AGU ADVANCING EARTH AND SPACE SCIENCE

Geophysical Research Letters

RESEARCH LETTER
10.1029/2020GL089566

Relationship Between C_4 Biomass and C_4 Agriculture During the Holocene and its Implications for Millet Domestication in Northeast China

Jian Wang[1,2,3], Xinying Zhou[1,2,3], Hai Xu[4], Junchi Liu[1,2,3], Qingjiang Yang[1,2,3], Chao Zhao[1,2], Qiang Gao[1], Keliang Zhao[1,2,3], Hermann Behling[5], and Xiaoqiang Li[1,2,3]

[1]State Key Laboratory of Vertebrate Evolution and Human Origin, Institute of Vertebrate Paleontology and Paleoanthropology, Chinese Academy of Sciences, Beijing, China, [2]CAS Center for Excellence in Life and Paleoenvironment, Beijing, China, [3]University of Chinese Academy of Sciences, Beijing, China, [4]Institute of Surface-Earth System Science, Tianjin University, Tianjin, China, [5]Department of Palynology and Climate Dynamics, University of Göettingen, Untere Karspüle 2, Göttingen, Germany

Key Points:

- Higher estimated C_4 biomass in the cultural layers of the Chahai site was related to human activity, mainly agricultural practices
- Change in regional C_4 biomass was nearly synchronous with the origin and development of millet agriculture in the early-middle Holocene
- Origin of millet agriculture in the early Holocene was driven both by human behavior and a favorable ecological environment

Supporting Information:

- Supporting Information S1
- Table S1
- Table S2
- Table S3

Correspondence to:

X. Zhou and X. Li
zhouxinying@ivpp.ac.cn;
lixiaoqiang@ivpp.ac.cn

Citation:

Wang, J., Zhou, X., Xu, H., Liu, J., Yang, Q., Zhao, C., et al. (2021). Relationship between C_4 biomass and C_4 agriculture during the Holocene and its implications for millet domestication in Northeast China. *Geophysical Research Letters*, *48*, e2020GL089566. https://doi.org/10.1029/2020GL089566

Received 6 JUL 2020
Accepted 30 NOV 2020

Abstract The origin of C_4 agriculture in China, foxtail millet (*Setaria italica*) and common millet (*Panicum miliaceum*), remains unclear. Here we conducted a comprehensive geochemical study of the archeological site of Chahai in Northeastern (NE) China and deduced that higher C_4 biomass in the cultural layers was mainly caused by agricultural practices and other human activities. To evaluate the anthropogenic factors involved in millet domestication, we produced a time series of contour maps of C_4 biomass for North China since 14 ka and integrated archaeological data. Results show that the origin and development of millet agriculture was nearly synchronous with the increase in C_4 biomass in the early-mid Holocene, but the synchrony was decoupled at ~4 ka when millet cultivation was established in NE China. Our findings suggest that both human management (possibly cultivation) of C_4 plants, and an environmental background of high C_4 biomass drove the origin of millet agriculture.

Plain Language Summary The evidence of the earliest domesticated millet comes from North China, however, it is unclear which factors were responsible. We conducted a multiproxy study on the archeological site of Chahai in NE China. The results show that higher estimated C_4 biomass in the cultural layers was related to human factors, mainly agricultural practices, in the step-by-step process of millet domestication. To further evaluate these factors, we used published data to determine the relationship between the regional C_4 biomass of the natural background and the history of millet agriculture. Research reveals a near-synchronous relationship between the origin and developmental stage of millet in the early-mid Holocene, but that these two processes became decoupled during the establishment of millet agriculture in the late Holocene. We conclude that human activities involving C_4 crops together with the favorable ecological background led to the origin of millet agriculture.

1. Introduction

The origin and propagation of agriculture not only promoted human socioeconomic development but also fundamentally changed the role of humans in Earth's ecosystems (Boivin et al., 2016; Fuller et al., 2014; Gremillion et al., 2014; Larson et al., 2014; Ruddiman et al., 2016). Two main domesticated C_4 crops, foxtail millet and common millet, were the staple foods in the semiarid regions of East Asia (Miller et al., 2016). Although the role of North China as the center of origin of millet agriculture has received widespread research attention (Barton et al., 2009; Cohen, 2011; Crawford, 2008; Lu et al., 2009; Yang et al., 2012), the factors driving the origin of millet cultivation are still debated (Cohen, 2011; Gignoux et al., 2011; Yang et al., 2018; Z. Zhao, 2011). Three types of hypotheses are commonly used to explain the rise of agriculture. One suggestion is that the principal driver was the stress induced by climatic instability (Bar-Yosef, 2011); a second is that it was related to socioeconomic competition (Hayden, 2009); and a third is that it was a co-evolutionary process with the environment (Bettinger et al., 2015). The key to testing these hypotheses is to distinguish between natural or anthropogenic factors during the transition, and to this end it is important to find a suitable region where evidence of early millet cultivation is available and which is sensitive to climate change.

10.1029/2020GL089566

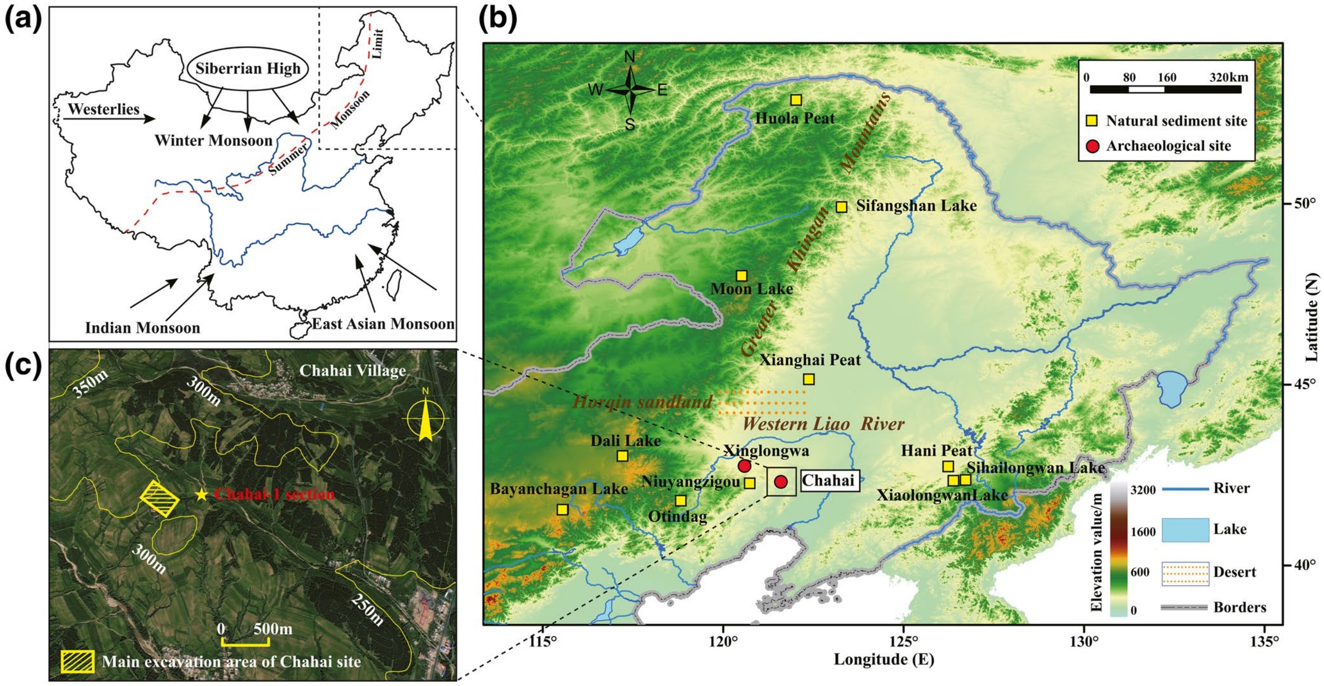


Figure 1. (a) Trajectories of the major atmospheric circulation systems of North China (after Xiao et al., 2004). (b) Topography and drainage of the study region and locations of the sampling site, and other sites mentioned in this study. (c) Location of the Chahai site and the Chahai-1 section.

