# The Role of the Local Environment in the Slow Pace of Emerging Agriculture in the Fertile Crescent

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# THE ROLE OF THE LOCAL ENVIRONMENT IN THE SLOW PACE OF EMERGING AGRICULTURE IN THE FERTILE CRESCENT

Simone Riehl[1]

*The origin of agriculture in the Fertile Crescent is among the most frequently investigated topics in Old World archaeology. Environmental pressure in relation with the Younger Dryas event is frequently discussed as a general determinant in the transition to cultivating domesticated cereals. Although there are data on the palaeoclimate and vegetation at the Pleistocene-Holocene transition in the Fertile Crescent, the role of environmental conditions at the emergence of agriculture on the local level has rarely been investigated. Archaeobotanical data from a number of Epipalaeolithic and aceramic Neolithic sites in the northern and eastern parts of the Fertile Crescent, as well as stable carbon isotope data on wild cereals from some of these sites, are investigated for their explanatory power regarding ancient ecological conditions of early cereal production and the slow pace of emerging agriculture. The data emphasize a high diversity on the taxonomic as well as on the inter-site level in the oldest aceramic Neolithic sites, supporting opportunistic resource use. At the same time, there is a trend toward higher amounts of small-seeded taxa in older sites with lower modern mean annual precipitation, as well as a generally stronger stress signal in large-seeded progenitor species than in PPNB (Pre-pottery Neolithic B) sites. Large-seeded progenitor species, in contrast, occur in greater amounts at younger sites with higher modern mean annual precipitation. Environmental variability in space and time seem to have strongly determined human choices in plant subsistence.*

**Keywords:**  *archaeobotany, stable isotope analysis, Near East, Neolithic, early agriculture*

## Introduction

It is today widely accepted that cultivation and domestication had multiple origins with locally distinctive sets of crop species and that a single core area for the origins of agriculture did not exist within the Fertile Crescent (Fuller et al. 2011; Larson 2011). The archaeobotanical evidence of Near Eastern sites of the aceramic Neolithic (syn. PPN – Pre-pottery Neolithic) suggests a slow transition from cultivating wild plant species to the appearance of the first genetically domesticated cereals, which probably took several hundreds of years (Fuller 2007; Fuller et al. 2012; Tanno and Willcox 2006; Willcox and Stordeur 2012). Explanations for this slow process have been sought in the possibility that wild cereals were collected from the ground (Kislev et al. 2004), were harvested in unripe conditions, or were replenished from wild stands (Willcox et al. 2009), which led either to suppression of the selection for mutants with domesticated traits or to continuous introgression of genes from wild cereals.

Explanatory models of why agriculture emerged at the transition from the Pleistocene to the Holocene are numerous and range from purely climatic deterministic explanations to culture-based behavioral models (Bar-Yosef 2009,

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2011; Binford 1968; Braidwood 1953, 1960; Byrne 1987; Childe 1928, 1936; Cohen 1977; Henry 1989; Richerson et al. 2001; Sage 1995; Watkins 2010, 2013; Wright et al. 1993). Archaeologists recently favor models that combine environmental and socio-cultural aspects, which is partially a procedural effect of the relatively coarse resolution of palaeoclimate proxies and the impossibility of directly linking these to the development of human populations (Asouti and Fuller 2013; Verhoeven 2004; Zeder 2008).

The linking of palaeoenvironmental results to archaeologically observed developments in cultural attributes is additionally impeded through regional differences within the Fertile Crescent that, despite of problematic chronology, become apparent in the palynological and stable oxygen isotope records (Supplementary Figure 1). While the Younger Dryas event is hardly visible in the pollen sequences of Ghab (Niklewski and van Zeist 1970; Yasuda et al. 2000) and Huleh (Baruch and Bottema 1999), it is very distinct in the records further inland. Deciduous oaks (*Quercus* spp.) at the Lakes Zeribar and Van increase very slowly after the Younger Dryas (Litt et al. 2009; van Zeist and Bottema 1977; Wick et al. 2003), but they were present in relatively high amounts in the coastal regions throughout the Late Glacial and the early Holocene (Wright and Thorpe 2003). While there were obviously regional differences in vegetation development within the Fertile Crescent, the different proxy records from each region are occasionally controversial, particularly moisture availability and the potential access to wild cereal resources. For example, Stevens et al. (2001) assume for Lake Zeribar continuously dry conditions after the end of the Late Glacial until 6000 cal yrs BP, contradicting the results of El-Moslimany (1987). How possible differences in local or regional development of the environment at the Pleistocene-Holocene transition affected wild plant resource availability is mostly unknown, and can only be investigated through archaeobotanical research (for detailed overviews of environmental conditions in the western, central, and eastern part of the Fertile Crescent and related availability of plant resources, see Deckers et al. 2009; Riehl et al. 2012, 2015).

The question of the role of the Younger Dryas in the development of agriculture has regained major interest recently, because the model of a protracted emergence of agriculture is largely accepted among archaeobotanists and can be supported with climate-deterministic arguments (Allaby et al. 2008; Fuller et al. 2011; Willcox et al. 2009). An important argument in this direction of thought was that cereals only developed into a major plant food resource after they increased in abundance in the early Holocene, whereas during the Younger Dryas, a much broader spectrum of small-seeded species were collected (cf. Hillman et al. 2001). Hunter-gatherers are thus thought to have used so-called low-ranked plant foods during the Younger Dryas with replacement by large-seeded grains of wild cereals at the beginning of the Holocene (Hillman et al. 1997; Weiss et al. 2004). It is necessary to examine whether such changes in plant resources can indeed be attributed to climate change, or if this shift in gathering strategy is multifactorial in nature. Pollen spectra, for example, do not fully support the argument of low cereal abundance during the Younger Dryas (Rossignol-Strick 1999; Bottema 2002; Wright and Thorpe 2003). With awareness of the geo-climatic diversity in the Near Eastern region, it seems obvious that

comparisons of local archaeobotanical assemblages with regional pollen assemblages or climate fluctuations recorded in the global palaeoclimate proxy archives of ice cores only allow for speculation about the relationship between local effects of climate fluctuations and the developmental steps into cultivation of wild cereals and emerging domestication.

Analysis of stable isotopes in plant remains is a contemporary approach that has led to important new research contributions regarding the investigation of local paleoenvironmental conditions. For cereals in arid and semi-arid environments $\delta^{13}C$ values provide a signal indicating the amount of water that was received by plants during the grain-filling period. Such data, thus, theoretically enable the reconstruction of seasonal fluctuations in past moisture conditions, which is important for addressing questions about agricultural and economic dynamics in ancient societies. Many studies address the drought-stress signal captured in ancient crop remains (Araus et al. 2001; Ferrio et al. 2012; Fiorentino et al. 2008; Flohr et al. 2011; Riehl et al. 2008, 2014). If applied to wild cereals in aceramic Neolithic sites, stable carbon isotope analysis can provide information about water availability at the emergence of agriculture, as artificial irrigation can be excluded for this period (Araus et al. 2014). Such local palaeoclimate records, which can be achieved through examination of archaeobotanical assemblages and stable carbon isotope analysis in plant remains, are indispensable for understanding the development of agriculture (Araus et al. 1998; Masi et al. 2013; Riehl et al. 2009).

