Vegetation History and Archaeobotany

Buckwheat: a crop from outside the major Chinese domestication centres? A review of the archaeobotanical, palynological and genetic evidence

--Manuscript Draft--

Manuscript Number:	VHAA-D-16-00084R2
Full Title:	Buckwheat: a crop from outside the major Chinese domestication centres? A review of the archaeobotanical, palynological and genetic evidence
Article Type:	Original Article
Corresponding Author:	Harriet Vaughan Hunt McDonald Institute for Archaeological Research Cambridge CB2 3ER , UNITED KINGDOM
Corresponding Author Secondary Information:	
Corresponding Author's Institution:	McDonald Institute for Archaeological Research
Corresponding Author's Secondary Institution:	
First Author:	Harriet Vaughan Hunt
First Author Secondary Information:	
Order of Authors:	Harriet Vaughan Hunt
	Xue Shang
	Martin Kenneth Jones
Order of Authors Secondary Information:	
Funding Information:	European Research Council (GA249642) — Prof Martin Kenneth Jones
	National Natural Science Foundation of China (41471167) — Dr Xue Shang
	National Scholarship Fund of China (201504910101) — Dr Xue Shang
	University of Cambridge Returning Carers' Scheme — Dr. Harriet Vaughan Hunt
Abstract:	The two cultivated species of buckwheat, Fagopyrum esculentum (common buckwheat) and F. tataricum (Tartary buckwheat) are Chinese domesticates whose origins are usually thought to lie in upland southwestern China, outside the major centres of agricultural origins associated with rice and millet. Synthesis of the macro- and microfossil evidence for buckwheat cultivation in China found just 26 records across all time periods, of which the majority are pollen finds. There are few or no identifying criteria distinguishing F. esculentum and F. tataricum for any sample type. The earliest plausibly agricultural Fagopyrum occurs in northern China from the mid-6th millennium cal BP. The archaeobotanical record requires reconciliation with biogeographic and genetic inferences of a southwestern Chinese origin for buckwheat. Scrutiny of the genetic data indicates limitations related to sampling, molecular markers, and analytical approaches. Common buckwheat may have been domesticated at the range margins of its wild progenitor before its cultivation expanded in the north, mediated by changing ranges of wild species during the Holocene and/or by cultural exchange or movement of early agriculturalists between southwest China, the Chengdu Plain, and the southern Loess Plateau. Buckwheat likely became a pan-Eurasian crop by the 3rd millennium cal BP, with the pattern of finds suggesting a route of westward expansion via the southern Himalaya to the Caucasus and Europe.
Response to Reviewers:	See comments to editor (as changes very minor)

Buckwheat: a crop from outside the major Chinese domestication centres? A review of the archaeobotanical, palynological and genetic evidence

Harriet V. Hunt[1*], Xue Shang[2*], Martin K. Jones[3]

[1]McDonald Institute for Archaeological Research, University of Cambridge, Downing Street, Cambridge CB2 3ER, UK
Tel: +44 1223 339330
e-mail: hvh22@cam.ac.uk

[2] Department of Archaeology and Anthropology, University of Chinese Academy of Sciences, 19A, Yuquan Road, Beijing 100049, China
Tel.: +86 10 88256417
e-mail: shangxue@ucas.ac.cn

[3]Division of Archaeology, University of Cambridge, Downing Street, Cambridge CB2 3DZ, UK

*Authors for correspondence

Abstract

The two cultivated species of buckwheat, *Fagopyrum esculentum* (common buckwheat) and *F. tataricum* (Tartary buckwheat) are Chinese domesticates whose origins are usually thought to lie in upland southwestern China, outside the major centres of agricultural origins associated with rice and millet. Synthesis of the macro- and microfossil evidence for buckwheat cultivation in China found just 26 records across all time periods, of which the majority are pollen finds. There are few or no identifying criteria distinguishing *F. esculentum* and *F. tataricum* for any sample type. The earliest plausibly agricultural *Fagopyrum* occurs in northern China from the mid-6th millennium cal BP. The archaeobotanical record requires reconciliation with biogeographic and genetic inferences of a southwestern Chinese origin for buckwheat. Scrutiny of the genetic data indicates limitations related to sampling, molecular markers, and analytical approaches. Common buckwheat may have been domesticated at the range margins of its wild progenitor before its cultivation expanded in the north, mediated by changing ranges of wild species during the Holocene and/or by cultural exchange or movement of early agriculturalists between southwest China, the Chengdu Plain, and the southern Loess Plateau. Buckwheat likely became a pan-Eurasian crop by the 3rd millennium cal BP, with the pattern of finds suggesting a route of westward expansion via the southern Himalaya to the Caucasus and Europe.

Keywords

Buckwheat; *Fagopyrum*; crop domestication; agricultural origins; China; Polygonaceae

Introduction

The transition to agriculture in China occurred independently in at least three recognised centres (Zhao 2011). Dry-land agriculture, with millets as the principal crops, began in the Loess Plateau and Yellow river catchment in north China; rice agriculture developed in the middle and lower Yangtze valley; and a third centre in tropical southern China, along the Zhujiang river south of the Nanling mountains, underwent an early agricultural transition in which roots and tubers, possibly including taro, were the main crops. The growth of Chinese archaeobotany in the last 10-15 years has rapidly advanced understanding of plant domestication in these regions and their interrelationships.