The West Liao River Basin in NE China is highly suited for an investigation of the origin and development of millet agriculture (Shelach, 2000). Analysis of the charred macrobotanical remains from the Xinglongwa site shows that morphology-based millets were an important food source for the local population during 8.0–7.5 ky BP (kilo years Before Present) (Y. G. Sun, 2015; Z. Zhao, 2011). Other archaeological studies of the early agriculture in the area have been conducted by predecessors (Jia et al., 2016; Liu et al., 2012, 2016; Shelach et al., 2019). However, previous research focused mainly on the origin and propagation of millet agriculture in time and space using the analysis of plant remains at archaeological sites, paying less attention to the factors driving the origin of millet agriculture based on analysis of buried cultural layers. Here, we conducted a study of the multiphase cultural strata of the Chahai archaeological site using Accelerator Mass Spectrometry (AMS) ^{14}C dating and analysis of stable carbon isotopes, pollen, and micro-charcoal of sediments. We compared the δ^{13}C values of the cultural layer with environmental records to determine the possible factors responsible for the domestication of millet. We also collected archeological data and carbon isotope data for North China since 14 ka to explore the relationship between the history of C_4 agriculture and the regional C_4 biomass for a better understanding of the origin of millet domestication.

2. Materials and Methods

The West Liao River Basin is located at the southeastern margin of the Eurasian steppe (Figures 1a and 1b). Most of the region experiences a semi-arid temperate monsoon climate, characterized by hot and humid summer with rainfall representing ~80% of the annual total. The mean annual precipitation and temperature are 300–600 mm and 5.0°C–6.5°C, respectively (Source: http://data.cma.gov.cn/). Due to its distinctive geographical location and natural conditions, the region has been a major corridor of human migration and cultural exchange since the late Paleolithic (Table S1). The Chahai site (42°11′2″N, 121°48′2″E, 274 m a.s.l), located ~2.5 km southwest of Chahai village, is one of the most important prehistoric sites in northern China. Abundant stone tools, dragon-patterned pottery and more than 30 houses have been discovered after seven systematic investigations (Liaoning Provincial Institute of Cultural Relics and Archaeology, 2012). The Chahai culture is dated to 8.2–7.0 ka, and multiple lines of evidence indicate the onset of sedentism and social hierarchy at this time (Dian & Yan, 1994). For these reasons, the site is known informally as "the birthplace of Chinese dragon culture" and "the first village in North China." The Chahai site is a typical example of the Xinglongwa culture, and the study area is generally regarded as the earliest millet farming center in North China (8.2–7.0 ka).

The Chahai-1 section is ~500 m from the main excavation area of the Chahai site (Figure 1c). The lithology of the section consists of seven layers of clay and sand, and it can be correlated with the strata at the main site based on radiocarbon dates and typological analysis of unearthed artifacts. Layers 2–5 belong to the cultural deposit, and its characteristics are closely related to human activities. Notably, carbonized seeds of foxtail millet were found at 160–180 cm, which is direct evidence of early millet-based agriculture. We collected 44 samples at 10-cm intervals for stable carbon isotope and pollen analysis and selected seven charcoal samples for AMS ^{14}C dating. The dating results and stratigraphic information are shown in Table S2 and Figures S1–S2. The C_4 biomass is the percentage of C_4 plants estimated for the surrounding area, which was calculated by applying the measured $\delta^{13}C$ values to an established mass-balance equation (Text S3, Table S3) (Wang et al., 2008). The detailed experiment information of stable carbon isotope and pollen analysis are given in Text S4.

3. Results and Discussion

3.1. Chronological Sequence and $\delta^{13}C$ Characteristics of Cultural Layers

The calibrated ^{14}C dates show that the section preserves an environmental record of the past >12.7 ka. Notably, there is a minor age reversal in the middle of the section. Causal factors such as analytical errors and tectonic influences and other natural disturbances can be excluded, and instead, given that several artifacts are present at this level, it is possible that the anomaly is related to human activities; a similar phenomenon exists at the main site (Liaoning Provincial Institute of Cultural Relics and Archaeology, 2012). Based on the chronology, the age ranges of the four cultural layers are 12.7–12.5 ka, 10.2–9.3 ka, 7.2–6.3 ka, and 2.1–1.9 ka, and the intervening strata may be affected by human activities or subsequent erosion (Q. J. Yang et al., 2020). The results of $\delta^{13}C$ and C_4 biomass for the Chaihai-1 section are presented in Figure 2a. Two major points can be made about the results: (1) the average $\delta^{13}C$ values of each cultural layer from 380 to 50 cm is −22.8‰, −22.3‰, −22.0‰, −21.9‰, and −21.4‰. This shows that, except for narrow intervals at the bottom and top of the section, the $\delta^{13}C$ values exhibit a gradually increasing trend. The mean C_4 biomass exhibits a similar trend. (2) The standard deviation of $\delta^{13}C$ values below 200 cm is 0.75 with the range of −22.2‰ to −21.2‰, and above 200 cm the amplitude of variation of the values is lower. No human-related remains were found in the interval of 440–380 cm, and the presence of micro-cross-bedding structures and the transition to the lower sand layer imply that the signals of carbon isotopes were affected by the water flow. Therefore, here we focus on the part of the section above 380 cm where there is no evidence of contamination.

Distinguishing the source of carbon isotopes in the cultural layers is a prerequisite for understanding their implications (Farquhar et al., 1989; Michener & Lajtha, 2008). Since comparison with similar natural records contributes to determining the factors controlling $\delta^{13}C$ values of the cultural layer, here we choose the section at Niuyangzigou, located 50 km west of the Chahai site (Lu et al., 2015). The $\delta^{13}C$ characteristics of the interval of 250–110 cm in the Chahai-1 section, which corresponds to the black loam S_0 soil, were compared with those of the paleosol layers S_0-S_5 in the Niuyangzigou section, which developed during the warm interglacial periods since 350 ka. The results show that the average values of the Chahai-1 section are ~2‰ higher than those of the paleosols (Figure 2b). Compared to the Holocene Climatic Optimum, temperatures during the formation of paleosols S_3 and S_5 were higher and therefore environmental conditions were more conducive to the growth of C_4 vegetation (Lyu et al., 2018). This suggests that differences in climatic factors were not responsible for the higher $\delta^{13}C$ values at the Chahai-1 section, which are 2~4‰ higher than those of the various sedimentary archives from elsewhere in NE China ($\delta^{13}C_{27-31}$ values have been corrected in Text S3). Furthermore, the $\delta^{13}C$ values at Chahai are similar to those on the northern Loess Plateau, at a lower latitude, indicating that the "latitude effect" of isotopic fractionation is insufficient to fully account for this difference. Therefore, we conclude that, in addition to natural factors, human activities have also influenced the carbon isotope composition of the cultural layers of the Chahai-1 section.