This study examines the selection criteria early gatherers may have adopted for using wild plant seeds and the environmental conditions under which cultivation developed in the Fertile Crescent, using multiple lines of evidence. The underlying working hypothesis is that climatic variability should have played a role in the availability of plant resources not only over time, but within and between regions due to geographical differences and these patterns should be reflected in the archaeobotanical data. If spatial and chronological variability played a role in the availability of plant resources, differences in the composition of plant assemblages detectable through numerical and statistical pattern-searching should also be visible in the $\delta^{13}C$ values of the barley (*Hordeum* spp.) grains.

## Materials and Methods

### Numerical Examination of Archaeobotanical Assemblages

The application of exploratory multivariate statistics in archaeobotany is often aimed at pattern-searching; statistical techniques are used to group samples or to identify major axes of variation on the basis of botanical taxonomic composition. The resulting patterns can then be interpreted in terms of behavioral or ecological relevance. Principal component analysis (PCA) is a widely used method in archaeology, but is less frequently applied to archaeobotanical data (Jones 1991; van der Veen 1992). In archaeobotany, use of PCA is similar to that of canonical correspondence analysis (CCA) and is an efficient exploratory tool for producing a two-dimensional rendering in a data matrix that allows examination of sample-
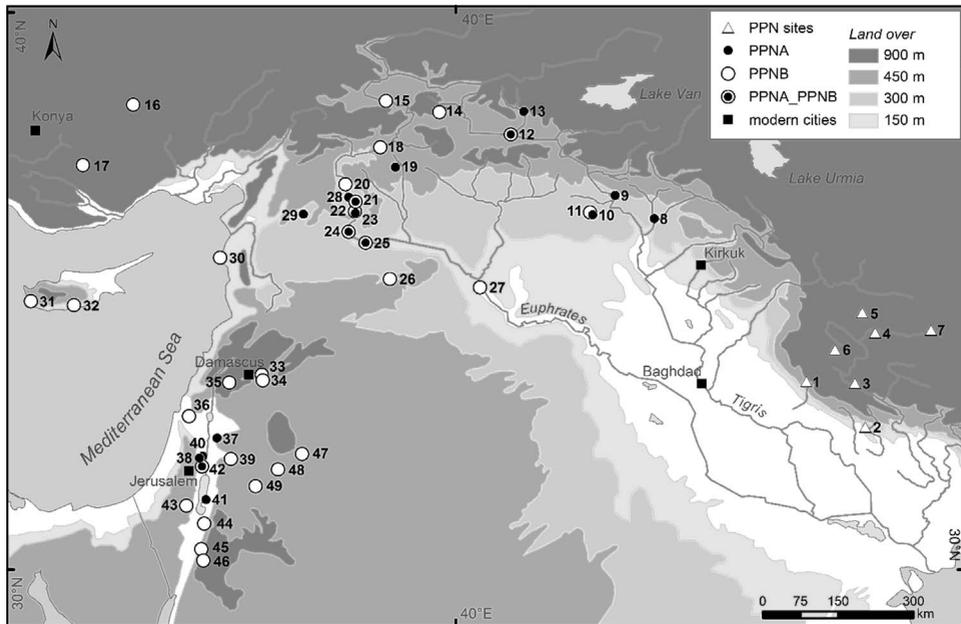
Figure 1. Map of aceramic Neolithic sites in the Near East: (1) Chogha Golan, (2) Ali Kosh, (3) Chia Sabz, (4) Ganj Dareh Tepe, (5) Sheikh-e Abad, (6) Jani, (7) Tepe Abdul Hosein, (8) M'lefaat, (9) Nemrik, (10) Qermez Dere, (11) Magzalia, (12) Körtik Tepe, (13) Hallan Cemi, (14) Cayonu, (15) Cafer Hoyuk, (16) Asikli Hoyuk, (17) Can Hasan III, (18) Nevali Cori, (19) Göbekli Tepe, (20) Akarçay Tepe, (21) Dja'de, (22) Halula, (23) Jerf al Ahmar, (24) Mureybit, (25) Abu Hureyra, (26) El Kowm I & II, (27) Bouqras, (28) Abr, (29) Qaramel, (30) Tell Ras Shamra, (31) Kissonerga, (32) Parekklisha-Shillourokambos, (33) Tell Ghoraifé, (34) Tell Aswad, (35) Tell Ramad, (36) Yiftah'el, (37) Iraq ed Dubb, (38) Gilgal, (39) 'Ain Ghazal, (40) Netiv Hagdud, (41) Dhra, (42) Jericho, (43) Nahal Hemar, (44) Wadi Fidan, (45) Beidha, (46) Basta, (47) Dhuweila, (48) Azraq 31, (49) Wadi Jilat 7.

based group formations differentiated by the taxonomic composition of the archaeobotanical assemblages. Such a picture also shows which archaeobotanical taxa are commonly associated with each other (cf. Baxter 1994). PCA was preferred over CCA, which is more frequently used for archaeobotanical pattern searching and would also be applicable here, because the focus in this analysis is on detecting inter-site differences which are better reflected with PCA rather than symmetrical analysis of sites and taxa. For the interpretation of the data arranged along axis 1 and 2, entities that plot in close proximity to one another are considered to be similar in their data structure, in terms of numerical abundance of the variables within the components of the entities, while dissimilar entities are farther apart from each other.

The raw data matrix comprising 100 archaeobotanical taxa has been extracted from published archaeobotanical reports (Figure 1, Table 1, and Supplementary Table 1), including data produced by the author from the Iranian aceramic Neolithic site Chogha Golan (Riehl et al. 2013, 2015). The data were generated from the Tübingen Archaeobotanical Database of Eastern Mediterranean and Near Eastern Sites (ADEMNES 2016) and subsequently used for numerical and

Table 1. The aceramic Neolithic archaeobotanical assemblages examined in this study. Absolute chronology, mostly according to Exoriente (2016) and own data for Chogha Golan.

