



Identification and exploitation of wild rye (*Secale* spp.) during the early Neolithic in the Middle Euphrates valley

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Abstract

Charred remains of wild rye from five sites in the Middle Euphrates region in Syria dated to the end of the Pleistocene and the beginning of the Holocene are examined. This period spans the transition from gathering to the beginnings of cultivation. Today wild rye cannot grow in the region because temperatures and aridity are too pronounced. Wild rye grains and wild two-grained einkorn are morphologically similar, which has led to difficulties in identification; in some cases rye may have been identified as two-grained einkorn or as *Triticum/Secale*. In this paper, with reference to modern specimens and re-examination of charred material from Dja'de el-Mughara, Jerf el-Ahmar and Mureybet, we examine the criteria for identification and revise the results for charred caryopses and wild spikelet bases. We then present these new results which show that at the early Neolithic sites of Jerf el-Ahmar, Mureybet, Dja'de el-Mughara and Tell 'Abr 3 wild rye frequencies are much higher than einkorn but wild barley is the dominant cereal. This is followed by discussions of how and why wild rye may have been exploited during the early Neolithic and why rye disappears from Euphrates sites with the advent of mixed farming.

Keywords Northern Syria · Early Holocene · *Secale* · Rye · Plant exploitation

Introduction

At the end of the Younger Dryas and the beginning of the Holocene, at least two Natufian sites and seven Pre-Pottery Neolithic villages were inhabited in the Middle Euphrates valley in northern Syria. As in other areas of the Fertile Crescent a wide variety of plants were exploited, including the eight taxa which make up the 'Neolithic founder crops' defined by Zohary. These include barley, einkorn, emmer, bitter vetch, chickpea, lentil, pea and flax (Weiss and Zohary 2011); to these, on the basis of recent finds, fig, broad (or horse) bean, timopheevi wheat and possibly wild rye should

be added (Denham 2007; Caracuta et al. 2017; Czajkowska et al. 2020).

With few exceptions, the exploitation of wild rye is restricted to the Middle Euphrates valley during the late Younger Dryas and the early Holocene. Significantly, wild rye cannot grow in the area today because the climate is too hot and arid. In the past, identifying wild rye and in particular distinguishing between charred grains of wild rye and those of two-grained wild einkorn has been problematic (Moore et al. 1975; Willcox 1996). Thus the identifications are sometimes referred to as *Triticum/Secale* (Willcox et al. 2008; Table 1). Hillman was the first to recognize rye grains in Natufian levels at Abu Hureyra, on the Euphrates (Moore et al. 1975; Hillman et al. 1989, 1997). He suggested that a few plump grains were domestic types (Fig. 12.6 and 12.23 in Hillman 2000). However, this was later nuanced (Hillman et al. 2001) and most archaeobotanists today agree that there is not enough evidence indicating domestic rye at Abu Hureyra (Colledge and Conolly 2010). *Hordeum spontaneum* (wild barley) is absent in Natufian levels at Abu Hureyra, only three grains were recovered from Natufian levels at Mureybet (van Zeist and Bakker-Heeres 1984; Willcox 2008), but it is dominant on the later early Holocene sites.

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Table 1 Summary of rye (or potential rye) finds from late Pleistocene and early Holocene sites in Southwest Asia

Site	Date/period	Rye identification	References
Abu Hureyra (N Syria)	Epipalaeolithic (11th mill. BC)	<i>Secale montanum</i> grains <i>S. vavilovii</i> grains <i>S. cereale</i> grains	Hillman 2000; Hillman et al. 2001; Colledge and Conolly 2010
Körtik Tepe (SE Anatolia)	Epipalaeolithic– Early Neolithic (11–10th mill. BC)	<i>Secale</i> grains <i>Secale cereale</i> brittle rachis	Coşkun et al. 2012; Benz et al. 2015; Rössner et al. 2018
Hallan Çemi (SE Anatolia)	PPNA (10th mill. BC)	<i>Triticum/Secale</i> grains	Savard 2018
Qermez Dere (N Iraq)	PPNA (10th mill. BC)	<i>Triticum/Secale</i> grains	Savard et al. 2006
Tell Mureybet (N Syria)	PPNA (10th mill. BC)	<i>Secale</i> spikelet impressions <i>Secale</i> grains (revised grains, among those previously identified as <i>T. boeoticum</i> ssp. <i>thaouadar</i>)	van Zeist and Casparie 1968; van Zeist and Bakker-Heeres 1984; Willcox and Fornite 1999; Willcox 2008
Jerf el-Ahmar (N Syria)	PPNA (10th mill. BC)	<i>Secale</i> spikelet bases impressions & charred remains <i>Secale</i> grains (revised grains, among those previously identified as <i>Triticum/Secale</i>)	Stordeur and Willcox 2009; Willcox and Stordeur 2012
Tell ‘Abr 3 (N Syria)	PPNA (10th mill. BC)	<i>Secale</i> grains	Stordeur and Willcox 2009; Yartah 2013
Dja’de el-Mughara (N Syria)	PPNA-EPPNB (10th–9th mill. BC)	<i>Secale</i> grains (including some of those previously identified as <i>Triticum/Secale</i>) <i>Secale</i> spikelet bases	Willcox 1996; Willcox et al. 2008; Douché and Willcox 2018
Çafer Höyük (C Anatolia)	EPPNB-LPPNB (8th–7th mill. BC)	<i>Triticum/Secale</i> grains and spikelet forks (cereals) <i>Secale montanum/vavilovii</i> grains (as wild/weed taxa)	De Moulins 1997

Attempts were made to identify the species of wild rye grains from Abu Hureyra using SEM examination but these were not successful (Hillman et al. 1989). Studies of the grain morphology from the Abu Hureyra material allowed G. Hillman and colleagues (Hillman et al. 1993) to suggest that some grains resemble the perennial wild species *Secale montanum* and this identification was purportedly confirmed by infra-red spectroscopy (Hillman et al. 1989, 1993 p. 106). In addition, another species, *S. vavilovii*, was identified (Hillman 2000).

Spikelet bases of wild rye were identified for the first time from impressions of chaff used as a tempering material for the pisé (i.e. daub or building earth) from a burnt house dated to Pre-Pottery Neolithic A at Tell Mureybet (Willcox and Fornite 1999). Unlike the grains, *Secale* spikelet bases are readily distinguishable from those of einkorn. Earlier analyses by W. van Zeist (van Zeist and Bakker-Heeres 1984) listed only two-grained einkorn grains (*Triticum boeoticum* ssp. *thaouadar*) and not wild rye. Thus the identification of wild rye spikelet bases in the same levels as charred two-grained einkorn suggest the possibility that wild rye had been overlooked or misidentified in the earlier studies.

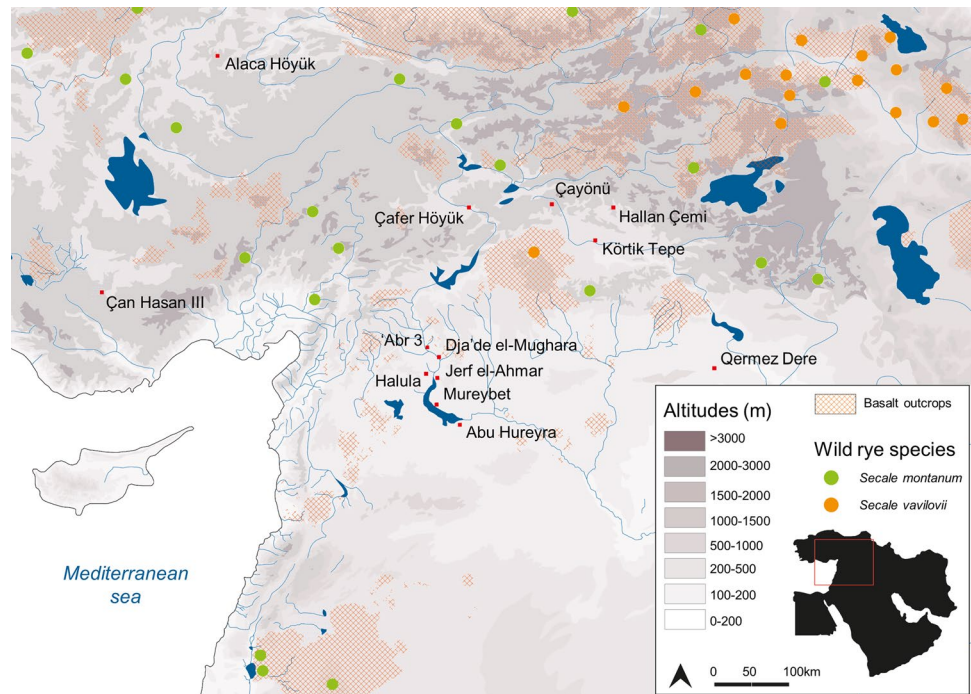
When in 2008 the results from three Euphrates sites were published (Willcox et al. 2008), einkorn and rye grains were not separated, thus a large proportion of

charred grains from Jerf el-Ahmar, Dja’de el-Mughara and Tell ‘Abr 3 were recorded as *Triticum/Secale* (Fig. 1 and Table 1). However, charred wild rye spikelet bases were identified among the assemblage and these were more frequent than einkorn spikelet bases. More comprehensive examination showed that wild rye grains were dominant over two-grained einkorn (Willcox and Stordeur 2012).

