.* (2010a). Given the above, the available data on chickpea finds, coupled with the C<sup>14</sup> record available from the EPPNB both at Tell Ain el-Kerkh and other sites may suggest a fast spread of domesticated chickpea out of the core area in south-eastern Turkey to northwestern Syria. The data from Cyprus including domesticated emmer, einkorn, and hulled barley, remains of lentil sp., other large seeded legumes and flax (*Linum* sp.) (Peltenburg *et al.*, 2001; Colledge, 2004; Colledge and Conolly, 2007) tend to further support the above reconstruction for cereals and may be for legumes and flax as well.

Let's consider these two examples to illustrate our point *vis à vis* the protracted model. If we follow Purugganan and Fuller's (2011) arguments and use the data presented by Tanno and Willcox (2006a, Fig. 1F), domestication was a process which has continued for several thousands of years starting in the very beginning of the PPN (at the site of Qaramel) sometime around almost 12,000 cal. years ago and not yet fully accomplished in the PN (Kosak Shamali site) some 7,500 cal. years ago. It is clear that [by Purugganan and Fuller's (2011) terms] while

this process was still on-going in the Near East [incomplete, because full dominance (100%) of domesticates was not yet achieved; or, can domestication be declared as completed when the domesticated type reaches 50-60-70-80 or 90% of the population?], in Europe, fields were already fully dominated by domesticated types (Coward *et al.*, 2008). For details see the site of Scamuso in Italy in a layer dated to the early eight Millennium cal. BP with einkorn and emmer, hulled barley as well as lentil and pea; or the Grotta dell'Uzzo in Sicily, a layer dated to the ninth Millennium cal. BP with einkorn, emmer, barley and lentil (Zohary and Hopf, 2000, p. 229). In other words, accepting the emerging protracted paradigm (Fuller, 2010) one has to assume that plant domestication (be it a process or an episode) was already completed in Europe while at the same time, the Near East Neolithic cultivators, being unable to distinguish brittle from non-brittle stocks (Purugganan and Fuller, 2011) were still "waiting" for the conclusion of the slow unconscious (automatic *sensu* Zohary, 2004) selection process in favor of non-brittle types which was taking place (albeit unnoticed) in their fields.

Wouldn't this, by definition, mean that plant domestication in Europe preceded domestication in the Near East? Shouldn't this logic lead to a statement that cereals were domesticated in Europe rather than in the Near East?

Indeed, Jones and Brown (2007, p. 46) stress that reproductive isolation of the 'predomesticated crop' must have preceded morphological domestication (e.g., attainment of non-brittle ear stocks of wheat or barley). In other words, Jones and Brown (2007) suggest that geographic expansion of 'predomesticated crops' towards the edge of the natural range of the wild progenitors, has created the opportunities for genetically distinct (e.g., cultivated emmer) populations to develop by way of reproductive isolation from their conspecific wild stands thriving across the oak pistachio woodland belt of the Fertile Crescent. Stated differently, emmer and einkorn wheat are unlikely to have been domesticated in the Near East, but elsewhere. Likewise, Allaby (2010) casts doubts: "... is it even possible for domestication to occur within the biogeographical range of the wild progenitor" or, in other words, is domestication possible before the cultivated (non-domesticated) stocks were taken out of their natural range? This is reminiscent of the response of Jones *et al.* (1998) to the pioneering study by Heun *et al.* (1997), with a similar statement. Can the alleged protracted process of domestication go on in the Near East while it has already been completed in Europe? Accepting this logic, should we start looking for a European center of domestication from which domesticated forms spread eastwards or at least the European source (core area) of the new ideas that opened up the eyes of the short-sighted cultivators in the Near East who could not consciously differentiate brittle from non-brittle cereals forms in their fields (Purugganan and Fuller, 2011)?

This extreme view ignores observations indicating that *wild-type vs. domesticated* phenotypes can be maintained even in the presence of gene flow (e.g., Papa and Gepts, 2003; Papa *et al.*,

2005, 2007). It also ignores the fact that stocks with similar phenotypes were "on the shelf" - the so called standing genetic variation mentioned by Doebley *et al.* (2006), Tang *et al.* (2010), Davies and Hillman (1992, pp. 212-213), and Honne and Heun (2009). We think that such an approach confuses between the socio-cultural and the biological aspects of plant domestication - between 'birth' (domestication episode) and 'growth.' Similarly, the definition of domestication as a (millennia long) protracted process confuses the domestication episode itself with crop evolution under domestication, and/or the process of the emergence of agriculture as an economic system (see later).