Buckwheat is an intriguing early Chinese crop whose origins appear not to fit the geography of any of these three recognised agricultural centres. In consequence, systematic evaluation of evidence for the origins of buckwheat has been neglected. Buckwheat is a pseudocereal belonging to the family Polygonaceae, with the grain either consumed whole after boiling or steaming, or ground into a (gluten-free) flour. Cultivated buckwheat comprises two species: common buckwheat, *Fagopyrum esculentum* L., and Tartary buckwheat (*F. tataricum* Gaertn.). The two species differ in importance and cultivated range. Common buckwheat is widespread in the temperate zones of the northern hemisphere (Ohnishi 1998b), while Tartary buckwheat is principally a crop of high-altitude zones, such as the circum-Himalaya region (Ohnishi 2000). Ecophysiologically, Tartary buckwheat has some frost tolerance, which is lacking in common buckwheat (Campbell 1997). The two species also differ in breeding system. Tartary buckwheat is self-fertile and largely inbreeding (Tsuji and Ohnishi 2000), while common buckwheat is an insect-pollinated, obligate outbreeder (Cawoy et al. 2009).

The aim of this paper is to elucidate the geographical origins and early chronology of both common and Tartary buckwheat within China, through a synthesis of the archaeobotanical (microfossil and macrofossil) data, in the context of biogeography and genetic evidence. This project is timely for several reasons. First, although it has been concluded from biogeographic and genetic data that both species originated in southwestern China (specifically eastern Tibet, northern Yunnan, and southwestern Sichuan; Konishi et al. 2005; Konishi and Ohnishi 2007; Ohnishi 2009), the congruence of the genetic and palaeobotanical data has never been examined. Second, the publication of palynological and macrofossil data from several new Chinese sites in recent years makes a review of the evidence for *Fagopyrum* appropriate. Third, the spread of agriculture into southwestern China and the Tibetan Himalaya region is a topic of much current interest (d'Alpoim Guedes 2011; d'Alpoim Guedes et al. 2013, 2014, 2015; Chen et al. 2015), to which an improved understanding of buckwheat origins and the differing ecologies of common and Tartary buckwheat is highly relevant. Finally, common buckwheat subsequently became a widespread crop in the Old World northern hemisphere, but the chronology of this globalization is

uncertain (Jones et al. 2011; Boivin et al. 2012). A recent review of the European palynological and macrobotanical data (de Klerk et al. 2015) has highlighted this uncertainty. Here we undertake a comparable review of the data set for China. Understanding the spatial and temporal picture of buckwheat origins in China is an essential step to resolving its global pattern, including the status of buckwheat finds in Europe. These issues in turn relate to the wider topic of east-west crop spread.

Methods

We aimed to collate all published data on archaeobotanical (comprising both macrofossil and microfossil) identifications of buckwheat/*Fagopyrum*/qiaomai/荞麦) within the present boundaries of China. We searched the English- and Chinese-language literature using Google scholar and the China National Infrastructure Database (www.cnki.net) respectively, using various combinations of the search terms '*Fagopyrum*', 'buckwheat', 'vegetation', 'China' on Google scholar and 'qiaomai/荞麦' (buckwheat) and 'yizhi /遗址' (archaeological site) on the China National Infrastructure Database. From each resulting record we extracted site information, the number of finds of *Fagopyrum*, taxonomic identifications, and chronological information or dating results. We would emphasise that this is a meta-data survey; if a record has been published in a suitable medium, then it has been included. We have not gone back to either the original specimens or primary context sheets to further scrutinise those records.

To plot sites on a map, we used longitude and latitude reported in the papers where this information was available, or estimated coordinates from other provided locality details using Google Earth. Maps were drawn using ArcMap v. 10.2, using imagery from NASA Blue Marble: Next Generation satellite imagery, originally produced Reto Stockli and obtained from NASA's Earth Observatory (NASA Goddard Space Flight Center); http://earthobservatory.nasa.gov/Features/BlueMarble/, and Adobe Photoshop CS4.

Results

Twenty-six reports of *Fagopyrum* in the archaeological/palynological record in China were found (Table 1). Ten reports were of macrofossils, fourteen of pollen records, and two of starch granules.

It is important to emphasise the diversity of formation processes leading to the deposition of these different categories of fossils, not all of which are well understood. Probably the most straightforward in depositional terms are the pollen grains from confined lakes and peat accumulations, contexts which have been subject to much study and analysis. Given the limited release of *Fagopyrum* pollen to the wind, one possible interpretation of these records is as the result of crop processing activities in the immediate vicinity, although they may also relate, for example, to the deposition of whole flowers in the water or peat. In the case of unconfined

waterways and active soils, it is more difficult to exclude either lateral or vertical movement of the contained pollen. In better studied crop species, charred macrofossil deposition is most frequently associated with crop processing, and the same is likely to be true of buckwheat, though very much dependent on whether that processing took place near or far from domestic fires. In taphonomic terms, the mechanisms of persistence of starch granules in archaeological deposits are not well understood. In summary, there is a range of depositional processes with a substantial potential impact on the recovered data.