Outside the Middle Euphrates (Table 1), *Triticum/Secale* has been reported from Hallan Çemi (Savard 2018), Qermez Dere (Savard et al. 2003, 2006) and Çafer Höyük (De Moulins 1997). Wild type *Secale* grains and chaff have been reported at Epipalaeolithic-early Neolithic Körtik Tepe (SE Anatolia), about 250 km northeast of the Euphrates sites (Coşkun et al. 2012; Benz et al. 2015; Rössner et al. 2018). Rye identified from later periods in Anatolia, for example at Çan Hasan III (Hillman 1978), Alaca Höyük (Gökgöl 1944) and in Europe, appear to be unrelated and morphologically different from the wild types from the Euphrates sites. Indeed, these later finds are large-grained domestic rye or weedy forms of *Secale cereale* (Behre 1992; Grikpëdis and Matuzevičiūtė 2016; Filatova et al. 2021) and are not included in this study.

Having re-examined the material from Jerf el-Ahmar, Dja’de el-Mughara, Tell ‘Abr 3 and Tell Mureybet, we

Fig. 1 Map showing the positions of the sites mentioned in the text, locations of modern stands of wild rye (not exhaustive) and major basalt outcrops



provide in this paper more precise identifications of wild rye found on these sites compared to previous publications.

The Middle Euphrates valley at the end of the Pleistocene and beginning of the Holocene

Today the area receives an average annual rainfall of between 150 and 300 mm. The vegetation is that of a highly degraded steppe and wild barley is the only wild cereal growing in the area today. However, during the early Holocene an open woodland steppe-forest with *Pistacia atlantica*, *Amygdalus* sp. and possibly *Quercus* sp. was present in the area, together with a rich riparian vegetation along the Euphrates river (Willcox 1996 p. 149, 2002; Helmer et al. 1998). Violent annual floods caused by a combination of snow melts in the Taurus and spring rains in April inundated the floodplain until dams were constructed upstream (Willcox and Roitel 1998). The settlements were protected from

flooding by being located on terraces some 10 m above the floodplain. The seasonal floods coincided with the point at which the cereals approached maturity, not during the growing season when moisture was necessary; their cultivation on the flood plain would have been impossible before the recent construction of dams. Similarly wild cereals could not have grown on the flood plain. Downstream in Iraq, where the Euphrates valley broadens and the flow is slower, water can be channeled away from the flood plain so that crops can be irrigated during the growing season, out of reach of all but the most extreme floods.

The site locations are given in Fig. 1. Seven sites are known to have been inhabited during the late Pleistocene/early Holocene in the Euphrates valley; of these, five produced finds of wild rye (dates for the sites are given in Table 2). Note that the PPNA (Pre-Pottery Neolithic A) – PPNB (Pre-Pottery Neolithic B) site of Cheikh Hassan

Table 2 List of archaeological sites located in the Middle Euphrates mentioned in the text and their dates of occupation

Site	Cultural period	Dates (cal BC)	References
Abu Hureyra	Late Natufian	ca. 11,100–10,000	Colledge and Conolly 2010
Tell 'Abr 3	PPNA	9th mill.	Yartah 2005
Jerf el-Ahmar	PPNA	ca. 9400–8900	Stordeur and Willcox 2009
Dja'de el-Mughara	PPNA, EPPNB	ca. 9310–8830, 8800–8290	Coqueugniot 2014
Tell Mureybet	PPNA, EPPNB, MPPNB	9500–8700, 8700–8200, 8200–8000	Ibáñez 2008
Tell Halula	MPPNB, LPPNB	8200–7500, 7500–7000	Molist 2013 (see Buxó and Rovira 2013)

is not included because there are no archaeobotanical data (see Abbès et al. 2001).

The occupation periods of these sites coincide with the climatic fluctuations occurring at the end of the Pleistocene and the beginning of the Holocene; thus Abu Hureyra I (late Natufian) dates to the end of the Pleistocene just before the Younger Dryas; Mureybet I (late Natufian) and Mureybet II (Khiamian) date to the Younger Dryas, a period of aridity and cooling. The PPNA sites of Jerf el-Ahmar, Tell ‘Abr 3 and Mureybet III date to the early Holocene, when the temperature increased but the climate was probably cooler and moister than today. Dja’de el-Mughara (late PPNA/early PPNB) also dates to the early Holocene. Jerf el-Ahmar, Mureybet, and Abu Hureyra are the most southerly sites, situated in an area which receives an average annual rainfall of 150–200 mm. Dja’de el-Mughara (Coqueugniot 2000, 2014) has an annual average rainfall of about 300 mm and is situated 50 km upstream from Jerf el-Ahmar. Tell ‘Abr 3 (Yartah 2004, 2005) is situated about 25 km farther north in an area with an annual rainfall similar to that of Dja’de el-Mughara.

Materials and methods

Modern species of wild rye

The classifications of wild ryes by botanists and geneticists are not always in agreement. This may be partly due to hybridization which can take place between different species. We use classification adopted by Maraci et al. (2018) which includes four species, two of which do not concern us: *S. cereale* which consists of several weedy and domestic subspecies and *S. sylvestris* which occurs outside our geographical range. Of the two remaining species which are relevant to this study, *S. vavilovii* is often cited as being the possible progenitor of domestic rye, and *S. strictum* (formerly *S. montanum*, the name we use here) has four subspecies and a wide range.

Secale cereale, *S. montanum* and *S. vavilovii* are heterogamous, unlike wheat and barley which are autogamous (self-fertilizing). This factor may have led to a more complex domestication process compared to wheat and barley and explains why the domestication of rye remains poorly understood. Interspecific hybridization is possible, for example between *S. cereale* and *S. montanum*, although this often leads to low-fertility hybrids (Stutz 1957; Singh et al. 1997). Genetic studies suggest that *S. vavilovii* is probably the wild rye that is closest to domestic rye (Schreiber et al. 2019), which evolved into a weedy form and then domestic *S. cereale* ssp. *cereale* (Sun et al. 2022).

Secale montanum is widely distributed in central and eastern Anatolia above 800 m a.s.l. on basalt soils (Figs. 1

and 2a, b) and was identified in the Akher Dagh, north of Kermanshah (Post and Dinsmore 1932; Davis 1985). Farther south, Willcox collected *S. montanum* at above 1,000 m on the Djebel Druze in southern Syria and it has been recorded on Mount Hermon in northern Israel. According to the *Flora Palaestina* (Feinbrun-Dothan 1986 pp. 178–179), the online Flora Syria (<http://florasyria.com/>) and Flora of Israel and adjacent areas (<https://flora.org.il/en/plants/sec-mon/>), *S. montanum* is the only wild rye species recorded in Syria. *S. vavilovii* has a more restricted distribution in eastern Anatolia (Map 7 in Zohary et al. 2012). Photos in Fig. 2c, d show wild stands, where in 1992 G. Hillman and his colleagues collected *S. vavilovii* on the foothills of Mount Ararat and around Lake Van. In conclusion, *S. montanum* has a more widespread distribution compared to *S. vavilovii*, which may be due to its wider tolerance to soil and climatic conditions.