10.1029/2020GL089566

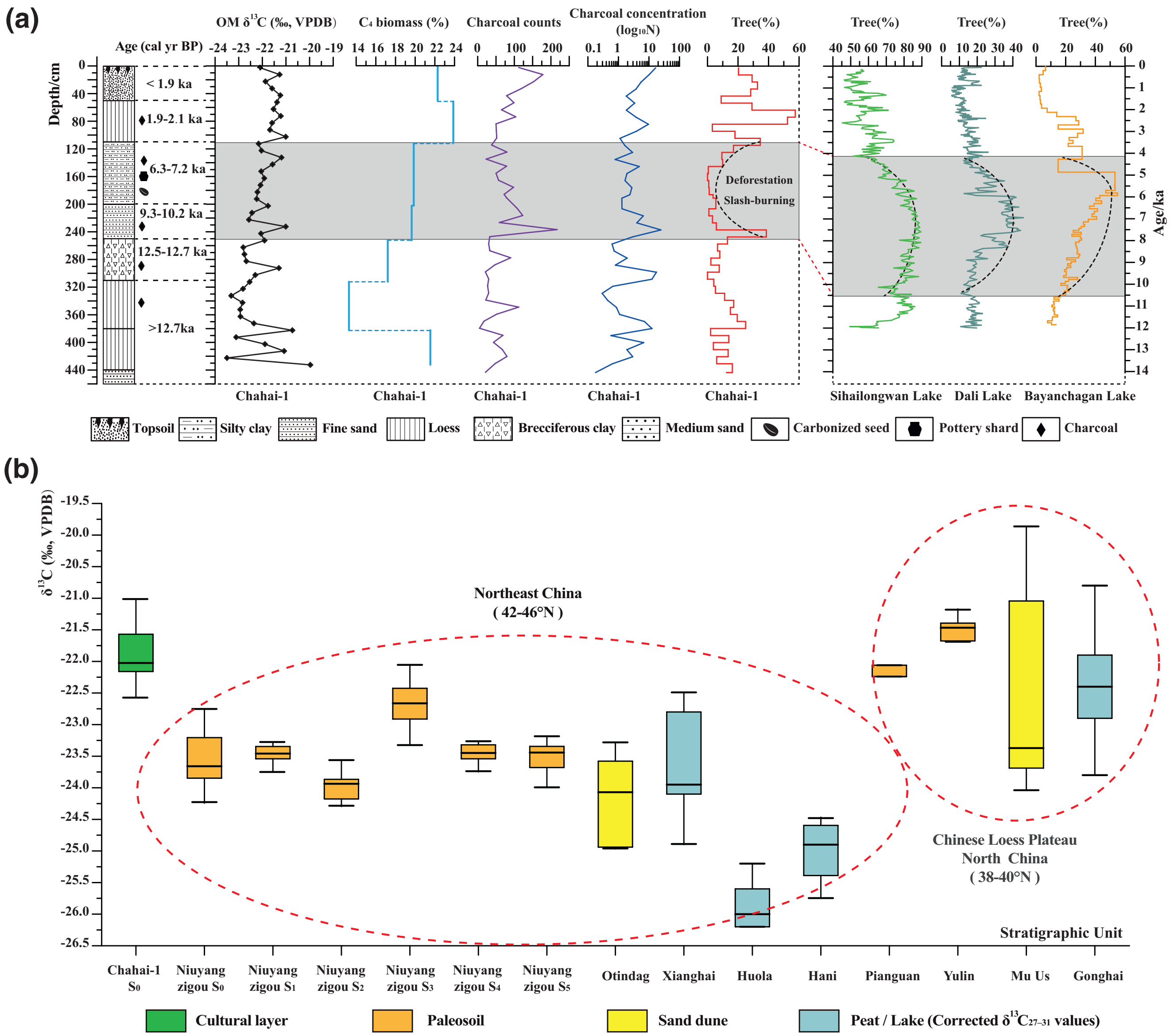


Figure 2. (a) Records of $\delta^{13}C$, C_4 biomass, charcoal concentration, and tree (%) pollen of the Chahai-1 section, and comparison with regional tree (%) pollen from three lake records (Jiang et al., 2006; Stebich et al., 2015; Wen et al., 2017). (b) Comparison of the $\delta^{13}C$ values from the Chahai-1 section with those of other sediments in North China.

The pollen and charcoal records from the Chahai-1 section reveal the influence of agriculture and deforestation during the early-mid Holocene. In contrast to the pollen records from Bayanchagan Lake, Dali Lake, and Sihailongwan Lake (Jiang et al., 2006; Stebich et al., 2015; Wen et al., 2017), calculations of the percentage tree cover in our section decreased by almost 35% during 7.2–6.3 ka, corresponding to the Holocene Optimum (Figure 2a). This suggests the occurrence of substantial deforestation within the study area. Although the concentration of micro-charcoal in the Chahai-1 section was not very high, field observations revealed the presence of abundant fine burnt material in 250–110 cm, implying the occurrence of slash-and-burn during this period. Moreover, the presence of carbonized domesticated millet seeds suggests that the deforestation, and associated swidden agriculture activities, were related to the expansion of C_4 cultivation, which is demonstrated by experimental studies showing that the C_4 biomass below 30-cm depth increased by 4.5%–5.0% on average per year by planting maize (Tu et al., 2018). Meanwhile, a high proportion of C_4 plants starch (millet and *Setaria* >90%) extracted from millstones at Chahai indicates the centralized utilization and likely cultivation of C_4 crops (Wu, 2015). The cumulative effect of this process would be expected to account for the ≥ 2‰ δ^{13}C difference in the cultural layer. The foregoing evidence suggests that land clearance, tillage, and cultivation, these critical steps in the crop domestication according to the foraging-to-agriculture continuum model (Fuller, 2007), occurred at Chahai in the early Neolithic.

3.2. Variation of C_4 Biomass in the Chahai-1 Section and Their Implications for C_4 Agriculture

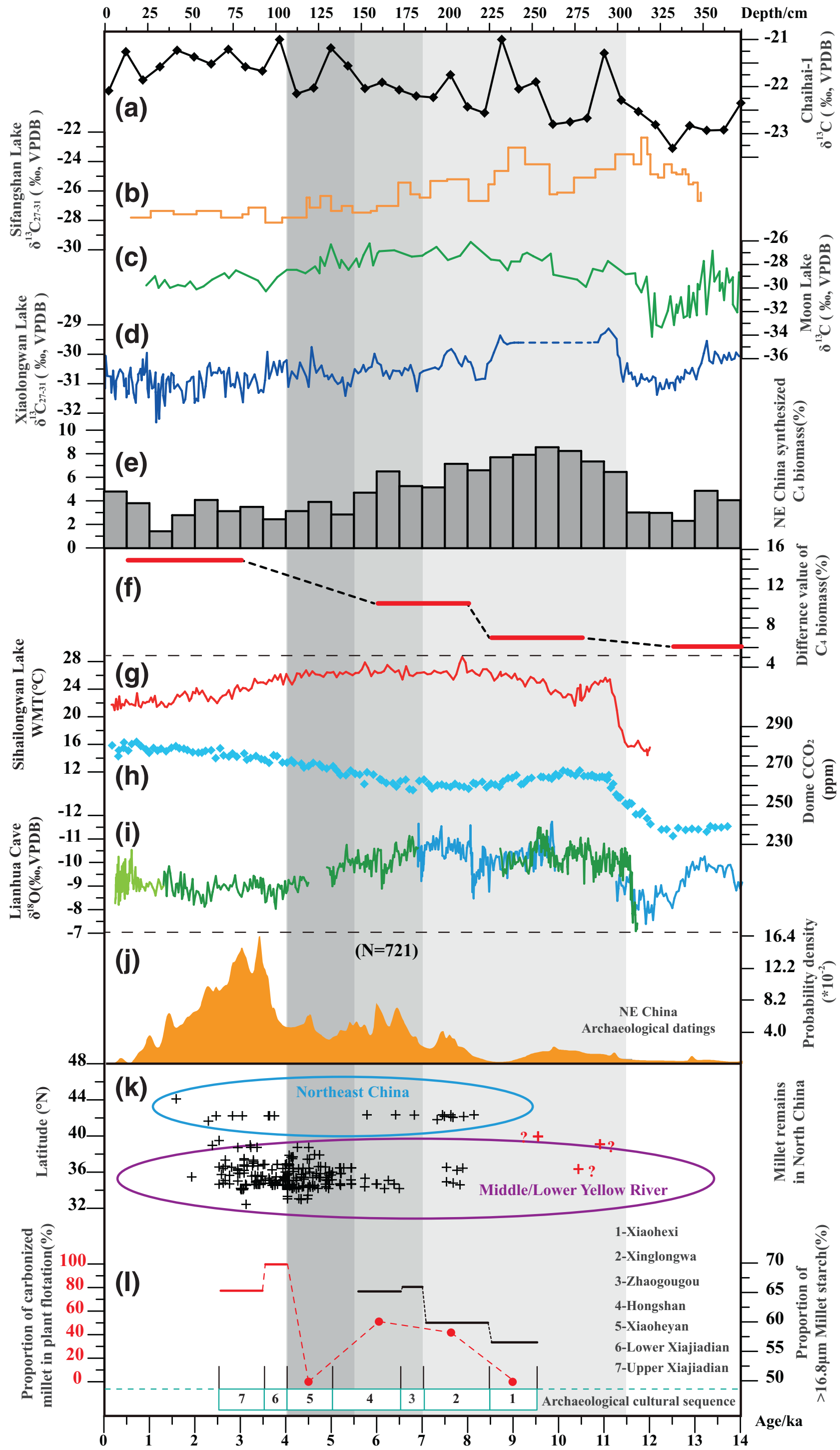
To interpret the δ^{13}C of the Chahai-1 section, we collated all of the published stable carbon isotopes records that involve soil organic matter and long-chain n-alkanes from nearby sites (Table S6). The latter was used to calculate the C_4 biomass of terrestrial vegetation using an empirically-based formula (Meyers & Lallier-Vergès, 1999) (Text S3). The time-slice maps with a 500-year resolution illustrate changes in the C_4 biomass of NE China since 14 ka. Three lake records with a higher resolution were selected to minimize bias caused by sediment types. Sifangshan Lake, Moon Lake and, Xiaolongwan Lake are Maar lakes, and the stable carbon isotopes measurements reflect a natural environment without human influences (Chu et al., 2014; Liu et al., 2010, 2017). The results show that the δ^{13}C values recorded in three Maar lakes increased by 4–6‰ from 13 ka to 11 ka (Figures 3a–3e). The near-simultaneous increasing trends in carbon isotope from multiple records indicate that the terrestrial C_4 vegetation in NE China expanded at the beginning of Holocene, with the average C_4 biomass increasing by ~5%. In the early Holocene, all of the carbon isotope records generally show high values or they continued to increase. Chahai-1 section shows a similar increasing trend. However, the δ^{13}C values of the lake sites gradually decrease and the average C_4 biomass was reduced by nearly 3% in the late mid-Holocene, while the values in the Chahai-1 section continue to increase.

