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Narrowing the harvest: Increasing sickle investment and the rise of domesticated cereal agriculture in the Fertile Crescent

Osamu Maeda [a], Leilani Lucas [b], Fabio Silva [b], Ken-Ichi Tanno [c], Dorian Q. Fuller [b, *]

[a] *Institute for Comparative Research in Human and Social Sciences, University of Tsukuba, Tsukuba 305-8571, Japan*
[b] *Institute of Archaeology, University College London, London WC1H 0PY, United Kingdom*
[c] *Faculty of Agriculture, Yamaguchi University, Yamaguchi 753-8515, Japan*

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ABSTRACT

For the first time we integrate quantitative data on lithic sickles and archaeobotanical evidence for domestication and the evolution of plant economies from sites dated to the terminal Pleistocene and Early Holocene (ca. 12000–5000 cal. BCE) from throughout the Fertile Crescent region of Southwest Asia. We find a strong correlation in some regions, throughout the Levant, for increasing investment in sickles that tracks the evidence for increasing reliance on cereal crops, while evidence for morphological domestication in wheats (*Triticum monococcum* and *Triticum dicoccum*) and barley (*Hordeum vulgare*) was delayed in comparison to sickle use. These data indicate that while the co-increase of sickle blades and cereal crops support the protracted development of agricultural practice, sickles did not drive the initial stages of the domestication process but rather were a cultural adaptation to increasing reliance on cereals that were still undergoing selection for morphological change. For other regions, such as the Eastern Fertile Crescent and Cyprus such correlations are weaker or non-existent suggesting diverse cultural trajectories to cereal domestication. We conclude that sickles were an exaptation transferred to cereal harvesting and important in signalling a new cultural identity of "farmers". Furthermore, the protracted process of technological and agricultural evolution calls into question hypotheses that the transition to agriculture was caused by any particular climatic event.

1. Introduction

The origins of agriculture transformed the social and natural worlds. Key plant species were transformed into domesticated crops, their micro-habitats became new ecosystems for weeds and pests (Willcox, 2012), and their annual seed produce was co-opted into cycles of harvest, storage and planting by people (Fuller, 2007; Harlan et al., 1973). During the same process human societies, economies and technologies changed, as sedentism increased (Belfer-Cohen and Goring-Morris, 2011), population densities increased (Kuijt, 2000) and subsistence shifted increasingly towards more intensive management of cultivated environments and land-ownership/private property (Bowles and Choi, 2013), as opposed to extensive hunting and gathering in communal territories. The development of agriculture was an entangled process where human society and the natural environment interplayed. Much of this process, however, remains poorly understood or actively debated. For example, there has been active debate between a hypothesis of rapid domestication driven by conscious human selection (Abbo et al., 2010a; Honne and Heun, 2009), and a protracted process in which selection pressures were lower and domestication traits were the unintended outcomes of human behavioural strategies of environmental management and species propagation (Allaby et al., 2010; Asouti and Kabukcu, 2014; Fuller et al., 2014). While the rapid expansion of archaeobotanical data over the past decade has provided more robust and quantitative models of crop evolution, which strongly favours slower domestication processes and weaker coefficients of selection of crops (Fuller et al., 2014; Purugganan and Fuller, 2011; Riehl et al., 2013; Tanno and Willcox, 2012), the integration of these data with evidence for human technologies, settlement structure and activity patterns has been more limited (Asouti and Fuller, 2013; Watkins, 2008). In the current contribution we present a comprehensive

Abbreviations: PPNA, Pre-Pottery Neolithic A period; PPNB, Pre-Pottery Neolithic B period; PN, Pottery Neolithic period.

* Corresponding author. University College London, Institute of Archaeology, 31-34 Gordon Square, London WC1H 0PY, United Kingdom.
E-mail address: d.fuller@ucl.ac.uk (D.Q. Fuller).

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and quantitative reanalysis of non-obsidian stone harvesting tools, i.e. sickle blades, from across the Fertile Crescent zone of Southwest Asia from ca. 12,000 to 5000 cal. BCE in order to trace the development of early agricultural practices (Fig. 1). For the first time large-scale, regional quantitative data on sickle use is directly compared to quantitative archaeobotanical evidence for the transformation of cereal crops towards morphologically domesticated forms, and the transformation in plant economies towards increasing reliance on crops over gathered wild foods. Our analysis, using quantile regression (detailed below) statistically examines a correlation between increasing use of, and investment in, sickle blades and increasing reliance on cereal crops, while at the same time questions a connection between sickle harvesting and evolution of non-shattering cereals (contrary to what has often been proposed, e.g., Wilke et al., 1972; Hillman and Davies, 1990). The paper below elucidates these patterns through a detailed consideration of regional lithic and archaeobotanical variation anchored to a uniformly applied chronometric timescale.

2. Harvesting and protracted domestication as entanglement of technology and ecology

The transformations of domestication can best be appreciated as a co-evolutionary entanglement between plant adaptations, human socioeconomic systems and technology. Many of the key traits that define the domestication syndrome in cereal crops can be tied directly to selection pressures caused by human actions, which modified the seed dispersal and germination parts of the plants' life cycle (Fuller and Allaby, 2009; Harlan et al., 1973). Thus, for example, harvesting methods that retain the entire cereal ear, such as uprooting or cutting by sickle, will favour non-shattering morphotypes, which have lost the wild type adaptation of spikelet dehiscence (Fuller et al., 2014; Harlan et al., 1973; Hillman and Davies, 1990). Larger seeds that lack germination inhibition will better compete at becoming established parts of crops planted in freshly tilled fields in contrast to smaller-seeded and dormant forms (Cunniff et al., 2014; Fuller, 2007; Harlan et al., 1973; Kluyver et al., 2013). There are, however, trade-offs from a human point of view. Non-shattering ears may be easier to harvest if one first invests in making tools, such as sickles for this purpose. However, once harvested, spikelets must be separated by threshing, which is not necessary for gathered mature spikelets; dehusking is required of both wild and domesticated cereals. Therefore, there are some additional labour investments, in sickle production and threshing, which become incumbent on the cultivators of domesticated cereals (Fuller et al., 2010). In addition, cultivated fields likely require some nutritional supplementation if they are to remain in use and support larger-seeded, more erect and tightly spaced domesticated plants.

Much recent discussion has cast agricultural origins as a particular form of ecological niche construction (Smith, 2011; Zeder, 2015). In this sense human activities of soil preparation, planting and harvesting created a new environment for crop life cycles, especially with regards to seed dispersal and germination. At the same time this economic environment, that included cultivation, formed a new niche to which humans had to adapt through labour investment, technology and cultivation practices. While for the plant, evolution can be seen as adaptation through natural selection for genetic changes, the evolution for the humans was phenotypic in the sense that it was cultural. As argued by Larson et al. (2013) such evolution fits the definition of exaptation (Gould and Vrba, 1982), in that existing techniques and technologies were co-opted into a new use and then gradually improved and modified for that purpose. One likely example of this is sickles (Fuller, 2007). In the case of Chinese rice domestication in the Yangtze, clear sickle tools only appear a millennium after morphological domestication (Fuller et al., 2007, 2009), and millennia after the start of cultivation. By contrast, in Southwest Asia sickles were in use for millennia before accepted evidence for pre-domestication cultivation (Willcox et al., 2008), suggesting that they were used for other tasks or a wider range of plant cutting needs. This contradicts the hypothesis that sickles were developed as part and parcel of domesticating cereals (Hillman and Davies, 1990; Wilke et al., 1972). Instead, there is a more complex relationship between the adoption of sickles for cereal harvesting with the evolution of domesticated cereals and the increasing importance of cereals economically.

