

The broad spectrum revisited: Evidence from plant remains

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The beginning of agriculture is one of the most important developments in human history, with enormous consequences that paved the way for settled life and complex society. Much of the research on the origins of agriculture over the last 40 years has been guided by Flannery's [Flannery, K. V. (1969) in *The Domestication and Exploitation of Plants and Animals*, eds. Ucko, P. J. & Dimbleby, G. W. (Duckworth, London), pp. 73–100] "broad spectrum revolution" (BSR) hypothesis, which posits that the transition to farming in southwest Asia entailed a period during which foragers broadened their resource base to encompass a wide array of foods that were previously ignored in an attempt to overcome food shortages. Although these resources undoubtedly included plants, nearly all BSR hypothesis-inspired research has focused on animals because of a dearth of Upper Paleolithic archaeobotanical assemblages. Now, however, a collection of >90,000 plant remains, recently recovered from the Stone Age site Ohalo II (23,000 B.P.), Israel, offers insights into the plant foods of the late Upper Paleolithic. The staple foods of this assemblage were wild grasses, pushing back the dietary shift to grains some 10,000 years earlier than previously recognized. Besides the cereals (wild wheat and barley), small-grained grasses made up a large component of the assemblage, indicating that the BSR in the Levant was even broader than originally conceived, encompassing what would have been low-ranked plant foods. Over the next 15,000 years small-grained grasses were gradually replaced by the cereals and ultimately disappeared from the Levantine diet.

Paleolithic hunter-gatherers in southwest Asia, according to Flannery (1, 2), relied primarily on small- to medium-sized ungulates, largely ignoring small mammals, birds, fish, tortoises, and crabs until later times. As they felt pressure from expanding populations, along with a reduction in the territory available for exploitation, hunter-gatherers gradually began to exploit these previously ignored low-ranked foods. The ultimate significance of this broadening of the resource base, according to Flannery (2), lay in its implications for the origins of cereal agriculture. The same pressures that encouraged hunters to capture previously ignored animal species also prompted them to collect small grass seeds, an essential first step in the process of domestication. Indeed, during the late Upper Paleolithic (UP; known as the Epi-Paleolithic in the Levant) wild cereals not only were considered worthwhile, they became staples, something that probably would not have happened before a broad-spectrum strategy was adopted (2).

Since Flannery proposed the "broad spectrum revolution" (BSR), researchers have found support for the hypothesis in faunal assemblages from sites across the Mediterranean basin dating back as early as 50,000 years ago (3–5). Among them are Stiner and colleagues (4–6), who went a step further and refined the BSR hypothesis by looking at dietary breadth in terms of "cost/benefits" rather than taxonomic species diversity. Cost is the effort expended in pursuit and handling compared with the energetic returns. When people began catching fast-moving small animals, such as hares (*Lepus capensis*) and partridges (*Alectoris chukar*), they broadened their diet to include foods that would have been low-ranked because of the greater amount

of work involved in capture compared with the return from food collected. Stiner and colleagues also proposed that "catchability" was tempered by "turnover" rates. Prey animals that reproduce quickly, such as hares, would have been more intensively exploited when there was pressure on food resources than "low-turnover" species, such as tortoises. Thus Stiner and colleagues see in the faunal data from the Mediterranean basin a BSR that entailed increasing reliance over time on small fast-moving prey animals with high turnover rates, beginning already during the Middle Paleolithic \approx 50,000 cal B.P. (cal, calibrated).

While many faunal studies have been carried out to test the BSR hypothesis, no one has conducted systematic tests using archaeobotanical data. It is not for lack of interest but for a scarcity of data. Compared with bone, plant remains preserve very poorly resulting in sparse botanical collections dating to the UP and Epi-Paleolithic. Indeed, direct evidence of plants (carbonized, mineralized, or waterlogged seeds, fruits, bark, and wood) from these periods is so rare that scholars have had to work with minuscule plant assemblages or rely on indirect evidence. Flannery (1) and Stiner (5), for example, draw on increasing numbers of ground stone tools and storage facilities as general indicators of growing reliance on plant foods.

Ohalo II: The Broad Spectrum Tested

With the excavations of Ohalo II in Israel in 1989–1991 and 1999–2001, a remarkable window into plant exploitation in the UP was opened. Dated at 23,000 cal B.P., during the height of the Late Glacial Maximum, the site yielded a stunning collection of >90,000 plant remains from 142 taxa, of which nearly 19,000 were grass grains, most of them superbly preserved (7). The plant remains from Ohalo II not only provide evidence for broad spectrum plant collecting (described in more detail below) but also push back the evidence for significant grass collecting 10,000 years earlier than previously had been known.

