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Isotope and morphometrical evidence reveals the technological package associated with agriculture adoption in western Europe

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This study aimed to reconstruct the environmental conditions and the crop management practices and plant characteristics when agriculture appeared in western Europe. We analyzed oak charcoal and a large number of cereal caryopsides recovered from La Draga (Girona, Spain), an early (5300 to 4800 cal. BC) agricultural site from the Iberian Peninsula. The carbon isotope discrimination ($\Delta^{13}C$) values of oak, the dominant forest species in the region, indicates prevalence of a wet climate at the site. Further, we reconstructed crop management conditions, achievable yield, and crop characteristics through the analysis of $\Delta^{13}C$, nitrogen isotope composition ($\delta^{15}N$), nitrogen content, and the reconstructed weight of wheat and barley caryopsides, following protocols developed by our team [Araus *et al.*, *Nat. Commun.* 5, 3953 (2014)] and comparison of these parameters with present-day organic agriculture in the region. In parallel, a regional perspective was achieved through the study of wheat and barley grains of seventeen Neolithic sites from the western Mediterranean. The results suggest that rather than small-garden cultivation, a more extensive agriculture was practiced under good water availability and moderate manuring. Moreover, results from La Draga evidence that grain weight and spike morphology were comparable to contemporary cereals. Growing conditions and the prevalence of improved crop traits indicate that agriculture was fairly consolidated at the time it reached the western edge of Europe.

agriculture | stable isotopes | Neolithic | Paleo reconstruction | cereals

Significance

The emergence and spread of agriculture represented a landmark in societal development, triggering the Neolithic revolution. The spread of agriculture from the Fertile Crescent to the western edge of Europe has been extensively researched, but our knowledge of the actual crop husbandry practices is still limited. We followed a dual approach: in-depth study of La Draga, one of the earliest agricultural settlements in the western Mediterranean and exceptional for its abundance and preservation of archaeobotanical remains, together with a regional perspective including other early agricultural sites. Our results support archaeological models of agriculture diffusion and denote favorable water conditions and evolved crop characteristics when agriculture reached Europe's western edge.

Agriculture spread about nine millennia ago from its origin in the Fertile Crescent, west through Europe to the continent's western shores, and arrived on the Iberian Peninsula around two millennia later (1–4). It comprised different cereals as the main crops, together with pulses as additional staples. While climate conditions during the early Holocene may have contributed to the emergence of agriculture, the causes of its progressive adoption throughout Europe until it reached Europe's western edge, whether associated with human migration (i.e., demic), the result of cultural transition or a mixed process (5, 6), is still open to debate. In the West Mediterranean, the archaeological record indicates a much faster rate of agricultural spread than in other European regions, which is coherent with a demic process driven by dispersal along coastal routes (7), even when interaction with local hunter-gatherers would have facilitated the process (8). Whatever the mechanisms responsible for agriculture adoption, be it demic, cultural, or something in between, it should have conferred comparative advantages over hunting and gathering. In that sense, unfavorable climate conditions might have contributed to its adoption, making agriculture more advantageous than gathering under the local climatic and environmental conditions. However, if agriculture confers benefits even under favorable conditions, this could also promote its diffusion and adoption by facilitating the creation of food surpluses. As a key point to solve this debate, it is necessary to gain further insight into the prevailing growing conditions and level of technology (agronomic/cultivation practices and intrinsic crop characteristics) when agriculture reached western Europe.

The Middle Holocene is characterized as a relatively climatic stable period. Nonetheless, different proxies show a global climate anomaly coinciding with the arrival of agriculture in western Europe around 5.5 to 5.0 kyr cal BC (9). This anomaly is documented in the NE Iberian Peninsula as an abrupt cooling, possibly related to a period with less precipitation (10–12). However, elucidating whether climate factors facilitated the adoption of agriculture is not always easy due to the difficulty of correlating different proxies with specific human occupations. In this regard, the isotopic study of archaeobotanical remains allows us to infer data on the climate and crop growing conditions local to the archaeological site and period in question. This is because the stable isotope composition in plant

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biomass of light elements reflects the environmental conditions in which the plant grew (13–15). In the case of carbon, plants are depleted in the heavier isotope ^{13}C relative to atmospheric CO_2. This is due to a fractionation process during photosynthesis, related to air diffusion through stomata and the carboxylation reaction (16). Under drought periods, stomatal closure reduces the CO_2 concentration in the intercellular space, limiting CO_2 availability for the carboxylating enzyme (Rubisco). This is linked to greater fixation of ^{13}C, consequently increasing carbon isotope composition ($\delta^{13}C$) and thus decreasing carbon isotope discrimination ($\Delta^{13}C$) values (16). The relationship between plant $\Delta^{13}C$ in woody tissues and climate variables is well demonstrated (17–19), with Mediterranean species such as *Quercus* spp. being sensitive to water stress (18, 20).

A second approach to address the drivers of agriculture spread is to assess the level of technology in the agricultural package at the time that agriculture was adopted. This includes an examination of the characteristics of the crop species cultivated and their growing conditions, including the agronomic practices displayed. Addressing these questions implies deciphering the characteristics of the agronomic components of grain yield. In the case of cereals, these components are the individual grain weight, the number of grains per spike and the density of ears per unit ground area. Increases in grain weight are likely a secondary trait associated with crop domestication that in general evolved much more slowly than the appearance of nonshattering spikelets, requiring several millennia to reach weights comparable to current cereal varieties (21, 22). The weight of original grains may be inferred from the linear dimensions of the charred remains (23, 24). This allows a direct comparison with grain weight values of modern cereals.

Increase in the grain number per spike is also considered a secondary trait related to domestication, but its evaluation is usually addressed by comparing wild progenitors with present-day landraces (25). However, the exceptional conditions of La Draga, where prevailing anoxic conditions have allowed the preservation of spike fragments (26, 27), enables a direct comparison between present-day landraces and ancient domesticated cereals. Finally, ear density (i.e., ears m^{-2}) is simultaneously affected by a number of environmental and cultural factors that make its inference a complex issue. Among these factors are the growing conditions (including availability of water and nutrients), crop management (sowing density, seedling emergence, weed control), and agronomic practices such as mixed cropping. These technological aspects, in particular, the water conditions, may be inferred from the $\Delta^{13}C$ of fossil grains (28–32), whereas nitrogen fertilization status, the level of manuring and, to some extent, the presence of intercropping, may be assessed through the nitrogen isotopic composition ($\delta^{15}N$) of the same grains (33, 34), and the nitrogen content of grains after correcting for carbonization (34, 35). In addition, the $\Delta^{13}C$ of grains also allows us to infer the potential grain yield attained by the crop (21, 36), which subsequently may provide clues about the total area under cultivation needed to support the site population (21, 37).

Here, we reconstructed climate and agricultural conditions at the time that agriculture reached the western Mediterranean using a dual approach: a detailed study at the local level together with a regional evaluation. For the local case, we ran an extensive study of archaeobotanical (wood and cereal grains) remains from La Draga, Girona, NE Iberian Peninsula. This is the richest early-Neolithic site (ca. 5300 to 4800 cal. BC) on the Iberian Peninsula in terms of abundance and preservation of archaeobotanical remains (26) (Fig. 1). By choosing La Draga as a case study we aimed to assess the climate conditions and to determine the degree of maturation of the agricultural package when agriculture was adopted. For climate reconstruction, the existing anthracology (38), pollen (39, 40), and $\Delta^{13}C$ of water-logged wood (41) records have been supplemented with new $\Delta^{13}C$ charcoal data and reexamined regionally. For the $\Delta^{13}C$ analysis in wood remains, we selected deciduous *Quercus* spp. because this taxon was the most abundant during the two occupation phases documented in La Draga (42) and is sensitive to water conditions. In terms of crops, we have focused on naked wheat (*Triticum durum/turgidum*) and two-row barley (*Hordeum vulgare* subsp. *distichum*). The former is the best represented cereal at La Draga, whereas barley, even though relatively frequent, seems to take the role of a secondary crop (26, 27). These two species allow the diachronic comparison with modern cereal agriculture in the region. For the regional evaluation, we performed a meta-analysis based on published sources and new data, aiming to attain an overall view of the agronomic conditions prevailing at the time agriculture was adopted in the western Mediterranean. For that, agricultural conditions were derived from the available $\Delta^{13}C$, $\delta^{15}N$, weight, and nitrogen content of naked wheat and barley grains from a set of seventeen Neolithic sites, mostly from the Iberian Peninsula. The questions on which the present study aims to shed light are i) what climatic conditions (dry or humid) prevailed at the time when agriculture appeared in western Europe, ii) the agronomic conditions of cultivation (soil moisture and fertility, grain nitrogen content), and iii) secondary domestication characteristics of the crop (grain weight and spike morphology).