| Site name | Absolute chronology (in cal yrs BC) | Cultural chronology | Number of samples | Number of taxa identified | Archaeobotanical publication |
|---|---|---|---|---|---|
| Tell Abu Hureyra 1 and 2 | 11,220–10,750 and 7,780–7,100 | Epipalaeolithic and PPNB | 21 and 83 | 82 | Hillman et al. 1989 |
| Chogha Golan AH XI-I | 9,550–7,600 | PPN | 54 | 64 | Riehl et al. 2013, 2015 and own unpublished data |
| Tell Ramad | 7,300–6,600 | PPNB | 40 | 60 | van Zeist and Bakker-Heeres 1982 |
| Tell Aswad IA and II/III | 9,300–8,350 and 8,620–7,520 | PPNA and PPNB | 6 and 24 | 50 | van Zeist and Bakker-Heeres 1982 |
| Netiv Hagdud | 9,300–8,850 | PPNA | 58 | 47 | Kislev et al. 1986; Kislev 1991, 1997 |
| Tell Mureybit I/II and III/IV | 10,150–9,250 and 9,200–7,950 | Epipalaeolithic and PPNA/B | 4 and 22 | 45 | van Zeist and Bakker-Heeres 1984b; Willcox and Fornite 1999 |
| El Kowm I and II | 7,000–6,500 | PPNB | 33 | 45 | de Moulins 2000; van Zeist 1986 |
| Tell Ghoraifé | 7,870 | PPNB | 35 | 42 | van Zeist and Bakker-Heeres 1982 |
| Sheikh-e Abad | 9,800–7,600 | PPN | 36 | 37 | Whitlam et al. 2013 |
| Tell Bouqras | 7,400–6,200 | PPNB | 28 | 35 | van Zeist and Rooijen 1985 |
| Ganj Dareh Tepe | 8,250–7,300 | PPNB | 94 | 32 | van Zeist et al. 1984 |
| Jerf el Ahmar | 9,450–8,600 | PPNA | 10 | 31 | Willcox 1996; Willcox and Fornite 1999; Willcox 2002 |
| Magzalia | ca. 7,500–5,400 | PPNB/PN | 3 | 28 | Willcox 2016; Personal pages |
| Ali Kosh | 8,700–7,000 | PPNB | unknown | 21 | Helbaek 1969 |
| Nahal Hemar | 8,200–7,080 | PPNB | 2 | 21 | Kislev 1988 |
| Tell Ras Shamra | ca. 7,500–7,000 | PPNB | 25 | 19 | van Zeist and Bakker-Heeres 1984a |
| M'lefaat | 9,650–8,850 | PPNA | 1 | 6 | Savard et al. 2003 |
| Yiftah'el | 7,950–7,480 | PPNB | unknown | 2 | Garfinkel et al. 1988; Kislev 1985 |

statistical analyses. It was expected that spatial and temporal variability in assemblages should be reflected in the archaeobotanical data.

The preparation of the data matrix for statistical analysis included the compression of the data set, in that taxa occurring in less than 9% of the samples were combined with the next higher unit (e.g., *Silene/Gypsophila* type were added to the Caryophyllaceae category). Where this was impossible, taxa of less than 9% frequency were deleted. This resulted in an overall availability of 100 taxa for data analysis. The generation of functional units resulted in 18 taxa groups that were used for PCA. The exclusion of rare taxa is common practice in archaeobotany (e.g., Jones 1991) because an inclusion of rare taxa may lead to obscure patterns in the data. Transformation of the data was automatically conducted by the software using logarithmization of the taxa counts.

For interpreting the meaning of the variables in the PCA plots (Figures 2 and 3) the variables were grouped according to functional (e.g., "fruits/nuts" including almond (*Amygdalus* sp.) and pistachio (*Pistacia* sp.), taxonomic (e.g., "barley" including *Hordeum vulgare* grains and rachis internodes), or ecological criteria (e.g., "salt indicator" including *Salsola kali*, *Suaeda* sp., etc.). The PCA plots based on aceramic Neolithic assemblage data provide information on how the sites differ in terms of functional or ecological floristic entities. Factor loadings for each variable—i.e., for each of the taxonomic groups, representing the data output of the PCA—provide information about the role of the variables in the formation of the axes (Table 2). The highest positive or negative factor loadings contribute most to the variation, whereas low loadings contribute little. For example, the high negative factor loading of "open dryland" and the positive factor loading of "Ornithogalum/Muscari" are responsible for the distribution of the sites along axis F1 and thus explain the taxonomic differences between the sites (compare Table 2 and Figure 2).

In addition to PCA, the archaeobotanical data are examined to determine if there was a shift from small-seeded to large-seeded taxa over time, and whether there are geographic factors contributing to trends (Figure 4). Two main categories were extracted from the data, (1) the large-seeded plants, such as the wild cereals and pulses that represent the wild progenitor species of modern crops, and (2) small-seeded taxa that include possible low-ranked food plants (Hillman et al. 1997) and probable arable weed species (Willcox 2012). Compositional analysis considering these two main categories was conducted by calculating proportions of major plant groups belonging to these categories. In all, a dataset of more than 1.5 million entries was analyzed for patterns to characterize plant use by ancient humans in terms of temporal and geographic variability in conditions of plant growth.

## Stable Carbon and Nitrogen Isotopes in Archaeobotanical Remains

Stable carbon and nitrogen isotope analysis of archaeobotanical remains has been widely used for reconstructing palaeoenvironmental conditions and the nutrient status of plants (Fiorentino et al. 2014). Stable carbon isotope analysis of archaeobotanical remains allows for directly linking climatic fluctuations and growing conditions in the past because $\delta^{13}C$ values in seed remains provide a drought stress signal when the amount of water received during the grain-filling
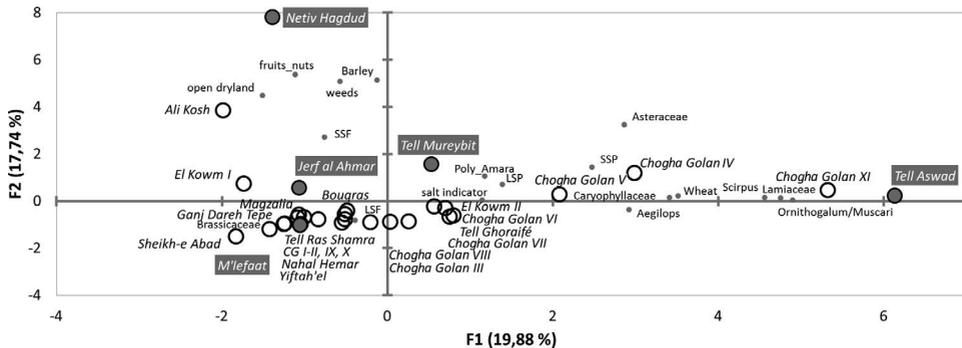
Figure 2. Principal component analyses of aceramic Neolithic archaeobotanical assemblages, without Tell Abu Hureyra. Grey circles indicate PPNA sites, white circles are PPNB sites; SSF: small-seeded Fabaceae, LSP: large-seeded Poaceae, SSP: small-seeded Poaceae, LSF: large-seeded Fabaceae; Biplot axes F1 and F2 account for 37.62 % of the variability.

period is low (Araus et al. 1997; Ferrio et al. 2005; Fiorentino et al. 2008; Riehl et al. 2008). The largest discrimination of the heavy carbon isotope in favor of the light one is during carbon fixation by the enzyme RuBisCO. Under optimal conditions, the stomata are fully open and the flow of $CO_2$ into the leaf is not limited, leading to maximum discrimination; i.e., increased use of the light isotope and depletion of the heavy $^{13}C$ isotope. Under water stress, the stomata are closed, increasing water use efficiency and leading to an enrichment of $^{13}C$.