For the pollen records, *Fagopyrum* or Polygonaceae pollen was in some cases (Jingbian, Fuxian and Wenhai Lake) present at a very low level along the entire depth of the core, as early as ~25,000 cal BP (Fig. 1). This great antiquity implies a wild form for it least the earlier part of the sequence, a point which is itself of interest. Taken at face value, this would suggest that a wild *Fagopyrum* species had a more extensive range in the past. This is in turn could have implications for where in China domestication may have taken place (see Discussion). For the purposes of this paper, we sought a plausible correlate for cultivation of *Fagopyrum*, and would propose that an abrupt increase in pollen count might be taken as a secure anthropic signal. We therefore took the date range for *Fagopyrum* pollen to report in Table 1 and Fig. 2 to equate to the time from which it underwent a sharp percentage increase (Fig. 1), in line with the dates suggested by the original reports for evidence of *Fagopyrum* cultivation. Given this criterion, all records fall within the time period 5500-700 cal BP.

Among the pollen cores or sections, ten use AMS 14C or OSL dating results, while three loess-paleosol sections use stratigraphic cross-dating to estimate the date of samples, and the one section from an archaeological site is cross-dated by reference to material cultural groups. These dating methods each have their own inherent constraints of precision and accuracy.

Eleven of the 14 pollen records are identified to genus-level, i.e. as *Fagopyrum*. Identifying criteria and taxonomic resolution of *Fagopyrum* pollen are discussed subsequently. While we comment on these, it was beyond the scope of this meta-survey to re-evaluate individual identifications, which would entail access to the original pollen samples.

The earliest abrupt increases in *Fagopyrum* pollen occur in the period 5500-4000 cal BP in a number of sites in northern China (Fig 1 and Fig 2A). Four of these sites have direct sediment dating records: Wangxianggou (4700 cal BP) in northeast China, Xindian (5500 cal BP) and Xishanping (4500 cal BP) in the northwest, and Chongming (4500 cal BP) at the mouth of the Yangtze. At all these sites, *Fagopyrum* pollen is associated with an abundance of cereal pollen, seeds or charcoal. In the 4th and 3rd millennia cal BP, additional directly-dated records with rises of *Fagopyrum* or Polygonaceae, likely *Fagopyrum*, pollen appear further upstream along the

Yangtze at Cauduntou and in southwest China at Wenhai Lake (Fig. 2B). A second major peak in *Fagopyrum* pollen occurred around 1300-700 cal BP, comprising signals from a number of additional sites in the northeast (Fig. 2C), and a second abrupt increase around 1100 cal BP in the Wangxianggou site. At two of these sites, Jinchuan and Lucheng, pollen is specifically identified as *F. esculentum*, but no criteria or justification are given.

The records above include pollen from confined lakes and peat accumulations (five sites); unconfined waterways (three sites) and active soils and sediments (six sites). Similar trends are observed in each of these groups. As indicated above, the confined lakes and peat accumulations, which are depositionally the most secure, display this pattern, and it is echoed in the depositional contexts that may be open to greater taphonomic complexity.

Contemporaneous with the latest of the first set of *Fagopyrum* pollen rises, culturally dated to around 4000 cal BP, are two published records of starch grains from northwestern China. At Chenqimogou, five starch grains identified as *F. esculentum* were present among a total of 48 from human dental calculus, although the number of samples was very small. At Changning, nine *qiaomai* (buckwheat) grains were among 152 reported from stone knives.

Fagopyrum macrofossils are in the form of charred seeds at all ten sites where they have been reported; these records are mostly limited by few samples and/or lack of any detailed information. Identifications are to species-level as *F. esculentum* (including the synonym *F. sagittatum*) or the vernacular *qiaomai*, with the exception of the record from Kyung-lung Mesa in southwestern Tibet, identified as *Fagopyrum* sp. and inferred to be a wild species on account of the small size (3 mm) of the preserved nutlets. Seven records are from the third millennium cal BP, spanning the Zhou dynasty, Warring States period and Han dynasty, and have a wide geographical distribution in northeastern, northwestern and southwestern China. At Haimenkou in Yunnan province, the earliest site with radiocarbon dating (3050-2750 cal BP), only three grains of *F. esculentum* were found, but the nearby site of Xueshan, dated culturally to the end of the third millennium BP, has 149 grains. At the three Han dynasty sites in the Yellow River/Loess plateau region, buckwheat was associated with pottery in tombs, but these excavations were carried out in the 1970s and minimal archaeobotanical detail was recorded.

Four grains of *F. esculentum* were recovered from each of two Liao dynasty sites in northeastern China (Bayantala and Sunchangqing). These coincide geographically and chronologically with the second major set of *Fagopyrum* pollen rises, around 1000-700 cal BP. The northeastern focus of buckwheat finds later than 2000 cal BP resonates with its modern importance, as inferred from the number of buckwheat accessions in the Chinese Crop Germplasm Information System (CGRIS).

A geographical outlier of similar period is the macrofossil record of possibly wild *Fagopyrum* sp. from the Zhangzhung kingdom site of Kyung-lung Mesa in southwestern Tibet.