Results

Charcoal and Grain $\Delta^{13}C$, Crop Water Status, and Yield. The $\Delta^{13}C$ values of deciduous *Quercus* sp. (oak) charcoal of the two occupation periods (ca. 5300 to 5050 and 5000 to 4800 cal BC, respectively) of La Draga were high, but on average increased near 1.5 ‰ from the first to the second period (*SI Appendix*, Table S1).

The mean $\Delta^{13}C$ of wheat grains remained rather steady throughout the occupation periods, with most values lying between 17.5 ‰ and 18.0 ‰ (Fig. 2). Mean values for present-day rainfed wheat grown under organic farming were below 17.0 ‰ (2016 to 2017) and 18.5 ‰ (2017 to 2018). Barley gave $\Delta^{13}C$ values around 17.0 ‰ and 18.5 ‰, respectively, for the two occupation periods, whereas for present-day rainfed barley under organic farming, the mean values were near 19.0 ‰ and above 20.0 ‰ for the two consecutive crop seasons (*SI Appendix*, Fig. S1).

Accumulated water inputs during grain filling of wheat, as inferred from the $\Delta^{13}C$ of grains, was around 150 mm throughout the occupation period, while for barley the water inputs were more variable, but also around 150 mm on average (*SI Appendix*, Fig. S2). Water input values during grain filling (from anthesis to crop maturity) in present-day organically farmed wheat and barley crops in 2017 were around 70 and 80 mm, respectively, and in 2018 were 210 and 270 mm, respectively, with the two consecutive years exhibiting the driest and wettest seasons of the decade.

Estimated wheat grain yield was around 2 Mg ha^{-1} throughout the occupation period (Fig. 3*A*), whereas for barley the values ranged from 1 to 1.5 Mg ha^{-1} (*SI Appendix*, Fig. S3). Present-day yields for rainfed wheat under organic farming in the area were nearly 3 Mg ha^{-1} (2016 to 2017) and 4 Mg ha^{-1} (2017 to 2018), whereas for barley were around 3.5 Mg ha^{-1} (2017 to 2018). Yields for organically farmed wheat grown in other regions with similar environmental conditions were comparable (Fig. 3*A*).

Grain Weight. The estimated mean grain weight for the whole set of samples was around 37 mg for both wheat and barley (*SI Appendix*, Fig. S4), with a higher SD for two-row barley. Mean wheat values across dated contexts ranged from 33 to 42 mg,

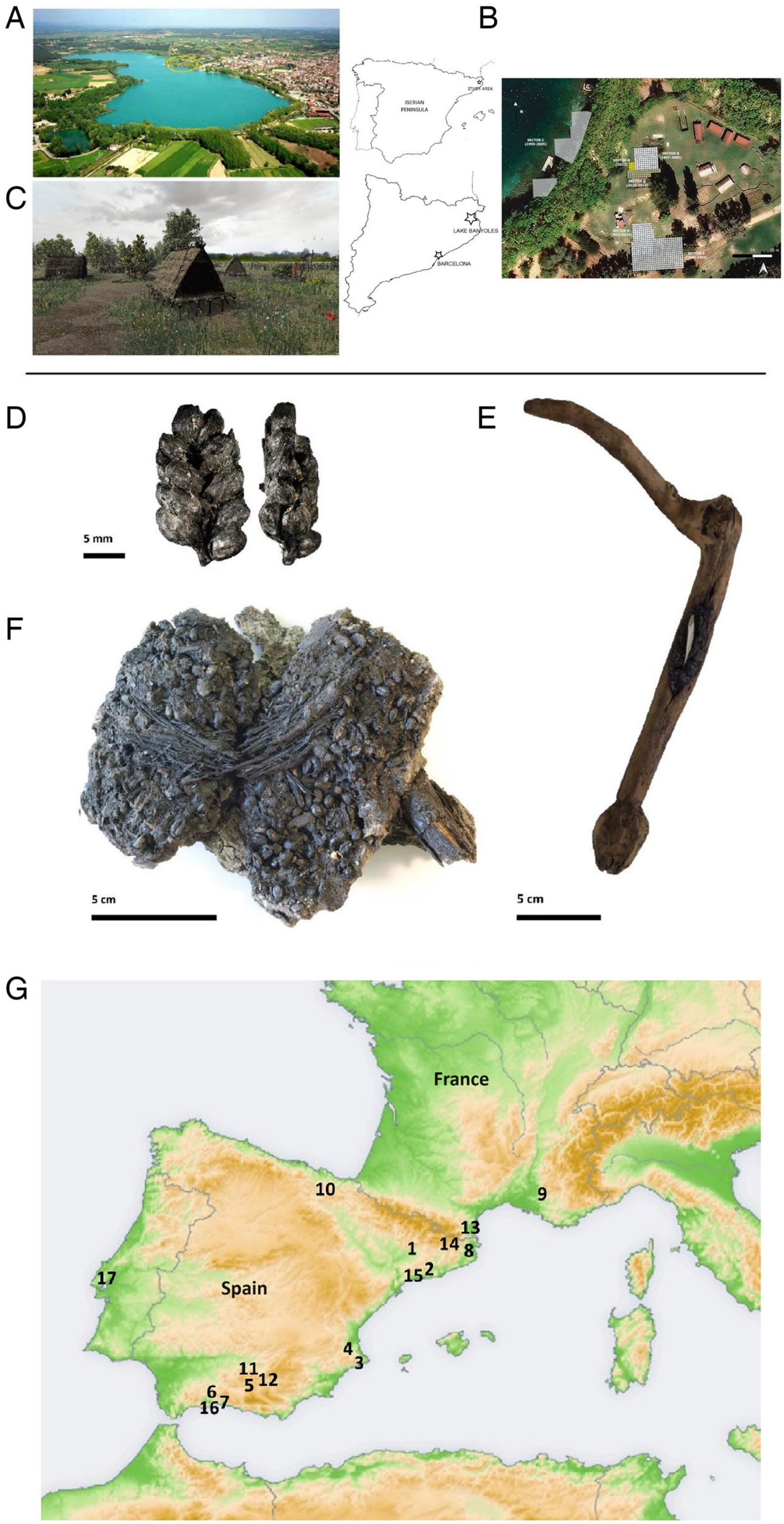

Fig. 1. Geographical location, map of La Draga, reconstruction of the site, and organic remains (dated 5300 to 4800 cal. BC) related to cereal agriculture with exceptional preservation thanks to the waterlogged conditions at La Draga. (*A*) Location of the La Draga site on the western shore of Lake Banyoles at 172 masl and 40 km from the Mediterranean coast of the NE Iberian Peninsula. (*B*) Locations of the excavation sectors at the La Draga site. Sector A is dry, sectors B–D are waterlogged and sector C is underwater. Samples analyzed originate from sectors B–D and A. (*C*) Hypothetical reconstruction of the early Neolithic wooden dwellings and environment at La Draga (Source: Equip Draga). (*D*) Spike fragment corresponding to durum wheat (Source: Ferran Antolín). (*E*) Wooden sickle. The handle is made of *Sambucus* sp. and the flint blade is fixed diagonally to the shaft. (*F*) remains of a carbonized basket presumably containing wheat grains (Source: Museu Arqueològic de Banyoles). (*G*) Map of the set of 17 Neolithic sites, mostly located on the Mediterranean shores of the Iberian Peninsula, from which wheat and barley grain data are presented in Fig. 4. Locations of the different sites are numbered in alphabetical order: 1—Auvelles, 2—Can Sadurní, 3—Cova de l'Or, 4—Cova de Sta Maira, 5—Cueva de los Mármoles; 6—Cueva del Toro, 7—Hostal Guadalupe, 8—La Draga, 9—Les Bagnoles, 10—Los Cascajos, 11—Los Murciélagos, 12—Montefrio, 13—Montou, 14—Plansallosa, 15—Pou Nou, 16—Roca Chica, and 17—Sâo Pedro de Canaferrím.