3. The use of sickles and sickle blades in the Fertile Crescent

The use of sickles for harvesting cereals can be attested in the archaeological record by the presence of sickle blades, a common stone tool used in prehistory. Sickle blades are usually made of flint or chert and used by being inserted in a wooden or bone handle, as evidenced in rare examples of complete sickles which have survived to date (Borrell and Molist, 2007; Edwards, 2007) or inferred

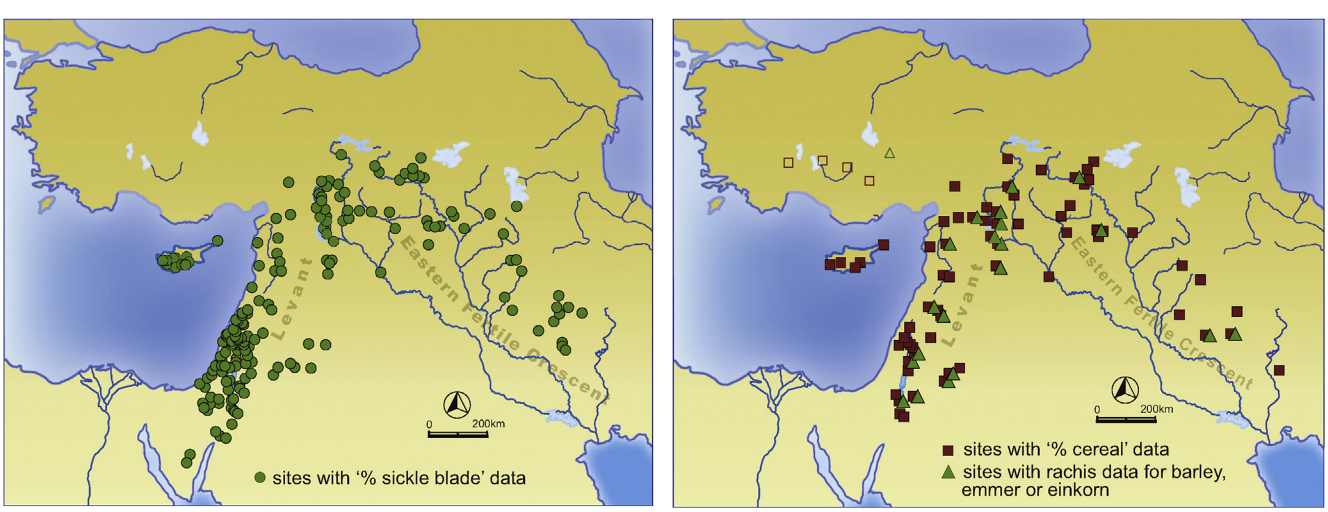


Fig. 1. Map of the Fertile Crescent showing the sites with the data for sickle blades and cereals.

from the trace of fixative remaining on their surface (Copeland and Verhoeven, 1996; Milevski et al., 2013). They are distinguished from other stone tools by having characteristic gloss, i.e. sickle gloss or sickle sheen, visible along the edges of blades. The gloss indicates their function as cereal harvesting tools since it is formed when used for cutting silica-rich plants, such as sedges or grasses, including wheat and barley (Fullagar, 1991).

The use of sickle blades in association with the development of agriculture has been investigated by various researchers particularly through typological studies (Cauvin, 1983; Gopher, 1989; Gopher et al., 1996) and microscopic use-wear analysis (Anderson, 1999; Clemente and Gibaja, 1998; Goodale et al., 2010; Unger-Hamilton, 1985; Vardi et al., 2010). It has been assumed that increasing use of sickle blades and their typological change throughout the Neolithic reflect an important role of sickle blades which contributed to increasing productivity of cereal crops (e.g. Borrell, 2015; Vardi and Gilead, 2013). However, such an assumption has never been tested against archaeobotanical data and often ignores regional diversity in agricultural development. The full-scale quantitative analysis of sickle blades, alongside archaeobotanical evidence for their harvested plant products, has not previously been undertaken. Here we do so on a chronological and geographical scale comparable to macro-regional processes of crop domestication and the transition to agriculture, facilitating comparison with regional archaeobotanical data.

4. Archaeobotanical trends in cereal domestication and consumption

Rather than seeing domestication and the origins of agriculture as a single “revolution”, recent research has indicated a protracted episode of evolution, in which both morphological domestication evolved slowly and the reduction in use of diverse wild foods declined gradually (Asouti and Fuller, 2012, 2013; Fuller et al., 2014). Non-shattering rachises is usually seen as a key trait making grain crops dependent on humans for reproduction by removal of the natural seed-dispersal mechanisms (Hillman and Davies, 1990; Zohary, 1969). In archaeological cereal remains this difference is documented by the preserved abscission scar on the base of the spikelets of the rachis segments (Fuller, 2007; Tanno and Willcox, 2006; 2012; Weide et al., 2015). Rather than the rapid replacement of shattering with non-shattering predicted under a strong selection model that assumed application of sickle harvesting from the beginnings of cultivation (Hillman and Davies, 1990), archaeobotanical evidence that has become available mostly in the past decade, for two wheats (*Triticum monococcum* and *Triticum dicoccum*) and barley (*Hordeum vulgare*) indicates a much more gradual transition to dominance in non-shattering rachises, taking 2000–2500 years (Fuller, 2007; Fuller et al., 2014; Tanno and Willcox, 2012).

5. Materials and methods

5.1. Chronology

The chronology of the lithic and botanical assemblages comes from available published radiocarbon dates (Table S1), and for a number of the sites, calibration information can be found in the supplementary material of Asouti and Fuller (Asouti and Fuller, 2013; Fuller et al., 2012). The dates were converted to a point estimate of age based on the median of summed calibrated radiocarbon dates, as described in Fuller et al. (Fuller et al., 2012, 2014). By this method all available dates for a site, or phase, were recalibrated and summed with OxCal 3.10 (Bronk Ramsey, 1995), using the IntCal13 calibration curve (Reimer et al., 2013). The median of the 1-sigma probability distribution was used.

This has the advantage of readily identifying and downplaying outlier dates in sites that have multiple dates, as the summed probability emphasizes the overlaps in like chronological range. The resulting median generally represents an estimate of the calibrated range that is most likely to fall during the site occupation and towards the middle of the timespan over which our studied assemblages formed. The summed probability approach has been used to combine multiple dates from single sites in regional studies of summed radiocarbon probability that use dates as data to infer demographic trends (e.g. Shennan and Edinborough, 2007; Shennan et al., 2013; Borrell et al., 2015; Flohr et al., 2015), and has been found to be a robust means of representing individual sites. While there has been debate over the use of summed probability plots at the regional level as proxies of past population (e.g. Williams, 2012), the approach has been robustly statistically tested (Timpson et al., 2014). In any case, our purpose is not demographic trends but merely to arrive at the best possible point estimate for placing assemblages in time, and therefore to understand general chronological trends in the use of cereals and sickle blades rather than to establish a very precise chronology for the start date, end date or occupation duration of any particular site. For this the use of summed probability is convenient and effective and does not require the time-consuming assessment and argumentation about quality of various ^{14}C-dates that is necessary to address some other questions (e.g. Flohr et al., 2015). As a result, a total of 1556 radiocarbon dates were used for the calibration of 181 archaeological sites/phases. For the other 119 sites/phases, for which radiocarbon dates were not available, the median age was either interpolated between later and earlier dates in the same sequence, or the median of the estimated date range provided in the publications, based on cultural materials, was used.

5.2. Sickle blades

Sickle blades recovered from 277 archaeological contexts across the Fertile Crescent (Fig. 1), covering about seven millennia, have been studied typologically and quantitatively. First, typology of sickle blades has been examined since it reflects the degree of investment on their production not necessarily in terms of labour and time consumption but in an attempt towards specialized production of these tools. Secondly, the frequency of sickle blades at each site/phase has been quantitatively evaluated to understand increasing importance of sickle use over time.