The question of the effects of late Pleistocene to early Holocene climatic fluctuations on wild cereals can be addressed, because the $\delta^{13}C$ signal reflects seasonal fluctuations in moisture conditions. This study is based on 158 $\delta^{13}C$ measurements from individual wild barley (*Hordeum spontaneum*) grains from the aceramic Neolithic site of Chogha Golan (Riehl et al. 2013), on measurements from 36 modern grains of *Hordeum spontaneum* from different locations in Israel and Turkey, collected by Mark Nesbitt (Kew Royal Botanic Gardens) between 1987–1990, also analyzed by the author, and on a dataset of 139 $\delta^{13}C$ values published by Araus et al. (2014) that were acquired mostly from sequences at the
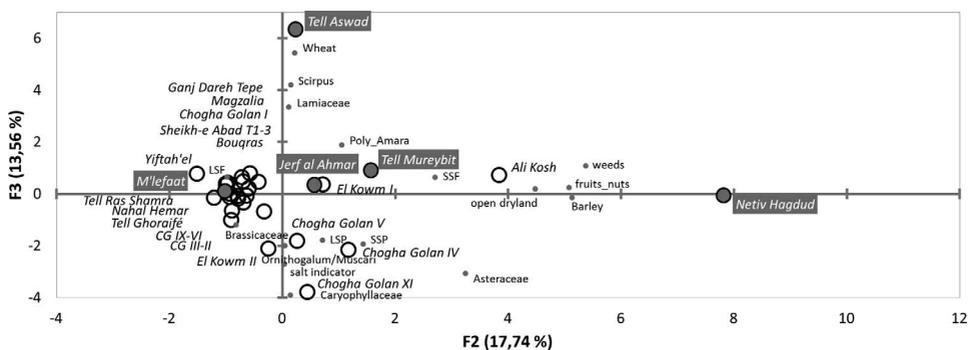


Figure 3. Principal component analyses of aceramic Neolithic archaeobotanical assemblages, without Tell Abu Hureyra and Tell Ramad; Biplot axes F2 and F3 account for 31.3 % of the variability; CG: Chogha Golan.

Table 2. Eigenvalues, percent of variation of axes F1–3 and the five highest positive and negative factor loadings for the different plant categories used in PCA; LSF: large-seeded pulses, SSF: small-seeded pulses.

| | Axis | Taxa groups | Neg. factor loadings | Taxa groups | Pos. factor loadings |
|---|---|---|---|---|---|
| | **F1** | | | | |
| eigenvalue | 3.58 | Open dryland | −0.25 | Ornithogalum/Muscari | 0.83 |
| % of variation | 19.88 | Weeds | −0.19 | Lamiaceae | 0.81 |
| | | LSF | −0.18 | Scirpus | 0.77 |
| | | SSF | −0.13 | Wheat | 0.60 |
| | | Fruits_nuts | −0.10 | Caryophyllaceae | 0.58 |
| | **F2** | | | | |
| eigenvalue | 3.19 | LSF | −0.16 | Weeds | 0.86 |
| % of variation | 17.74 | Brassicaceae | −0.13 | Barley | 0.82 |
| | | Aegilops | −0.06 | Fruits_nuts | 0.81 |
| | | n.a. | | Open dryland | 0.72 |
| | | n.a. | | Asteraceae | 0.52 |
| | **F3** | | | | |
| eigenvalue | 2.44 | Aegilops | −0.57 | Wheat | 0.76 |
| % of variation | 13.56 | Caryophyllaceae | −0.55 | Scirpus | 0.59 |
| | | Asteraceae | −0.43 | Lamiaceae | 0.47 |
| | | Salt indicator | −0.38 | Poly_Amara | 0.26 |
| | | Ornithogalum/Muscari | −0.28 | Weeds | 0.15 |

aceramic Neolithic sites of Jerf el Ahmar, Dja'de, and Akarçay Tepe (Supplementary Table 2).

Measurements of $\delta^{13}C$ in archaeobotanical *Hordeum spontaneum* grains from Chogha Golan and modern *Hordeum spontaneum* were carried out at the Institute of Geosciences of the University of Tubingen, Germany, on a FinniganMAT252 gas source mass spectrometer with a ThermoFinnigan GasBench II/CTC Combi-Pal autosampler. Prior to mass-spectrometric measurements, the barley grains were reacted with 5% HCl to eliminate sedimentary carbonate. The common standard of $\delta^{13}C$ VPDB (Vienna Peedee belemnite ‰) was applied to the measurements of the $^{13}C/^{12}C$ ratios to calculate $\delta^{13}C$ in the barley grains. Changes in atmospheric $CO_2$ concentration ($\delta^{13}C$ air) over time were taken into account by calibrating our $\delta^{13}C$ from ancient barley to $\Delta^{13}C$ values by using the approximation AIRCO2_LOESS (Barnola et al. 1987; Ferrio et al. 2005).

In modern domesticated barley (*Hordeum vulgare*), 40 mm total water input (TWI) equals a $\delta^{13}C$ value of roughly −23‰, corresponding to a $\Delta^{13}C$ of approximately 16‰ (Riehl et al. 2014). Ancient, calibrated values between 17‰ and 16‰ may be considered to indicate moderate drought stress and values below 16‰ to characterize an increased drought stress. There are, however, other researchers (Wallace et al. 2015) who consider values of 18‰–17‰ in two-row barley and up to 19‰ in six-row barley to indicate stress. Such high values appear unrealistic because measurements are typically below 19‰ in archaeobotanical grains from Near Eastern sites (Riehl et al. 2014), which would mean
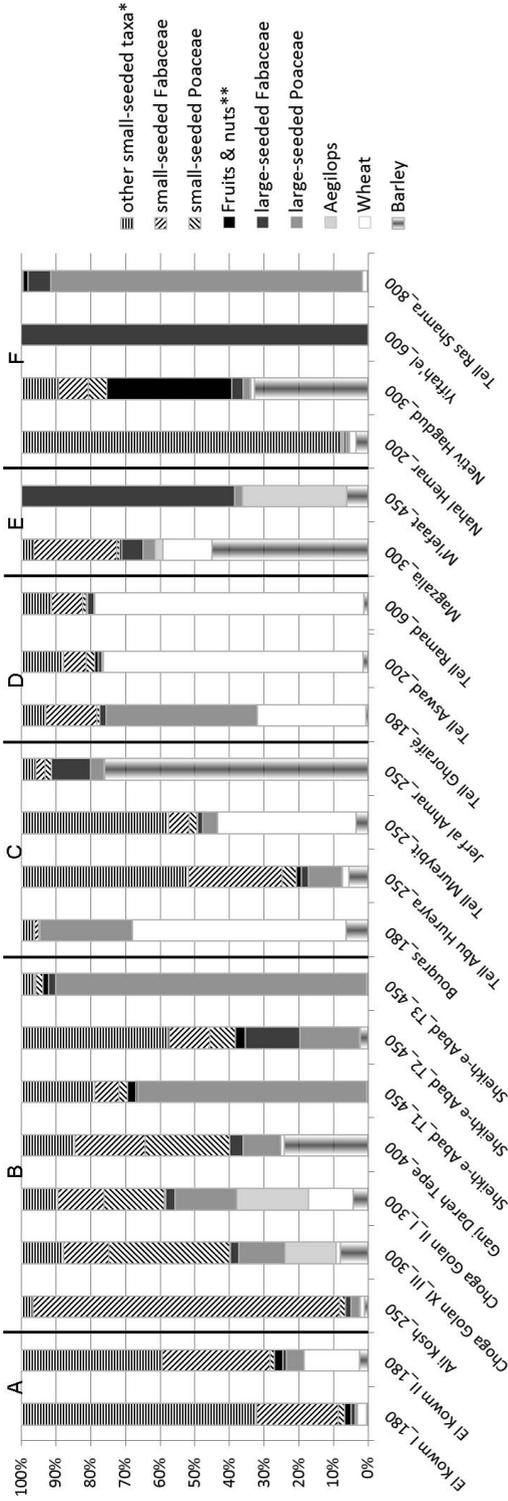
Figure 4. Seed percentage proportions of large-seeded (barley, wheat, Aegilops, large-seeded Poaceae, large-seeded Fabaceae, fruits and nuts in grayscale signatures) and small-seeded categories (small-seeded Poaceae, small-seeded Fabaceae, other small-seeded taxa in line signatures) in the different archaeological sites. The sites are arranged under consideration of three different factors that are superimposed on each other: (1) geographic region (A: Syrian desert; B: Iran, C: Euphrates, D: Damascus region, E: upper Tigris; F: southern Levant), (2) modern mean annual precipitation in mm/a provided as extension in the site name, and (3) age. Arrangement is according to dating only within the same region, if mean annual precipitation and site name are identical. Other small-seeded taxa*: Caryophyllaceae, Lamiaceae, Brassicaceae, Asteraceae, Polygonaceae, Chenopodium spp., Helianthemum sp., Aizoon sp., Gypsophila spp., Suaeda sp., Beta sp., Scirpus sp., Ornithogalum/Muscari type. Fruits & nuts**: Vitis sp., Ficus sp., Pistacia spp., Prunus spp.