There have been no positive identifications of *F. tataricum* among any sample type at any period in China.

Discussion

Interpreting the Fagopyrum *pollen and macrofossil record*

The majority of records were identified to genus level as *Fagopyrum*. Chinese palynological work predominantly uses the reference criteria of Wang et al. 1995, Zhou et al. 2003, and Chen et al. 2014. These authors consider that *Fagopyrum* pollen cannot be identified to species based on size, shape or surface ornamentation. Zhou et al. (2003) describe the pollen morphology of the genus *Fagopyrum* Mill. in China as 'prolate, or often subprolate/prolate to spheroidal in shape, and elliptical from equatorial view, circular from polar view, with their germination aperture being all 3-colporate'. Wang et al. (1995) agree that *Fagopyrum* species produce prolate shape, tricolpate pollen with reticulate ornamentation. Palynologists from Europe also describe *Fagopyrum* pollen as tricolporate, oval with branched columellae, with variable sizes from 40 – 60 µm (in glycerine); sizes are dimorphic in heterostylous species including *F esculentum* (Fægri and Iversen 1989; Moore et al. 1991; de Klerk et al. 2015). However, work on *Fagopyrum* pollen in Europe has more often attempted to distinguish *F. esculentum* and *F. tataricum*, following the identification criteria of van Leeuven et al. 1988, who consider that the two species are distinguishable on the base of basal truncs - distinct (*F. esculentum* – branched columellae in the mesocolpium as well as at the apocolpium, and very thick exine) or indistinct (*F. tataricum*). For the two sites in China (Jinchuan and Lucheng) where pollen identifications are reported to species-level as *F. esculentum*, insufficient detail or explanation of identification criteria is given to infer whether this taxonomic precision is appropriate.

It has been claimed that the pollen of a number of African genera of Polygonaceae (*Oxygonum*, *Antigon*, and *Afrobrunnichia*) is morphologically similar to that of *Fagopyrum* (de Klerk et al. 2015), but the basis of their claim is unclear and African genera are in any case unlikely to be relevant to the topic of this paper. Chinese pollen morphology studies show that the *Fagopyrum* pollen has surface sculpture distinguishing it from other genera, which allows confident genus-level identification in sedimentary pollen diagrams (Wang et al. 1995).

Seed and pollen records of *Fagopyrum* in China outside the south-west are generally assumed to represent cultivation of one of the two domesticated taxa, even in the absence of species identification (Fuller et al. in press). Two lines of reasoning lead to this assumption. First, most wild *Fagopyrum* species, including *F. esculentum* subsp. *ancestralis* and *F. tataricum* subsp.

potanini, are restricted to southwestern China (Fig. 3), although it should be noted that perennial buckwheat (*F. dibotrys*) is more widespread across southern China and as far north as Henan, Shaanxi and southern Gansu provinces (Yamane et al. 2003) and (http://www.efloras.org/florataxon.aspx?flora_id=2&taxon_id=242100052); the implications of this are discussed below. Second, by reference to associated taxa, *Fagopyrum* pollen always appears within an open landscape or forest clearance episodes. *Fagopyrum* pollen is invariably encountered in low numbers, on account of its being entomophilous or self-pollinated, with poor production, and limited dispersal capacities on account of the large pollen grain size, as well as the coarse sculpture of the exine (Miras 2009; Pidek 2009; de Klerk et al. 2015). The levels of *Fagopyrum* pollen in surface samples *in situ* and near contemporary buckwheat fields are markedly low (Miras 2009; Pidek 2009; de Klerk et al. 2015). We therefore tentatively suggest that a high incidence of buckwheat pollen might be explained by crop processing in the vicinity.

Trigonous nutlets are not uncommon in carbonised macrofossil assemblages, and are typically attributable to one of two families, Cyperaceae and Polygonaceae, on the basis of surface patterning and terminal attachments. Within the Polygonaceae, details of these features along with cross section, sharpness of lateral ridges and overall size normally allows further attribution to genus (cf. Katz et al. 1965) The large size and surface texture of *Fagopyrum* nutlets are distinctive, and published records unlikely to be problematic. Within the genus, species identification may be suggested on the basis of size (*F. tataricum* is on average rather shorter than *F. esculentum*, though there is some overlap in their ranges). Their pericarps have structures distinctive to particular species, which may also be discerned in surface patterning (Winton and Winton 1932).

The paucity of buckwheat macrofossil records from China is striking. As indicated above, in better studied crop taxa, the incidence of charred macrofossils is related to crop processing activities in the vicinity of routine fires (generally domestic fires of some kind). Not all ethnographically attested crop processing occurs near fire; indeed some are actively kept distant from fires, in which case they leave no charred record. It is thus perfectly possible, if conjectural, that a low incidence of macrofossils relates to the proximity of crop processing activities and fires, rather than any underlying level of incidence in the agrarian landscape.

There is also an increasing interest in starch granules, with some attributions to *Fagopyrum* (Li et al. 2010; Qiao 2014). Both the criteria for genus and species identification, and the circumstances that might allow their millennial persistence are matters for ongoing investigation.