The use patterns of sickle blades, based on their typology and quantitative trends, can be classified into 12 groups (Fig. 2). Typological classification is based on their shape, type of blank and manner of retouch, referring to previous studies (e.g. Cauvin, 1983; Gopher, 1989). It has been suggested that the shape of sickle blades reflect the shape of sickle handles and the way in which they were hafted (Bar-Yosef, 1987; Cauvin, 1983). However, recent discoveries of complete sickles demonstrate that the way sickle blades were hafted was not so easily predictable (e.g. Borrell and Molist, 2007). Therefore, types of handles and hafting are not considered here in detail. The definition of 12 groups is detailed in supplementary information and summarized in Table S2.

Quantitative data of sickle blades used at each site were calculated as the percentage of sickle blades to all retouched flint/chert tools by count and plotted in the chronological order provided by Table S1 (Fig. 3a, b). The figures were calculated from published data with the exception of new data from Hasankeyf Höyük (Table S3). Any glossed pieces (including those made on flakes) or those described as “with sheen” in published lithic data were counted as sickle blades while retouched tools involve any pieces which have edge modification, including retouched and used

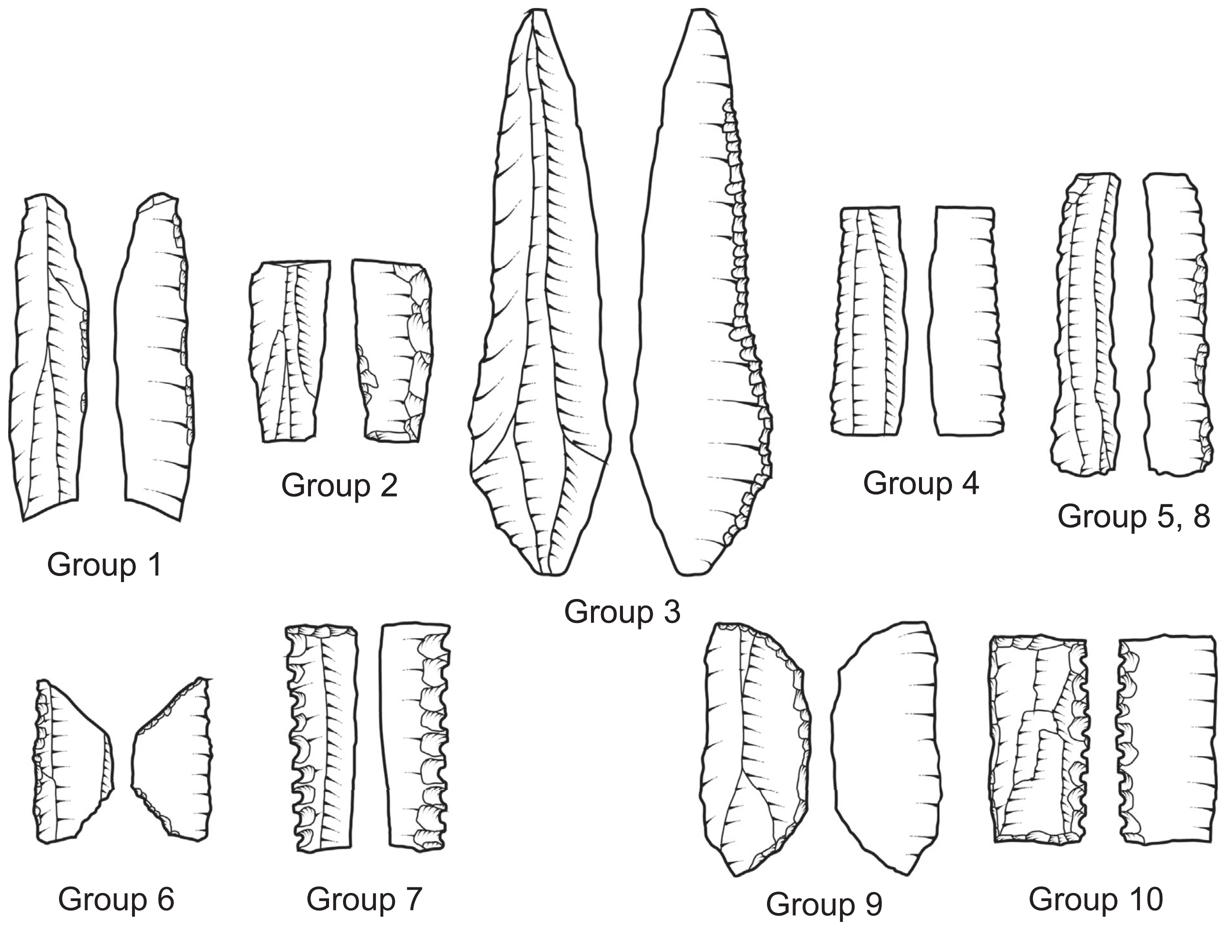


Fig. 2. Schematic drawing of typological groups of sickle blades. Group 11 is defined for the Cyprus area where the typological features of sickle blades vary between different sites and periods and cannot be represented by a single type. Group 12 is defined for the Levantine arid area where the use of sickle blades is very infrequent and their typology is not standardised.

blades and flakes. It is known that gloss can be produced on the edge of lithic tools by activities such as reed-cutting (Winter 1994) or use of threshing sledges (Anderson, 1999; Gurova, 2013) so glossed blades do not exclusively indicate cereal harvesting. Nevertheless, we assume that the scale of these other activities during the Neolithic would be outweighed by cereal cutting when cereal cultivation is a significant part of the economy. Therefore, in this study all the glossed tools reported from Epi-Palaeolithic and Neolithic sites are regarded as plausible cereal harvesting tools for the purpose of exploring regional and chronological quantitative patterns and how these correlate with data on cereal use and domestication. Experimental studies have demonstrated that only a few hours work of cereal cutting develops gloss on the edge (Quintero et al., 1997) and thus the misidentification of sickle blades due to the lack of gloss should be minimal.

When the amount of sickle blades has been reported as “rare” or “virtually absent”, a numerical value of 1% was chosen for the purposes of quantitative analysis. For some sites the percentage of sickle blades are presented as a range value (e.g. 15–20%) in Table S3. This is for sites where the quantity of sickle blades are only reported as a range of percentage and their numerical counts are not available, or in instances where there are two or more datasets obtained from different excavations at one site but correlations between them are difficult. In this case the median values were used for the quantitative analysis in Fig. 3.

The percentage of sickle blades can be biased by various factors, such as a number of blades inserted to one sickle and longevity of each blade but it is unlikely to affect the general pattern in our overall dataset. Another factor which may bias quantification of sickle blades is the use of obsidian blades for cereal harvesting. Since distinctive sickle gloss is not formed on obsidian (Fullagar, 1991), it is not possible to identify obsidian sickle blades with the naked eye. This could misrepresent the percentage of sickle blades used at sites where obsidian was a major raw material. Although recent progress in use wear analysis on a microscopic level allows us to identify the use of obsidian for harvesting purposes, those methods have not been widely enough applied to be useful for the quantitative analysis in the present paper. For this reason, sites in Central Anatolia, where obsidian accounts for the majority of lithic assemblages, are not included in this study. Elsewhere, obsidian is usually a minority, ca. 0–30% of all lithics (Ibáñez et al., 2015), and therefore has a minor effect on the estimated percentage of sickle blades based on flint/chert examples.