## V. DISCUSSION

The debate concerning the nature of plant domestication in general and in the Near East in particular is conducted within three intellectual spheres. One sphere concerns aspects of the biology of the crop plants and their wild progenitors, their biogeography, ecology, physiology, reproductive biology, genetics, and agronomy, upon which most of our above arguments are founded. The second circle concerns aspects of human culture and behavior, which are fundamental to the question regarding the role of conscious *vs.* unconscious processes in plant domestication and later crop evolutionary processes (discussed below). And the third one encompasses the context of the students of the subject and how it shapes their intellectual assumptions and affects their interpretation of evidence (*sensu* Harris, 1989).

### A. The Role of Conscious vs. Unconscious Selection

Our work on the domestication of Near Eastern grain legumes lends strong support to the notion of a highly conscious and knowledge-based domestication episode. This includes the selection for nutritionally superior chickpea types (Kerem *et al.*, 2007), the ancient selection of vernalization-insensitive chickpea types and the invention of the summer cropping to stabilize its yields (Abbo *et al.*, 2003b). The fact that domesticated plants in the Near East appear in the form of a balanced 'crop assemblage' (Zohary and Hopf, 2000, pp. 246; and see Gepts, 2004) with a very good yield buffering ability (Abbo *et al.*, 2010b) and nutritional and agronomic complementation between cereals and legumes (Gepts, 2004) is a testimony to the deep biological insight of the early Neolithic farmers and the thoughtful recruitment of crop species. Similarly, Ladizinsky's (1987, 1989, 1993) work on wild lentils, which was severely criticized by Zohary (1989) and Blumler (1991) and flatly dismissed by Davies and Hillman (1992, p. 201), also points in this direction by showing that lentil 'cultivation' is highly unlikely to have taken place prior to the availability of a free germinating stock (Ladizinsky, 1987). Indeed, the meager yield of naturally occurring wild lentil populations corroborates Ladizinsky's contention by stressing the fact that wild lentil is unlikely to have been a staple for hunters-gatherers (Abbo *et al.*, 2008b). Therefore, it is impossible to view lentil domestication as an outcome of a long mutual interdependence of a predator-prey interaction (man-lentil liaison) *à la* Rindos (1980), as a result of weedy

tendencies (Hawkes, 1970; Abbo *et al.*, 2005) or in terms of niche construction activities (Smith, 2007; Laland and O'Brien, 2010; Rowley-Conwy and Layton, 2011). Similarly, recent experimental cultivation of wild pea (Abbo *et al.*, 2011b) suggests that pea domestication is also unlikely to have resulted by way of a protracted unconscious selection process. The alternative, of course, is a knowledge-based, well-focused, and highly conscious domestication episode. After all, rather than considering plant domestication as a result of long-term mutualism, the present-day interdependence of mankind and crop plants on each other can be seen as the result of the domestication episode and later crop evolution processes.

## B. The Methodological Implications of the 'Protracted Domestication' Assumption

As noted by Harris (1989), proper definitions of 'cultivation,' 'domestication,' 'agriculture,' and other terms are highly important, and not just for semantic reasons. This is because the way such terms are understood by students of the subject directly affects the layout of experiments and, most importantly, data (archaeological, biological, agronomic, etc.) treatment and literature interpretation and integration into a coherent reconstruction. These definitions (see Box 1) are especially relevant to the interpretation of genetic differences, as measured at both the DNA and gene expression levels, between crop plants and their wild progenitors.