Located on the shores of the Sea of Galilee, Ohalo II was submerged and left undisturbed until the recent excavations (8, 9). In this anaerobic environment the charred plant remains were beautifully preserved (10, 11), making it possible to identify much of the material to genus and even species level.

When the lake's water level dropped, archaeological remains covering some 2,000 m² were exposed. These included the remains of several brush huts, hearths, a human grave, an assemblage of flint and ground stone tools, and a wide faunal spectrum (mammals, birds, rodents, fish, mollusks), as well as a plant assemblage (8, 9, 11–20).

The principal plant foods appear to have been grass seeds, augmented with a variety of other plants from different habitats (7). These include Mount Tabor oak acorns, almonds, pistachios, wild olives, and fruits and berries such as Christ's thorn, raspberry, wild fig, and wild grape. There were also

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Abbreviations: UP, Upper Paleolithic; BSR, broad spectrum revolution; cal, calibrated; SGG, small-grained grasses; PPNB, Prepottery Neolithic B.

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Table 1. The primary SGG and cereals at Ohalo II

Latin name	English name	Quantity
SGG		
<i>Alopecurus utriculatus/arundinaceus</i>	Bladder/creeping foxtail	1,814
<i>Bromus pseudobrachystachys/tigridis</i>	Brome	10,995
<i>Hordeum glaucum</i>	Smooth barley	932
<i>Hordeum marinum/hystrix</i>	Seaside/Mediterranean barley	574
<i>Puccinellia cf. convoluta</i>	Alkali grass	1,853
Cereals		
<i>Hordeum spontaneum</i>	Wild barley	2,503
<i>Triticum dicoccoides</i>	Wild wheat	102
Total		18,773

Data are from refs. 7, 21, and 47.

several plants from the borage (Boraginaceae) and sunflower (Compositae) families, as well as a small quantity of pulses. The largest component of the assemblage, the grasses, includes the wild cereals emmer wheat and barley, progenitors of the domesticates, and an enormous quantity of small-grained grasses (SGG). Most of these have not been reported from other archaeological sites. They include brome (*Bromus pseudobrachystachys/tigridis*) (the great majority), foxtail (*Alopecurus utriculatus/arundinaceus*), alkali grass (*Puccinellia cf. convoluta*), and others (Table 1).

Weiss *et al.* (21) proposed that these SGG were a staple food at Ohalo II, based on several lines of evidence: (i) the large number of grains; (ii) the fact that all grains were fully mature; (iii) the ethnographic parallels for the use of SGG among hunter-gatherers as well as present-day agriculturalists. Moreover, SGG and cereal grains were found in one of the site's huts concentrated around a grinding stone, which was discovered *in situ* in the second floor layer supported by small pebbles, much like an anvil or a working surface (22).

The ethnographic parallels for the use of SGG as food are many and involve agriculturalists as well as hunter-gatherers. In central Chile mango (*Bromus mango*) was a domesticated crop plant (23, 24). Several native North American groups gathered wild brome grains (25): the Neeshenam exploited *Bromus carinatus* (26); the Mendocino (27) and the Gosiute collected (28) *Bromus marginatus*; the Cahuilla, *Bromus tectorum* (29); the Karok (30), Luiseño (31), and Miwok (32) gathered *Bromus diandrus*; and the Karok collected *Bromus hordeaceus* (30). In Australia indigenous peoples collect *Panicum australiense* and *Fimbristylis oxystachya* (33). In Ethiopia the minute grains of tef (*Eragrostis tef*) are the staple food. In the Sahara *Aristida pungens*, *Cenchrus biflorus*, and *Panicum turgidum* are widely eaten, and the latter is harvested wherever it occurs as far east as Afghanistan and Pakistan (34, 35). In central and Eastern Europe crabgrass, *Digitaria sanguinalis*, and *Glyceria fluitans* were important foods until recently (34).

The SGG at Ohalo II vastly outnumbered barley and emmer (16,000 SGG to 2,503 barley grains and 102 emmer grains) (9, 36). But the cereals represent a far greater mass of food because of the much larger size of the individual grains (discussed below), one of the pivotal reasons for their consumption and ultimately domestication (36).