5.3. Plant data: non-shattering rachises and percentage of cereals

In order to address the relationship between sickles and economic change, we have taken two straightforward indices from the archaeobotanical record, the proportion of non-shattering (domesticated morphotype) cereals, from 9148 rachises, and the overall proportion of cereals in archaeobotanical assemblages, totaling 742,860 charred specimens from all assemblages across 113 sites (Tables S4 and S5). While these data are not always available from all sites, nor from the same sites, they can

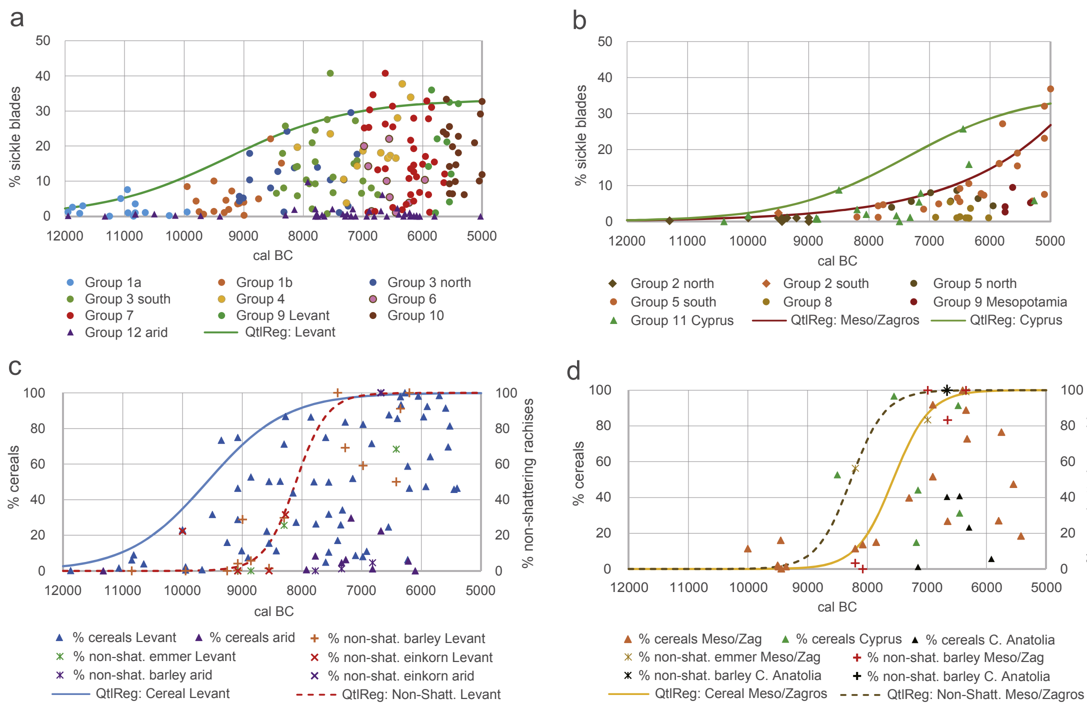


Fig. 3. Changes in sickle blade frequency and cereal frequency over time, with trends indicated by 90% quantile regression. a. Sickle blade frequencies in the Levant. b. Sickle blade frequencies in Mesopotamia, the Zagros and Cyprus. c. Percentages of cereals and percentages of non-shattering cereal rachises at sites in the Levant. d. Percentages of cereals and percentages of non-shattering cereal rachises at sites in Mesopotamia, the Zagros and Cyprus.

nevertheless be plotted chronologically (by median age) and grouped by region as defined by the sickle blade groups presented in Section 5.2 (Fig. 3c, d).

The percentage of non-shattering spikelet bases in cereals recovered from archaeological contexts has been used previously (Fuller et al., 2014) to document the evolution of the domestication syndrome. By calculating the percentage of non-shattering in an archaeological assemblage and plotting against an estimate of time, it is possible to document the slow progression over time to the dominance of non-shattering rachises. The evidence for non-shattering rachises in barley (*Hordeum vulgare*) comes from previously published datasets presented earlier by Fuller et al. (2014) (Table S4). The limited rachis datasets for emmer (*Triticum dicoccum*) and einkorn (*T. monococcum*) (Table S4) has been expanded from that presented earlier (Fuller et al., 2014) with additional emmer rachis data from Chogha Golan (Weide et al., 2015) included. Differences between data presented earlier by Fuller et al. (2014) and the present dataset are rachises that were not determined to be either shattering or non-shattering (i.e. 'indeterminates') were not taken into consideration in this study, although presented in the tables, and the estimated standard deviations are not presented.

While the broader trends in the evolution of non-shattering are similar across the Fertile Crescent the importance of cereals in the diet varied greatly across sites and regions. To see the growth in cereal production over time, we have taken a percentage of the number of cereal specimens (including grains and chaff of barley, wheats and rye, whether wild or domestic) out of all counted charred plant remains (Table S5). In other words this is the total number of identifiable specimens of all cereals combined, rather than attempting to estimate the number of specimens by combining chaff and grain from the same species. Although chaff to grain ratios differ across cereal crops, and the proportion of chaff to grain differ between different products and by-products of crop-processing stages (Hillman, 1984; Stevens, 2003), it is unrealistic to attempt to account for this across all assemblages. For one thing, numbers and ratios are subject to variations in sampling, sorting and reporting strategies of different archaeobotanists. In addition, different patterns in which crop-processing stages were exposed to fire and preserved may structure the proportions of chaff and grains, and this may differ across cereal types (e.g. between glume wheats and barley), systematic variation in this regard is as likely to differ across contexts within an individual site as it is between sites. It is the case that sites include a range of contexts and context types, therefore providing some balance between intra-site variations. Nevertheless, biases will tend to balance out when all cereal types are considered. Thus, for example, a greater input from dehusking by-product will be expected to increase glume wheat representation, while less dehusking will favour more barley or rye and fewer glume wheats. It has also been experimentally demonstrated that chaff rich assemblages before charring will be made to look grain-rich through the charring process (Boardman and Jones, 1990). Taking into account all of these concerns we took a simple summed frequency approach as this requires the least assumptions, except that archaeobotanical evidence reflects some recurrent aspects of plant use on a site, and it is straightforward in terms of using existing archaeobotanical evidence, i.e. closer to the primary data as reported.

5.4. Quantile regression and the analysis of covariance

In order to objectively identify trends, we used quantile regression of the 90th percentile. Unlike an ordinary least squares regression, which approximates to the conditional mean, a quantile regression can approximate to any quantile of the dataset being analysed (Koenker, 2005). This is quite useful when trying to understand, as in our case, the evolution not of the mean but of the top-end of the dataset, that is driving the process of adoption (for more on this see Section 6.2).

The shape of the regression curve chosen was logistic as this best mimics the data. It is also the case that logistic curves are the predicted form on many evolutionary processes, including selection for domestication traits and the transition to agricultural economies over foraging (Rindos, 1984; Hillman and Davies, 1990). In addition, a logistic curve replicates on theoretical grounds the process of development/adoption of an innovation (Fitzhugh, 2001). The regressions were done using the quantreg package (Koenker, 2013) for R (R Core Team, 2014). It is worth noting that quantile regressions focusing on such trends are robust to minor variation to both horizontal and vertical axis values, which means minor differences in the observational error between sites should not affect the overall trends. For example, even if median dates are misestimated somewhat, by a couple of centuries in either direction, for example, the logistic quantile regression is unaffected.

To then quantitatively compare the different identified logistic curves, particularly in what relates to their covariance with time, an analysis of covariance (ANCOVA) was applied (e.g. Garcia-Berthou, 2001). This type of analysis evaluates whether a series of given trends are equal across different levels of a categorical independent variable, in our case, between cereals and sickle blades across the same, or different regions. Because ANCOVA is a general linear model that combines ANOVA (analysis of variance) with regression, it requires that the relationship between the dependent and independent variables be linear. As mentioned above, a logistic curve is the best representation of our data, and this required the data to be logit-transformed so as to recover a linear relationship with time. The ANCOVA test that uses quantile regression, available from the quantreg package mentioned above, was then applied to compare the different trends. A significant effect of the categorical variable, given by a low p-value, is then interpreted as a lack of covariance – in other words, the two trends being compared are significantly different from each other.