Doebley *et al.* (2006) reviewed two approaches for identifying the molecular genetic basis of 'crop domestication,' later termed by Ross-Ibarra *et al.* (2007) as 'Top-down' and 'Bottom-up' approaches (see also Gross and Olsen, 2010; Hamblin *et al.*, 2011). The starting point of the first (classical) approach is the phenotype (e.g., non brittle *vs.* brittle rachis in Near Eastern cereals), and special populations are then used to study the genetic control (e.g., Peleg *et al.*, 2011) and later map and clone such major genes (or QTL) affecting those phenotypes (e.g., Dorweiler *et al.*, 1993; Doebley, 2004; Uauy *et al.*, 2006). The second approach is based on population genetic tools to compare the wild *vs.* domesticated gene pools by estimation of selection signatures, demographic history and past evolutionary bottlenecks. In this approach it is possible to obtain genome-wide information on all regions, which were subject to selection or genetic drift (either direct, or indirect – conscious or unconscious), without *a priori* assumptions about the role of any specific phenotype(s) (Doebley *et al.*, 2006; Ross-Ibarra *et al.*, 2007; Hamblin *et al.*, 2011).

According to Ross-Ibarra *et al.* (2007), the major drawback of the top-down approach is that it can identify only the genomic regions affecting the phenotypic changes thought to be associated with the domestication phenotype (e.g., loci determining rachis brittleness in cereals or pod dehiscence in legumes). This is exactly the advantage of the second approach with which one is not limited to the tagging of genomic regions affecting *a priori* determined phenotypes (therein). However, as noted by Doebley *et al.* (2006) the latter approach will identify regions

associated with the domestication episode as well as regions associated with all later selection events, which were part of the on-going crop evolutionary history under domestication; termed 'crop improvement signatures' by Doebley *et al.* (2006).

Decades of pea genetic studies, following the 'top-down' attitude have led Weeden (2007) to indicate that a minimum of 15 genes, in addition to few major quantitative trait loci (QTL) were critical to the pea domestication process. However, based on Ladizinsky's (1987, 1989, 1993) arguments and our experimental wild pea nurseries (Abbo *et al.*, 2011b), we argue that it is only the seed dormancy trait that can be regarded as 'critical' to pea domestication *sensu strictu*. There is no doubt that pea stocks (and likewise lentil and chickpea) with indehiscent pods would minimize yield losses, but such a trait is not an imperative for profitable pea growing (Abbo *et al.*, 2011b). With the possible exception of seed quality (including taste) QTL, the other traits listed by Weeden (2007, Table 1) may have evolved at any time during pea evolution under domestication that followed the domestication episode. Of course, genes linked to the dormancy locus in which allelic changes may have occurred as a correlated response to the initial selection, would also be flagged by top-down analyses.

Recently, Burke *et al.* (2007) have noted that differentiating between 'domestication-related' and 'improvement-related' genes is not a matter of academic curiosity, and stressed the importance of such differentiation for the study of crop evolution and future breeding. This distinction, by definition, implies that one deals with two groups of traits, each with its own different evolutionary history. Indeed, Hamblin *et al.* (2011) argue that the selective history of crop plants and their population genetic structure interact in complex ways with the standing genetic variation. Such complex interactions may result in different genetic architectures, of the respective traits of interest and, therefore, bear important implications for our ability to further manipulate crop plants for desirable phenotypes. Although without specifying the respective time frames, these authors referred to the impact of domestication in terms of genetic bottlenecks and phenotypic selection, and also to 'ongoing evolution under domestication,' thereby implying two distinct phases in crops' histories (Hamblin *et al.*, 2011). The recognition that the domestication bottlenecks did not only involve mere reduction in population size, but also strong novel selection operating on suites of traits, grants the reconstruction of crops' evolutionary histories a special importance. This is because under such circumstances the distinction between mono- or poly-phyletic origins, geographically focused, or highly diffused origins, and protracted or contracted domestication episodes (each with its different population dynamics and selection profiles) become highly significant (Abbo *et al.*, 2011a). This is because of the unique effects of each of the above options on the genetic pathways underlying agronomic (and other) traits, as well as the genetic architecture of the nascent crops populations as a whole. Therefore we argue that a reliable reconstruction of evolutionary histories of crops is primarily dependent upon intimate

understanding of all aspects of the biology of the respective crops and their wild progenitors.