This remarkable archaeobotanical assemblage from Ohalo II allows us to test the BSR hypothesis with plant remains, specifically by examining the breadth of grasses represented. We focus on grasses because they appear to have been the staple plant food at Ohalo II, representing >90% of the edible seeds recovered. Grasses were also the staple of later Levantine communities, which we examine later in the paper to trace the evolution of the BSR in plant foods.

Ohalo II's assemblage supports both Flannery's original formulation and Stiner and colleagues' refinement of the hypothesis. The Ohalo diet was diverse and included what must be considered low-ranked foods, the SGG. These are consistent with the work of Stiner and colleagues in that the net cost involved in gathering the SGG is high relative to the amount of food collected. Like wild barley, the grains must be freed from the hulls through a labor-intensive dehulling process, but because the grains are so small they "produce" relatively little for the effort. Fig. 1 shows how the grain sizes of the SGG compare with those of wild barley and emmer wheat. The largest small grain is a minute 12 mm³ and most are under 5 mm³, whereas barley and emmer average 42 mm³ and 47 mm³, respectively. The SGG would have been more difficult to gather than wheat and barley as well, because the low-growing plants (with an average height of 61 cm in the southern Levant today) would have required more bending and stooping than would have been the case for the cereals (with an average height of 125 cm) (37). In sum, the plant remains from Ohalo II prove that broad-spectrum foraging was a strategy for plant collecting as well as for hunting

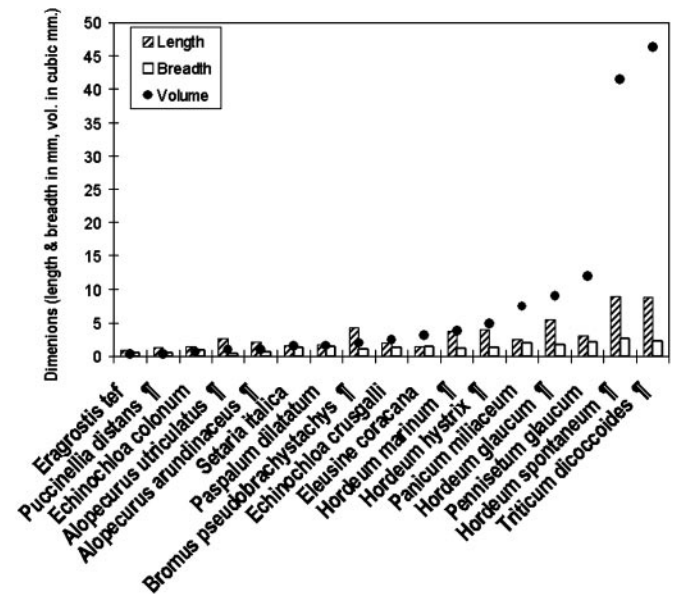


Fig. 1. Grain sizes of SGG occurring at Ohalo II and in contemporary agriculture; the Ohalo II species are indicated with †. The species are arranged in order of increasing grain volume (calculated using refs. 48–50). Length, breadth, and thickness are mean measurements in mm; volume is in mm³. Volume was calculated by multiplying length, breadth, and width. The cereals (wild emmer wheat and wild barley) included for comparison, highlight how large these grains are compared with the SGG.

Table 2. Volume of SGG and wild cereal species occurring in southwest Asian archaeological sites from the UP to the Late PPNB