6. Results and discussion

6.1. Diverse investment: sickle blade types and sickle blade frequency in the Neolithic tool-kits

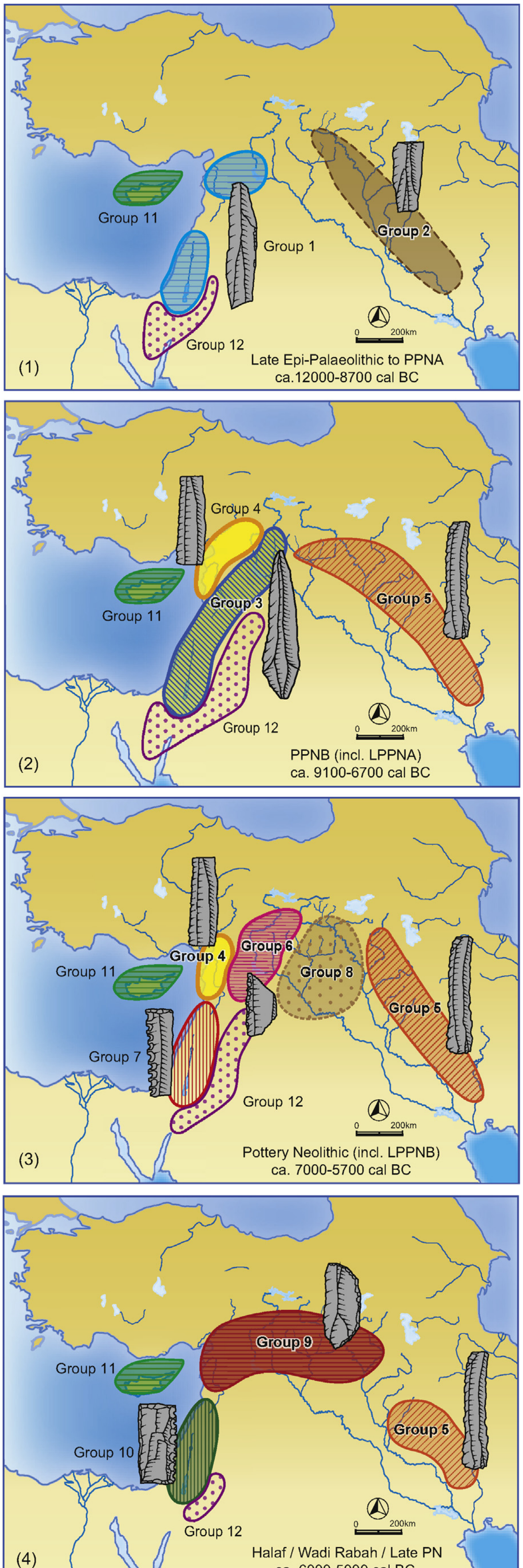
Our study demonstrates the increasing investment in production and the use of sickle blades as well as their regional diversity. While Fig. 3a and b shows a general quantitative trend of sickle blade use, the chronological and geographical distributions of different types of sickle blades defined in section 5.2 (Fig. 2, Table S2) can be represented in four time slices (Fig. 4). Cyprus is dealt with separately because sickle blade typology in Cyprus does not exactly match the situation in the mainland, although a close relationship between Cyprus and Levantine coastal regions is inferred from lithic industry as a whole (McCartney and Todd, 2005). The following time slices show the chronological change of sickle blade typology, which reflect the change in degree of their specialized manufacture.

(1) During the last phase of the Epi-Palaeolithic to the PPNA (ca. 12,000 to 8700 cal. BCE), the use of sickle blades is limited across all the area. Sickle blades used in the northern and southern Levant (Group 1) are of a simple rectangular type made of less-standardised blades from which other retouched tools were also manufactured. The percentage of sickle blades are mostly less than 5% (Fig. 3a, Table S3). In the Eastern Fertile Crescent (Mesopotamia and Zagros) sickle blades are extremely rare (Group 2). When present they are made of simple blades or rather irregular flakes.

(2) From the last phase of the PPNA to the PPNB (ca. 9100 to 6700 cal. BCE), sickle blades begin to increase at some sites in the Levant and regional difference in their typology and quantity becomes clearer between the Levant and Eastern Fertile Crescent (Fig. 3a and b). In the northern and southern Levant, sickle blades made of bi-directional blades produced from opposed platform cores become common (Group 3) and their percentage increases through time up to about 30% at some sites but remains low at others (Fig. 3a, Table S3). The same type of sickle blades is distributed in the arid zone but in a very small quantity. Although the production of bi-directional blades are highly specialized (Abbès, 2003), these blades were used for various types of tools and it indicates the production of sickle blades was not specialized with respect to other lithic types. On the other hand, specialized production of sickle blades is witnessed in the north-western Levant in the Late PPNB (Group 4), where sickle blades were made of standardised uni-directional blades produced from single-platform prismatic cores (Arimura, 2011; Borrell, 2015). It is assumed that this type of blade was specifically produced to be used for sickle blades while other tools were usually made of bi-directional blades through a separate production sequence. In the Eastern Fertile Crescent the occurrence of sickle blades increase from the previous period up to 10% (Fig. 3b, Table S3) and becomes more standardised (Group 5). They are made of uni-directional blades produced from bullet-shaped cores using pressure detachment technique (Inizan and Lechevallier, 1994), as are other tools. Except for the presence of gloss these sickle blades are basically identical to ordinary retouched blades used for various purposes. Thus, although the pressure blade detachment requires higher skill, the production of sickle blades was not particularly specialized.

(3) In the later phase of Late PPNB and the Pottery Neolithic (PN) (ca. 7000 to 5700 cal. BCE), Group 4 continued in the north-western Levant, and sickle blade types changed in other areas of the Levant. The maximum percentages of sickle blades in an assemblage levels off (Fig. 3a). In the north Levant crescent-shaped sickle blades became popular (Group 6). Although their production from irregular blades/flakes is not highly skilled, their distinctive shape and the orientation of gloss oblique to the blade edge indicates that they were apparently different from ordinary retouched blades and produced to be inserted into sickles in a specific manner (Cauvin, 1973; Nishiaki, 1997). Another distinctive type is seen in the southern Levant (Group 7), where sickle blades made of uni-directional blade/flake segments with coarsely denticulated retouch become common. The higher degree of retouch indicates higher investment in their production (Gopher et al., 1996). In the Eastern Fertile Crescent, Group 5 continues in the Zagros foothills and the percentage of sickle blades remains more or less the same. On the other hand, sites in northern Mesopotamia experienced a drop in the use of sickle blades at this time (Group 8).

(4) In the Late PN to the beginning of the Chalcolithic (ca. 6000 to 5000 cal. BCE), the Halaf culture expands across the northern half of both the Eastern Fertile Crescent and the Levant. In this area crescent sickle blades were used alongside rectangular ones (Group 9) (Arimura, 1999). Despite the typological commonality from east to west, the quantitative differences of sickle blades remained with a low frequency in the Eastern Fertile Crescent (Fig. 3a, b). In the southern half of Eastern Fertile Crescent where Group 5 continues, however, the percentage of sickle blades begins to increase and catches up with Levantine assemblages by the end of this period.



Sickle blades used in the southern Levant were carefully made into standardised rectangular segments (Kadowaki, 2005; Vardi and Gilead, 2013) and those with backed retouch and truncated ends prevail (Group 10).

We have then classed the assemblages into four grades that reflect increasing levels of effort in production, and plotted their occurrence over time (Fig. 5, Table S2). The production of Group 1 sickle blades were not separated from that of ordinary retouched blades, which are morphologically identical to sickle blades. It is thus likely that sickle blades were simply selected from ordinary retouched blades and inserted into handles to be used for harvesting. The same is true for Group 3 sickle blades. The appearance of the Group 3 sickle blades made on fine bi-directional blades at the end of the PPNA should be regarded as an outcome of the change in overall blade production rather than specialized production of sickle blades. The specific production of sickle blades targeted to be only used as sickle blades comes to the fore in the Pottery Neolithic in the Levant. Sickle blades of Groups 4, 6, 7, 9 and 10 are those produced for the specific use as harvesting tools. This suggests a trend towards increasing interest in sickle production through time (Fig. 5). Taken together with the trend of increased numbers of sickles, this typological change highlights the increasing importance of this tool category over the course of the Neolithic.