Multiple records have confirmed that temperature was the principal factor controlling changes in the stable carbon isotope composition of vegetation in NE China and the expansion of C_4 vegetation, and its positive effect exceeds the negative bias of precipitation and atmospheric CO_2 content (Lu et al., 2015; Lyu et al., 2018) (Figures 3g–3i). However, temperature control cannot explain the continuous increase in the δ^{13}C value after 7.0 ka at Chahai. Therefore, we conclude that anthropogenic factors, mainly agricultural practices, began to exert an increasing influence on the δ^{13}C values of the cultural layers at Chahai (Figure 3f). Moreover, farmers typically plow and loosen the upper ~30 cm of the topsoil to increase the crop yield, resulting in the mixing and homogenization of the tillage layer (Alcántara et al., 2016). Given the emergence of agricultural implements such as stone plow and stone hoe in the study area at 6.5–6.0 ka (J. X. Liu & Dong, 1996), the decreasing variance of δ^{13}C values over time (the standard deviations for the lower, middle and upper parts of cultural deposits are 0.36, 0.12, and 0.07) may indicate an increasing intensity of the cultivation practices associate with C_4 crops in the transition from foraging to farming.

To test the above viewpoint, we further collated the published archaeological data in the study area (Figures 3j–3l). These data consist of the following: (i) the probability distribution of archaeological dates in NE China since 14 ka, which is considered a reasonable proxy for prehistoric demographic fluctuations (Wang et al., 2014) (Figure 3j). (ii) Latitudinal changes in the occurrence of millet remains in northern China (Leipe et al., 2019; Li et al., 2020) (Figure 3k). (iii) The proportion of millet remains in the flotation results and millet starch grains extracted from the grinding tools at Neolithic sites located within 0–150 km northwest of the Chahai site (Jia et al., 2016; Ma et al., 2016; Y. G. Sun, 2015) (Figure 3l), which can be used to semi-quantitatively evaluate the importance of millet in the prehistoric human economies (Gremillion, 2014). The results indicate an increasing population size with an increasing focus on C_4 crop cultivation that ultimately ended with the domestication of millet, consistent with the stable carbon isotope measurements at Chahai. The average difference value of C_4 biomass between the Chahai-1 section and the integrated natural record may indicate the enhancement of early human management and planting of C_4 crops at the Chahai locale (Figure 3f).

3.3. Relationship Between C_4 Biomass and the History of C_4 Agriculture in North China During the Holocene

To assess the changes in the relative influences of anthropogenic and natural factors in millet domestication from a wider spatio-temporal scale, we established a new database by summarizing the published dates of archaeological sites and millet remains in North China since 14 ka. We divided the history of millet agri-


Depth/cm
Chaihai-1
δ13C (‰, VPDB)
Sifangshan Lake
δ13C27-31 (‰, VPDB)
Moon Lake
δ13C (‰, VPDB)
Xiaolongwan Lake
δ13C27-31 (‰, VPDB)
NE China synthesized
C4 biomass(%)
Differnce value of
C4 biomass(%)
Sihailongwan Lake
WMT(°C)
Dome CCO2
(ppm)
Lianhua Cave
δ18O(‰,VPDB)
(N=721)
NE China
Archaeological datings
Probability density
(*10-2)
Latitude (°N)
Northeast China
Middle/Lower Yellow River
Millet remains
in North China
Proportion of carbonized
millet in plant flotation(%)
Proportion of
>16.8μm Millet starch(%)
1-Xiaohexi
2-Xinglongwa
3-Zhaogougou
4-Hongshan
5-Xiaoheyan
6-Lower Xiajiadian
7-Upper Xiajiadian
Archaeological cultural sequence
Age/ka

10.1029/2020GL089566

culture into the following five stages: exploratory (14.0–11.5 ka), origin (11.5–7.0 ka), development (7.0–5.5 ka), spread (5.5–4.0 ka), and maturity (4.0–0.0 ka), based on the distribution of the probability density (Figure S3). In addition, we collated the published carbon isotope data and produced the first C_4 biomass contour maps for the whole of northern China for the five periods defined above.

Figure 4 shows that the northern boundary of the C_4 ecosystem advanced by ~4° northward in 12.0–10.0 ka. The mean C_4 biomass reached its highest level during 10.0–9.0 ka and maintained a high value with 6%–8% until 7.0 ka. The earliest domesticated millet appeared in NE China during this interval (Zhao, 2014). The 5%–20% contour line of the central and western parts of northern China, including at Chahai, continued to advance northward during 7.0–6.0 ka, although the average C_4 biomass decreased slightly (mainly in the eastern part of NE China). However, the C_4 ecosystem retreated by 2°–3° to lower latitudes during 5.5–4.0 ka. Millet remains almost disappeared in NE China while expanding rapidly in the Yellow River Basin (Hosner et al., 2016), which may be caused by a temperature decrease at the end of Holocene Optimum given that millets are characterized by a high sensitivity to temperature changes (Marcott et al., 2013; Nematpour et al., 2019). The C_4 biomass continued to decrease slightly, but millet reappeared and expanded in NE China after 4.0 ka (Jia et al., 2016).