Morphology of modern wild rye species

Spikelet bases

Spikelet bases of wild rye are readily distinguishable from other cereal spikelet bases. Their identification, unlike that of the grains, provides unequivocal evidence for the presence of wild rye. Rye species, except for *S. sylvestre* (Schlegel 2016 p. 11), contain two fertile florets (two grains per spikelet) alternating in two ranks. The lemmas of wild rye are long with an awn and characterized by “pectinate-ciliate keels” (Willcox and Fornite 1999) which do not occur on einkorn (Fig. 3a, b). In general, the glumes of rye are reduced but thick at the base and are inserted into the spikelet base at a more horizontal angle (aprox. 90°) than the glumes of einkorn, which are wide and thin at the base and inserted into the rachis at a more vertical angle. In addition, einkorn spikelet bases exhibit a primary keel arising at the same level as the abscission scar. The abscission scars of rye and einkorn can also be distinguished: the scar of the former is deep and defined by a pronounced lip; on the latter it is wide and shallow. Finally, vertical lines running along the internodes of rye are highly pronounced compared to einkorn.

Grains

Hillman (2000) provided the following observations on rye: (1) the grains are relatively narrow and triangular in transverse section; (2) the ventral furrow forms a lacunate T-shape in cross-section and extends around the apical end; (3) the apical end is conoidal-truncate in side view; (4) the coleoptile is narrow and pointed. Because the distinction between the caryopses of wild rye and wild two-grained einkorn has been problematical in the past (Willcox 1996),



Fig. 2 Photos of wild rye. **a** Wild rye (*Secale montanum*) flowering at Jalès, France (photo taken by G. Willcox in 1995), **b** Wild stand in the Karadağ (Turkey) including a mixture of oat, wheat and rye

(photo taken G. Willcox in 2004), **c** Photos of *S. vavilovii* growing on the foothills of Mount Ararat (Turkey) and **d** along a roadside (photos taken by P. Anderson in 1992)

we attempt here to clarify the morphological differences between two-grained einkorn and wild rye (see Table 3; Fig. 3c–f). The ventral surface of wild rye is slightly convex, whereas for two-grained einkorn it is flat (Kreuz and Boenke 2002). A ridge and striations often run longitudinally on the dorsal surface of wild rye, while a single dorsal line formed by a shallow groove is usually visible on einkorn. Two-grained einkorn grains are also characterized by the presence of a longitudinal line running on their lateral side due to the pressure of the glumes (Weide et al. 2021), and they sometimes present a ventral compression (notch) at the apex, whereas rye is more truncated. Rye and einkorn also differ in the size of the embryo which is relatively long for rye and short for einkorn. Finally, the cell pattern of the epidermis is often clearly visible on rye grains and forms longitudinal lines, formed by large cells seen in a lateral view (Hillman et al. 1993).

Charring affects grain morphology. Recent experimental charring indicates that wild rye grains (*Secale cereale* ssp. *vavilovii*) become more rounded when charred at

260–300 °C (Weide et al. 2021). Our results from charring experiments on *S. vavilovii* at lower temperatures (150–200 °C) produced shrinkage (Fig. 4). In general, experimental charring of cereal grains has demonstrated that various distortions (i.e. shrinkage or puffing) can occur, depending on several conditions such as humidity, temperature, oxygen levels etc. which would produce a wider size range compared to fresh material (Willcox 2004; Braadbaart 2008; Charles et al. 2015).

Archaeological material

For details of recovery and processing of the charred material see van Zeist and Bakker-Heeres (1984), Hillman (2000), Willcox et al. (2008) and Douché and Willcox (2018). Samples collected from a variety of archaeological contexts (including floors, pits, accumulated ash and hearths) were processed by flotation. Six cereal taxa were identified at the five sites. For simplicity we use the ‘traditional taxonomy’ (Zohary et al. 2012 p. 29) as follows: (1)

Fig. 3 Modern specimens of **a** *Secale vavilovii*, spikelet base (MNHN, LAB 2621), **b** *Secale montanum*, spikelet base (MNHN, G1986-181), **c** *Secale vavilovii*, grain (MNHN, LAB 2621), **d** *Secale montanum*, grain (MNHN, G1986-181), **e** *Secale sylvestre*, grain (IPK R1129), **f** *Triticum boeoticum* 2gr. (Beysehir, Turkey—Groningen collection). Note the angle and the position of where the glumes joint the rachis on wild rye and the flat ventral face in 2gr. einkorn caryopsis. MNHN Muséum National d’Histoire Naturelle (LAB Reference collection of the archaeobotanical laboratory; G “Graineterie”/seedbank), IPK Leibniz Institute of Plant Genetics and Crop Plant Research. Scale bars = 1 mm



Table 3 Morphological differences between wild two-grained einkorn and wild rye based on our observations, and descriptions given by Kreuz and Boenke (2002) and Nesbitt (2017)

	2gr Einkorn (<i>Triticum boeoticum</i>)	Wild rye (<i>Secale</i> spp.)
Spikelet and floret		
Lemma	Lemma wide with a long awn	Lemma wide with a medium awn. Keel pectinate-ciliate
Glumes	Wide but thin at the base. Little or no veining near the base. Glume inserted into the rachis at an oblique angle. Primary keel, arising at the same level as the attachment scar	Narrow but thick at the base. Little or no veining near the base. Glume inserted into the rachis at an abrupt angle (c. 90°)
Internode		Vertical lines
Abscission scar	Wide and shallow	Deep with protruding lips
Caryopsis		
Shape		
Ventral face	Flat	Slightly more convex
Dorsal ridging		Sharp ridge running longitudinally on the back
Dorsal markings	Single dorsal groove	Striations
Lateral view	Groove impression left by the glumes often visible	Groove impression left by the lemmas rarely visible
Apex	Ventral compression ending well short of the apex (notch)	Truncation
Embryo		
Scutellum size	Narrow and short (1/6 of the grain length)	Long (1/4 – 1/3 of the grain length)
Scutellum shape	Linear short	Basal V-shape
Bran		
Epidermis		Cell pattern of the epidermis forming well defined longitudinal lines

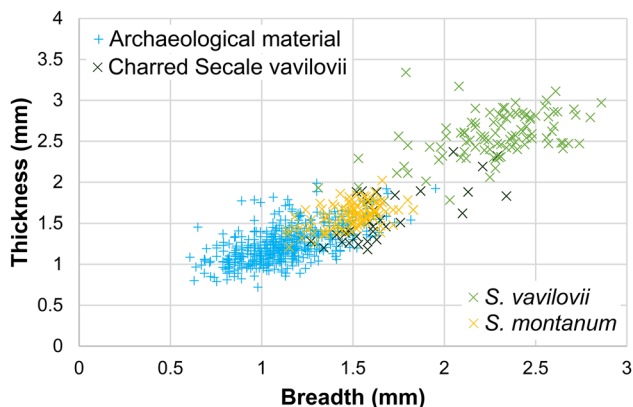


Fig. 4 Scatter diagram giving measurements of archaeological grains from Abr'3 (n=90), Jerf (n=273), Mureybet (n=50) and Dja'de (n=75) compared to modern fresh *S. montanum* and *S. vavilovii* and charred *S. vavilovii* (experimental charring made by G. Willcox). The charred *S. vavilovii* grains exhibit shrinkage compared to the fresh material due to charring. The archaeological charred grain are the smallest, the group nearest in size to them are uncharred *S. montanum*. While more work needs to be carried out, the best match for the early Neolithic rye grain is with *S. montanum*; see Supplementary material 1 for measurement details

Hordeum spontaneum (wild barley); (2) *Triticum boeoticum* ssp. *aegilopoides* (wild single-grained einkorn); (3) *T. boeoticum* ssp. *thaoudar* or *T. urartu* (two-grained einkorn); (4) *T. turgidum* ssp. *dicoccoides* (wild emmer); (5) *Secale* spp.

(wild rye); with problematic grains identified as *Triticum/Secale*. This taxonomy is based on morphology and may or may not reflect the underlying biomolecular taxonomy.

As is the case for other early Neolithic sites, the cereal grains were often fragmented, and it is for this reason that we adopted the method pioneered by S. Colledge where only breadth and thickness measurements were used (Willcox 2004; Colledge and Conolly 2010).