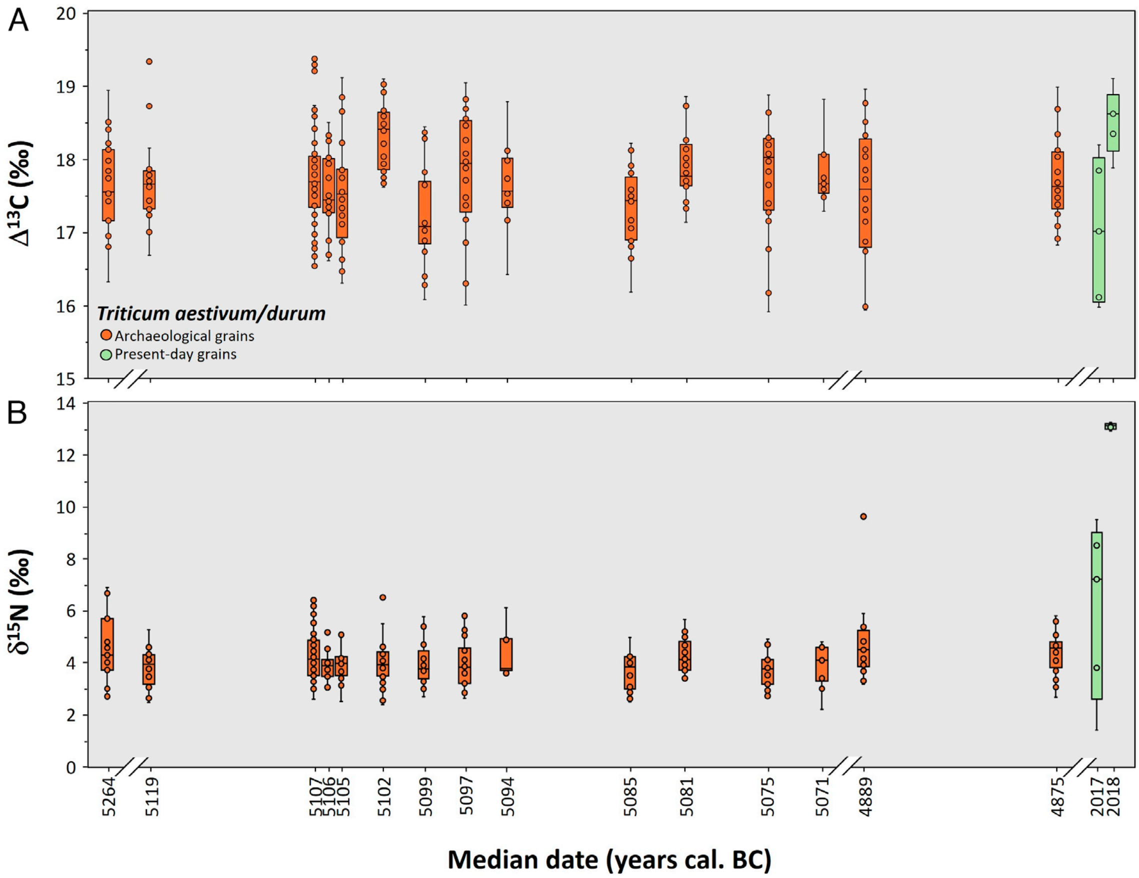

Fig. 2. Carbon isotope discrimination "$\Delta^{13}C$" (*A*) and nitrogen isotope composition "$\delta^{15}N$" (*B*) in the grains of naked wheat from La Draga. $\Delta^{13}C$ values were calculated from the analysis of carbon isotope composition of the grains and the inferred carbon isotope composition of the air. The *Right* side of the main figure shows the values for present-day organic crops in the area, grown under rainfed conditions in a nontillage regime, rotated with pulses, during two consecutive seasons (2016/17 and 2017/18 crop seasons). Results are presented as box-and-whisker plots using the exclusive median for calculating the interquartile range. The boundary of the box closest to zero indicates the 25th percentile, the line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whisker caps above and below the box indicate the minimum and maximum values calculated as the mean ± SE, and the scattered values denote all data points.

except for the last date, where grain weight was 27 mg (Fig. 3*B*). Barley values diverged strongly between the earliest (22 mg) and second-earliest (46 mg) dated contexts (*SI Appendix*, Fig. S5) and weights of individual grains of both dates together correlated positively with $\Delta^{13}C$ of grains (*SI Appendix*, Fig. S6). Grain weight of present-day organically farmed crops in the area were 35 and 37 mg for wheat, and 35 and 45 mg for two-row barley during the two consecutive seasons (2016/17 and 2017/18). Grain weight values reported for rainfed organically farmed wheats grown in agroclimatic regions comparable to present-day La Draga were also consistent with these results (Fig. 3*B*).

Grain Nitrogen Concentration and $\delta^{15}N$. The grain nitrogen concentration of wheat remained steady (around 2.0 %) during the entire lifetime of the site, except for the last occupation period, when values slightly decreased (Fig. 3*C*). For barley, the nitrogen concentration clearly decreased from around 2.7 % in the first phase to 1.6 % in the second phase (*SI Appendix*, Fig. S7). Present-day (2016/17 and 2017/18) values from organic farming in the region were higher (around 3.0 %) for wheat and comparable (1.7 %) for barley. Values for organically farmed wheat in other regions of comparable agroecological conditions were around 2.5 % (Fig. 3*C*). Both grain weight and nitrogen concentration values for wheat at La Draga were lower in the most recent samples, compared to the previous ones (*SI Appendix*, Table S2).

The nitrogen isotope composition ($\delta^{15}N$) of grains remained quite stable, with median values around 4 ‰ for both crops, while for values from present-day organic farming the median ranged from around 7 to 13 ‰ for wheat (Fig. 2) and 3 to 11 ‰ for barley (*SI Appendix*, Fig. S8).

Early Agriculture Conditions: A Regional Perspective. Data on $\Delta^{13}C$, $\delta^{15}N$, weight, and nitrogen concentration of naked wheat and barley grains from a set of another 17 Neolithic sites from western Europe (Spain and France) were studied (Fig. 1*G*). Most of the sites (15) were placed on the Mediterranean shores of Spain and France. $\Delta^{13}C$ values were in general slightly lower than in La Draga but overall above 16 ‰ and 16.5 ‰ for wheat and barley, respectively (Fig. 4*A* and *SI Appendix*, Fig. S9). Grain weight values were also slightly higher at La Draga than those of the sites where values were available (Fig. 4*D*). By contrast, $\delta^{15}N$ values (between 4 and 6 ‰ for both species) and nitrogen content (around 2 % for wheat and 1.5 % for barley) of grains were quite similar across sites (Fig. 4 *B* and *C*), including La Draga. When all the sites and dates were considered together, positive correlations were observed for barley, as well as for barley plus wheat combined (and a trend for wheat alone) between the date of the samples and the mean $\delta^{15}N$ for each site and date (*SI Appendix*, Fig. S10).

Discussion

Different proxies show a global climate anomaly around 5.5 to 5.0 kyr cal BC (9) that also affected the northeast (NE) Iberian Peninsula (10–12) causing an abrupt cooling, and possibly less