Our research shows that millet cultivation in NE China originated and developed under the ecological background of increasing C_4 biomass, and its propagation stage likely corresponds to the decrease of C_4 biomass. Therefore, the history of millet agriculture and the change of C_4 biomass have a certain synchronous relationship in the early-mid Holocene although there is a 2.0 ka time difference between the first peak of the two (C_4 biomass in 9.5–10 ka and millet agriculture in 7.5–8.0 ka). However, the re-emergence of millet at the Lower Xiajiadian culture sites in NE China and its absolute dominance in human economies despite a low natural C_4 biomass background marked a decoupling of the synchronization between environments C_4 and anthropogenic C_4 cultivation around 4.0 ka. This may indicate that anthropogenic factors began to surpass natural factors in millet domestication within a certain interval threshold of C_4 biomass.

Research on the relationship between C_4 biomass and C_4 agriculture contributes to the exploration of the driving factors and mechanisms of the origin of millet agriculture. For the arid and semi-arid regions of North China, the increasing C_4 biomass implies an amelioration due to its high coincidence with modern isohyets (S. Yang et al., 2015). Therefore, our results suggest that continuous human behavior (perhaps management or cultivation) of C_4 plants, against the natural environmental background of the increasing C_4 biomass, providing an important setting for the origin of millet agriculture. These two factors drove the origin of millet agriculture in NE China in the following aspects. First, the increasing C_4 biomass resulted in an increase in the number and diversity of potential C_4 crops, including millets and their wild ancestors, which increased the probability of millet being utilized by humans (Z. Zhao, 2005). Second, previous studies have indicated that the expansion of C_4 vegetation played a critical role in dune stabilization of north deserts by reducing soil erosion and enhancing soil organic matter accumulation (Guo et al., 2019), acting to maintain a favorable environment for sedentary prehistoric humans. Third, the expansion of the C_4 biomass is accompanied by a wetter climate and a more productive ecosystem, increasing the availability of potential food resources (L. Liu et al., 2016). This provided more opportunities for humans to attempt to manage various C_4 plants. The final amelioration of the climate was followed immediately by the beginnings of C_4 plant intensive resource use strategies in some areas, which led to the emergence of early C_4 agriculture and the growth of population. Also, an increasing population necessitated an increased food supply, which fur-

Figure 3. Comparison of carbon isotope records, climate indices and archaeological data in NE China since 14 ka. The vertical bars with shadows correspond to the history of millet agriculture (more details see Section 3.3). (a) $\delta^{13}C$ values of the Chahai-1 section (this study). (b) $\delta^{13}C_{27-31}$ values at Sifangshan Lake (Liu et al., 2017). (c) $\delta^{13}C$ values of bulk organic matter at Moon Lake (Liu et al., 2010). (d) $\delta^{13}C_{27-31}$ values at Xiaolongwan Lake (Chu et al., 2014; Sun et al., 2016). (e) Change in C_4 biomass (500-year resolution) for NE China since 14 ka (this study). (f) Average difference in C_4 biomass between the Chahai-1 section and synthesis natural records without human influences (this study). (g) Pollen-based warmest-month temperature record from Sihailongwan Lake (Stebich et al., 2015). (h) Ice core record of CO_2 concentration from Dome C (Monnin, 2001). (i) East Asian Summer Monsoon variations indicated by the $\delta^{18}O$ record of Lianhua cave (Zhang et al., 2013). (j) Probability density of archaeological dates in NE China since 14 ka (data from Dong et al., 2020; Wang et al., 2014). (k) Latitudinal and temporal distribution of the millet sites in North China (data from Leipe et al., 2019; Liu et al., 2008). (l) Proportion of millets in flotation samples (red curve) and millet starch extracted from grinding tools (black curve) from Neolithic sites in the study region (data from Jia et al., 2016, Ma et al., 2016; Y. G. Sun, 2015).

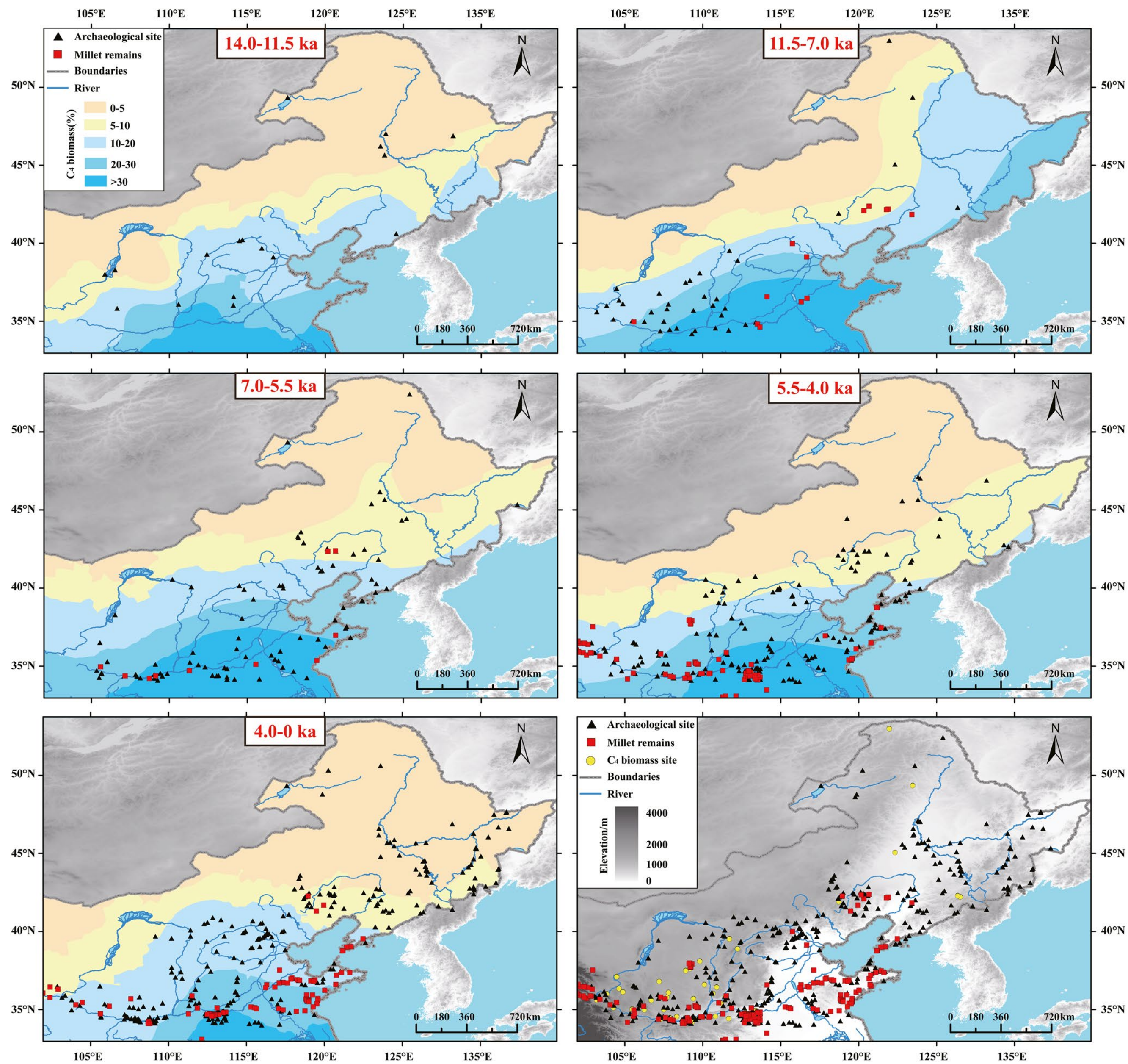


Figure 4. Contour maps of C_4 biomass and the spatiotemporal distribution of archaeological sites with millet remains in northern China since 14.0 ka (data from Dong et al., 2020; Leipe et al., 2019; Liu et al., 2008; Wang et al., 2014).

ther promoted the intensification and spread of millet agriculture (Lele et al., 1989). This positive feedback shows a progressive co-evolutionary model. Furthermore, the ∼2-ky offset between the first peak in the C_4 biomass and millet remains further confirms that the domestication of wild plants was typically a process rather than an event (Flannery, 1973; Rindos, 2013). Overall, it is undeniable that C_4 biomass expansion and human behavior were the prerequisites for the rise to prominence of millet as a cultivar in NE China.