6.2. Comparing trends of sickle blades and cereals

Fig. 3c and d shows the chronological trends in the proportion of non-shattering cereals (barley, emmer and einkorn) and the percentage of cereals (barley, *Triticum* spp. and rye) out of all charred remains. While a few sites in the Levant have large minorities of non-shattering einkorn or emmer early in the Neolithic (10,000-9000 cal. BCE), sites with a majority of domesticated rachis remains or approaching 100% all date to the later PPNB (after 7500 cal. BCE) (Fig. 3c). There is less data from the Eastern Fertile Crescent, which indicates both a late appearance of non-shattering barley (after 8000 cal. BCE), one early appearance of a high proportion (large minority) of non-shattering emmer at Chogha Golan (Riehl et al., 2013; Weide et al., 2015), and otherwise the fixation of non-shattering in populations after 7000 cal. BCE (Fig. 3d).

What is evident is that cereals only start to occur as a majority of the archaeobotanical assemblages in a few sites in the Levant just before 9000 cal. BCE, but lower proportions are more common until after 7000 cal. BCE when assemblages low in cereals disappear, except for in the arid area. Data are more limited in the eastern Fertile Crescent and Cyprus but the trend towards cereal consumption appears later than in the Levant (Fig. 3d). In the arid zone of the southern Levant cereals remain rare throughout the period considered and at most of these sites wild cereals persist, raising the possibility that either cereal collecting persisted or that selection for non-shattering did not occur in this region.

We tested whether on individual sites we could see a strong correlation between cereal statistics and sickle frequency, but there is no clear regression by which proportion of sickle blades predicts the amount of cereal use or domesticated cereals (Fig. 6). Nevertheless, there are some tendencies for sites with more specialized sickle types to have more cereals and sites with few cereals to have fewer sickles.

Thus patterns emerge only at the regional level, but even at this

Fig. 4. Map of the Fertile Crescent showing the regional typological groups of sickle blades in four time slices.

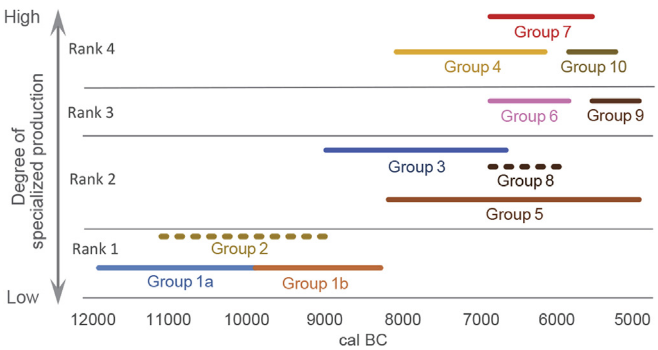


Fig. 5. The occurrence of sickle typological groups over time, classed into 4 ranks of increasingly specialized production and investment.

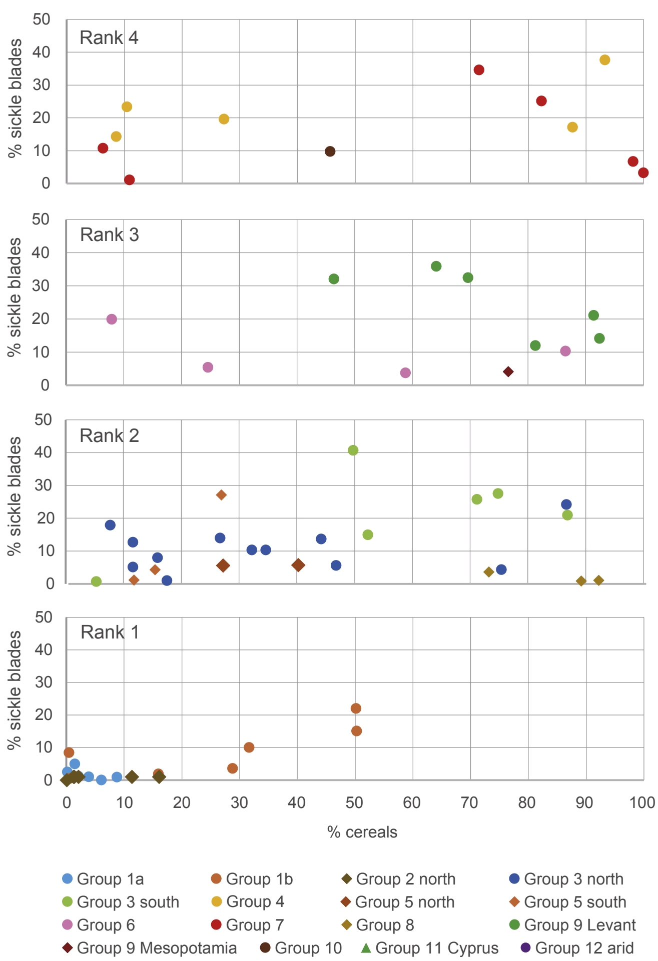


Fig. 6. Sickle blade frequency and cereal frequency at individual sites. Each dot represents an individual site for which data for % sickle blade and % cereal are both available.

level there are sites that are further in the innovation adoption process than others, as Fig. 3 makes clear. As we are more interested in these "innovators" we cannot simply look at how the conditional mean evolves through time. Instead, one should look at the top quantiles of the conditional distribution or, in other words, focus our analysis on what is driving the process regionally. We have, as noted in Section 5.4, conducted quantile regression to the top 90th percentile in order to recover the top-end of the range, adopting a logistic regression curve (curved lines in Fig. 3), and subsequently did ANCOVA analyses on the identified trends.

The resulting curves in Fig. 3 allow for a direct comparison of these maximum trends between the variables and regions analysed, which can be seen in Fig. 7, and is supported by the ANCOVA tests of covariance whose results are shown in Table S7. We can observe that, in the Levant, the logistic growth curves for % sickle blades and % cereal seem to co-vary with time (Fig. 7a), however they are significantly different (p-value of 0.03393). Cereals reach the turning point (50%) around 9600 cal. BCE, whereas sickle blades do so three centuries later. Non-shattering cereals, on the other hand, only reach the turning point fifteen hundred years later, around 8100 cal. BCE. The trend of the curves for % sickle blades and % cereal is very different in Mesopotamia and Zagros (Fig. 7b), and this is again supported by the ANCOVA tests (highly significant p-value of 0.0002187).