Biogeography and genetic evidence for the origins of cultivated buckwheat

The geography of cultivated buckwheat origins has been inferred primarily from biogeographic and genetic data. China is the centre of species diversity of *Fagopyrum*, which comprises around 16 species, many of which have a narrow endemic distribution in southwestern China (Ohnishi and Yasui 1998; Chauhan et al. 2010). The taxa characterised in recent years include the wild progenitors of both common and Tartary buckwheat. Wild *F. esculentum*, designated *F. esculentum* subsp. *ancestralis*, resembles cultivated common buckwheat morphologically and as a self-infertile, heterostylous, outcrossing diploid taxon with 2n=16 chromosomes, but differs in its smaller flowers and achenes, thicker blades, strong seed dormancy, shattering of premature achenes, a more branching habit at lower nodes, and a longer vegetative growth period (Ohnishi 1991; Ohnishi 1998a). Its known distribution is limited to an ~250 km radius in northern Yunnan province, southwestern Sichuan province and eastern Tibet, where it typically grows on rocky cliffs and roadsides (Ohnishi 1998a,b, 2009; Ohnishi and Yasui 1998; Ohnishi and Konishi 2001; Ohnishi and Tomiyoshi 2005; Fig. 3). Its progenitor status was inferred from the typical wild species traits above, and the resolution of subsp. *esculentum* and subsp. *ancestralis* as sister taxa within phylogenies of *Fagopyrum* based on morphological traits, isozyme variability, and RFLPs of cpDNA (Ohnishi and Matsuoka 1996).

Within the narrow distribution of *F. esculentum* subsp. *ancestralis*, the Sanjiang area along the Tibet-Sichuan border, where three major rivers (Changjiang, Mekong and Salween) flow north-south in deep valleys between 3000-4000 m high mountain ranges, the Sanjiang area has been inferred to be the geographic origin of domesticated *F. esculentum* (Fig. 3). This inference follows from genetic analyses of wild populations and sympatric domesticated landraces using amplified fragment length polymorphism (AFLP), simple sequence repeat (SSR) and isozyme markers, based on the monophyly of the cultivated populations and their close relationship to wild populations from this area (Konishi et al. 2005; Konishi and Ohnishi 2007; Ohnishi 2009).

A wild subspecies of Tartary buckwheat, *F. tataricum* subsp. *potanini* Batalin, has a relatively wide distribution in northern Sichuan province, southern Tibet, Kashmir and northern Pakistan, and more sporadically in Gansu and Qinghai provinces (Ohnishi 1993a, 1994, 1998a,b; Fig. 3). In Tibet it reaches altitudes of up to 4900 m (Ohnishi 1993a). Like cultivated Tartary buckwheat, subsp. *potanini* is a self-fertile, homostylous, inbreeding diploid with 2n=16 chromosomes. The literature describing its morphology is difficult to access. Weedy types of Tartary buckwheat also exist, distributed in northern Pakistan, and are described as morphologically similar to cultivated landraces but with wild-subspecies-like characters including a shattering habit, strong dormancy, and highly branched (Ohnishi 1994).

Fagopyrum tataricum [subsp. *tataricum*] and *F. tataricum* subsp. *potanini* were confirmed as sister taxa (Ohnishi and Matsuoka 1996), from which the authors inferred *F. tataricum* subsp.

potanini to be the wild ancestor of cultivated Tartary buckwheat. Isozyme, RAPD, and AFLP variability was found to be substantially higher in wild than in cultivated or weedy Tartary buckwheat (Ohnishi 1998b; Tsuji and Ohnishi 2000, 2001), and the authors inferred that the cultivated subspecies was domesticated in eastern Tibet/ Yunnan / Sichuan provinces on the basis of the high genetic diversity in wild populations from this area, despite the genetic similarity of cultivated landraces to wild populations from Tibet and Pakistan (Ohnishi 1998b; Tsuji and Ohnishi 2000, 2001). Weedy *F. tataricum* was dispersed among wild and cultivated groups in the RAPD phylogenetic analyses and it was suggested that these forms arose from hybridization between wild and cultivated plants in Yunnan or Sichuan, with later spread to northern Pakistan as a weed of cultivated *F. tataricum*.

Limitations of the genetic data

The inference of the Sanjiang region as the centre of origin of cultivated *F. esculentum* (Konishi et al. 2005; Konishi and Ohnishi 2007; Ohnishi 2009) may constitute overinterpretation of the limited genetic data to date. Very few samples, particularly of cultivated *F. esculentum,* were included in these genetic studies. As the authors admit, their failure to sample the cultivated taxon from outside southwest China is a serious weakness, which limits the robustness of inferences of the relationship between subsp. *ancestralis* and subsp. *esculentum.* The genetic markers used are now outdated, with particular weaknesses being the low level of variability detected by isozymes, and problems of dominance and false monophyly associated with AFLPs (Allaby and Brown 2003). We also suggest that the data in Ohnishi (2009) offer inadequate support for an origin in Sanjiang, as this interpretation relies on the weak statistic of genetic distance measures and moreover virtually all the wild populations analysed are genetically close to the cultivated samples. Given the geographical range of *F. esculentum* subsp. *ancestralis*, the origin of *F. esculentum* subsp. *esculentum* somewhere in the eastern Tibet/ northern Yunnan / western Sichuan region seems uncontroversial, but more precise definition is premature.