that barley was always cultivated under drought throughout prehistoric and historic times.

Interpretation of $^{15}$N signals from archaeobotanical remains is not straightforward because of the considerable number of factors involved in the soil–plant system (Amundson et al. 2003; Högberg 1997). Soil processes that lead to nitrogen loss, such as nitrate lixiviation through precipitation, generally result in relative enrichment of the heavy isotope, which is also captured in plant matter. At the same time, nitrogen input through fertilizers, which results in nitrogen excess, also leads to an enrichment of $^{15}$N (Bogaard et al. 2007; for an overview on the sources of variability in nitrogen isotopes, see Fiorentino et al. 2014). For the beginnings of cultivation and emerging agriculture, we assume that manuring was not practiced and that enriched $^{15}$N values indicate naturally fertile soils. However, enriched values could also be a consequence of increased rainfall. Factors that could cause depletion of $^{15}$N, such as soil salinity, would require additional consideration of the archaeobotanical assemblage for indicator species of saline conditions (Handley et al. 1997; Yousfi et al. 2009). The results presented here can be considered as a step into this direction.

## Results

### Archaeobotanical Assemblage Structure at Aceramic Neolithic Sites

Principal component analysis provides an overview on how the various sites differ from each other based on functional, taxonomic, and ecological classification of archaeobotanical taxa[1] (Figures 2 and 3). The most significant pattern in the currently available data is the high inter-site diversity of archaeobotanical assemblages from Epipalaeolithic and PPNA sites, whereas sites dated later than 10,800 cal yrs BP (PPNB) appear more similar to each other in terms of plant composition (Figures 2 and 3).

The first three axes of the PCA account for 51.17% of the data variation (Table 2). Considering the highest factor loadings for each axis, the open dryland group appears to occur together with the fruits/nuts group and barley, in contrast to wheat (*Triticum* spp.), which occurs on axes F1 and F3 with *Scirpus* sp. This suggests an association of different growing habitats of the two wild cereals, with barley growing in drier and wheat in moister vegetation units. Related to this, differences in the frequency of ancient people using these different habitats may have been relevant for the formation process of the archaeobotanical assemblage.

Most of the younger sites, culturally equivalent to the PPNB, accumulate in the left part of the diagrams (Figure 2 and 3), whereas the older sites (Epipalaeolithic and PPNA) are distributed in all sectors and dominantly appear at the most distant spots from the center of the axes, indicating that each of the older archaeobotanical assemblages differs considerably from those of other old sites. This was particularly the case for the sites of Abu Hureyra and Tell Ramad, leading to amalgamation of all other sites. Therefore the assemblages from Abu Hureyra and Tell Ramad were excluded for the production of Figures 2 and 3.

Looking at the taxonomic diversity of the archaeobotanical assemblages (i.e., at the number of different taxa recorded at each site), the oldest sites appear to be

taxonomically more diverse, Netiv Hagdud and Tell Aswad in particular, as well as Abu Hureyra and Tell Ramad (Table 1). The predefined taxonomic, functional, and ecological categories characterize the assemblages. For example, wheat species and a number of small-seeded taxa dominate the assemblage from Tell Aswad, but at Netiv Hagdud, fruits, nuts (mostly pistachio [*Pistacia* sp.] and almonds [*Amygdalus* sp.]), and barley account for the dominant taxa.

There are three recognizable factors that influence the abundance of small- and large-seeded taxa and that superimpose on each other: the geographic region, site chronology, and human dietary choice based on palaeoclimatic diversity (Figure 4). The geographic region in which sites are located determines the composition of the floristic assemblages through the habitat structure and a region's range of precipitation. For example, locations with lower modern mean annual precipitation show higher amounts of small-seeded taxa than those sites that are within an area that exhibited either higher mean annual rainfall or productive aquifers and major rivers. Within the different geographic regions, chronology also appears to play a role, with a trend towards higher amounts of large-seeded progenitor species in younger sites.

There are few exceptions to the relationship between the dominance of either small- or large-seeded taxa and geographic and chronological parameters that likely relate to human choice in palaeoclimatically diverse landscapes. For example, while the modern mean annual precipitation at Tell Bouqras is approximately 180 mm, its close vicinity to the Euphrates River riparian corridor surely played a role in the availability of ancient water resources. Additionally, local climate at Tell Bouqras was likely moister than today, particularly during the first half of the site's occupation. Similarly the Damascus region is known for being located above highly productive aquifers (Tübinger Atlas des Vorderen Orients [TAVO] A II 5), which may have compensated for the regionally low rainfall and enabled the growth of large-seeded wild progenitor species of modern crops.

Examination of the archaeobotanical assemblages indeed confirms earlier observations of decreasing low-ranked, small-seeded plant taxa over time, but suggests that the decreasing taxonomic diversity is also associated with the regional precipitation ranges and floristic composition in the vicinity of the sites. Whether these patterns are related to climatic fluctuations at the Pleistocene-Holocene transition cannot be answered on the basis of the composition of archaeobotanical assemblages alone.