Another interesting observation is the similarity between the % non-shattering regression curves for both the Levant and the Mesopotamia/Zagros regions with a point difference sum of merely 171.14 (Fig. 7c). All three parameters for these curves are very similar, their turning points differ by a mere 170 years. The ANCOVA test returned a non-significant p-value of 0.25753, meaning that

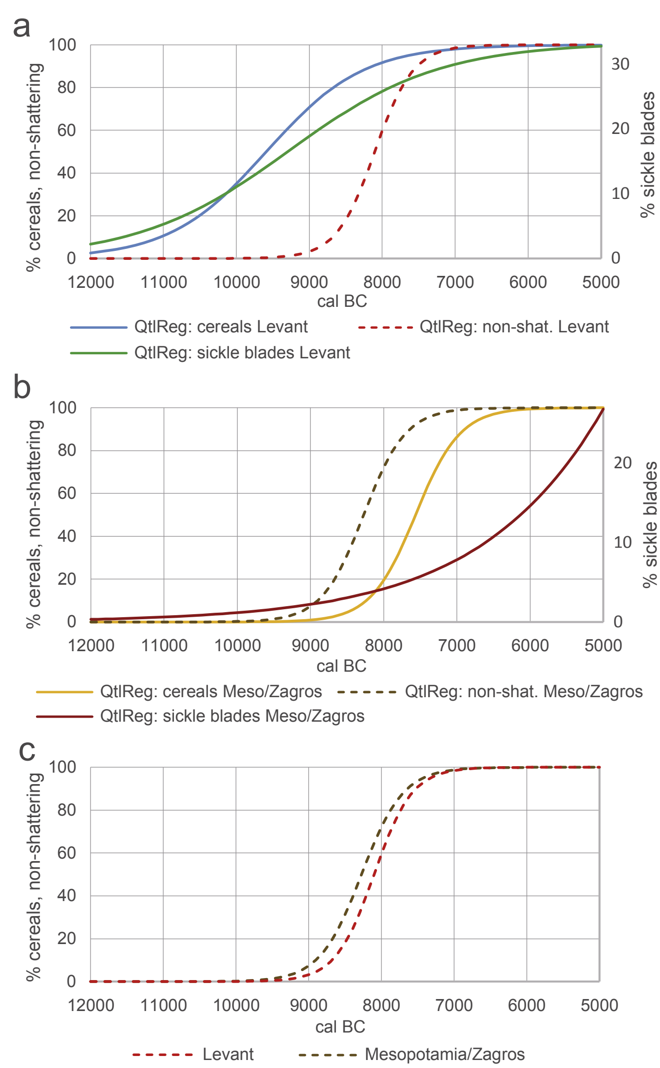


Fig. 7. A comparison of the quantile regression trends in sickle blade frequency, cereal frequency and domesticated cereal frequency. a. For the Levant, b. For Mesopotamia and the Zagros, c. A comparison of the cereal domestication trends (non-shattering rachides) for the Levant and Mesopotamia plus the Zagros.

the two trends are not significantly different. However, the curve for the Mesopotamia/Central Zagros regions is based on only eight data points and the error margins for this curve are too elevated (Table S6). Their similarity should therefore be taken as merely suggestive.

Nevertheless, these data may suggest cereals across the whole region shared in the same general trend, as assumed in recent studies of domestication rate (Fuller et al., 2014; Purugganan and Fuller, 2011), and can be regarded as a single meta-population. This means that although early cereal cultivation patches were geographically dispersed and separated, between them there was enough gene flow that new alleles could spread between cultivated patches through the bridge of intervening wild populations as well as through human exchanges of seed (Allaby, 2010). Such a pattern is consistent with the view that cereal domestication evolved as a geographical mosaic drawing on several local populations in parallel (Allaby, 2015). Such a pattern is strongly indicated in recent genomic analyses on domesticated and wild barley (Poets et al., 2015), and consistent with available analyses of wheat genetics (Kilian et al., 2007; Civáň et al., 2013).

The close correspondence between the timing of the increases in tough rachis cereals in both the Levant and the Mesopotamia/Zagros regions raises the possibility that tough rachis cereals were introduced into the Mesopotamia/Zagros region from the west, and this could have taken place in several waves. At Chogha Golan, for example, after a shift in the plant assemblage that suggests some subsistence reorganization at ca. 8200 BCE, emmer with a high proportion of non-shattering rachises (~56%) appears, and this could indicate introduction of cultivars further along the evolutionary path to non-shattering, rather than in situ selection for this trait. Further archaeobotanical evidence is needed to test whether the hypothesis of independent cereal domestication in the eastern Fertile Crescent (e.g. Riehl et al., 2013, 2015) can be sustained.

6.3. *Alternative regional investments in sickles and cereals*

The trends in quantile regression show the correlation between sickle use and cereal use. In both the northern and southern Levant a clear trend towards increasing sickle production, compounded by the appearance of highly specialized sickles, correlates with a rise in consumption of cereals, with the trend in sickles lagging slightly behind that for cereal consumption. This suggests that the increasing investment on sickle blades was driven by the growth of cereal production. However, at the same time, the use of sickle blades clearly demonstrates regional diversity in these trends. In the Eastern Fertile Crescent and Cyprus both trends begin later. While sickle blades increase after 9000 cal. BCE and reach the peak around 7000 cal. BCE at many sites in the Levant, those in the Eastern Fertile Crescent begin to increase only after 6500 cal. BCE. In Cyprus, although the early introduction of cereals may be associated with elevated rates of becoming domesticated (Lucas et al., 2012), the late adoption of sickles appears unconnected to this process. These regional differences demonstrate that different technological trajectories occurred in the development of agriculture across Fertile Crescent regions. This is also supported by the regional differences of sickle blade typology as discussed in section 6.1. Therefore, even if cereal domestication can be seen as a region-wide process affecting cereal meta-populations, the accompanying cultural evolution was regionally varied with a mosaic of cultural pathways. Indeed a number of authors have argued for a Neolithic cultural mosaic, despite geographical proximity and long-distance trade (e.g. Asouti and Fuller, 2013; Belfer-Cohen and Goring-Morris, 2011; Watkins, 2008). It is definitely worth exploring what causes these regional differences in agricultural trajectories. Multiple factors can be considered, such as, resource availability, including the degrees to which legumes or animal resources contributed to protein consumption, climate differences, population density, settlement pattern, and social tradition relating to land tenure or ownership. But enquiry into these potential causes requires further substantial research beyond the scope of this paper.

The lag between the rise of sickles and the rise towards fixation in non-shattering cereal ears contradicts a long-standing hypothesis of sickle pressure, i.e. that use of sickles drove the evolution of non-shattering rachises (Harlan, 1992; Hillman and Davies, 1990; Wilke et al., 1972). This hypothesis presupposes strong selection of domestic-type cereals during sickle reaping because shattering (wild-type) spikelets more likely drop when the ears are shaken by contact with sickles (or people holding sickles), whereas non-shattering forms have a high likelihood of being harvested via sickle and sown the next year. Proponents of the hypothesis of domestication via sickle pressure have argued that sickle reaping prompted rapid evolution of non-shattering rachises, taking cultivated cereal populations from morphologically wild to genotypically fixed for non-shattering morphotypes in less than 200 years and perhaps as fast as a few decades (Hillman and Davies, 1990). Our study, on the contrary, supports the contention that sickles were not necessary for non-shattering cereals to evolve, particularly when their evolution was a slow, prolonged process (Fuller, 2007; Fuller et al., 2009; Sauer, 1958). It is assumed that the use of sickle did not prevent the evolution of non-shattering rachises but it did not prompt it either.

It is more likely that the evolution of non-shattering types was caused by other sources of weak selection (Fuller, 2007; Fuller et al., 2010), through annual harvesting and sowing cycles. First, simple by virtue of being cultivated and re-sown by people, the wild state in which natural selection favours shattering is overturned thus allowing for tough rachis mutants to accumulate in cultivated populations. The timing of harvesting, i.e. late harvests, may then select for non-shattering. As wild cereals are non-synchronous in their ripening, their exploitation, including under early cultivation, would have necessitated multiple harvests, for example weekly over a period of 4–6 weeks of cereal ripening. The latest of such harvests would have included larger proportions of non-shattering mutants. Therefore if this last harvest was saved for sowing, even by rare households, something like 1 household in 20, there would be a basis of selection for non-shattering to increase overall in regional populations. By similar reasoning it is also plausible that occasional households experimented with sickle harvesting of cereals, long before this became a standard practice, and this would have contributed to selection for non-shattering. This rare experimentation with sickles for cereal harvests in due course became a fad and a more widely accepted standard practice.