The centre of origin of Tartary buckwheat is in principle less geographically constrained, given the wide range of *F. tataricum* subsp. *potanini* and indeed the lack of any specific archaeobotanical records of *F. tataricum* in any period (remembering the general paucity of records discussed above, a situation that could be mitigated by further research). The argument that the domestication of *F. esculentum* in eastern Tibet/ Yunnan / Sichuan supports a domestication of *F. tataricum* in the same region (Ohnishi 1998b; Tsuji and Ohnishi 2000, 2001) is constrained by the lack of associated archaeological evidence for nascent agriculture. The actual genetic evidence for domestication in this region relies solely on maximum genetic diversity, but this inference is made on the basis of very few variable loci, which was a frequent problem of first-generation molecular markers. It is also notable that *F. tataricum* landraces are phylogenetically closer to wild populations in central Tibet and Pakistan. Tsuji and Ohnishi (2000)

speculate that these morphologically wild populations are descended from hybrids between cultivated and wild populations in Yunnan or Sichuan, but their data do not directly support this hypothesis.

Buckwheat domestication and cultivation in China: where and when?

On the basis of the above evidence, the direct sediment dating records, associated with *Fagopyrum* pollen together with the abundance of cereal pollen, seeds and charcoal, are consistent with buckwheat cultivation arising in northern China from 5500 BP. This is outside the inferred centres of domestication of both common and Tartary buckwheat in eastern Tibet/ Yunnan / Sichuan, where the genus does not appear in the archaeobotanical record (pollen or macroremains) until the third millennium cal BP. This incongruence of the archaeobotanical and genetic evidence demands further attention, and has hitherto been underplayed: d'Alpoim Guedes et al. (2014) state that the palyonological evidence for buckwheat from northeastern and northwestern China and the lower Yangtze 'postdates 2000 BC', citing Boivin et al. (2012). However, Boivin et al. (2012)'s paper actually mentions dates from 2400-2500 BC, and omits mention of the earlier records from Xindian and Beizhuangcun.

The possible scenarios that explain buckwheat origins in the light of these differing lines of evidence are necessarily speculative, given the very limited state of knowledge about domestication traits, role in subsistence, and taxonomic specificity in cultivated *Fagopyrum.* Nevertheless, they highlight some important avenues for further investigation.

First, the possibility that buckwheat (particularly *F. esculentum*) underwent an initial domestication from *F. esculentum* subsp. *ancestralis* at the margins of the latter's range in southwestern China, but was not substantially cultivated until it spread beyond that range into the north, is interesting in relation to the obligate outbreeding nature of *F. esculentum*. Reproductive isolation of outcrossing crops from their wild progenitors, a keystone of both morphological and phylogenetic concepts of domestication, is expected to be slower and /or more complicated compared with selfing species. The empirical evidence gives some support to this expectation, although it is difficult to disentangle the effect from associated traits, in particular annuality (Glémin and Bataillon 2009). Although geographical isolation of domesticated crops from their wild progenitors appears to be the exception rather than the norm (Dempewolf et al. 2012), we can postulate that northwards 'translocation' (in the loosest sense, see below) of *F. esculentum* populations characterised by some domestication traits facilitated fixation of these traits to make a sufficiently productive crop to reach detectable levels in the archaeobotanical record.

This hypothesis would demand explanation of the mechanism of geographical isolation or translocation. One obvious possibility is that the range of *F. esculentum* subsp. *ancestralis*

extended into northern China in the mid-Holocene. Palynological vegetation reconstructions indicate that temperate forests extended further north in China, including around the Xindian site in the southern Loess Plateau, than they do today (Shang and Li 2010; Ni et al. 2014). The range of *F. esculentum* subsp. *ancestralis* in Yunnan, Sichuan and eastern Tibet today appears also to fall broadly within a forest rather than grassland biome, providing some support for this idea, but much further work is needed on the precise ecological niche of the wild taxon, and the abiotic and biotic factors that may govern this. As a related issue, cultivated buckwheat today predominates in steppe or forest-steppe zones (Fig. 4), suggesting the interesting possibility of a shift in ecological adaptation following domestication.