## Stable Carbon and Nitrogen Isotope Analysis of Cereal Grains

Stable carbon isotope ratios measured in barley from different aceramic Neolithic sites appear to be relatively stable in their range throughout the early Holocene (Figure 5). However, consideration of the means and minima indicates comparatively dry conditions at the earliest sites (the left five sites in Figure 5, dating between 11,220–10,830 cal yrs BP). Such drier conditions at the beginning of the Holocene may have affected the growth of wild cereals. The mean $\Delta^{13}C$ values at the sites Jerf el-Ahmar and Chogha Golan in samples older than 10,800 cal yrs BP are generally lower than those of later periods, including modern values of *Hordeum spontaneum*.
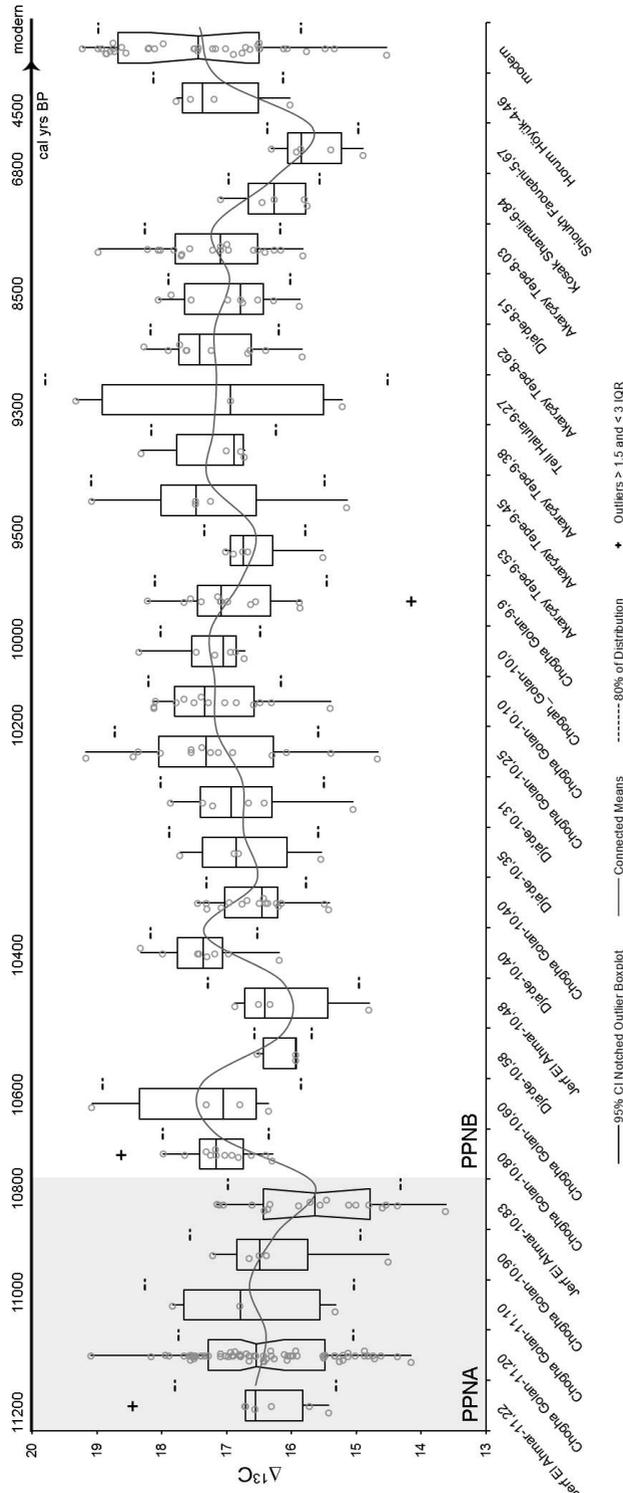
Figure 5. Stable carbon isotope measurements in *Hordeum* species from different early Holocene sites. Dating given in ky BP as extension in the site name.
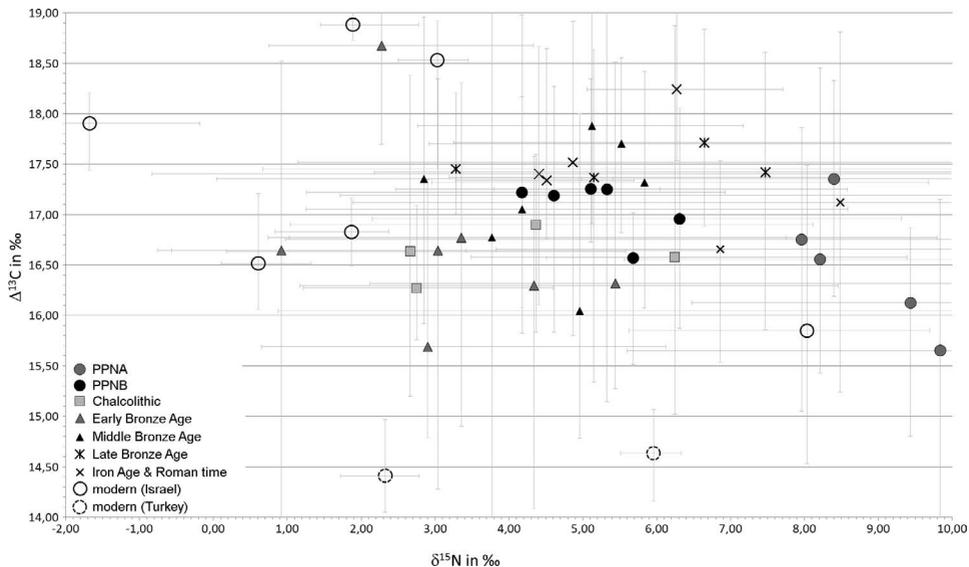
Figure 6. Mean stable carbon and nitrogen measurements in barley from different historic and prehistoric sites with minima and maxima values in both directions.

Examination of $\delta^{13}$C and $\delta^{15}$N values in barley illustrates an interesting pattern (Figure 6). Modern mean $^{15}$N values are generally depleted, whereas values from samples older than 10,300 cal yrs BP are generally enriched in $^{15}$N. Comparatively depleted $^{15}$N values also occur in Early and Middle Bronze Age samples, but some of the Late Bronze and Iron Age sites show high $\delta^{15}$N, which may be an effect of manuring domesticated barley fields. Late Bronze and Iron Age samples also show $\delta^{13}$C values of relatively sufficient moisture availability for barley growth, in contrast to the mean values of the Chalcolithic and Early Bronze Age samples, which more frequently indicate drought stress.

A relatively clear chronological pattern is also indicated when comparing different taxa of cereal, such as free-threshing wheat (*Triticum aestivum/durum*), emmer wheat (*Triticum dicoccum*), rye (*Triticum/Secale*), einkorn (*Triticum boeticum* and *T. monococcum*) and barley (*Hordeum spontaneum* and *H. vulgare*) from early Holocene sites (Figure 7). Wild cereal grains from locations that date to sequences older than 10,400 cal yrs BP generally show a stronger stress signal and extreme water stress appears to have presented a problem only in the oldest sites (Abu Hureyra and the older levels of Jerf el Ahmar). The $\delta^{15}$N values are relatively enriched in sites older than 10,400 cal yrs BP and samples dated after 9,400 cal yrs BP never have $\delta^{15}$N values higher than 7‰.