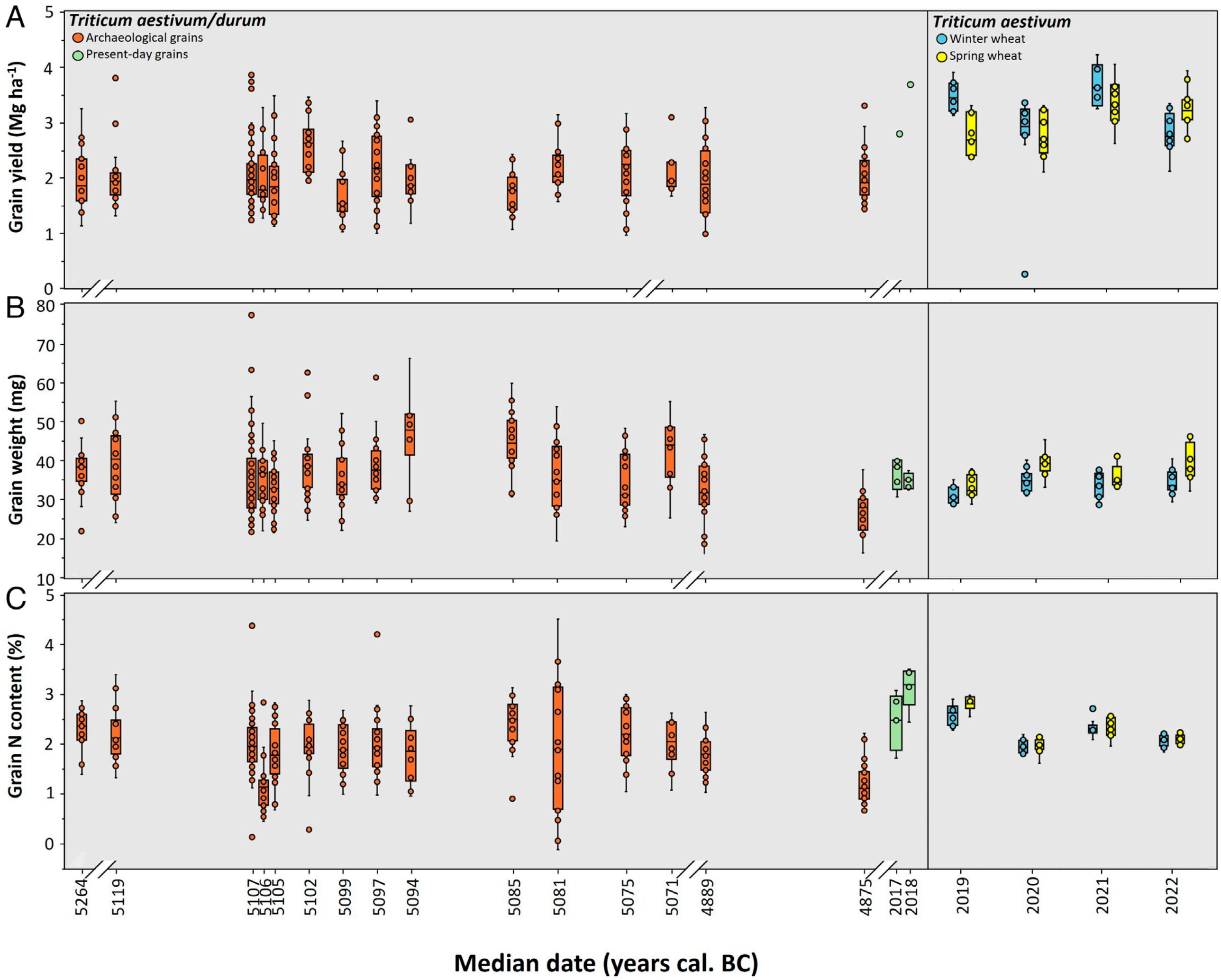

Fig. 3. Grain yield (*A*), weight of individual grains (*B*), and nitrogen concentration in the grains (*C*) of naked wheat from La Draga. Grain yield was estimated on the basis of the $\Delta^{13}C$ of charred grains according to the models developed by our team (34, 43, 44). Grain weight was estimated from the dimensions (length, width, and thickness) of charred grains according to the models developed in Ferrio et al. (23). Grain N content was calculated after correcting for their actual weight. The *Right* side of the main frame of the figure shows the values for present-day grain yield, grain weight, or grain nitrogen content of organic wheat crops in the area grown under rainfed conditions during two consecutive seasons (2016/17 and 2017/18 crop seasons). The wheat was bread wheat (*Triticum aestivum*) c.v. Valbona, fertilized with compost derived from pig and chicken manure plus chopped straw. The *Right* smaller figure frame depicts the values of the last four crop seasons (2018/19 to 2021/22) published by GENVCE (https://genvce.org/productos-genvce/informes/) for winter and spring bread wheat cultivated under organic farming conditions in regions with ecoclimatic conditions comparable to the present-day La Draga site. Results are presented as box-and-whisker plots using the exclusive median for calculating the interquartile range. The boundary of the box closest to zero indicates the 25th percentile, the line within the box marks the median, and the boundary of the box farthest from zero indicates the 75th percentile. Whisker caps above and below the box indicate the minimum and maximum values calculated as the mean ± SE, and the scattered values denote all data points.

precipitation, coinciding with the onset of agriculture in the region. However, the prevalence of humid conditions during the emergence of agriculture in La Draga (48) is supported by published palynological (39, 40) and anthracological (38, 49, 50) records that indicate a densely wooded landscape at that time, with the landscape dominated by deciduous forests, and oak as the most abundant taxon. The charcoal $\Delta^{13}C$ results from approximately the time of the site's establishment (18.3 ‰) expand the temporal range of previous studies (41) that compared the $\Delta^{13}C$ of subfossil (19.4 ‰) and extant (18.0 ‰) samples of deciduous oak (Dataset S1), and suggest greater water availability during the emergence of agriculture at the site than at present. However, the anthracological record showed that while oak and laurel (*Laurus nobilis*) were still predominant, they decreased during the second occupation phase, whereas there was a significant increase in *Buxus sempervirens*, a pioneer species that colonizes degraded oak woodland (51) and is likely associated with increasing anthropization of the landscape. Published pollen records also suggest a decrease in deciduous oak and riparian forest species, probably as a result of forest exploitation (38, 39). Nevertheless, deforestation of the site by Neolithic communities apparently did not modify the local climate toward drier conditions: The $\Delta^{13}C$ values of charcoal, already high at the time of agriculture's arrival (18.3 ‰ on average), clearly increased during Phase II (19.7 ‰), and the presence of mesophilous trees (i.e., *Tilia*, *Corylus*) other than oak even expanded (40, 52, 53). All together, these results seem to disprove the existence of an environmental limitation preventing continuation of hunting and gathering activities as a cause for the adoption of agriculture in the Iberian Peninsula. In the case of La Draga, the most plausible scenario is a mechanism of migrating population (7, 8), since the site and the region were mostly unpopulated, even by hunter-gatherer standards during the few centuries before agriculture appeared (54–56).

The high grain $\Delta^{13}C$ values throughout the occupation time at La Draga (near 18.0 ‰), which correspond to approximately 150 mm water input during grain filling (25, 30), suggest that wheat grew