We should regard sickles as having been developed as a cutting tool for raw materials such as reeds and sedges for basketry, matting or thatch. The extensive use of grass culms, reeds and sedges for such purposes, including for lining burials, has been inferred from phytolith analyses at some Natufian sites (e.g. Portillo et al., 2010; Power et al., 2014). We suggest that sickles were later, over the course of the PPNB, transferred to agricultural harvesting, in cultural evolutionary terms an exaptation (Fuller, 2007; Larson et al., 2013). Attributing a role to sickles in morphological evolution of cereal domestication appears to be an anachronism, and the imposition of modern "agronomic" thinking on early forager-cultivator societies. This conclusion also makes sense in comparative global terms, as archaeological evidence argues against a role for sickles or other harvesting knives in the domestication of rice, where sickles were instead adopted in the later Fourth millennium cal. BCE, after *Oryza sativa* was already domesticated and non-shattering (Fuller et al., 2007, 2009).

This disconnection between sickles and cereal domestication in evolutionary terms, then, raises the question as to why sickles were adopted into agriculture. While this can be considered to increase efficiency, especially if measured in terms of harvest yield per unit of area (Bar-Yosef, 1998; Fuller, 2007), the regional differences indicate that there were also cultural factors. For one thing many sites have low sickle percentages throughout the period of study even if quantile regression shows a steady trend of an increase in the upper limits of frequency. On a regional level, the use of sickle blades remains humble in northern Mesopotamia during the Pottery Neolithic (Group 8 in Fig. 4) while the use of cereals had already begun to rise at this time (Fig. 3b,d). This means that sickles were not always requisite for cereal harvesting. In fact, sickle harvesting is not necessarily more efficient than other methods (e.g. Hillman and Davies, 1990). It has also been reported that hand plucking of wheat and barley by Bedul Bedouin is as efficient as harvesting with lithic and metal sickles (Simms and Russell, 1997). Even if sickle harvesting has a slight advantage in harvest yield per unit, the difference in time investment to harvest a certain area must be only few hours when compared with other methods. Sickles also require investment in manufacture, and as the data indicate this investment in each sickle also tended to increase over time (Fig. 5). It is indeed not our intention to exclude an economic factor promoting sickle use in cereal harvesting. However, we believe that the economic advantage of sickles is subtle and was not a sufficient motivation for their adoption into agriculture. Our study clearly shows that the growth in cereal consumption and sickle use are correlated but it also shows that it was a process which cannot be simply explained by cause-and-effect relations in economic terms. In this sense those regions like the Levant, where sickles became increasingly prominent, followed historically contingent trajectories in which sickle use made sense within the cultural and ecological logic of that cultural tradition. We would suggest that as a focus of labour investment sickles were adopted as a character of the cultural package of farming. Cultural transmission processes such as conformist bias (Acerbi and Bentley, 2014), could contribute to explaining this pattern in the Levant, beyond mere content biases such as efficiency. Conformist bias means that people mostly copy the behaviours that they see as more common or frequent in the society around them, on the assumption that what is common is “right” or “better”. In a sense then the adoption of sickles was as much stylistic, conforming to styling oneself to be a “farmer”, as it was about efficiency, and that cultural evolution was not a straightforward adaptive process, but developed by cultural exaptation, a solution that was efficient enough and developed from retooling an existing technology (blades) for a new purpose (cereal harvesting), i.e. exaptation. The stylistic aspects of sickles as signalling the cultural identity of a farmer may provide part of the explanation for the curious later development of fired clay sickles in the Ubaid period of Mesopotamia (Benco, 1992). While this has sometimes been attributed to the lack of lithic raw materials in the floodplains of Mesopotamia, such an explanation fails to explain why such tools have been found in the northern Mesopotamia, e.g. Tepe Gawra (Oates, 2010), where lithic materials for more efficient stone-blade sickles would have been readily available. Therefore, we infer that the protracted transition to agriculture in the Near East was in part a matter of developing the cultural logic of being a farmer, which in the Levant included the use of sickles.

The long-term co-evolutionary trajectory that we have highlighted between cereal cultivation and sickle use has a number of implications for re-framing explanations for the origins of agriculture. Clearly there is no single event, or step change, apparent as we might expect in relation to hypotheses of simple climatic triggers for the origins of agriculture. There is certainly no indication that the Younger Dryas or its termination was a dividing line between foraging and cultivation that precipitated rapid change (e.g. Bar-Yosef, 1998; Hillman et al., 2001; Blockley and Pinhasi, 2011). Nevertheless, the onset of the Holocene and the PPNA, after ca. 10,000 cal. BCE (as per Blockley and Pinhasi, 2011) does correlate with start of the upward trend in cereal use and sickle blades, and the first reports of a few non-shattering wheat or barley on very few sites, but this is only the beginning of a 2000 year trend that levels off after 8000 cal. BCE. Borrell et al. (2015) argue that around 8000 cal. BCE there was a climate driven break in population in the northern Levant and this transition led to the establishment of agriculture and new blade production patterns after this dry event. While the abandonment of sites in this region at this period is compelling (Borrell et al., 2015), the trend illustrated by our study from archaeobotanical and lithic data across the wider region fit with what still appears a gradual and macro-regional pattern of change. Elsewhere, such as in western Iran this same dry event (ca. 8200-8000 cal. BCE) correlated with other subsistence shifts, such as the brief appearance and then abandonment of non-shattering barley at Chogha Golan, followed by its replacement by semi-domesticated emmer wheat (Riehl et al., 2015). As Riehl et al. (2015) argue, the protracted process of domestication would have included a period of stasis, or even reversal, at least on a local level, facilitated by the resilience that was inherent in mixed strategies of foraging and landscape management.

A further implication of the reviewed evidence is that we need to broaden the study of early cereal domestication from the traditional focus on non-shattering rachises. There is a long tradition of regarding non-shattering ears as the single most important trait differentiating domesticated crops from their wild ancestors. This has been called “the main diagnostic character that serves for distinction of wild cereals from their cultivated counterparts (Zohary, 1969, p. 157–158), or “the most conspicuous… crucial in maintaining the disruptive selection that effectively maintains separation of the two kinds of populations” (Harlan, 1992, p. 118). Non-shattering rachises remain important for at least two reasons: first, they are an archaeobotanically recoverable trait that is less ambiguous than most in studying cereal evolution under cultivation. Second, non-shattering helps to maintain a dependence of domesticated species on humans for sowing, and subsequent selection and maintenance of varietal differences in cereals is facilitated by co-dependence of humans and cereals that do not readily reseed themselves. Nevertheless, and contrary to Harlan’s (1992) inference, this trait may not have been so crucial during domestication. Instead, traits like even germination and ripening, reliability of yield (e.g. Abbo et al., 2010b), and increased food value brought about by better grain filling and larger grains (Fuller et al., 2010) may have been at least as important, alongside the storability of cereals and how they fit with traditions of food preparation and consumption, such as the flour-based foods that were characteristic of the Near East (e.g. Haaland, 2007; Fuller and Rowlands, 2011).

7. Conclusions

It is suggested that to the extent that change was directional—on a regional level but not in every locality— it was directed by an internal logic of cultural evolutionary processes, including conformist bias and exaptation of pre-existing technologies to new uses, that in some cases may have produced marginal efficiency gains or, in others, non-significant efficiency losses. This would then predict considerable scope of variation between regions as cultural traditions drifted in alternative directions. Variations in traditions of harvesting, such a tool choice, harvesting height, when and how many times during ripening, and which temporal portion of the harvested cereals were stored for re-sowing would have all contributed to creating varied levels of selection for domestication traits (as per Fuller, 2007; Fuller et al., 2010). Nevertheless the slow accumulation of domestication traits amongst cereals across a macro-regional meta-population could have promoted but not required becoming a more committed sickle-harvester of cereals. Trends towards human population increase and sedentism would have similarly provided more opportunities to commit to this trend towards a cereal producer identity, even if local collapses and climate shock may have sometimes gone the other way. What is nevertheless clear is that the net regional trend was to establish a high commitment to cereals, sickles and fixation on non-shattering domesticated forms throughout the Fertile Crescent by the sixth millennium cal. BCE.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.quascirev.2016.05.032.

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