Spikelet bases recovered at Dja'de el-Mughara and Jerf el-Ahmar are particularly well preserved, presenting the base of the lemmas in line with the abscission scar (Fig. 5a–d). The characteristic pectinate-ciliate keels on the lemmas seen in the impressions (Willcox and Fornite 1999) are not preserved in the charred material. However, the thick glume bases present an angle of approximately 90° to the axis and the internodes bear vertical lines. Compared to einkorn (Fig. 5e), on the wild specimens of rye the abscission scars are wide, deep and delimited by protruding lips. The domestic-type specimens have a fragment of the adjacent spikelet adhering to the scar (Fig. 5b). Concerning the grains (Fig. 5f–j), the ventral sides are slightly convex. The dorsal ridge extends along the middle in the dorsal view towards a truncated apex (Fig. 5g–i). The cell patterns of the epidermis are aligned longitudinally and are clearly visible, especially in the lateral view.

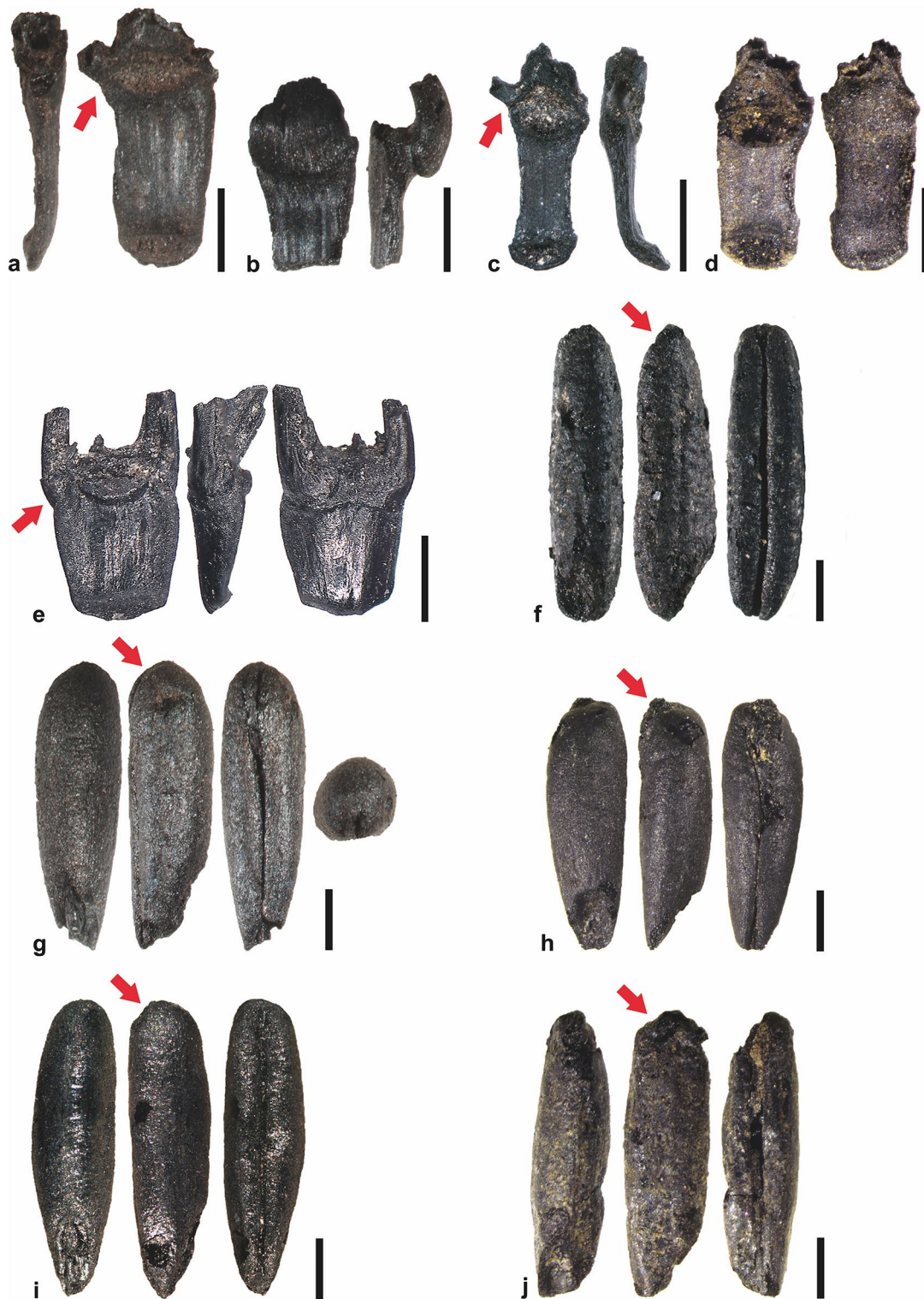


Fig. 5 Example of archaeological charred material; **a** rye spikelet base of wild-type recovered at Dja'de el-Mughara, **b** rye spikelet base of domestic-type from Dja'de, **c** rye spikelet base of wild-type from Jerf. This specimen is very narrow, **d** rye spikelet base of wild-type from Jerf (with a more regular shape), **e** example of einkorn spikelet

base of wild type from the Neolithic site of Dispilio (Greece), **f** example of 2gr. einkorn caryopsis from Aswad, **g** rye grain from Dja'de, **h** rye grain from Jerf, **i** rye grain from Mureybet, **j** rye grain from 'Abr 3. Scale bars = 1mm

Results: revised identifications

Table 4 presents new revised identifications of wild rye and wild einkorn from Dja'de el-Mughara, Jerf el-Ahmar and 'Abr 3, originally listed in Willcox et al. (2008) as *Triticum/Secale*. The data from Dja'de el-Mughara include additional results from samples from the earliest levels (DJ I) taken after the 2008 publication (Douché and Willcox 2018). Results from Mureybet (Ibáñez 2008) are based on a re-examination of the material originally identified as wild two-grained einkorn (van Zeist and Casparie 1968; van Zeist and Bakker-Heeres 1984). We thank Prof. René Cappers for allowing C. Douché to access the material from Mureybet at the University of Groningen. The numbers for Abu Hureyra were obtained from S. Colledge, who states “As none of the original score sheets are available we calculated numbers of taxa per sample by measuring the bar lengths in Fig. 12.7 in Moore et al. 2000 [...] our totals are therefore approximations” (Colledge and Conolly 2010 p. 130).

These new results make it clear that wild rye grains were dominant over wild einkorn grains and spikelet bases at these sites. Wild einkorn grains were rare with the exception of Abu Hureyra and Dja'de el-Mughara III. We separated one- and two-grained einkorn but present them as a single taxon in Table 4 because present-day wild two-grained einkorn has a mixture of one- and two-grained spikelets (Fig. 12.3 in Willcox 2007). Thus the grains should be considered as coming from populations of *Triticum boeoticum* ssp. *thaoudar*.

Taken as a whole, the finds of both charred grains and spikelet bases indicate morphologically wild populations. In order to distinguish between wild and domestic spikelet

bases, we used the criteria described by Tanno and Willcox (2012) and Weide et al. (2015). Dja'de el-Mughara II produced 8% domestic-type rye spikelet bases, but the proportion is not high enough (< 10%) to designate morphological domestication (see Discussion below).