Summarizing the results, Epipalaeolithic and PPNA archaeobotanical assemblages are generally highly diverse, on the taxonomic as well as on the inter-site level, compared with later assemblages that are more similar to each other in composition and show a trend to decreased numbers of taxa. In other words, a loss of diversity in plant use can be observed throughout time. Although chronology surely plays a role in the composition of the plant assemblages, the geographic region and climatic background are also important factors. There is a
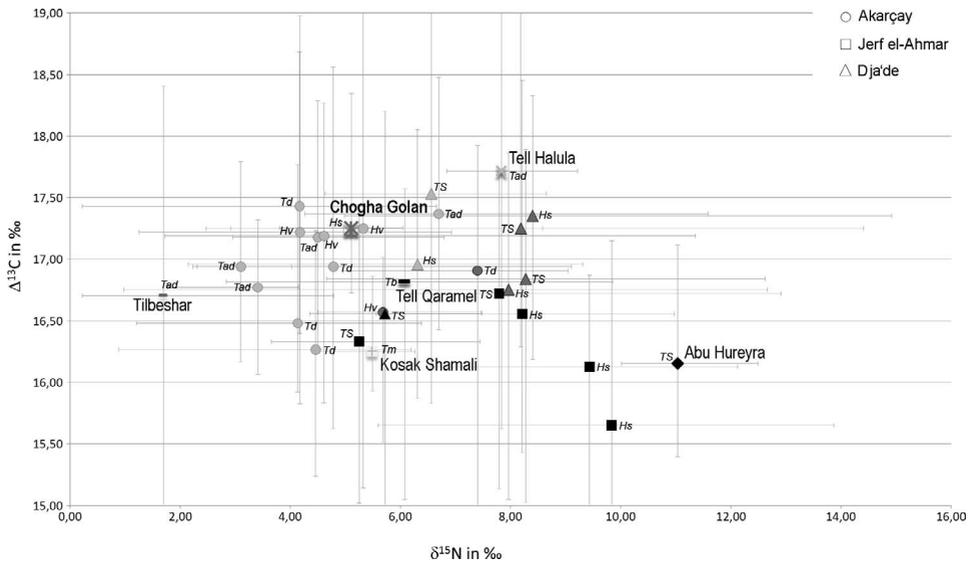
Figure 7. Mean stable carbon and nitrogen measurements in different cereal taxa (*Tad-Triticum aestivum/durum, Td-Triticum dicoccum, Tm-Triticum monococcum, Tb-Triticum boeoticum, TS-Triticum/Secale, Hv-Hordeum vulgare, Hs-Hordeum spontaneum*) from different early Holocene sites. Chronology: black symbols: samples older than 10,400 BP, dark Grey symbols: samples dating between 10,400 BP and 9,500 BP, light Grey symbols: samples dating between 9,400–8,000 BP, Kosak Shamali and Tilbeshar are younger than 8,000 BP.

trend of higher amounts of small-seeded taxa in older sites with lower modern mean annual precipitation in contrast to large-seeded progenitor species that occur in higher amounts at younger sites with higher modern mean annual precipitation. These results are supported by the $\delta^{13}C$ record that indicates a stronger stress signal in sites older than 10,800 cal yrs BP (Figure 5) than in samples of younger age. Additionally, samples younger than 10,300 cal yrs BP are depleted in $^{15}N$ but only until the end of the Middle Bronze Age (Figure 6). Given that the isotopic trends are visible across the different wild cereal species, the pattern is environmental rather than species-specific.

## Discussion

The data presented in this study can be interpreted at multiple levels, suggesting first that climatic fluctuations that created regionally drier conditions favored higher amounts of small-seeded taxa that were gathered in an opportunistic way. Second, these patterns are superimposed with gradually increasing numbers of large-seeded wild progenitors of modern crops, leading to the cultivation of wild cereals and pulses over time.

Archaeologists consider the question of why agriculture developed in the early Holocene by highlighting environmental limitations through low $CO_2$ concentrations in the atmosphere (Richerson et al. 2001) and/or arid and cool climatic conditions as during the Younger Dryas event (Bar-Yosef 2011).

Alternatively the advent of agriculture can be interpreted favoring explanations that focus on the development of humans' social-cognitive skills (Watkins 2013), which is referred to as the "cultural intelligence hypothesis" (Herrmann et al. 2007; van Schaik and Burkart 2011). Although it is impossible to say whether increased cultural intelligence was a prerequisite for developing agriculture, it is obvious from an evolutionary standpoint that social-cognitive skills developed alongside the necessity to improve human survival and reproductive success under increased stress, which was probably a factor during times of resource pressure. This study cannot contribute to the role of human cognition in the development of agriculture, but it can address environmental factors that influenced the availability of plant resources on the basis of archaeobotanical and stable isotope data.

### Ecological and Human Behavioral Patterns

Small-seeded taxa in aceramic Neolithic sites have been sometimes interpreted as low-ranked food items (Hillman et al. 2001; Weiss et al. 2004), in contrast to the mostly large-seeded wild progenitor species of so-called founder crops. Small-seeded taxa naturally occur in much higher diversity than large-seeded taxa. The high diversity of small-seeded plant taxa, as is observed in a number of Epipalaeolithic and aceramic Neolithic sites, has been linked to Kent Flannery's "broad spectrum revolution" because the high diversity in plant taxa, similar to that in animal species (Zeder 2012), could have been a consequence of human adaptation to food shortages (Weiss et al. 2004). The reduced diversity and ubiquity of small-seeded taxa from the Epipalaeolithic until the early PPNB has been suggested to indicate increasing importance of cultivating founder crops (Willcox et al. 2008). Although broadening of the diet during the Epipalaeolithic and an increasing importance of wild progenitor species of modern crops with the beginning of the aceramic Neolithic were likely coupled to human behavioral development, the data presented here suggest climatic fluctuations and regional environmental conditions as additional important factors in early cultivation. The diversity of climate geography defining different ranges of precipitation and floristic realms set the background for peoples' options and explains why (e.g., in regions with precipitation extremes, either positive or negative) a strict chronological trend of decreasing small-seeded and increasing large-seeded taxa did not occur (Figure 4). Short-term climatic fluctuations over some years surely affected resource availability for early Neolithic human populations, which may be reflected in adverse trends in using small-seeded or large-seeded taxa (e.g., Chogha Golan IV and V in Figure 4; Riehl et al. 2015).

Although it is possible to describe archaeobotanical assemblages with an autecological approach (Willcox et al. 2009), the data presented here emphasize the high diversity in the oldest aceramic Neolithic sites, supporting opportunistic resource use, such as is generally attributed to hunter-gatherer communities, rather than reflecting intentional attempts to increase plant productivity or targeting of specific plant taxa (see Figures 5 and 6). In this context, high ubiquities of floodplain plants in the oldest Neolithic and Epipalaeolithic sites

can be explained by the gatherers' choices to settle in floodplains and to make use of nearby resources.