The lentil (Ladizinsky, 1987, 1989, 1993; Zohary, 1989; Blumler, 1991), chickpea (Abbo *et al.*, 2003b; Kerem *et al.*, 2007), pea (Abbo *et al.*, 2011b) and wheat (Peleg *et al.*, 2011) cases are good illustrations to the imperative of obtaining deep understanding of the biology of crop plants and their wild progenitors. Such understanding is fundamental for defining the ‘critical’ domestication traits for each and every crop plant, based on its specific biological features, and for differentiating those critical traits from other features known to differ between the cultigens and their wild progenitors (Gross and Olsen, 2010, p. 533). No less important, intellectual assumptions [e.g., the necessity of a pre-domestication cultivation stage (e.g., Fuller, 2007), the need for reproductive isolation from the wild progenitor (e.g., Jones and Brown, 2007), the occurrence of Neolithic labor traps (Fuller *et al.*, 2010b) the lack of rationality in Neolithic decision making (Barker, 2011), or the role of seed dormancy vs. pod shattering in legumes domestication (Zohary, 1989)], cannot possibly replace agronomic and biological understanding of crop plants and their wild progenitors.

It is in this context that our attempt to separate between the domestication episode (event) and the following crop evolutionary long-term history comes into play. We argue that by assuming a protracted domestication process, which lasted for millennia (e.g., Barker, 2006, pp. 396–397; Tanno and Willcox, 2006a; Allaby *et al.*, 2008a, 2008b; Brown *et al.*, 2009; Fuller, 2010; Purugganan and Fuller, 2011, and citations), one (by definition) needlessly opts to operate within an intellectual framework that does not allow to differentiate between the decisive (critical) domestication loci and genomic regions which have evolved later during the crop dissemination and improvement phases (Jones and Liu, 2009, last statement), which followed the domestication episode in the so-called ‘living fields’ (Harlan, 1995).

To illustrate the consequence of this lack of delimitation between the domestication episode and following crop evolution processes we present the following examples. First, is a book chapter by Rindos entitled ‘Darwinism and its role in the explanation of domestication.’ In his introduction, Rindos (1989) stated that his intent is to shed some light on the evolution of agricultural systems, by looking at human culture and culture change. Indeed, most of the concrete examples given to support his mostly theoretical discussion concern the adoption of maize by prehistoric communities of the area known as the American Bottom at about 800 AD, after being ‘incidental domesticators’ of local nut-bearing trees and starchy and oily native seed plants (Rindos, 1989). While a change in the crop repertoire is certainly an interesting case of evolution of agricultural systems, and must have required that the introduced (Mesoamerican) species harbored adequate adaptive genetic variation to allow successful cropping in the new region, in our view it could hardly be argued to be relevant in any way to the episode of maize domestication, which, according to Piperno and Flannery (2001), occurred in

present-day Mexico more than five millennia earlier. Second, the short note on agricultural transition as a *historical process* (*italics* in original) by Zvelebil (2009), who argued that the origin and dispersal of farming can be comprehended in terms of a three-phase availability model; namely, the availability phase (equivalent to our invention phase), the substitution phase (representing the negotiation-adoption of our model), and the consolidation phase representing the period of a fully established agro-economic system (Zvelebil, 2009). We do not deny the rationale of these phases as descriptors of the cultural dynamics both in the origin of agriculture and in the dispersal of agriculture. However, the concrete examples given by Zvelebil (2009) mostly concern the adoption of the Near Eastern package by the complex “transegalitarian” hunter-gatherer communities of Europe. There is no doubt that such modeling is instrumental in explaining such transitions to agriculture by way of migration, cultural contact, trade or else. However, while such geographic movement of crops and livestock must have involved major evolutionary changes in the relevant crop populations similar to those documented by Jones *et al.* (2008), van Heerwaarden *et al.* (2011) and Erskine *et al.* (1998, 2011), we cannot see its relevance to plant domestication in a world with NO adjacent (or indeed remote) farming communities.