A second possibility for northwards movement of common buckwheat in China is small-scale cultivation and localised domestication in the southwest followed by anthropogenic translocation to central and northern China. The development of agriculture in the Chengdu Plain and southwest China are a topic of increasing interest in Chinese archaeology (d'Alpoim Guedes 2011; d'Alpoim Guedes et al. 2013, 2014, 2015), although virtually always from the perspective of south- and westward movement of millet and rice agriculture and agriculturalists. Evidence of plant cultivation (of foxtail and broomcorn millet) appears from around 5500 cal BP at the Neolithic sites of Changdu Karuo in eastern Tibet, and Haxiu and Yingpanshan in northern Sichuan (d'Alpoim Guedes 2011). All these sites lie further north, by around 500 km, than the region of origin of domesticated *F. esculentum* proposed by Ohnishi and colleagues. In Yunnan province, the earliest evidence for agriculture comes from rice remains, and may date from around 4500 cal BP at Haidong in eastern Yunnan and Baiyangcun, although systematic flotation and reliable dating only comes from around 3600 cal BP at Haimenkou, where buckwheat is also present in levels dated around 3050-2750 cal BP. A recent analysis of site chronology from the Nujiang valley in northwestern Yunnan, the area inferred from biogeography and genetics as the centre of origin of domesticated *F. esculentum*, found convincing evidence for Neolithic settlement of the region only from ~4200 cal BP. Earlier dates (~5100 cal BP) exist from the first stage of Haimenkou, but may not be reliable (Liu et al. 2016). Prior to this period, there is evidence for occupation of a handful of late Palaeolithic sites in the region by hunter-gatherers, such as Tangzigou (~8000 cal BP; Liu et al. 2016). In summary, unless these hunter-gatherer populations were independently experimenting with buckwheat cultivation and sustained this until cultural exchange with northern China began in the 6th millennium cal BP, the currently-understood chronology of Neolithic/agricultural sites around the Yunnan/Sichuan/Tibet border postdates apparent buckwheat cultivation in the north by as much as 1000 years. However, given the clear cultural links between central Sichuan and northern China by the mid-6th millennium cal BP, we could speculate regarding a Sichuan common buckwheat domestication and its northward expansion ‘contraflow’ to that of millet, perhaps through the Majiayao and Yangshao cultures. This scenario requires that the past range of *F. esculentum* subsp. *ancestralis* extended further to

the north than today. Although any of these scenarios demands much substantiation, resolving the domestication and expansion of buckwheat within China is of interest precisely because its geography is atypical of other elements of the agricultural package, and may well add complexity to the emerging narrative of Neolithic cultural interactions.

Buckwheat as a Tibetan plateau/Himalayan crop

The expansion of cultivated buckwheat (both *F. esculentum* and *F. tataricum*) is also of interest in relation to the arrival of agriculture on the Tibetan plateau. Both common and Tartary buckwheat, and their respective wild ancestors, are native to the low-mountain zones at the southeastern edge of the region.

Research on agricultural spread to the Tibetan plateau has focused chiefly on the major cultigens found in archaeobotanical assemblages from the region, which are wheat, barley, and broomcorn and foxtail millets. Their potential ranges have also been assessed using ecological modelling (d'Alpoim Guedes et al. 2014, 2015; Chen et al. 2015). The potential limits of cultivation of common and Tartary buckwheat have not yet been comparably modelled, and beyond the sites of Haimenkou, Xueshan and Wenhai Lake at the southeastern margins of the Tibetan Plateau, no sites in the eastern part of the Plateau have yielded *Fagopyrum* remains. However, the majority of archaeobotanical investigations have been in the northeastern plateau (Chen et al. 2015), and more research is needed on sites in its southeast. Some 1000-1500 km to the west, to the south of the Tibetan plateau in the Himalaya, *Fagopyrum* remains appear in western-central Nepal from 3000 cal BP in the Jhong river valley at 3000-4000 m altitude (both *F. esculentum* and *F. tataricum*; Knörzer 2000), around 1000 cal BP at Kohla at 3350 m (a single grain of *Fagopyrum* cf. *esculentum*), and in southwestern Tibet small nutlets, possibly of a wild species, around 700-880 AD at Kyung-lung Mesa (d'Alpoim Guedes et al. 2014). It has been suggested that the cereal remains were transported to these sites from lower altitudes rather than cultivated *in situ*. From the very limited data available, we can postulate that domesticated *F. esculentum* spread westward along the southern slopes of the Himalaya by the third millennium cal BP; whether *F. tataricum* followed a similar expansion or was a local Himalayan domesticate remains an open question. From the current distribution of *F. esculentum* and *F. tataricum*, Ohnishi (1993a) concludes that buckwheat did not cross the Himalayas [i.e. into the central Tibetan plateau].

Spread into western Eurasia

The arrival of cultivated and Tartary buckwheat in Europe is widely considered to date back only to the Late Mediaeval period (see de Klerk et al. 2015 for a summary of the history of this idea and references). However, the presence of earlier *Fagopyrum* pollen records in Europe prompted Janik (2002), Jones (2004) and Jones et al. (2011) to challenge this narrative, raising the possibility that cultivated buckwheat spread into Europe as early as the 7th millennium cal BP. To

explore this hypothesis further, de Klerk et al. (2015) assembled a comprehensive data set of European pre-Mediaeval records, identifying some 232 pollen and ten macrofossil records attributable to *Fagopyrum* dating prior to 650 cal BP. The earliest time-slice with layers containing *Fagopyrum* pollen is before 11700 cal BP, suggesting that a non-agricultural explanation is required in any case for at least some of these pre-Mediaeval finds. Many of the sites collated in this survey contained just a single pollen grain attributed to *Fagopyrum*, and an assessment of indicators of cultivation using criteria comparable to this paper was not made. De Klerk et al. (2015) suggest that pollen records prior to 4000 cal BP could represent a wild *Fagopyrum* or related Polygonaceae species now extinct in Europe. The few Bronze Age and earlier macrofossil records in Europe require further scrutiny.