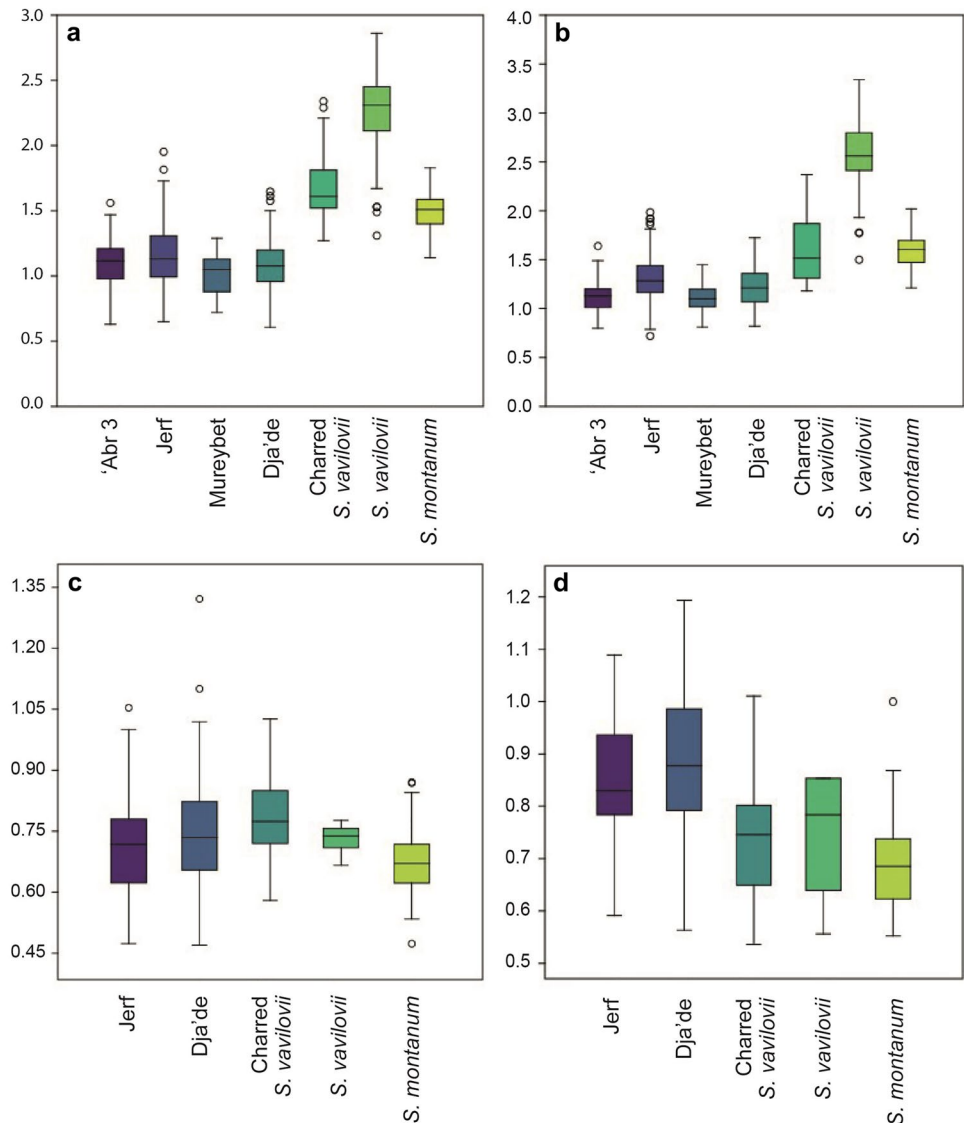
The identification of the charred rye to species level is tenuous to say the least, due to the incompleteness of the charred spikelet bases and the distortions of grains caused by charring. In addition, the morphological similarity of modern species of wild rye makes the distinction even more difficult. The only criterion we were able to use was grain size. Measurements of the grains (and spikelet bases) from Dja'de el-Mughara, Jerf el-Ahmar, Tell 'Abr 3 and Mureybet (Figs. 4 and 6) show a strong clustering, suggesting that they come from the same population and therefore probably the same species. Taking into account the present-day distributions and the environmental constraints of wild ryes, the two most likely candidates are *S. montanum* and *S. vavilovii*. The former has smaller grains than the latter. Overlaps occur but overall, the ancient charred grains are smaller than those of fresh *S. montanum*, and smaller than charred *S. vavilovii*. Given that charring often causes shrinkage, the ancient grains appear to be closer in size to *S. montanum* than to *S. vavilovii*. In conclusion, more work needs to be carried out in order to reach a more secure species identification. This is not an easy task, considering specialists are not in agreement with regard to the taxonomy and specimens in reference collections or from gene banks may be inaccurately identified. Caution is also necessary because there is the possibility that we are dealing with an extinct species.

Table 4 Revised counts of charred grains and spikelet bases (spk) of wild rye and wild einkorn from the five sites. Impressions of wild rye spikelet bases found at Jerf and Mureybet III are not included. An

explanation of the counts for Abu Hureyra is given in the text. Note that wild rye has much higher frequencies than wild einkorn for grains and spikelet bases

Site	Dja'de			Jerf	Abr 3	Mureybet				Abu Hureyra
	I	II	III			IA	II	III	IV	
Phase										
Period	PPNA	PPNB		PPNA	PPNA	Natufian	Khiamian	PPNA	PPNB	Natufian
<i>Triticum boeoticum</i> (1 and 2 grained) grain	4	42	222	67	90	5	1	89		252
<i>Triticum boeoticum</i> spk		9		59				1		
<i>Triticum/Secale</i> grain		12	48	694	8	1	2	461		303
<i>Secale montanum/vavilovii</i> grain	57	273	287	1,778	2,991	3	5	1,734	7	333
<i>Secale</i> spk (indetermined type)	8	308	20	34						
<i>Secale</i> spk (wild)	2	266		88						
<i>Secale</i> spk (domestic type)		50								

Fig. 6 Box plots showing comparison of archaeological material and modern specimens of rye; **a** breadth of grains, **b** thickness of grains, **c** ratio of scar thickness: scar width (mm), **d** ratio scar width: rachis width (mm). Grains measurements: 'Abr 3 n=90, Jerf n=273, Mureybet n=50, Dja'de n=75, *S. vavilovii* experimentally charred n=32, *S. vavilovii* n=100, *S. montanum* n=100. Spikelet bases measurements: Jerf n=80, Dja'de n=76, *S. vavilovii* experimentally charred n=30, *S. vavilovii* n=7, *S. montanum* n=40. The box plots were obtained using the free software Past 4 (Hammer et al. 2001); see Supplementary material 2 a–d for measurement details



Discussion

In previous studies, wild einkorn and wild rye were not clearly distinguished on early Neolithic Middle Euphrates sites (Willcox et al. 2008). In some later publications this was partially corrected (Stordeur and Willcox 2009; Willcox and Stordeur 2012). This study attempts to elucidate the distinction between wild rye and wild einkorn and update earlier results. The new results clearly indicate that wild rye was dominant over wild einkorn at the four sites examined and that during the Natufian it was the most frequent cereal at Abu Hureyra (for Mureybet I and II frequencies are too low to make comparisons). During the PPNA and EPPNB wild rye was the dominant cereal at Mureybet III and second to wild barley at Jerf el-Ahmar and Dja'de el-Mughara (Fig. 7). On these sites, there are no signs of domestication. The small percentage

of domestic spikelet bases from Dja'de el-Mughara II (8%, n=50 out of 624) should not be considered morphological domestication because similar small percentages have been found occurring in wild cereal populations (Kislev 1989 p. 150, 1992). The identification at species level remains problematical, particularly when comparing charred material with fresh uncharred specimens. Hillman separated grains of *S. montanum* and *S. vavilovii* (Hillman 2000; Hillman et al. 2001). Our data, based on grain size, suggest closer similarities with the perennial *S. montanum* than with *S. vavilovii*. Although *S. montanum* is not adapted to today's environmental conditions in the Middle Euphrates area, of all the wild rye species it has the widest geographical range and hence the widest environmental tolerance, including high altitudes (Akhalkatsi and Girgvliani 2016). At the end of the Pleistocene and beginning of the Holocene when the climate was cooler, its range could

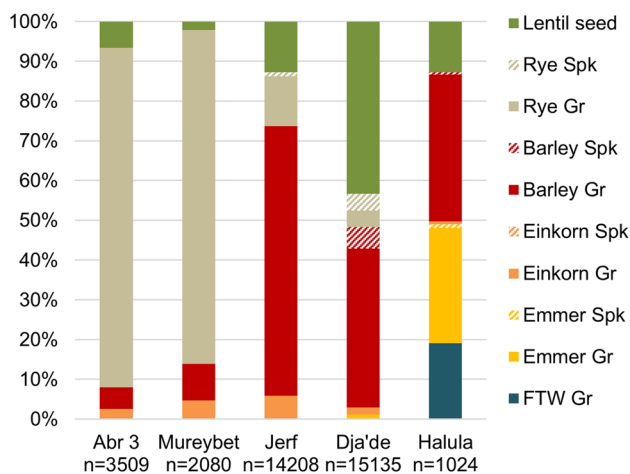


Fig. 7 Bar charts comparing the percentages of selected taxa (including rye) from sites located in the Middle Euphrates valley. The Natufian results from Abu Hureyra are not included due to the absence of counts in the publication (approximate extrapolated counts for rye and einkorn are provided in Table 4). Counts from Mureybet and Dja'de combine all periods (for counts by period see Table 4). Results from Halula come from MPPNB levels. FTW Free-threshing wheat, Gr grain, Spk Spikelet/Rachis

have been more widespread, allowing it to grow closer to the Middle Euphrates area than today. Where exactly the wild rye which was exploited at these sites was growing, is difficult to establish. Furthermore, we cannot exclude the possibility of long-distance transport on the Euphrates river itself or the possibility that these finds represent an extinct species of wild rye.