Site	Average age, cal B.P.	Period	Cereal grains			SGG			Ref.
			Quantity	Volume, mm ³	% of volume total	Quantity	Volume, mm ³	% of volume total	
Ohalo II	23,000	UP	2,620	108,801	65.4	16,168	57,671	34.6	7
Abu Hureyra I	12,500	Natufian	611	15,942	78.2	1,547	4,446	21.8	51
Mureybet I,II	11,000	PPNA	31	900	82.9	90	185	17.1	52
Netiv Hagdud	10,800	PPNA	1,999	44,097	98.6	237	632	1.4	53
Wadi el-Jilat 7	10,800	Early PPNB	309	20,480	95.8	207	897	4.2	54
Nevali Çori	10,100	Early PPNB	879	30,645	98.9	44	332	1.1	55
Çayönü	10,100	Early PPNB	191	4,267	96.8	44	140	3.2	56
Mureybet III	10,100	Early PPNB	2,898	65,522	99.9	28	55	0.1	52
Ganj Dareh	10,500	Middle PPNB	252	21,625	99.2	328	167	0.8	57
Abu Hureyra 2A	10,000	Middle PPNB	339	15,913	79.2	749	4,479	20.8	58
Aswad II	9,800	Middle PPNB	2,720	105,007	90.1	2,624	11,524	9.9	59
Asikli Höyük	9,800	Middle PPNB	106	4,831	97.6	14	117	2.4	60
Ghoraifé	9,200	Middle PPNB	298	11,649	90.5	259	1,220	9.5	59
Ali Kosh (BM)	8,800	Middle PPNB	514	19,145	96.5	302	686	3.5	61
Tell Bouqras	8,800	Late PPNB	4,270	289,225	99.9	37	254	0.1	62
Ramad I	8,800	Late PPNB	396	15,513	94.5	226	894	5.5	59
Abu Hureyra 2B	8,800	Late PPNB	1,277	17,248	87.3	359	2,511	12.7	58
El Kowm II-Caracol	8,300	Late PPNB	138	10,614	94.1	140	665	5.9	63
Atlit-Yam	8,300	Late PPNB	1,472	54,261	99.5	39	272	0.5	64

Average cal B.P. dates were calculated by using the available dates for each site and do not reflect the total time span of occupation. Volume was calculated by using figures by Kislev and colleagues (48–50). PPNA, Prepottery Neolithic A.

in the UP. We will not know, however, the specific hunting practices at Ohalo II until a quantitative analysis of its faunal assemblage is published.

How widespread was this pattern of broad-spectrum plant foraging in the Levant during the Late Glacial Maximum? Unfortunately, because of the rarity of plant data from this period from other sites we have no idea of its extent. Nor can we look for older examples of dietary change in the UP, also because of a lack of data (38–43). Plant assemblages from the Middle Paleolithic, however, do shed a faint light on even earlier diets.

Middle Paleolithic: Prelude to the Broad Spectrum

In Middle Paleolithic Kebara Cave (~60,000–48,000 thermoluminescence years ago), Mount Carmel, Israel, Lev and associates (41, 44) found 3,956 charred seeds representing 52 taxa. On the basis of ethnographic observations and the fact that this plant assemblage was retrieved mainly from the immediate environment of the hearths, we assume that these seeds represent the Mousterian cave dwellers' diet. Most of the seeds (3,300) were legumes but there were also acorns (*Quercus* sp.) and pistachio (*Pistacia atlantica*) nuts, as well as the seeds of giant golden-drop (*Onosma gigantean*), podonosma (*Podonosma orientalis*), Judean bugloss (*Echium angustifolium/judaeum*), safflower (*Carthamus* sp.), and wild grape (*Vitis vinifera*). Only ten grass grains, including two of wild barley (*Hordeum spontaneum*), were recovered. In light of the generally good preservation of plant remains in the cave, Lev and colleagues concluded that cereal grains were an insignificant food source. It is notable, however, that they had made their way into human hands by this time, albeit in modest amounts.

Less compelling evidence of the Middle Paleolithic diet comes from Amud Cave (~70,000–55,000 thermoluminescence years ago) in the Upper Galilee, Israel. On the basis of phytolith assemblages, Madella *et al.* (42) concluded that the cave's Neanderthals exploited herbaceous plants, ligneous parts of trees and shrubs, and mature grass panicles, and proposed that broad-spectrum exploitation of plants had started at least by the end of the Middle Paleolithic. Because phytoliths, minute silica bodies in plant cells, are identified only to family group and not

species, this proposal needs further support with seeds, which can be more precisely identified.

Post-Epipaleolithic: The Shrinking Spectrum

On the basis of this meager evidence it appears that the BSR in plant collecting probably did not begin in the Middle Paleolithic. Relying on the currently available information, it is likely that the BSR started during the UP. The Late Glacial Maximum period may have seen the apogee of this strategy because the spectrum of plant foods appears to have shrunk progressively thereafter, based on a survey of later sites.