4. Conclusions

We conducted a comprehensive study of the cultural layer of the Chahai site, combined with a comparison with available environmental records, to show that the higher C_4 biomass in the vicinity of the site was caused by practices associated with C_4 plants cultivation and related human activities. To evaluate changes in anthropogenic factors behind the millet domestication, we mapped the spatiotemporal changes of C_4 biomass and integrated archaeological data reflecting the history of millet agriculture in North China since 14 ka. Results show that millet agriculture originated and developed in the context of a higher C_4 biomass, with a near-synchronous relationship; however, the two became decoupled at ~4 ka, when millet cultivation became established but the environmental background of C_4 biomass decreased. Our findings suggest that human activities such as the management or cultivation of C_4 plants, against the background of a high C_4 biomass, were together responsible for the origin of millet agriculture.

Data Availability Statement

The research data have been submitted to the datasets of 4TU Centre for Research Data (http://doi.org/10.4121/uuid:55149db6-76ca-4dff-9923-02440aa5ce84).

Acknowledgments
The authors appreciate Lu Huayu, Xiao Jule, Jiang Wenying, Wen Ruilin, Wang Yong, and Guo Licheng for kindly providing the carbon isotope and pollen data. Special thanks to Jan Bloemendal for English improvement. The authors gratefully acknowledge the Editor Valerie Trouet and three anonymous reviewers for their constructive comments. This work was supported by the Strategic Priority Research Program of Chinese Academy of Sciences (grant numbers XDB26000000), the National Natural Science Foundation of China (grant numbers 41730319, 41888101, and 41772371), and the China Scholarship Council.

References

Alcántara, V., Don, A., Well, R., & Nieder, R. (2016). Deep ploughing increases agricultural soil organic matter stocks. *Global Change Biology*, *22*(8), 2939–2956. https://doi.org/10.1111/gcb.13289

Bar-Yosef, O. (2011). Climatic fluctuations and early farming in west and East Asia. *Current Anthropology*, *52*(S4), S175–S193. https://doi.org/10.1086/659784

Barton, L., Newsome, S. D., Chen, F. H., Wang, H., Guilderson, T. P., & Bettinger, R. L. (2009). Agricultural origins and the isotopic identity of domestication in northern China. Proceedings of the National Academy of Sciences of the United States of America, 106(14), 5523–5528. https://doi.org/10.1073/pnas.0809960106

Bettinger, R. L., Garvey, R., & Tushingham, S. (2015). *Hunter-gatherers: Archaeological and evolutionary theory*. Springer.

Boivin, N. L., Zeder, M. A., Fuller, D. Q., Crowther, A., Larson, G., Erlandson, J. M., et al. (2016). Ecological consequences of human niche construction: Examining long-term anthropogenic shaping of global species distributions. Proceedings of the National Academy of Sciences of the United States of America, 113(23), 6388–6396. https://doi.org/10.1073/pnas.1525200113

Chu, G., Sun, Q., Xie, M., Lin, Y., Shang, W., Zhu, Q., et al. (2014). Holocene cyclic climatic variations and the role of the Pacific Ocean as recorded in varved sediments from northeastern China. *Quaternary Science Reviews*, *102*, 85–95. https://doi.org/10.1016/j.quascirev.2014.08.008

Cohen, D. J. (2011). The beginnings of agriculture in China: A multiregional view. *Current Anthropology*, *52*(S4), S273–S293. https://doi.org/10.1086/659965

Crawford, G. W. (2008). East Asian plant domestication. *Archaeology of Asia*, 77–95. https://doi.org/10.1002/9780470774670

Dian, C., & Yan, X. (1994). Three excavations (1987-1990) in Chahai ruins in Fuxin County, Liaoning. *Cultural Relics*, *11*, 4–19 (in Chinese).

Dong, G., Li, R., Lu, M., Zhang, D., & James, N. (2020). Evolution of human–environmental interactions in China from the late paleolithic to the Bronze age. *Progress in Physical Geography*, *44*(2), 233–250. https://doi.org/10.1177/0309133319876802

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*(1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.0024403

Flannery, K. V. (1973). The origins of agriculture. *Annual Review of Anthropology*, *2*(1), 271–310.

Fuller, D. Q. (2007). Contrasting patterns in crop domestication and domestication rates: Recent archaeobotanical insights from the old world. *Annals of Botany*, *100*(5), 903–924. https://doi.org/10.1093/aob/mcm048

Fuller, D. Q., Denham, T., Arroyo-Kalin, M., Lucas, L., Stevens, C. J., Qin, L., et al. (2014). Convergent evolution and parallelism in plant domestication revealed by an expanding archaeological record. Proceedings of the National Academy of Sciences, 111(17), 6147–6152. https://doi.org/10.1073/pnas.1308937110

Gignoux, C. R., Henn, B. M., & Mountain, J. L. (2011). Rapid, global demographic expansions after the origins of agriculture. Proceedings of the National Academy of Sciences of the United States of America, 108(15), 6044–6049. https://doi.org/10.1073/pnas.0914274108

Gremillion, K. J., Barton, L., & Piperno, D. R. (2014). Particularism and the retreat from theory in the archaeology of agricultural origins. Proceedings of the National Academy of Sciences of the United States of America, 111(17), 6171–6177. https://doi.org/10.1073/pnas.1308938110

Gremillion, K. (2014). Plant Domestication and Cultivation in Archaeology. In C.Smith (Ed.), *Encyclopedia of Global Archaeology*, (5964–5973). New York: Springer. https://doi.org/10.1007/978-1-4419-0465-2_70

Guo, L. C., Xiong, S. F., Dong, X. X., Ding, Z. L., Yang, P., Zhao, H., et al. (2019). Linkage between C_4 vegetation expansion and dune stabilization in the deserts of NE China during the late Quaternary. *Quaternary International*, *503*, 10–23. https://doi.org/10.1016/j.quaint.2018.10.026

Hayden, B. (2009). The proof is in the pudding: Feasting and the origins of domestication. *Current Anthropology*, *50*(5), 597–601. https://doi.org/10.1086/605110

Hosner, D., Wagner, M., Tarasov, P. E., Chen, X., & Leipe, C. (2016). Spatiotemporal distribution patterns of archaeological sites in China during the Neolithic and Bronze Age: An overview. *Holocene*, *26*(10), 1576–1593. https://doi.org/10.1177/0959683616641743

Jiang, W. Y., Guo, Z. T., Sun, X. J., Wu, H. B., Chu, G. Q., Yuan, B. Y., et al. (2006). Reconstruction of climate and vegetation changes of lake Bayanchagan (Inner Mongolia): Holocene variability of the East Asian monsoon. *Quaternary Research*, *65*(3), 411–420.

Jia, X., Sun, Y. G., Wang, L., Sun, W. F., Zhao, Z. J., Lee, H. F., et al. (2016). The transition of human subsistence strategies in relation to climate change during the Bronze Age in the West Liao River Basin, Northeast China. *Holocene*, *26*(5), 781–789. https://doi.org/10.1177/0959683615618262

Larson, G., Piperno, D. R., Allaby, R. G., Purugganan, M. D., Andersson, L., Arroyo-Kalin, M., et al. (2014). Current perspectives and the future of domestication studies. Proceedings of the National Academy of Sciences of the United States of America, 111(17), 6139–6146. https://doi.org/10.1073/pnas.1323964111

Leipe, C., Long, T., Sergusheva, E. A., Wagner, M., & Tarasov, P. E. (2019). Discontinuous spread of millet agriculture in eastern Asia and prehistoric population dynamics. *Science Advances*, *5*(9), eaax6225. https://doi.org/10.1126/sciadv.aax6225

Lele, V., Stone, S. W., Quinn, V. J., French, H. F., Barbier, E. B., Pearce, D. W., et al. (1989). *Population pressure, the environment and agricultural intensification; variations on the Boserup hypothesis*. Washington, DC (EUA): Banco Mundial.