Significantly, with the increase in temperature after the Younger Dryas during the early Holocene, wild rye becomes less frequent and disappears from the middle PPNB onwards in the Middle Euphrates area. For example, it was absent from Middle PPNB Tell Halula (Buxó and Rovira 2013), located at about 5 km north of Jerf el-Ahmar and was rare in Middle PPNB levels at Abu Hureyra compared to the Natufian levels (De Moulins 1997 p. 400; Hillman 2000). But factors other than climate may have contributed to the decline of *Secale*; in particular, on Middle PPNB sites important economic and cultural changes occurred (Goring-Morris and Belfer-Cohen 2011, 2014), with widespread cultivation of domestic emmer and barley and a sudden increase in settlement size (Kuijt 2006, 2008; Willcox et al. 2009; Goring-Morris and Belfer-Cohen 2010; Tanno and Willcox 2012). During the same period of warming, *H. spontaneum*, which was absent during the Younger Dryas at Abu Hureyra, becomes dominant in the PPNA and PPNB levels at Jerf el-Ahmar, Mureybet and Dja'de el-Mughara at the beginning of the Holocene and can still be found growing in the area today where it tolerates the current hot and arid climate.

Wild rye as a food resource has an advantage over wild barley and wild einkorn in that the grains are easily released from the glumes and lemmas, as in free-threshing cereals. But in order to take advantage of this benefit, the crop cannot be mixed with hulled cereals during processing, and indeed wild rye does appear to have been processed separately. For example, at Tell 'Abr 3 a large amount of pure charred wild rye grains was recovered from a large burnt communal building, where it had been stored (Yartah 2013). A large-scale sampling at Jerf el-Ahmar demonstrated that *Secale* was dominant in some samples, suggesting that it was harvested and processed separately from *Hordeum* (Fig. 9 in Willcox and Stordeur 2012). Whether wild rye was cultivated or gathered from the wild cannot be demonstrated. Arguments have been given for evidence of pre-domestic cultivation at Dja'de el-Mughara and Jerf el-Ahmar (Willcox et al. 2008, 2009; Willcox 2012), and a recent study based on functional ecology suggests low levels of disturbance (Weide et al. 2022). Furthermore, it is not clear which of the cereals and/or pulses may have been cultivated; it is possible that some cultivation may have been practiced, supplemented with harvests from wild stands. Hillman argued that because *S. montanum* was perennial and is not known to have ever been cultivated, it was gathered from wild stands (Hillman et al. 1993 p. 100). But the possibility that wild perennials were cultivated should not be totally ruled out, especially since *S. montanum* can grow as a weed in cereal fields (Davis 1985 p. 257). Whatever the case, the evidence from Abu Hureyra, 'Abr 3, Jerf el-Ahmar, Mureybet and Dja'de el-Mughara suggests that the wild rye found on these Middle Euphrates sites was a distinct crop and separate from wild barley; the two wild cereals are not found in the same habitats today. At present we have no evidence to indicate how wild rye was consumed at these sites. Rye grains can be prepared in various ways, to make black bread, rye porridge, or used for fermentation (Balcerek et al. 2016).

Conclusions

Today wild ryes are not adapted to the climatic conditions of the Middle Euphrates. However, we have demonstrated that wild rye was used as a discrete crop there at the end of the Pleistocene/beginning of the Holocene but then abruptly ceases to be exploited. The finds of wild rye on these sites are intriguing, because (1) environmental conditions today are totally unsuited to wild rye and (2) it proceeded from being the most common cereal in the Natufian to being abandoned by the period of the Middle PPNB in the Middle Euphrates area and (3) it was found with wild barley despite the fact that these cereals have different habitat

requirements. The high frequencies of wild rye and the absence of wild barley during the Natufian at Abu Hureyra may reflect cooler climatic conditions during the Younger Dryas, while the occurrence of wild barley and the decline of wild rye at Jerf el-Ahmar and Dja'de el-Mughara may reflect the warmer conditions of the early Holocene. The data from Tell 'Abr 3 and Mureybet are problematical due to small sample size, and the samples from Tell 'Abr 3 come from a single context, which was a burnt storage area. It is not possible to know where the wild rye was harvested. It could have been local or imported from farther afield. Today the nearest stands of wild rye are found growing in southeastern Turkey, Israel and southern Syria, some 250–300 km away, where they are found above 1,000 m a.s.l. Altitudinal zoning is pronounced in the Near East and zones may have been lower during cool periods in the past. The wild rye species that the charred grains represent is difficult to establish; we suggest tentatively the perennial *S. montanum*.

With regard to whether wild rye was gathered or cultivated, Willcox (2012) and colleagues (Willcox et al. 2008) have suggested that several lines of evidence indicate the cultivation of cereals and/or pulses at Jerf el-Ahmar and Dja'de el-Mughara, in particular the presence of a potential arable weed assemblage that occurs on later sites with cultivated domesticated plants. This remains controversial due to the low identification level of wild/weed taxa (Weide et al. 2022) and to complicate the issue, cultivation and gathering may have occurred simultaneously or gone into and out of use during the period of pre-domestic cultivation. Because *S. montanum* is a perennial (if indeed that is the species we are dealing with), gathering would appear to be more probable; however, the fact that perennial rye has been found in arable habitats does suggest that cultivation would have been possible.

Note: After acceptance of the manuscript, we received results of ^{14}C AMS dates (Lyon-19,947 GrM) obtained exclusively from rye caryopsis recovered from Dja'de which gave DJI: 9188-8777 cal BC, DJII: 8818-8614 cal BC, DJIII: 8635-8389 cal BC. They are consistent with the established chronology of the site.

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Declarations

Conflict of interest None.

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References

- Abbès F, Bellot-Gurlet L, Bressy C et al (2001) Nouvelles recherches sur l'obsidienne de Cheikh Hassan (vallée de l'Euphrate, Syrie) au Néolithique: PPNA et PPNB ancien. *Syria* 78:5–17. <https://doi.org/10.3406/syria.2001.7727>
- Akhalkatsi M, Girgvliani T (2016) Landraces and wild species of the *Secale* genus in the georgia (Caucasus Ecoregion). *Agric Res Technol: Open Access J* 1:78–84. <https://doi.org/10.19080/artoaj.2016.01.555567>
- Balcerek M, Pielech-Przybylska K, Strak E, Patelski P, Dziekońska U (2016) Comparison of fermentation results and quality of the agricultural distillates obtained by application of commercial amyolytic preparations and cereal malts. *Eur Food Res Technol* 242:321–335. <https://doi.org/10.1007/s00217-015-2542-7>
- Behre K-E (1992) The history of rye cultivation in Europe. *Veget Hist Archaeobot* 1:141–156. <https://doi.org/10.1007/BF00191554>
- Benz M, Deckers K, Rössner C et al (2015) Prelude to village life. Environmental data and building traditions of the epipalaeolithic settlement at Körtik Tepe, Southeastern Turkey. *Paléorient* 41:9–30. <https://doi.org/10.3406/paleo.2015.5673>
- Braadbaart F (2008) Carbonisation and morphological changes in modern dehusked and husked *Triticum dicoccum* and *Triticum aestivum* grains. *Veget Hist Archaeobot* 17:155–166. <https://doi.org/10.1007/s00334-007-0134-6>
- Buxó R, Rovira N (2013) Tell Halula: arqueobotánica de los restos de semillas y frutos. In: Molist Montaña M (ed) *Tell Halula, un poblado de los primeros agricultores en el valle del Éufrates, Siria: memoria científica*. Ministerio de Educación, Cultura y Deporte, Secretaría General Técnica, Madrid, pp 359–389
- Caracuta V, Vardi J, Paz Y, Boaretto E (2017) Farming legumes in the pre-pottery neolithic: new discoveries from the site of Ahihud (Israel). *PLoS ONE* 12:e0177859. <https://doi.org/10.1371/journal.pone.0177859>
- Charles M, Forster E, Wallace M, Jones G (2015) “Nor ever lightning char thy grain”¹: establishing archaeologically relevant charring conditions and their effect on glume wheat grain morphology.