To trace broad-spectrum plant foraging after the occupation of Ohalo II we examined all published reports from excavations in the Levant and selected the 19 archaeobotanical assemblages that contained 100 or more grass and cereal caryopses, dating from the Natufian (14,500–11,500 cal B.P.) through the end of the Prepottery Neolithic B (abbreviated PPNB; 8,200 cal B.P.). We weighed differences in preservation and sampling techniques at the various sites to make sure that they did not distort the value of the overall comparisons. The archaeobotanical assemblages derive from generally similar contexts, mostly dumping zones between houses or in abandoned structures in the Neolithic mounds. All of the samples were retrieved by various flotation techniques, using a flotation machine or a simple water tank. Although these methods were not identical, all of the sites we chose produced SGG, which we consider to be evidence for a similar general level of recovery. We excluded Jericho (45) because only dry sieving was sometimes used, and no SGG were found, suggesting the mesh was large and the recovery rates lower than the other sites.

As in the case of Ohalo II, we tested for broad-spectrum foraging with the ratios of SGG volume to wild cereal volume. That is, we tried to determine how broad a range of grasses contributed to the foragers' diet in terms of total food mass. For each site we tabulated the volume of the SGG and cereals, as well as their collective total (see Table 2). To determine the relative contribution of each to the total, we calculated the percentage that SGG and cereals each represented. The higher the figure for SGG, the broader the foraging base and, conversely, the higher

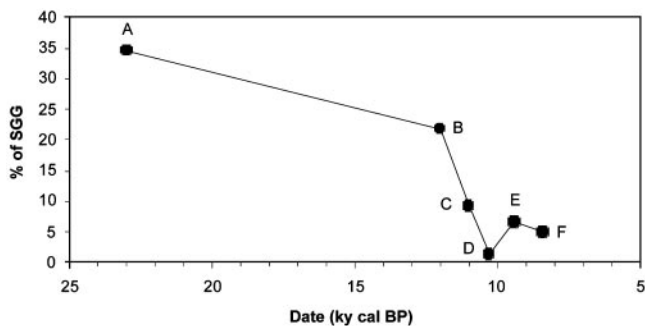


Fig. 2. Averages, per period, of the percentage of SGG relative to the total grasses at each site. Dates are median dates for each period [A, UP; B, Natufian; C, Prepottery Neolithic A (PPNA); D, Early PPNB; E, Middle PPNB; F, Late PPNB]. The graph shows a decline in SGG from the UP to the Early PPNB and their negligible significance thereafter.

the percentage of cereals, the narrower the base. Because sample sizes and numbers differ from site to site, the volume ratios give a more valid comparison than sheer quantity of different taxa. For Ohalo II the figure is 34.6%, which reflects the greatest dietary breadth in the samples considered here. Thereafter, the percentage of SGG declines in a very clear trend. By the Late PPNB, SGG had fallen to <1% of the cereal/grass assemblage at several sites, and the grass component of the diet had become vastly dominated by cereals. This trend is shown graphically in Fig. 2, which plots the averages, per period, of the percentage of SGG relative to the total grasses in each site.

Conclusions

Flannery's original formulation of the BSR (1) proposed that Paleolithic foragers gradually expanded their resource base to include a broad range of foods that had once been ignored. Several decades of research, primarily on faunal remains, has shown that foragers were indeed casting their nets wider, starting

perhaps 50,000 years ago. This research has also shown not only that the new animal foods were taxonomically more diverse than in earlier periods but also that they were more costly in terms of effort to procure (4–6, 46). Whether plant foods went along on this broad-spectrum ride has never been demonstrated for lack of archaeobotanical data. Now with the remarkable collection of plant remains from Ohalo II it is possible to examine the plant component of the Late Paleolithic economy and prove that plant foods were indeed part of the BSR. The assemblage of some 90,000 plant remains shows that wild cereals were gathered at 23,000 cal B.P., pushing back the floral component of the broad-spectrum revolution some 10,000 years earlier than previously suggested. Perhaps more remarkable is the evidence that broad-spectrum foraging was even broader than Flannery originally conceived. In addition to cereals, the foragers of Ohalo II gathered large quantities of more than five different SGG which, like much of the fauna hunted during the Late Paleolithic, were costly to procure compared with the returns. On the basis of the currently published archaeobotanical assemblages, we can say that such dietary breadth was never seen again in the Levant. At sites from later periods the number of SGG declined sharply and was negligible by the end of the PPNB, giving way entirely to the cereals, which by that time were domesticated. As Flannery proposed, the real significance of the BSR was that it led to cereal domestication. But at the time he wrote no one knew that broad-spectrum foraging for cereals went back at least 23,000 years ago and included a dalliance with minute grass seeds.

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