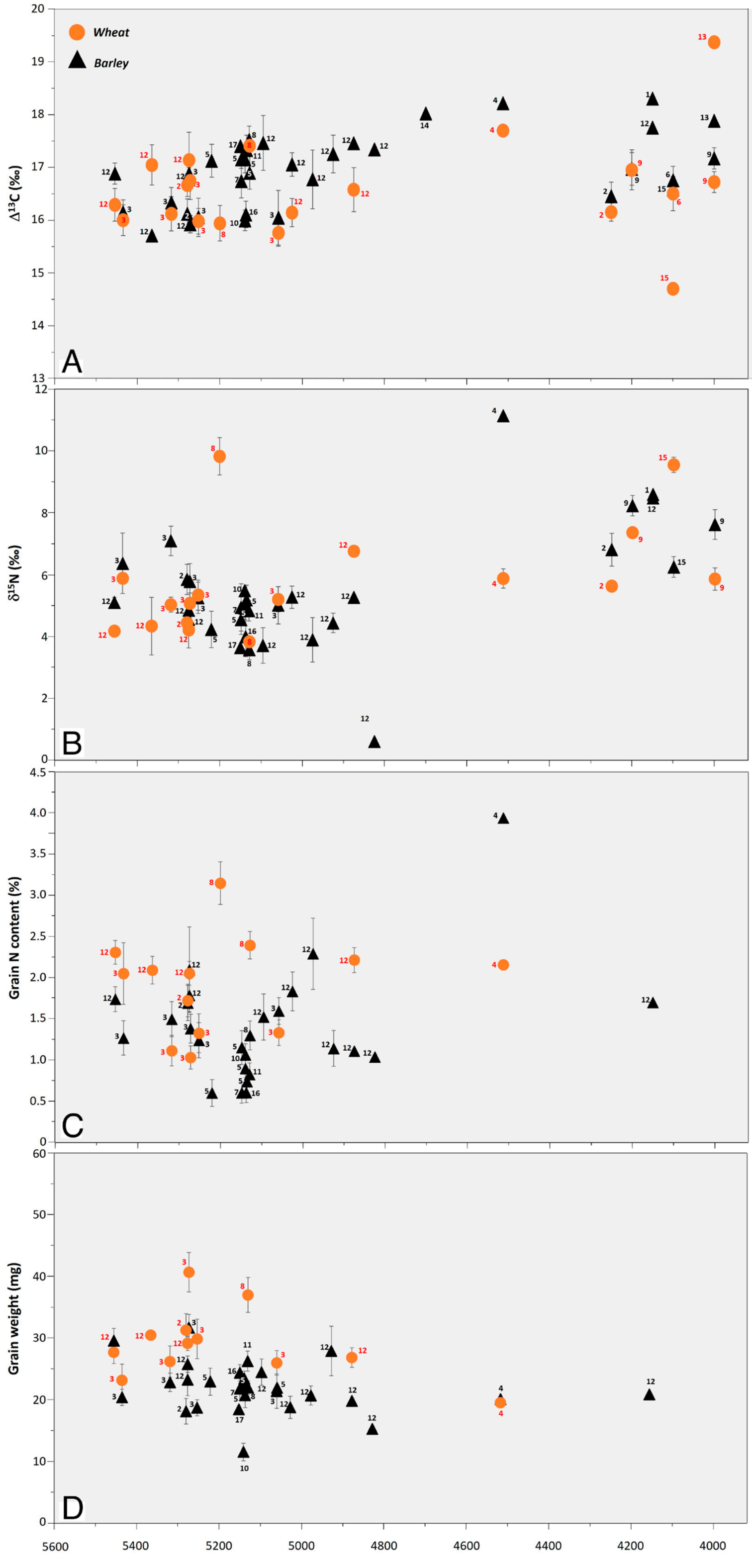

Fig. 4. Data on $\Delta^{13}C$ (*A*), $\delta^{15}N$ (*B*), nitrogen content (*C*) and weight (*D*) of grains from naked wheat and barley grains of a set of 17 Neolithic sites, detailed in Fig. 1*G*. Values presented were derived from published sources (28, 34, 45–47) and new data (Dataset S5) and are means ± SE, whereas the scattered values around the means denote all data points, except for the Sâo Pedro de Canaferrím and Plansallosa sites, where only the average values were available. Numbers close to the symbols refer to specific sites as referred in the map in Fig. 1*G*. Values from La Draga in this figure are new and not included in the other figures in this study because these samples were obtained during preliminary campaigns.

under relatively wet conditions and was rather unaffected by annual variability in rainfall and temperature (14, 15, 29). The rather low intrasample variability in $\Delta^{13}C$ values also supports cultivation under naturally wet conditions (57). This finding agrees with the humid environment prevalent at the site, as inferred from anthracological isotopic evidence. While cultivation on the shores of a lake with a shallow soil water table may have contributed to the constancy of wet conditions, the relatively low

$\delta^{15}N$ values at the site do not support the cultivation of temporarily waterlogged soils of a lake shore (58). In the case of barley $\Delta^{13}C$ values, although they were also in the range of good water conditions, they were more variable, which suggests this crop was somewhat secondary (57).

Grain nitrogen concentrations, which were around 2 % for wheat throughout the occupation of La Draga and slightly below this for barley during the second occupation, agree with the most common values for present-day crops (59–61). These values suggest moderate-to-good nitrogen fertilization conditions. Animal manuring, whether it was conscious or unconscious, was the most usual way of crop fertilization in the Neolithic (62). We examined grain $\delta^{15}N$ as a proxy for manuring. The results do not discount some degree of manuring, probably associated with herding (63). However, the rather low $\delta^{15}N$ in grains, around 4 ‰ throughout the occupation period, does not support intensive manuring. In fact, the estimated $\delta^{15}N$ values of herbivore forage (i.e., essentially unmanured plants) in La Draga, inferred from $\delta^{15}N$ values of bone collagen of wild herbivores would be just slightly lower (around 1 to 1.5 ‰) than those of cereals in La Draga (64). Zooarchaeological remains allow us to dismiss extensive herding practices in favor of a more diversified farming strategy, where pigs, cattle, goats, and sheep would have been raised and had occasional access to the arable plots (26). The absence of spores of coprophilous fungi off-site suggests a limited impact of grazing on the landscape (39), which could be a sign of a very local management (on-site) of the animals. Manuring associated with the consumption of fish or mollusks from a lake as small as Banyoles would be insignificant, and had it been practiced to any extend, this nutrient source would have decreased $\delta^{15}N$ (65). Another possibility particularly associated with the establishment of agriculture could be *burning/shifting cultivation.* Soil and vegetation $\delta^{15}N$ values would have increased, but in a transient and frequently moderate manner (66). In the case of La Draga, no evidence of slash-and-burn has been found during the occupation of the site (40). The effects of tillage and plowing in raising $\delta^{15}N$ are usually minor (66), and even more so in early agricultural sites such as La Draga where tillage practices were of moderate depth due to the use of digging sticks for soil disturbance (67). The $\delta^{15}N$ values of grain cereals at La Draga are consistent with reports on the grain $\delta^{15}N$ of cereals from early agricultural sites of the Fertile Crescent (21) as well as eastern and central Europe (63, 68), and the same may be concluded for our meta-analysis of Mediterranean western Europe, with average values usually below 6‰. These results suggest that in most cases manuring fertilization was modest. Moreover, the $\delta^{15}N$ values of grain cereals from present-day organic farming subjected to intensive manure were clearly higher. In this sense, the study of Bogaard et al. (63) suggests that long-term absence of manure was associated with cereal grain $\delta^{15}N$ values below 3 ‰, whereas under intensive manuring $\delta^{15}N$ values would be above 6 ‰. Other studies (68) report comparable results, suggesting a cutoff value of 6.3 ‰, to differentiate between low and high inputs of manure. In this sense, for barley grains manured with 25 Mg per hectare every fourth year, with the most recent addition two years before harvest, $\delta^{15}N$ values of 8.9 ‰ were reported (69), in line with the values found for present-day organic wheat and barley crops in the Lake Banyoles area. From the evidence above, we may conclude that cultivation would be placed within the low (i.e., residual from previous land-use history only) range of manuring rates (60, 63). Moreover, unlike the Near East (21) and different early agricultural sites in Europe (68, 70), the $\delta^{15}N$ values do not support higher manuring for wheat than barley.

Rotation or intercropping of cereals with pulses or forage legumes might represent an alternative explanation for the moderate $\delta^{15}N$ values of charred seeds (60, 71). In the absence of N fertilization, pulses exhibit near zero $\delta^{15}N$ values because they fix atmospheric N_2 as a source of nitrogen (72). Thus, evidence from eastern Europe (mainland Greece) dating from the 6th millennium BC already point to the use of selective farming strategies including rotation with nitrogen-fixing pulses to maximize the yield of free-threshing wheat, likely grown exclusively for human consumption (73). However, $\delta^{15}N$ values (<2 ‰) of wheat grains in these Greek sites are clearly lower than at La Draga and the other western European sites examined, where in addition no clear differences in $\delta^{15}N$ between wheat and barley were evidenced. In fact, almost no pulses have been recovered from La Draga (26), which discards intercropping or rotation with these crop species as a cause for their low $\delta^{15}N$ values. Moreover, even when the presence of wild legumes such as *Vicia villosa*, *Vicia sepium*, and *Lathyrus aphaca* as weed plants has been reported, their relative importance seems minimal (26).

Therefore, while the use of selective crop farming strategies, such as manuring and rotation with legumes, depending on the local environmental settings, has already been suggested for European agriculture before it reached the western edge of the continent (73), our study does not support the implementation of these practices at the time of agriculture's adoption in the western Mediterranean. In fact, and since growing conditions were globally adequate in the western Mediterranean, there was little need to develop selective farming strategies at the time that agriculture was established. Nevertheless, the meta-analysis shows higher $\delta^{15}N$ values in the more recent Neolithic sites, suggesting that manuring increased with time after agriculture emerged (74). On the other hand, we demonstrated some regional differences in crop water status, with more humid conditions (higher grain $\Delta^{13}C$) in the north and central areas/regions compared with the southern Mediterranean shores of the Iberian Peninsula. However, overall water conditions were favorable, in line with regional differences reported for example in barley cultivation between coastal and inner areas of the Near East (57). Moreover, the nitrogen content of the grains at La Draga and other western Mediterranean sites is comparable to that of present-day crops, confirming that nitrogen fertility did not represent a limitation to the early stages of agriculture when it was established in pristine soils (21, 37, 41). Values of grain nitrogen content comparable to present-day crops have also been reported for barley and wheat at the advent of agriculture in other European regions (74). The development of management practices at later stages during the Neolithic (73, 74) may be the result of adaptative strategies that aimed to palliate loss of fertility due to continued cultivation. In fact, lack of sustainability of agricultural systems has been already suggested for early Euromediterranean sites (34). Nevertheless, most evidence of resource limitation due to land degradation has been linked to population growth that was clearly after the Neolithic (21, 75). Interestingly, although $\Delta^{13}C$ and even $\delta^{15}N$ exhibited no clear changes, the decrease in grain weight and nitrogen concentration values for wheat at La Draga in the most recent samples, compared to the previous ones, suggests that nitrogen fertility conditions had already begun to decline.