- STAR: Sci Technol Archaeol Res 1:1–6. <https://doi.org/10.1179/2054892315Y.0000000008>
- Colledge S, Conolly J (2010) Reassessing the evidence for the cultivation of wild crops during the younger Dryas at tell Abu Hureyra, Syria. *Environ Archaeol* 15:124–138. <https://doi.org/10.1179/146141010X12640787648504>
- Coqueugniot E (2000) Dja'de (Syrie), un village à la veille de la domestication (seconde moitié du IXe millénaire av. J.-C.). In: Guilaine J (ed) *Premiers paysans du monde: naissance des agricultures* (Séminaire du Collège de France). Editions Errance, Paris, pp 63–79
- Coqueugniot E (2014) Dja'de (Syrie) et les représentations symboliques au IXe millénaire cal. BC. In: Manen C, Perrin T, Guilaine J (eds) *La transition néolithique en Méditerranée: actes du colloque 'Transitions en Méditerranée, ou comment des chasseurs devinrent agriculteurs'*. Muséum de Toulouse, 14–15 avril 2011. Arles, Editions Errance, pp 91–108
- Coşkun A, Benz M, Rössner C et al (2012) New results on the younger Dryas occupation at Körtik Tepe. *Neo-lithics* 1/12:25–32
- Czajkowska BI, Bogaard A, Charles M et al (2020) Ancient DNA typing indicates that the “new” glume wheat of early eurasian agriculture is a cultivated member of the *Triticum timopheevii* group. *J Archaeol Sci* 123:105258. <https://doi.org/10.1016/j.jas.2020.105258>
- Davis PH (1985) *Flora of Turkey and the East Aegean Island, Gramineae*, vol 9. Edinburgh University Press, Edinburgh
- De Moulins D (1997) Agricultural changes at Euphrates and steppe sites in the mid-8th to the 6th millennium B.C. *BAR International Series* 683. Hedges, Oxford
- Denham T (2007) Early fig domestication, or gathering of wild parthenocarpic figs? *Antiquity* 81:457–461. <https://doi.org/10.1017/S0003598X00095326>
- Douché C, Willcox G (2018) New archaeobotanical data from the early neolithic sites of dja'de el-Mughara and tell Aswad (Syria): a comparison between the Northern and the Southern Levant. *Paléorient* 44:45–58
- Feinbrun-Dothan N (1986) *Flora Palaestina. Part 4: Alismataceae to Orchidaceae*. Israel Academy of Sciences and Humanities, Jerusalem
- Filatova S, Claassen B, Torres G et al (2021) Toward an investigation of diversity and cultivation of rye (*Secale cereale* ssp. *cereale* L.) in Germany: methodological insights and first results from early modern plant material. *Agronomy* 11:2451. <https://doi.org/10.3390/agronomy11122451>
- Gökgöl DM (1944) Samen, die bei den Ausgrabungen in Alaca Höyük im Jahre 1936 gefunden worden sind. In: Kosay HZ (ed) *Ausgrabungen von Alaca Höyük*. Türk Tarih Kurumu, Ankara, pp 185–186
- Goring-Morris N, Belfer-Cohen A (2010) Different Ways of being, different Ways of seeing ... changing Worldviews in the Near East. In: Finlayson B, Warren G (eds) *Landscapes in transition: 8*, Illustrated edition. Oxbow Books, Oxford, pp 9–22
- Goring-Morris N, Belfer-Cohen A (2011) Neolithization processes in the Levant. *Curr Anthropol* 52:S195–S208. <https://doi.org/10.1086/658860>
- Goring-Morris N, Belfer-Cohen A (2014) The neolithic in Southern Levant: yet another ‘unique’ phenomenon. In: Manen C, Perrin T, Guilaine J (eds) *La transition néolithique en Méditerranée: actes du colloque transitions en Méditerranée ou comment des chasseurs devinrent agriculteurs*, Muséum de Toulouse, 14–15 avril 2011. Editions Errance, Arles, pp 59–73
- Grikkpēdis M, Matuzevičiūtė GM (2016) The beginnings of rye (*Secale cereale*) cultivation in the East Baltics. *Veget Hist Archaeobot* 25:601–610. <https://doi.org/10.1007/s00334-016-0587-6>
- Hammer Ø, Harper DAT, Ryan PD (2001) PAST: paleontological statistics software package for education and data analysis. *Palaeontol Electron* 4:9
- Helmer D, Roitel V, Sana M, Willcox G (1998) Interprétations environnementales des données archéozoologiques et archéobotaniques en Syrie du nord de 16000 BP à 7000 BP, et les débuts de la domestication des plantes et des animaux. In: Fortin M, Aurenche O (eds) *Espace naturel, espace habité en Syrie du nord (10e-2e millénaires av. J.-C.)* (Natural space, inhabited space in Northern Syria (10th-2nd millennium B.C.): actes du colloque tenu à l'Université Laval (Québec) du 5 au 7 mai 1997. Maison de l'Orient méditerranéen, Lyon, pp 9–34
- Hillman G (1978) On the origins of domestic rye—*Secale cereale*: the finds from aceramic can hasan III in Turkey. *Anatol Stud* 28:157–174
- Hillman GC (2000) The plant food economy of Abu Hureyra 1 and 2. In: Moore AMT, Hillman GC, Legge AJ (eds) *Village on the Euphrates: from foraging to farming at Abu Hureyra*. Oxford University Press, Oxford, pp 327–398
- Hillman GC, Colledge SM, Harris DR (1989) Plant food economy during the epipalaeolithic period at Tell Abu Hureyra, Syria: dietary diversity, seasonality and modes of exploitation. In: Harris DR, Hillman GC (eds) *Foraging and farming: the evolution of plant exploitation: symposium on recent advances in the understanding of plant domestication and early agriculture*. Unwin Hyman, London, pp 240–268
- Hillman G, Hedges R, Moore A, Colledge S, Pettitt P (2001) New evidence of Lateglacial cereal cultivation at Abu Hureyra on the Euphrates. *Holocene* 11:383–393. <https://doi.org/10.1191/095968301678302823>
- Hillman GC, Legge AJ, Rowley-Conwy PA (1997) On the Charred Seeds from Epipalaeolithic Abu Hureyra: food or fuel? *Curr Anthropol* 38:651–655. <https://doi.org/10.1086/204651>
- Hillman G, Wales S, McLaren F, Evans J, Butler A (1993) Identifying problematic remains of ancient plant foods: a comparison of the role of chemical, histological and morphological criteria. *World Archaeol* 25:94–121. <https://doi.org/10.1080/00438243.1993.9980230>
- Ibáñez JJ (2008) *Le site néolithique de tell Mureybet (Syrie du Nord), en hommage à Jacques Cauvin*. Archaeopress, Oxford
- Kislev ME (1989) Pre-domesticated cereals in the pre-pottery neolithic a period. In: Hershkovitz I (ed) *People and culture in change: proceedings of the second symposium on upper palaeolithic, mesolithic and neolithic populations of Europe and the mediterranean basin*. *BAR international series* 508. Archaeopress, Oxford, pp 147–151
- Kislev ME (1992) Agriculture in the near east in the 7th millennium B.C. In: Anderson PC (ed) *Préhistoire de l'agriculture: nouvelles approches expérimentales et ethnographiques (the prehistory of agriculture: new experimental and ethnographic approaches)*. Editions du CNRS, Paris, pp 87–94
- Kreuz A, Boenke N (2002) The presence of two-grained einkorn at the time of the Bandkeramik culture. *Veget Hist Archaeobot* 11:233–240. <https://doi.org/10.1007/s003340200026>
- Kuijt I (2006) *Life in neolithic farming communities: social organization, identity, and differentiation*. Kluwer Academic/Plenum Publishers, New-York
- Kuijt I (2008) Demography and storage systems during the southern levantine neolithic demographic transition. In: Bocquet-Appel J-P, Bar-Yosef O (eds) *The neolithic demographic transition and its consequences*. Springer, Dordrecht, pp 287–313
- Maraci Ö, Özkan H, Bilgin R (2018) Phylogeny and genetic structure in the genus *Secale*. *PLoS ONE* 13:e0200825. <https://doi.org/10.1371/journal.pone.0200825>