## VI. CONCLUDING REMARKS

Near Eastern plant domestication was basically a cultural move initiated by Neolithic sedentary hunter-gatherer societies. Thus, the study of plant domestication should consist of an integration of botanical, ecological, agronomic, genetic and archaeological (cultural or socio-cultural) evidence. Plant evolution under domestication, however, is an independent (albeit related) school of thought (e.g., Evans, 1993; Ladizinsky, 1998b), in the past mostly relying on agronomic, genetic, and ethnographic knowledge, and today also on “bottom-up” approaches (e.g., Doebley *et al.*, 2006; Burke *et al.*, 2007; Ross-Ibarra *et al.*, 2007; van Heerwaarden *et al.*, 2011). It should be noted that the socio-cultural dynamics critical to the understanding of plant domestication (the episodic invention phase) and its adoption may contribute only little to the study of crop evolution under domestication.

Similarly, understanding the adaptive evolutionary processes involved in the spread of crop plants out of their ‘core domestication area’ (*sensu* Lev-Yadun *et al.*, 2000; Gopher *et al.*, 2001; Abbo *et al.*, 2006, 2010a) into and across different agro-climatic zones (e.g., Badr *et al.*, 2000; Jones *et al.*, 2008; van Heerwaarden *et al.*, 2011) can make only a minor contribution to clarify the fundamentals of plant domestication episodes in their pristine core areas. A good illustration to this point is the case of the barley photoperiod response genes studied by Jones *et al.* (2008). These authors have demonstrated that wild barley from Iran is the likely source of the photoperiod nonresponsive *ppd-H1* phenotype prevalent in certain European barley landraces (Jones *et al.*, 2008), and therefore concluded that their finding is in accord with a presumed area of barley domestication east of

the Fertile Crescent as suggested by Morrell and Clegg (2007). However, without any supporting archaeological evidence for the presumed (Oriental) barley domestication center (see Abbo *et al.*, 2010a) the finding by Jones *et al.* (2008) may as well be interpreted as the likely result of crop evolution under domestication processes. Namely, that during the spread of domesticated barley eastward, natural mutations and/or introgression with surrounding locally adapted wild *H. spontaneum* occurred, which enriched the domesticated stocks with naturally occurring advantageous local alleles, similar to the process documented for maize (van Heerwaarden *et al.*, 2011). This (and other) introgressed genetic variation have enabled to expand barley cropping into the temperate high-latitude growing regions of Europe as expressed in the latitude dependent geographic gradient of the barley *ppd* polymorphism (Jones *et al.*, 2008). Indeed, a similar latitude-associated photoperiod response gradient exists in domesticated lentil (Erskine *et al.*, 1990, Fig. 5), but was never interpreted as related in any way to lentil domestication, but rather as the long-term process of lentil evolution under domestication (Erskine *et al.*, 1998, 2011).

Therefore, in our view, the ‘protracted domestication’ assumption, while providing an apparently harmonic and easy to comprehend scenario, lacks experimental (and other type of) support. It is thus not only unacceptable, but it is also not helpful in understanding the foundations of Near Eastern plant domestication, nor is it helpful for the study of crop evolution under domestication. Upon critical inspection of the arguments, and with mounting experimental evidence against its basic assumptions (e.g., Abbo *et al.*, 2011b; Peleg *et al.*, 2011), the protracted domestication model appears to undermine the resolution power of the study of plant domestication and crop evolution and emerges as an intellectual construct (*sensu* Harris, 1989) rather than as an evidence-based model.

In our final notes we wish to resort to the (above) third sphere of discussion concerning the intellectual spheres within which students of plant domestication operate. First, we find it peculiar that criticism of the theoretical basis of the phylogenetic analyses (Allaby and Brown, 2003, 2004; Allaby *et al.*, 2008a, 2008b, 2010; Allaby, 2010) was aimed mostly at studies performed with Near Eastern cereals (Heun *et al.*, 1997, 2008; Badr *et al.*, 2000; Özkan *et al.*, 2002, 2005; Salamini *et al.*, 2002, 2004; Honne and Heun, 2009). Problems related to the theoretical foundations of the procedures used to compute the genetic similarity parameters used to identify the geographic origin of crop plants, based on DNA profile of living plants (e.g., Allaby, 2010; Gross and Olsen, 2010), have far reaching implications. Therefore, if valid, such theoretical considerations should have been applied to numerous studies which have suggested single origin of crops which include: maize (Matsuoka *et al.*, 2002), potato (Spooner *et al.*, 2005), sunflower (Harter *et al.*, 2004), pearl millet (Oumar *et al.*, 2008), Meso-American common bean (Kwak *et al.*, 2009), soybean (Guo *et al.*, 2010), cassava (Olsen and Schaal, 2001), African rice (Li *et al.*, 2011), and indeed Asian rice as well (Molina *et al.*, 2011).