Liaoning Provincial Institute of Cultural Relics and Archaeology. (2012). *The excavation report of Chahai neolithic settlement site*. Beijing: Relic Press (in Chinese).

Li, R., Lv, F., Yang, L., Liu, F., Liu, R., & Dong, G. (2020). Spatial-temporal variation of cropping patterns in relation to climate change in Neolithic China. *Atmosphere*, *11*(7), 1–12. https://doi.org/10.3390/atmos11070677

Liu, J. X., & Dong, X. L. (1996). Initial discussion of agricultural economics of Zhaobaogou culture. *Archaeology*, *2*, 61–65 (in Chinese).

Liu, L., Duncan, N. A., Chen, X., & Ji, P. (2016). Plant-based subsistence strategies and development of complex societies in Neolithic Northeast China: Evidence from grinding stones. *Journal of Archaeological Science: Reports*, *7*, 247–261. https://doi.org/10.1016/j.jasrep.2016.04.014

Liu, C. J., Jin, G. Y., & Kong, Z. C. (2008). *Archaeobotany: Research on seeds and fruits*. Beijing: Science Press (in Chinese).

Liu, X. Y., Jones, M. K., Zhao, Z. J., Liu, G. X., & O'Connell, T. C. (2012). The earliest evidence of millet as a staple crop: New light on neolithic foodways in North China. *American Journal of Physical Anthropology*, *149*(2), 283–290. https://doi.org/10.1002/ajpa.22127

Liu, Q., Li, Q., & Luo, W. (2010). Stable carbon isotope record of bulk organic matter from a sediment core at Moon Lake in the middle part of the Da Xing an Range Northeast China during the last 21ka BP. *Quaternary Sciences*, *30*(6), 1069 (in Chinese).

Liu, J. L., Liu, Q., Wu, J., Chu, G. Q., & Liu, J. Q. (2017). N-alkanes distributions and compound-specific carbon isotope records and their paleoenviromental significance of sediments from Lake Sifangshan in the Great Khingan Mountain, Northeastern China. *Journal of Lake Sciences*, *29*(2), 498–511 (in Chinese).

Lu, H. Y., Zhang, J. P., Liu, K., Wu, N. Q., Li, Y. M., Zhou, K. S., et al. (2009). Earliest domestication of common millet (*Panicum miliaceum*) in East Asia extended to 10,000 years ago. *Proceedings of the National Academy of Sciences*, *106*(18), 7367–7372. https://doi.org/10.1073/pnas.0900158106

Lu, H. Y., Zhang, H. Y., Zeng, L., & Lv, A. Q. (2015). Loess records of pleistocene vegetation in northeast China affected by temperature. *Quaternary Sciences*, *35*(4), 828–836 (in Chinese).

Lyu, A., Lu, H., Zeng, L., Zhang, H., Zhang, E., & Yi, S. (2018). Vegetation variation of loess deposits in the southeastern Inner Mongolia, NE China over the past ~1.08 million years. *Journal of Asian Earth Sciences*, *155*, 174–179. https://doi.org/10.1016/j.jseaes.2017.11.013

Marcott, S. A., Shakun, J. D., Clark, P. U., & Mix, A. C. (2013). A reconstruction of regional and global temperature for the past 11,300 years. *Science*, *339*(6124), 1198–1201. https://doi.org/10.1126/science.1228026

Ma, Z. K., Yang, X. Y., Zhang, C., Sun, Y. G., & Jia, X. (2016). Early millet use in West Liaohe area during early-middle Holocene. *Science China Earth Sciences*, *59*(8), 1554–1561. https://doi.org/10.1007/s11430-015-5257-5

Meyers, P. A., & Lallier-Vergès, E. (1999). Lacustrine sedimentary organic matter records of Late Quaternary paleoclimates. *Journal of Paleolimnology*, *21*(3), 345–372. https://doi.org/10.1023/A:1008073732192

Michener, R., & Lajtha, K. (2008). *Stable isotopes in ecology and environmental science*. John Wiley & Sons.

Miller, N. F., Spengler, R. N., & Frachetti, M. (2016). Millet cultivation across Eurasia: Origins, spread, and the influence of seasonal climate. *Holocene*, *26*(10), 1566–1575. https://doi.org/10.1177/0959683616641742

Monnin, E. (2001). Atmospheric CO_2 concentrations over the last glacial termination. *Science*, *291*(5501), 112–114. https://doi.org/10.1126/science.291.5501.112

Nematpour, A., Eshghizadeh, H. R., & Zahedi, M. (2019). Drought-tolerance mechanisms in foxtail millet (*Setaria italica*) and proso millet (*Panicum miliaceum*) under different nitrogen supply and sowing dates. *Crop and Pasture Science*, *70*(5), 442–452. https://doi.org/10.1071/CP18501

Rindos, D. (2013). *The origins of agriculture: An evolutionary perspective*. Academic Press.

Ruddiman, W. F., Fuller, D. Q., Kutzbach, J. E., Tzedakis, P. C., Kaplan, J. O., Ellis, E. C., et al. (2016). Late Holocene climate: Natural or anthropogenic?. *Reviews of Geophysics*, *54*(1), 93–118.

Shelach, G. (2000). The earliest neolithic cultures of northeast China: Recent discoveries and new perspectives on the beginning of agriculture. *Journal of World Prehistory*, *14*(4), 363–413. https://doi.org/10.1023/A:1011124209079

Shelach, G., Teng, M., Goldsmith, Y., Wachtel, I., Stevens, C. J., Marder, O., et al. (2019). Sedentism and plant cultivation in northeast China emerged during affluent conditions. *PloS One*, *14*(7), e0218751. https://doi.org/10.1371/journal.pone.0218751

Stebich, M., Rehfeld, K., Schlütz, F., Tarasov, P. E., Liu, J., & Mingram, J. (2015). Holocene vegetation and climate dynamics of NE China based on the pollen record from Sihailongwan Maar Lake. *Quaternary Science Reviews*, *124*, 275–289. https://doi.org/10.1016/j.quascirev.2015.07.021

Sun, Y. G. (2015). *Research on plant remains from neolithic to early bronze age in Upper West Liao River region (PhD thesis). Inner Mongolia Normal University* (in Chinese).

Sun, Q., Xie, M., Lin, Y., Shan, Y., Zhu, Q., Xu, D., et al. (2016). An n-alkane and carbon isotope record during the last deglaciation from annually laminated sediment in Lake Xiaolongwan, northeastern China. *Journal of Paleolimnology*, *56*(2–3), 189–203. https://doi.org/10.1007/s10933-016-9904-4

Tu, C. L., Liu, C. Q., Quine, T. A., Jones, M. W., Liu, T. ., Li, L. B., & Liu, W. J. (2018). Dynamics of soil organic carbon following land-use change: Insights from stable C-isotope analysis in black soil of Northeast China. *Acta Geochimica*, *37*(5), 746–757. https://doi.org/10.1007/s11631-018-0282-7

Wang, G., Feng, X., Han, J., Zhou, L., Tan, W., & Su, F. (2008). Paleovegetation reconstruction using δ^{13} C of Soil Organic Matter. *Biogeosciences*, *5*(5), 1325–1337. https://doi.org/10.5194/bg-5-1325-2008

Wang, C., Lu, H., Zhang, J., Gu, Z., & He, K. (2014). Prehistoric demographic fluctuations in China inferred from radiocarbon data and their linkage with climate change over the past 50,000 years. *Quaternary Science Reviews*, *98*, 45–59. https://doi.org/10.1016/j.quascirev.2014.05.015

Wen, R. L., Xiao, J. L., Fan, J. W., Zhang, S. R., & Yamagata, H. (2017). Pollen evidence for a mid-Holocene East Asian summer monsoon maximum in northern China. *Quaternary Science Reviews*, *176*, 29–35. https://doi.org/10.1016/j.quascirev.2017.10.008

Wu, W. W. (2015). Preliminary analysis of subsistence economy at Chahai site in Fuxin, Liaoning Province: Indication of results from analysis of starch granules. *Agricultural Archaeology*, (3), 1–9 (in Chinese).