Increases in grain size are a feature associated with domestication (76), which in the case of einkorn (77, 78) and barley (21) took as much as a few millennia to reach fully domesticated values. Original grain weight can be inferred from the length, width, and thickness of archaeological grains (23, 24). In fact, reported grain weights estimated for naked wheat and barley from Near East sites, encompassing several millennia following the emergence of agriculture, did not surpass 30 mg (21), far below the typical grain weight of present-day landraces from the region (30, 79). However, the grain weight values of wheat from La Draga are comparable to those of present-day rainfed cultivation, not only under organic farming (Fig. 3) but also for conventional agriculture (61). These values are just slightly lower than in durum wheat landraces cultivated under optimal conditions, with values around 45 mg (30, 79). Barley grain weights from La Draga are also comparable to present-day values, but both are more variable than wheat. From the beginning of agriculture to the present, barley has been grown under less fertile conditions than wheat in the Mediterranean basin (34). In fact, while grain weight may be affected by water conditions, a positive relationship between $\Delta^{13}C$ and grain weight has been reported in barley from La Draga. In other Neolithic sites from the region (e.g., Montefrio, Andalusia), lower grain weights alongside a consistently lower $\Delta^{13}C$ (around 1 ‰) than in La Draga have been reported for both wheat and barley crops, with values placed between 15 and 30 mg (34). In the case of Near East sites that were contemporary with and later than La Draga, lower $\Delta^{13}C$ (between 16 to 17 ‰) and grain weight values (again between 15 and 30 mg) have been reported (21, 37). Given the nonlinear response of grain $\Delta^{13}C$ to water input (29, 32) an increase in $\Delta^{13}C$ of between 17 and 18 ‰ (about 1 ‰) under Mediterranean evapotranspirative conditions may represent a concomitant increase in water inputs during grain filling from 120 to 200 mm, and between 16 and 18 ‰ (about 2 ‰) to near triple the water input during grain filling. Therefore, the good environmental water conditions experienced at La Draga, probably also favored by its lacustrine nature, may have allowed full expression of the genetic potential of crops (particularly of wheat) in terms of grain weight. However, in Neolithic sites from the Fertile Crescent (more than two millennia older than La Draga), with good water status (in terms of precipitation versus evapotranspiration) inferred from grain $\Delta^{13}C$ (43), grain sizes are clearly smaller (30) than those of La Draga. In the same sense, the grain weights of barley and wheat for Neolithic agriculture in Scandinavia are also smaller than those of La Draga, whereas the $\Delta^{13}C$ was similar or higher (74). Therefore, it was not only good water status but probably also the genetic characteristics of the wheat that reached the western Mediterranean that allowed for grain weights comparable to modern cereals. Agronomic selection may have reinforced natural selection leading to a relatively narrow range of seed sizes in species like wheat, whereas cultivated types retained high plasticity for seed number (80). For example, deeper tillage, as could be supported by cattle osteological evidence (81), may create a selective advantage for larger seeded genotypes (82), but to date no direct evidence for the use of the plow has been found at La Draga. Further, the provenance of the seeds recovered may bias grain weight estimations; e.g., from silos or other storage structures as in La Draga or just gathered in disparate fashion from dwelling places where seed fragments and discarded seeds may be more abundant. On the other hand, the preservation of grains at La Draga is superior to any other site on the Iberian Peninsula, thanks to the prevailing waterlogging conditions, and hence measurements at other sites may be underestimated. In any case, our results support the fact that by the time agriculture appeared in the western Mediterranean, cereal crops had already achieved present-day grain sizes.

The spike fragments of durum wheat (26) recovered from La Draga (Fig. 1*D*) also suggest spike morphology (83) and kernel number per spike comparable to those of present-day landraces (range = 27 to 37 grains) from the Iberian Peninsula (30) and cultivars bred for organic agriculture. There is clear evidence that naked hexaploid (bread) wheat (*T. aestivum*) was established by the seventh millennium BC in central Anatolia and elsewhere in the Middle East, but not in Greece until the sixth millennium BC (84). In the case of the early agricultural site of La Draga, dating from the end of the sixth millennium BC, the presence of hexaploid wheat, even if marginal at less than 0.5 % of rachis segments (26, 27, 85), is coherent with a rapid dispersion of a fairly consolidated agriculture (at least in terms of growing conditions and genotypes cultivated) to the western Mediterranean.

The higher estimated yields of wheat compared to barley agree with previous reports for the early agricultural sites of the Near East (21) and the Iberian Peninsula (34, 43) and were further confirmed by our meta-analysis. For the Iberian Peninsula, the evidence suggests higher wheat and barley yields in the northeast than the southeast, due to greater water availability in the former (43). However, the estimated yields for ancient cereal agriculture at La Draga are even higher than the means reported for other Neolithic sites on the NE Iberian Peninsula (43), where La Draga is located. With some exceptions (30, 44), yields of both cereals at La Draga are also well above those of Neolithic sites of the Near East (21). The main factor contributing to higher yields at La Draga is its better water status, as inferred from $\Delta^{13}C$ (32). While grain yield values estimated via grain $\Delta^{13}C$ probably represent the upper limit of achievable yields, actual yields were probably lower because of miscellaneous factors such as incidence of weeds, pests, and diseases, and inadequate planting and/or soil fertility in general, which affect plant tillering and therefore the number of spikes m^{-2}. Nevertheless, yield inferences allow estimation of the cultivated land area needed to feed the site's population. Assuming an average requirement of 300 kg of grains per person y^{-1} to fulfill nutritional and sowing needs (21, 30, 37) and a yield of around half the estimated maximum yield the minimum cultivated land required per inhabitant at La Draga would be around 0.25 ha. For a Neolithic settlement like La Draga, with few dwellings, we can assume a population of not more than 50 to 100 inhabitants, which agrees with the estimation of similar early Neolithic settlements in the region (86), but is smaller than sites in the Eastern Mediterranean. Labor availability may have been the limiting factor at la Draga (87), further justifying the deployment of extensive agricultural practices, which is understood as a system of crop cultivation using small amounts of labor and inputs in relation to the area of land being farmed. Therefore, the required cultivated land would have ranged between 15 and 25 ha. However, such an estimation does not consider hunting and gathering activities, which may result in far lower requirements for land cultivation. Whereas the evidence does not support hunting as an important activity at La Draga (26), fruit gathering seems relevant (88) similar to other Neolithic sites (89). In addition, evidence suggests the use of digging sticks as agricultural tools at La Draga (67), which is not a high-throughput planting method and therefore not consistent with large-scale extensive cultivation. Nevertheless, small-garden cultivation may be disregarded as the only way that cereals were grown at La Draga, when considering that the area of the site covered just one tenth of the land required to entirely fill the food needs of the site's population (68). The relatively low $\delta^{15}N$ of the grains, indicating only moderate manuring, also supports the presence of extensive agriculture at La Draga, while rotation or intercropping with pulses can be discarded as a common practice, which is in line with the pioneering nature of agriculture in the western Mediterranean. The $\delta^{15}N$ values of the grains from the other western Neolithic sites reported in our study also suggest the prevalence of similar cultivation practices. This contrasts to some extent with the evidence from Neolithic sites of similar antiquity in the eastern Mediterranean, where either more intensive manuring (63) or rotations with pulses (73) were already practiced. Nevertheless, extensive agriculture, together with improved crop traits and cultivation under good water conditions, supports a fairly consolidated agriculture by the time it reached the western edge of Europe. Despite the fact that regional differences existed, cultivation under favorable water conditions was a prevalent trend when agriculture appeared in the region, as inferred from the high $\Delta^{13}C$ values of most of the sites. Thus, we can conclude that cultivation under good water conditions was a common feature at the regional level, and reject the hypothesis that unfavorable climate conditions triggered cultivation in this area. This might have ensured that good yields were achieved, and allowed the storage of agricultural outputs, as has been well documented in La Draga (85). Aspects such as the progressive loss of soil fertility, with its negative consequences in terms of nutrient and water status, would only appear following continued cultivation, and once agriculture was already well consolidated.