Second, a growing number of scholars recently describe the transition from foraging to farming and domestication of plants in terms of niche constructions (e.g., Smith, 2007; Laland and O’Brien, 2010; Rowley-Conwy and Layton, 2011). Some even suggest that “farming originated not as a deliberate process of intensifying resource production, but as a series of small, accidental changes in the way that niches were constructed” (Rowley-Conwy and Layton, 2011). Such claims, thereby, imply that niche construction activities can be seen as exerting non-deliberate and therefore unconscious selection pressures on the surrounding biota, which in turn exposed the rarely occurring mutants thereby giving rise to domesticated plants. At the same time, these authors describe the intimate natural knowledge of the hunter-gatherers as expressed in the intricate ways with which they may have managed wild gazelle herds, or other game populations (Rowley-Conwy and Layton, 2011, pp. 852–853). Therefore, the role of a ‘cultural regressive’ stage in this reconstruction of the prehistoric processes is puzzling. Namely, what is the basis for the assumption that the early Neolithic farmers have abandoned their immense natural knowledge and high awareness in favor of unconsciousness? Apparently, without such a component in the reconstruction, one needs not assume that the early Neolithic farmers have had to wait “between one and two or even three millennia, as the frequencies of the non-shattering form gradually increased” (Rowley-Conwy and Layton, 2011, p. 856). Of course, such an approach is in line with the conclusions of Purugganan and Fuller (2011) regarding the inability of the Neolithic farmers to identify subtle changes in the composition of their plant populations, let alone to differentiate between brittle- and non-brittle ear types in their fields (therein).

Third, Jones and Brown (2007, p. 46) have recently stated the following: “The fully domesticated crop therefore emerges when the predomesticated population goes beyond the edge of the wild range and becomes reproductively isolated.” Similarly, Allaby (2010, p. 938) suggested that dominance of the domesticated genotypes in the cultivated plant populations might have been achieved only out of the natural range of the wild progenitors. This is because only out of the biogeographic context of the wild progenitors no introgression of wild-type alleles could have occurred, thereby ‘liberating’ the nascent crops from the load of wild-type alleles contamination (Jones and Liu, 2009). That is, escaping the introgression of *WT* alleles of spike disarticulation genes in cereals from wild cereals stands surrounding the ancient Near Eastern fields. Accordingly, Allaby (2010) suggests that domestication might have been the result of human expansions out of the natural range of the wild progenitors. In the Near Eastern context, this means that plant domestication was possible only west and northwest of the Balkans, south of the Levant, and east of the Kopet-Dag range in Iran-Turkmenistan, where most of the wild progenitors of the Near Eastern crops (except from *Hordeum spontaneum*, *Lens orientalis* and *Linum bienne*) are not native. Such a claim must be based on implicit or explicit assumptions similar to Purugganan and Fuller’s (2011)

statement about the inability of Neolithic cultivators to distinguish brittle rachis from non-brittle rachis types in their cereals fields. Otherwise, why need present-day students of the subject (e.g., Jones and Brown, 2007; Allaby, 2010), or the incipient Levantine cultivators in antiquity worry about introgression of brittle rachis alleles from the wild as an obstacle for domestication? In our view, the requirement for biogeographic (and therefore cultural) isolation (Jones and Brown, 2007) for domestication together with portraying the Near Eastern Neolithic ‘cultivators’ as unable to selectively propagate useful and/or desired stocks is in a way akin to an Orientalistic world-view (Said, 1979).

## NOTE

1. Based on the on-line Cambridge, Merriam-Webster and Oxford dictionaries, we herein use the word ‘episode’ to denote the following: A single event; an event that is distinctive; an incident or period considered in isolation. In our discussion herein, the term ‘domestication episode’ is used as opposed to the notion of protracted domesticated process for the origins of crops (Abbo *et al.*, 2011a).

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