Xiao, J. L., Xu, Q. H., Nakamura, T., Yang, X. L., Liang, W. D., & Inouchi, Y. (2004). Holocene vegetation variation in the Daihai lake region of North-central China: A direct indication of the Asian monsoon climatic history. *Quaternary Science Reviews*, *23*(14–15), 1669–1679. https://doi.org/10.1016/j.quascirev.2004.01.005

Yang, S., Ding, Z., Li, Y., Wang, X., Jiang, W., & Huang, X. (2015). Warming-induced northwestward migration of the East Asian monsoon rain belt from the Last Glacial Maximum to the mid-Holocene. Proceedings of the National Academy of Sciences of the United States of America, 112(43), 13178–13183. https://doi.org/10.1073/pnas.1504688112

Yang, X. Y., Wan, Z. W., Perry, L., Lu, H. Y., Wang, Q., Zhao, C. H., et al. (2012). Early millet use in northern China. Proceedings of the National Academy of Sciences, 109(10), 3726–3730. https://doi.org/10.1073/pnas.1115430109

Yang, X., Wu, W., Perry, L., Ma, Z., Bar-Yosef, O., Cohen, D. J., et al. (2018). Critical role of climate change in plant selection and millet domestication in North China. *Scientific Reports*, *8*(1), 1–9. https://doi.org/10.1038/s41598-018-26218-6

Yang, Q. J., Zhou, X. Y., Zhao, C., Gao, Q., Liu, J. C., Jia, W. M., et al. (2020). Human occupation, slash-burning and vegetation response from the final Pleistocene to the middle Holocene, Daling River basin, NE China. *Review of Palaeobotany and Palynology*, *275*, 104158. https://doi.org/10.1016/j.revpalbo.2020.104158

Zhang, H. L., Yu, K. F., Zhao, J. X., Feng, Y. X., Lin, Y. S., Zhou, W., & Liu, G. H. (2013). East Asian Summer Monsoon variations in the past 12.5ka: High-resolution $\delta^{18}O$ record from a precisely dated aragonite stalagmite in central China. *Journal of Asian Earth Sciences*, *73*, 162–175. https://doi.org/10.1016/j.jseaes.2013.04.015

Zhao, Z. (2005). Palaeobotanical studies on the origin of agriculture and civilization. *Management and Review of Social Sciences*, *2*, 82–91 (in Chinese).

Zhao, Z. (2011). New Archaeobotanic data for the study of the origins of agriculture in China. *Current Anthropology*, *52*(S4), S295–S306. https://doi.org/10.1086/659308

Zhao, Z. J. (2014). The process of origin of agriculture in China: Archaeological evidence from flotation results. *Quaternary Sciences*, *34*(1), 73–84 (in Chinese).

References From the Supporting Information

Brugnoli, E., & Farquhar, G. D. (2000). Photosynthetic fractionation of carbon isotopes. In *Photosynthesis* (pp. 399–434). Springer.

Clark, R. L., & RL, C. (1982). *Point count estimation of charcoal in pollen preparations and thin sections of sediments*.

Collister, J. W., Rieley, G., Stern, B., Eglinton, G., & Fry, B. (1994). Compound-specific $\delta^{13}C$ analyses of leaf lipids from plants with differing carbon dioxide metabolisms. *Organic Geochemistry*, *21*(6–7), 619–627.

Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon Isotope Discrimination and Photosynthesis. *Annual Review of Plant Physiology and Plant Molecular Biology*, *40*(1), 503–537. https://doi.org/10.1146/annurev.pp.40.060189.002443

Guo, D. S. (2002). *Lower Xiajiadian culture. The Archaeology of Northeast China* (pp. 161–195). Routledge.

Hamlin, J. K., Wynn, K., & Bloom, P. (2007). Social evaluation by preverbal infants. *Nature*, *450*(7169), 557–559.

Jia, X., Sun, Y. G., Wang, L., Sun, W. F., Zhao, Z. J., Lee, H. F., et al. (2016). The transition of human subsistence strategies in relation to climate change during the Bronze Age in the West Liao River Basin, Northeast China. *The Holocene*, *26*(5), 781–789. https://doi.org/10.1177/0959683615618262

Leipe, C., Long, T., Sergusheva, E. A., Wagner, M., & Tarasov, P. E. (2019). Discontinuous spread of millet agriculture in eastern Asia and prehistoric population dynamics. *Science Advances*, *5*(9), eaax6225. https://doi.org/10.1126/sciadv.aax6225

Li, X. Q., & Du, N. Q. (1999). The acid-alkali-free analysis of Quaternary pollen. *Journal of Integrative Plant Biology*, *41*(7) (in Chinese).

Li, X. Q., Shang, X., Zhou, X. Y., & Zhang, H. B. (2006). Integrative method of sieving and heavy liquid in pollen analysis of loess. *Arid Land Geography*, *29*(5), 663–667 (in Chinese).

Liu, C. J., Jin, G. Y., & Kong, Z. C. (2008). *Archaeobotany: Research on seeds and fruits*. Beijing: Science Press (in Chinese).

Moore, P. D., Webb, J. A., & Collison, M. E. (1991). *Pollen analysis*. Blackwell scientific publications.

Nordt, L. C., Boutton, T. W., Jacob, J. S., & Mandel, R. D. (2002). C_4 plant productivity and climate-CO_2 variations in south-central Texas during the late Quaternary. *Quaternary Research*, *58*(2), 182–188.

Rao, Z.G., Chen, F., Cheng, H., Liu, W., Lai, Z., & Bloemendal, J. (2013). High-resolution summer precipitation variations in the western Chinese Loess Plateau during the last glacial. *Scientific Reports*, *3*, 2785.

Rao, Z.G., Jia, G., Zhu, Z., Wu, Y., & Zhang, J. (2008). Comparison of the carbon isotope composition of total organic carbon and long-chain n-alkanes from surface soils in eastern China and their significance. *Chinese Science Bulletin*, *53*(24), 3921–3927. https://doi.org/10.1007/s11434-008-0296-3

Reimer, P. J., Bard, E., Bayliss, A., Beck, J. W., Blackwell, P. G., Ramsey, C. B., et al. (2013). IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0–50,000 Years cal BP. *Radiocarbon*, *55*(4), 1869–1887. https://doi.org/10.2458/azu_js_rc.55.16947

Schmitt, D. N., & Lupo, K. D. (2012). The Bonneville Estates Rockshelter rodent fauna and changes in late Pleistocene–middle Holocene climates and biogeography in the Northern Bonneville Basin, USA. *Quaternary Research*, *78*(1), 95–102.

Sun, Y. G. (2015). *Research on plant remains from Neolithic to early bronze age in Upper West Liao River Region (PhD thesis)*. Inner Mongolia Normal University (in Chinese).

Suo, X. F., & Li, S. B. (2011). Studies on Hongshan culture. *Acta Archaeol Sin*, *3*, 301-326 (in Chinese).

Suo, X. F., & Li, S. B. (2013). On the Types of Xinglongwa Culture. *Archaeology*, (11), 52-61 (in Chinese).

Wang, G., Feng, X., Han, J., Zhou, L., Tan, W., & Su, F. (2008). Paleovegetation reconstruction using $\delta^{13}C$ of Soil Organic Matter. *Biogeosciences*, *5*(5), 1325–1337. https://doi.org/10.5194/bg-5-1325-2008

Zhao, Z. (2011). New Archaeobotanic Data for the Study of the Origins of Agriculture in China. *Current Anthropology*, *52*(S4), S29s5–S306. https://doi.org/10.1086/659308