In summary, this study gives insights into the existence of a certain level of proficiency within the agricultural package when agriculture reached western Europe. Despite a limited labor force capacity, cultivation under suitable conditions (particularly under good water conditions, as shown by the high $\Delta^{13}C$ values of grains) contributed to stable (through time and across sites) and quite productive crops. Therefore, the main factor contributing to increasing yield, which was probably already well understood by early farmers, was to secure proper crop management in terms of water and nutrients. Besides a rather favorable climate, the farmers of the time were likely skilled enough to select the most fertile soils available, and more in the context of there being low competition among the farmers for agricultural land due to low demographic pressure. In terms of breeding, it is unlikely that farmers were selecting consciously for higher yields, but it is evident that good agronomic conditions may have assisted a more rapid genetic advance compared to cultivating crops under harsh conditions. Nevertheless, grain size was probably a more tangible trait for selection, given its relevance to quality. This was probably achieved over time by keeping large grains for planting. In the case of La Draga, because cultivation took place under good environmental and management conditions, this allowed full expression of genetic traits like grain weight, achieving values comparable to present day crops.

Materials and Methods

The Site. The lacustrine settlement of La Draga (90) is located on the eastern side of the Lake of Banyoles, Spain (42°07′36″N 2°45′31″E) 172 masl, 50 km south of the Pyrenees and 35 km from the current shoreline of the Mediterranean Sea (Fig. 1). The area currently has a climate that is defined as humid Mediterranean or sub-Mediterranean, with warm, dry summers and mild winters, and a mean annual rainfall of 850 to 800 mm and temperature of 15 to 14 °C (https://www.meteobanyoles.com/). The region currently belongs to the evergreen oak formation (*Quercetum illicis galloprovincialis pistacietosum*). Around the lake there are still vestiges of riparian forest (Alno-Padion), where mixed forests of *Quercus ilex* and *Quercus pubescens* are also preserved as well as typical wetland vegetation (91). The maximum area of the site is thought to be less than 3 ha (90). A precise estimate of population size is not possible because no necropolis or even single burials have been found to date. However, from the size of the site and the information already available from other Neolithic sites in Catalonia, it can be inferred that it was populated by a group composed of several dozens of people. Different sectors can be distinguished according to the position of their archaeological levels with respect to groundwater (Fig. 1*B* and *SI Appendix*, *La Draga Description*).

Archaeobotanical Material. Agronomic conditions and genetic characteristics of ancient cereal crops, mainly of wheat and barley, were inferred from different traits of charred grains. A total of 318 grains of naked wheat (*T. aestivum/durum*), 27 grains of barley (*H. vulgare* subsp. *distichum*) and 22 charcoal remains of deciduous *Quercus* sp. were analyzed. Cereal kernels and wood remains were found in a carbonized state (as charred kernels and charcoal) and most of them were clustered in a disparate manner from domestic fires, cooking ovens, and cellar floors, whereas others were found stored in silos. Each grain was analyzed individually for its stable carbon and nitrogen isotope signature, nitrogen content, and size. The chronology of archaeobotanical samples was based on stratigraphic dating and radiocarbon ages (48). Calibrated ages were determined using the computer program CALIBTH3 (92). Further analysis was undertaken of 22 of charcoal fragments of *Quercus* sp. from different archaeological levels corresponding to structures associated with the two phases documented at La Draga (*SI Appendix*, Table S1). From Phase I, 11 fragments from Level VII, located in Sector B, were analyzed, while the other 11 fragments corresponded to charcoal remains from two different structures located in Sector A that corresponded to Phase II. The average size of the charcoal fragments was 12 mm × 7 mm × 9 mm, with an average number of rings per fragment of 10.6 ± 5.5 (SD).

Modern Grains. Grain samples from rainfed organic modern spring wheat (*T. aestivum*, c.v. Valbona) and barley (*H. vulgare*, c.v. Shuffle) crops cultivated near the site were collected during the 2016 to 2017 and 2017 to 2018 crop seasons, and grain yields recorded. Wheat was fertilized with pig, chicken, and chopped straw slurry, and barley with cow manure. Both crops were rotated with grain legumes. In addition, data on grain yield, grain weight, and protein content from organic winter and spring bread wheat cultivated during the previous four seasons (2018 to 2019 to 2021 to 2022) at different locations on the Iberian Peninsula (Spain) with agroclimatic conditions comparable to Lake Banyoles, were also used for comparison. The above data were obtained from annual reports (https://genvce.org/productos-genvce/informes/) published by GENVCE (Grupo para la Evaluación de Nuevas Variedades de Cultivos en España).

Stable Carbon and Nitrogen Isotope Analyses. Carbonate crusts in fossil grains and charcoal were removed following the procedure of DeNiro and Hastorf (93) with further adjustments (34, 35, 45). Thus, each grain and charcoal fragment was soaked separately in 1 mol HCl for 24 h at room temperature and then the kernel was rinsed repeatedly with distilled water. All samples (modern and archaeological) were oven dried at 60 °C for 48 h before milling to a fine powder for isotope analyses. Given that the wood remains were found carbonized (as charcoal fragments), extracting cellulose was not feasible (41). As a consequence, carbon isotope analyses were performed on the whole charcoal instead. The stable isotope composition of carbon ($\delta^{13}C$, referred to the VPDB standard) and nitrogen ($\delta^{15}N$, referred to N_2 in air) as well as carbon and nitrogen concentrations (%C, %N) were determined by elemental analysis and isotope ratio mass spectrometry (EA/IRMS). Grain samples were analyzed at the Isotope Services of the University of Barcelona (Barcelona, Spain) as described elsewhere (21). The overall analytical precision was about 0.1 ‰ for $\delta^{13}C$, 0.2 ‰ for $\delta^{15}N$, 0.6 % for %C and 0.1 % for %N. For the grains, different international secondary standards of known $^{13}C/^{12}C$ ratios (IAEA CH7, IAEA CH6, IAEA 600, and USGS 40) calibrated against Vienna Pee Dee Belemnite carbonate, and $^{15}N/^{14}N$ ratios (IAEA-N-1, IAEA-N-2 ammonium sulfate, IAEA-NO3, and USGS 40) referring to N_2 in air, were used. The $\delta^{13}C$ of charcoal samples was analyzed by EA/IRMS at the Stable Isotope Analysis Laboratory (Autonomous University of Barcelona, Spain). Reference standard IAEA-600 was measured as a quality control check of samples during analysis. Analytical precision was about 0.04 ‰.

Carbon isotope discrimination ($\Delta^{13}C$) of archaeobotanical samples was calculated from sample $\delta^{13}C$ and from the $\delta^{13}C$ of atmospheric CO_2, as follows:

$$\Delta^{13}C\ (‰) = (\delta^{13}C_{air} - \delta^{13}C_{plant}) / [1 + (\delta^{13}C_{plant} / 1{,}000)], \qquad [\mathbf{1}]$$

where $\delta^{13}C_{air}$ and $\delta^{13}C_{plant}$ denote air and plant $\delta^{13}C$, respectively (16). The $\delta^{13}C_{air}$ was inferred by interpolating a range of data from Antarctic ice-core records together with modern data from two Antarctic stations (Halley Bay and Palmer Station) of the NOAA ESRL Carbon Cycle Cooperative Global Air Sampling Network (https://gml.noaa.gov/aftp/data/trace_gases/co2c13/flask/), as described elsewhere (21, 32). The locally weighted least squares (LOESS) fitted curve and the Excel tool used to interpolate $\delta^{13}C_{air}$ data are available at https://data.mendeley.com/datasets/btwpwh8292/.