- Moore AMT, Hillman GC, Legge AJ (1975) The excavation of tell Abu Hureyra in Syria: a preliminary report. *Proc Prehist Soc* 41:50–77. <https://doi.org/10.1017/S0079497X00010902>
- Moore AMT, Hillman GC, Legge AJ (eds) (2000) *Village on the Euphrates: from foraging to farming at Abu Hureyra*. Oxford University Press, Oxford
- Nesbitt M (2017) *Identification guide for near eastern grass seeds*. Routledge, London
- Post GE, Dinsmore JE (1932) *Flora of Syria, Palestine and Sinai: a handbook of the flowering plants and ferns, native and naturalized from the Taurus to ras Muhammad and from the Mediterranean Sea to the syrian desert*. American University of Beirut Press, Beirut
- Rössner C, Deckers K, Benz M, Özkaya V, Riehl S (2018) Subsistence strategies and vegetation development at Aceramic Neolithic Körtik Tepe, southeastern Anatolia, Turkey. *Veget Hist Archaeobot* 27:15–29. <https://doi.org/10.1007/s00334-017-0641-z>
- Savard M (2018) Archaeobotanical and geographical perspectives on Subsistence and Sedentism: the case of Hallan Çemi (Turkey). In: Lightfoot E, Liu X, Fuller DQ (eds) *Far from the hearth: essays in honour of Martin K. Jones*. McDonald Institute for Archaeological Research, Cambridge, pp 117–125
- Savard M, Nesbitt M, Gale R (2003) Archaeobotanical evidence for early neolithic diet and subsistence at M'lefaat (Iraq). *Paléorient* 29:93–106. <https://doi.org/10.3406/paleo.2003.4756>
- Savard M, Nesbitt M, Jones MK (2006) The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. *World Archaeol* 38:179–196. <https://doi.org/10.1080/00438240600689016>
- Schlegel RHJ (2016) *Rye: genetics, breeding, and cultivation*. CRC Press, Boca Raton
- Schreiber M, Himmelbach A, Börner A, Mescher M (2019) Genetic diversity and relationship between domesticated rye and its wild relatives as revealed through genotyping-by-sequencing. *Evol Appl* 12:66–77. <https://doi.org/10.1111/eva.12624>
- Singh KB, Malhotra RS, Saxena MC, Bejiga G (1997) Superiority of winter sowing over traditional spring sowing of chickpea in the mediterranean region. *Agron J* 89:112–118. <https://doi.org/10.2134/agronj1997.00021962008900010017x>
- Stordeur D, Willcox G (2009) Indices de culture et d'utilisation des céréales à Jerf el Ahmar. In: Fabre D (ed) *De Méditerranée et d'ailleurs ... Mélanges offerts à Jean Guilaine*. Archives d'Ecologie Préhistorique, Toulouse, pp 693–710
- Stutz HC (1957) A cytogenetic analysis of the Hybrid *Secale Cereale L. x Secale Montanum Guss.* And its progeny. *Genetics* 42:199–221. <https://doi.org/10.1093/genetics/42.3.199>
- Sun Y, Shen E, Hu Y et al (2022) Population genomic analysis reveals domestication of cultivated rye from weedy rye. *Mol Plant* 15:552–561. <https://doi.org/10.1016/j.molp.2021.12.015>
- Tanno K, Willcox G (2012) Distinguishing wild and domestic wheat and barley spikelets from early holocene sites in the Near East. *Veget Hist Archaeobot* 21:107–115. <https://doi.org/10.1007/s00334-011-0316-0>
- Van Zeist W, Bakker-Heeres JAH (1984) Archaeobotanical studies in the Levant. Late-Palaeolithic Mureybit *Palaeohistoria* 26:171–1993
- Van Zeist W, Casparie WA (1968) Wild einkorn wheat and barley from tell Mureybit in northern Syria. *Acta Bot Neerl* 17:44–53
- Weide A, Arranz-Otaegui A, Schmidt AF et al (2021) Identification of the triticoid-type grains (Poaceae) from archaeobotanical assemblages in southwest Asia as *Heteranthelium piliferum* (Banks & Sol.) Hochst. *Veget Hist Archaeobot* 30:657–674. <https://doi.org/10.1007/s00334-020-00822-x>
- Weide A, Green L, Hodgson JG et al (2022) A new functional ecological model reveals the nature of early plant management in southwest Asia. *Nat Plants* 8:623–634. <https://doi.org/10.1038/s41477-022-01161-7>
- Weide A, Riehl S, Zeidi M, Conard NJ (2015) Using new morphological criteria to identify domesticated emmer wheat at the aceramic neolithic site of Chogha Golan (Iran). *J Archaeol Sci* 57:109–118. <https://doi.org/10.1016/j.jas.2015.01.013>
- Weiss E, Zohary D (2011) The neolithic southwest asian founder crops: their Biology and Archaeobotany. *Curr Anthropol* 52:S237–S254. <https://doi.org/10.1086/658367>
- Willcox G (1996) Evidence for plant exploitation and vegetation history from three early neolithic pre-pottery sites on the Euphrates (Syria). *Veget Hist Archaeobot* 5:143–152. <https://doi.org/10.1007/BF00189445>
- Willcox G (2002) Evidence for ancient forest cover and deforestation from charcoal analysis of ten archaeological sites on the Euphrates. In: Thiébaud S (ed) *Charcoal analysis: methodological approaches, palaeoecological results and wood uses: proceedings of the Second International Meeting of Anthracology, Paris, September 2000*. Archaeopress, Oxford, pp. 141–145
- Willcox G (2004) Measuring grain size and identifying Near Eastern cereal domestication: evidence from the Euphrates valley. *J Archaeol Sci* 31:145–150. <https://doi.org/10.1016/j.jas.2003.07.003>
- Willcox G (2007) Agrarian change and the beginnings of cultivation in the Near East: evidence from wild progenitors, experimental cultivation and archaeobotanical data. In: White P, Denham T (eds) *The emergence of agriculture: a global view*. Routledge, New-York, pp 217–241
- Willcox G (2008) Les nouvelles données archéobotaniques de Mureybet et la néolithisation du moyen Euphrate. In: Ibáñez J-J (ed) *Le site néolithique de tell Mureybet (Syrie du Nord), en hommage à Jacques Cauvin*. BAR International Series. Archaeopress, Oxford, pp 103–114
- Willcox G (2012) Pre-domestic cultivation during the late Pleistocene and Early Holocene in the northern Levant. In: Gepts PL, Famula TR, Bettinger RL et al (eds) *Biodiversity in agriculture: domestication, evolution, and sustainability*. Cambridge University Press, Cambridge, pp 92–109
- Willcox G, Fornite S (1999) Impressions of wild cereal chaff in pisé from the 10th millennium uncal B.P. at Jerf el-Ahmar and Mureybet: Northern Syria. *Veget Hist Archaeobot* 8:21–24. <https://doi.org/10.1007/BF02042838>
- Willcox G, Roitel V (1998) Rapport archéobotanique préliminaire de trois sites précéramiques du Moyen-Euphrate (Syria). *Cahiers de l'Euphrate* 8:65–84
- Willcox G, Stordeur D (2012) Large-scale cereal processing before domestication during the tenth millennium cal BC in northern Syria. *Antiquity* 86:99–114. <https://doi.org/10.1017/S0003598X00062487>
- Willcox G, Buxo R, Herveux L (2009) Late pleistocene and early Holocene climate and the beginnings of cultivation in northern Syria. *Holocene* 19:151–158. <https://doi.org/10.1177/0959683608098961>
- Willcox G, Fornite S, Herveux L (2008) Early holocene cultivation before domestication in northern Syria. *Veget Hist Archaeobot* 17:313–325. <https://doi.org/10.1007/s00334-007-0121-y>
- Yartah T (2004) Tell 'Abr 3, un village du néolithique précéramique (PPNA) sur le Moyen Euphrate. *Première approche Paléorient* 30:141–158. <https://doi.org/10.3406/paleo.2004.1017>
- Yartah T (2005) Les bâtiments communautaires de tell 'Abr 3 (PPNA, Syrie). *Neo-Lithics* 1:3–9
- Yartah T (2013) *Vie quotidienne, vie communautaire et symbolique à tell 'Abr 3 – Syrie du Nord. Données nouvelles et nouvelles réflexions sur l'horizon PPNA au nord du Levant 10 000–9 000 BP*. Thèse de doctorat en Langues, Histoire et civilisations des mondes anciens, Université Lumière Lyon 2

Zohary D, Hopf M, Weiss E (2012) Domestication of plants in the Old World: the origin and spread of domesticated plants in Southwest Asia, Europe, and the Mediterranean Basin, 4th edn. Oxford University Press, Oxford

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