**A Potential Role for Water Stress**

The drier conditions of the Younger Dryas event and the relatively low $CO_2$ concentrations during the Pleistocene are among the most famous environmental arguments put forward in the discussion of when humans began to cultivate wild species and why domestication emerged in the early Holocene and not earlier (Hillman et al. 2001; Richerson et al. 2001; Sage 1995; Willcox et al. 2009). Both arguments involve stress on plant resources and, through this, assumed food stress for ancient humans. While generalizations that moisture increased due to higher rainfall in the early Holocene compared to the previous Younger Dryas event can be made, the Pleistocene-Holocene transitional increase in moisture may have been a continuous development that did not happen abruptly. This would allow for the possibility that sites that date to the earliest Holocene, such as Jerf el-Ahmar or the oldest levels of Chogha Golan, may still have experienced relatively dry conditions, at least to a degree that caused some drought stress in a larger proportion of the wild barley plants.

Paleoclimate proxy records that support the assumption of a gradual warming after the Younger Dryas exist at the global and regional levels. According to the chronology of ice cores, the transition from the Younger Dryas to typical Holocene $\delta^{18}O_{ice}$ values took approximately 1,500 years, although this included step-like changes within a temperature range of 5–10 °C within only several decades (Severinghaus et al. 1998). The Soreq Cave oxygen isotopes show a two-step transition from the Younger Dryas to the Holocene, with a jump from $-4,4‰$ to modern values of $-5,2 ‰ \delta^{18}O$ within only decades and then continuing to a maximum of $-6‰ \delta^{18}O$ by approximately 9,900 cal yrs BP; i.e., within ca. 1,200 years (Bar-Matthews et al. 2003; see also Supplementary Figure 1). Comparing the dates of the earliest Holocene sites considered here to the $\delta^{18}O$ record from Soreq Cave, the sites fall into a sequence of continuously decreasing $\delta^{18}O$, which further decreased until 9,600–9,500 cal yrs BP (Bar-Matthews et al. 1999). These trends are in line with the differences in composition of the archaeobotanical assemblages. They are also in line with the $\Delta^{13}C$ record in barley grains and with the increased $\delta^{15}N$ values (higher than 7‰) for the earliest Holocene sites.

Although the global paleoclimate development during the Pleistocene-Holocene transition is well investigated and some regional paleoclimate proxy records also highlight the climatic fluctuations of the Younger Dryas and the beginning Holocene, there is little direct local information on the environmental impact on the use of plant resources during this time. Although some argue for the early beginnings of pre-domestication cultivation during the Younger Dryas (Hillman et al. 2001), cultivation of wild plant species is generally considered to have begun with the early Holocene, as indicated at 11 archaeological sites, among them Netiv Hagdud, Abu Hureyra, Jerf el Ahmar, Dja'de, and Chogha Golan (Riehl et al. 2013; Tanno and Willcox 2012; Willcox 2013).

Archaeobotanical studies of aceramic Neolithic assemblages of the Euphrates region describe a slow replacement of rye and small-seeded floodplain plants by

increasing barley frequencies starting during the Younger Dryas until the beginning of the Holocene (Willcox et al. 2009). This chronologically correlates with the decreased $\delta^{15}N$ values in barley and could indicate that either the soils were already less fertile compared with the Epipalaeolithic soils or conditions were dry or were accompanied by increased salinity. Many researchers suggest for the Late Glacial/Early Holocene transition that temperatures were high and therefore so were the evaporation rates that would have supported the emergence of more saline environments. The high frequencies of rye during the Younger Dryas may be a sign of cool conditions. The fact that people were focusing on floodplain plants indicates that they exploited the resources in and around rivers (see also Coşkun et al. 2011) and suggests generally drier environments farther away from the river valleys. The slow decrease in rye until its disappearance in the early Holocene suggests that this cereal species could not survive the increasing temperatures (Willcox et al. 2009) and/or would no longer be competitive with other cereal species. The precipitation increase to optimal conditions for wild cereals was relatively slow and reached its optimum only around 10,800 cal yrs BP. This is reflected in global paleoclimate proxies, such as the $\delta^{18}O$ record from the GRIP (Greenland Ice Core Project) core, as well as in local proxies, such as the $\delta^{13}C$ in barley (see Figure 5). Additionally, seasonal differences in some regions also changed to higher summer rainfall as was discussed for Lakes Zeribar and Mirabad in Iran, supporting the growth of wheat species (El-Moslimany 1987; Stevens et al. 2001).

Although the cultivation of wild plant species appears to have been in place by 11,200 cal yrs BP (Tanno and Willcox 2012), it was only several hundred years later that moisture availability reached a level that could support the maximum productivity of large-seeded progenitor species of modern crops, particularly in areas farther from the Levantine coast (Figure 4). This is supported by the $\delta^{13}C$ record (Figure 5) as well as by the ratios of large-seeded to small-seeded archaeobotanical species at the sites considered here.

## Conclusions

The analyses presented in this paper support previous models arguing for a general pattern of increased use of small-seeded plants in Epipalaeolithic and PPNA sites. These results show that the use of small-seeded plants was also related to times of and regions with higher aridity and that using large-seeded plants was preferred during times and in regions of increased moisture availability. Recent studies of archaeobiological assemblages and the stable carbon isotope record allow for a detailed description of local environmental sequences and for linking those to the developmental steps towards cultivating wild progenitor species of modern crops, though information on the role of human behavior in the slow pace of the emergence of agriculture is still limited. Gathering of a wide range of small-seeded grains was practiced for a long period including the Last Glacial Maximum and the Younger Dryas; however, large-seeded grains of wild progenitor species of modern crops do not dominate plant assemblages dating to before 10,000 cal yrs BP. Nonetheless, indisputable signs of

the pre-domestic cultivation of large-seeded cereals and pulses appear earlier, in 11,200 cal yrs BP, approximately coinciding with the transition from the Younger Dryas event to the early Holocene. There are clear signs in the stable carbon isotope record that the earliest cultivated wild barley (e.g., at Jerf el Ahmar and Chogha Golan) had to face the still drier soil conditions than later early Holocene sites after 10,800 cal yrs BP. In drier environments and during times of increased aridity, small-seeded plants, however, remained an important foodstuff until at least 9,000 cal yrs BP. Continuously increasing the cultivation of wild cereals from approximately 10,500 cal yrs BP onwards led to genetically changed cereals only some hundred years later, whereas assemblages dominated by domesticated grains appeared not before 8,500 cal yrs BP.

### Note

[1] With the current state of the research, far more PPNB (Pre-pottery Neolithic B; ca. 10,600–9,500 cal yrs BP [short chronology according to radiocarbon dates at Exoriente 2016], ca. 10,800–8,400 cal yrs BP [long chronology according to Akkermans and Schwartz 2003]) than older sites, culturally belonging to the Epipalaeolithic and PPNA (Pre-pottery Neolithic A; ca. 11,700–10,800 cal yrs BP) have been investigated for their archaeobotanical remains, which makes a diachronic comparison of the assemblages difficult.

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