Charring Effects on $\delta^{13}C$, $\delta^{15}N$, and Nitrogen Concentration. Most of the studies available on cereal grains have reported that $\delta^{13}C$ (30, 32, 34, 94) and $\delta^{15}N$ (33, 34, 95, 96) are not significantly affected by carbonization within the expected range for carbonization and sample preservation (~200 to 400 °C).

In fact, the color, distortion, and internal structure of grains were considered good enough for the purpose of isotope analysis (97). However, nitrogen concentration in grains is affected by carbonization. Fortunately, the nitrogen concentration of charred kernels can be partly corrected based on the carbon concentration value of the sample (34). Thus, considering that %C in extant cereal grains is nearly constant regardless of the species and environmental conditions (28, 32, 94) we fitted a linear regression model relating the original grain %N (%N_{corr}) to the %N and %C values of charred grains as reported by Aguilera et al. (34):

$$\%N_{corr} = \%N - 0.094\ \%C + 3.9810. \quad [2]$$

The validity of the adjustment for carbonization of the grain N concentration is further proved by the positive relationship between the N and the C concentration of fossil grains and the fact that modern grain values fit within the relationship (*SI Appendix*, Fig. S11).

Concerning charcoal, despite reports of consistent changes in $\delta^{13}C$ for ground wood in response to different carbonization treatments (98), our team's previous results from experimental charring of wood blocks of angiosperm trees and shrubs (including the genus *Quercus*) have shown negligible shifts in $\delta^{13}C$ (45, 94, 99). Nevertheless, the clearly lower total carbon concentration from Phase II compared with Phase I suggests a higher charring temperature at Phase I, with the consequent effect of decreasing $\delta^{13}C$. The correction introduced for samples with total carbon values above 65%, resulted in an increase in $\delta^{13}C$, and a consequent decrease in $\Delta^{13}C$ of samples from Phase I. This may have consequences for the interpretation of results, increasing the $\Delta^{13}C$ of Phase I to values comparable to those published before (Dataset S1). However, the low carbon content at Phase II could be an effect of the oxidation of the charcoals. Thus, following Moureaux et al. (100), Fourier transform infrared (FTIR) spectroscopy was performed on the charcoal samples from both phases by attenuated total reflectance FTIR spectroscopy using a Bruker Tensor 27 spectrometer. Measurements were run at the scientific facilities of the Autonomous University of Barcelona. The IR spectra were recorded with a Bruker spectrophotometer model Alpha II with a single-reflection diamond ATR module (Model Platinum ATR). The IR spectra of the samples were recorded without any pretreatment. After being recorded, the same spectral treatment was applied to all the spectra in order to facilitate spectral visualization and interpretation. Tools within the equipment software (OPUS vs. 7.8.44) were used: baseline correction with the elastic tape correction method and spectrum smoothing with 17 points. Spectra are included as a dataset (Dataset S2) in the study. Except for a couple of cases that showed unclear spectra, the results suggested that carbonization in both phases took place above 400°C (100). Indeed, as reported before (45, 100), while the increase in the temperature of carbonization from 300 to 400 °C clearly makes $\delta^{13}C$ more negative, further increases in temperature to 500 °C have a minor effect. These results suggest that differences in $\delta^{13}C$ between both phases due to carbonization were minor.

Estimation of Kernel Weight from Charred Samples. Kernel weight (KW, mg) of wheat and barley can be assessed from the dimensions in mm (length, L; width, W; thickness, T) of charred kernels using the products of L × W and L × T, which are not significantly affected within the range of carbonization conditions allowing for sample preservation and identification (23). We used specific models for wheat and barley according to the following formulae (23):

For wheat:

$$KW = -15.4 + 2.47 \times (L \times W), \quad [3]$$

$$KW = -15.1 + 2.98 \times (L \times T), \quad [4]$$

For barley:

$$KW = 0.21 \times (L \times W)^{1.60}, \quad [5]$$

$$KW = 0.78 \times (L \times T)^{1.28}. \quad [6]$$

KW was then estimated as the mean value of both formulae (L × W and L × T). The range of grain dimensions and carbonization conditions of this model covered the expected range for the archaeological material. It should be noted that these models were calibrated with experimentally charred grains across multiple charring conditions (200, 250, and 300 °C in oxidant and anoxic atmospheres). The robustness of this approach for grain weight estimation was further validated with the use of a different dataset of modern, uncharred material (*SI Appendix*, Fig. S12 and Dataset S3).

Estimation of Water Inputs from the $\Delta^{13}C$ of Cereal Kernels. The $\Delta^{13}C$ of cereal kernels presents a strong positive relationship to water inputs (precipitation or precipitation plus irrigation) during grain filling across a wide range of Mediterranean conditions (29, 32, 94). In fact, other sources of variability in $\Delta^{13}C$ such as the genotypic effect, its interaction with environmental conditions or the intraspike variability are considered as being minor (28–32, 61). We followed the same modeling approach as in earlier studies (24, 32, 34). Thus, past wheat and barley water inputs (mm) were estimated as detailed in *SI Appendix*, *Estimation of Cereal WI*.

Estimation of Grain Yield from $\Delta^{13}C$ and Kernel Size. Grain yield of cereals was estimated using the models previously developed by our team (34, 43, 44). The model accounts for the water status (through the $\Delta^{13}C$ of kernels), together with changes in Harvest Index (the ratio of KW to total aerial biomass) due to the Green Revolution and the effect of lower CO_2 levels than before the Industrial Revolution (about 270 µL L^{-1}). Equations used are detailed in *SI Appendix*, *Estimation of Cereal Yield*.

Assessing the Effect of Manuring on the Grain $\delta^{15}N$ at La Draga. We examined grain $\delta^{15}N$ as a proxy for manuring, since plant $\delta^{15}N$ increases by a variable amount depending on the type and quantity of fertilizer and the duration of its application (66). In that sense the average $\delta^{15}N$ values from bone collagen (4.9 ± 1.1 ‰) of wild herbivores at La Draga (101) were used to estimate the reference $\delta^{15}N$ values for unmanured plants (63). The $\delta^{15}N$ value of wild herbivores was 4.9 ± 1.1 ‰, lower by ~1.2 ‰ than other early agricultural sites from the region. However, the domestic herbivores were significantly ^{15}N enriched by 0.6 ‰ compared to the wild ones at La Draga (101). To estimate the $\delta^{15}N$ values of the plant diet consumed by the wild herbivores, a 3 ‰ decrease in ^{15}N was initially applied between bone collagen and diet (102, 103). This implied that the $\delta^{15}N$ values of plants eaten by wild herbivorous were slightly below 2 ‰. In the case of cereals crops, since the $\delta^{15}N$ of grains in cereals may be slightly enriched compared with the leaves (104) or the straw (59), and particularly under high fertilization conditions, 1 ‰ was subtracted, which places the $\delta^{15}N$ values of the herbaceous crops and the straw around 3 ‰. The dataset for each of the archaeological grains from La Draga and the modern cereal grains is included (Dataset S4).

Assessing Conditions of Early Agriculture in Mediterranean Western Europe. Data on $\Delta^{13}C$, $\delta^{15}N$, weight, and nitrogen content of fossil grains from naked wheat and barley from a set of 17 Neolithic sites, mostly located on the Mediterranean shores of the Iberian Peninsula, were derived from published and new data, using the same analytical methods as for La Draga. New and published data as well as the extended Montefrio (34) data with corrected radiocarbon chronologies are included as a dataset (Dataset S5). The sites considered and the sources of the information are as follows: Cova Santa Maira (45), Cova Cova de l'Or [(45) and Dataset S5], Cueva del Toro (28), Montefrío (34), Montou and Plansallosa (46), Auvelles, Les Bagnoles and Pou Nou (47), Can Sadurní [(47) and Dataset S5], and Los Cascajos, La Draga, Hostal Guadalupe, Cueva de Los Mármoles, Los Murciélagos, Roca Chica, and Sâo Pedro de Canaferrím (all from Dataset S5). Values of $\Delta^{13}C$, $\delta^{15}N$, grain weight, and nitrogen content in these studies were assessed using the same approaches described above. Besides La Draga, the set included 14 sites located on the Mediterranean shores of the Iberian Peninsula, another in southern France (Les Bagnoles), one near the Atlantic coast of central Portugal (Sâo Pedro de Canaferrím) and the last one in northern Spain (Los Cascajos).

Data, Materials, and Software Availability. All study data are included in the article and/or supporting information.

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