In the period between 4000 and 2800 cal BP, many of the samples containing buckwheat come from the Bronze Age (3500-3400 cal BP) Georgian cemetery of Saphar-Kharaba (Kvavadze 2007). Interestingly, this chronology in the Caucasus is comparable to new data on the earliest firm evidence for broomcorn and foxtail millet in the region (Lucie Martin and Nana Rusishvili, pers. comm.), cereals with some ecological similarities to buckwheat whose spread from China to Europe has sometimes been considered together (Jones 2004, Jones et al. 2011). In contrast to the Asian millets, however, for which the macrofossil picture in the Central Asian Bronze Age has been clarified considerably by recent work (Spengler and Willcox 2013; Spengler et al. 2013; Spengler et al. 2014a,b,c), no *Fagopyrum* macrofossil records for Central Asia have emerged. It is also notable that buckwheat is absent from the diverse range of excellently-preserved cultigens at Bronze Age cemetery sites in Xinjiang in the far northwest of China, in which broomcorn and foxtail millet typically feature prominently (Jiang et al. 2007, 2013; Jia et al. 2011; Li et al. 2013).

The pattern and drivers of buckwheat globalization

In summary, although the initial zone of buckwheat domestication requires clarification, the archaeobotanical data evidence its cultivation in northern China from at least the mid-6th millennium cal BP, and in southwestern China and the Tibetan plateau/Himalaya from at least the end of the 4th millennium cal BP. It may also have been cultivated in the Caucasus from the 4th millennium cal BP. De Klerk et al. (2015) conclude from the upturn in European pollen- and macrofossil record numbers that buckwheat cultivation in Europe was very likely already widespread in the third millennium cal BP, and possibly from 3800 cal BP. The absence of Central Asian records of buckwheat, together with these positive identifications in the Himalayan and Caucasus regions [in the 4th-3rd millennia cal BP], could suggest that buckwheat spread to Europe via a southerly route. This would indicate a westward expansion separate from broomcorn millet; the archaeobotanical data for foxtail millet have rarely been considered independently. Most authors suggest that the eastward spread of buckwheat to Japan occurred from around 4000 cal BP (de Klerk et al. 2015, Fuller et al. in press); the significance of the earlier (5500 cal BP)

buckwheat pollen record of Tsukada et al. (1986), as with similarly early *Fagopyrum* pollen finds in Europe, are hard to interpret, with possibilities comprehensively discussed by de Klerk et al. (2015).. Genetic data addressing the route of spread of buckwheat are very limited (Ohnishi 1993b,c; Murai and Ohnishi 1996) and appear to give conflicting answers. Further genetic and palynological/archaeobotanical work are needed to clarify the routes of spread and whether the geographical 'gap' in Russia and central Asia or around the Caspian can be bridged.

Returning to the narrative of 'arrival' of common buckwheat in Europe in the Late Mediaeval, we can hypothesise that its increased presence in the macrofossil record from this period may instead relate to an episode of intensification. It would be interesting to seek parallels between this and the possible earlier intensification in northern China. The dynamics of intensification of common buckwheat cultivation could be peculiar to its biology as an insect-pollinated crop. Specifically, modern data show that honeybee pollination substantially increases buckwheat yield (Klein et al. 2007). This raises the interesting possibility that human management of bee populations was among the drivers of buckwheat globalization.

Data access and Supplementary Material

Data accompanying this publication are directly available within the publication. Further details relating to the data reviewed here are cited in references.

Acknowledgements

MKJ and HVH were supported by a European Research Council Advanced Investigator award to MKJ (GA249642, 'Food Globalization in Prehistory)'. HVH was supported by a University of Cambridge Returning Carers' Scheme award. SX was supported by grants from the National Natural Science Foundation of China (41471167), and National Scholarship Fund of China (CSC no. 201504910101). We thank Cameron Petrie for advice on data mapping and Lucie Martin and Nana Rusishvili for sharing unpublished data on archaeobotany in the Caucasus. The helpful comments of two anonymous reviewers are acknowledged.

References

Allaby RG, Brown TA (2003) AFLP data and the origins of domesticated crops. Genome 46:448-453

Boivin N, Fuller DQ, Crowther A (2012) Old World globalization and the Columbian exchange: comparison and contrast. World Archaeol 44:452-469

Chauhan RS, Gupta N, Sharma SK, Rana JC, Sharma TR, Jana S (2010) Genetic and Genome Resources in Buckwheat - Present Status and Future Prospects. Eur J Plant Sci Biotech 4:33-44

Chen FH et al. (2015) Agriculture facilitated permanent human occupation of the Tibetan plateau after 3600 B.P. Science 347:248-250

Chen ML, You YL, Wen HH, Li Y (2014) The breeding system and reproductive ecology of the endangered plant *Fagopyrum dibotrys* (D. Don) Hara. Bangladesh J Bot 43: 197–205

Cheng Y, Jiang W (2011) Vegetation and climate changes since the last glacial maximum in the northern Loess Plateau (Mo Ci Sheng Bing Qi Yi Lai Shaanbei Huang Tu Gao Yuan De Zhi Bei He Qi Hou Bian Hua). Quat Sciences 31:982-989. In Chinese

d'Alpoim Guedes J (2011) Millets, Rice, Social Complexity, and the spread of agriculture to the Chengdu Plain and southwest China. Rice 4:104-113

d'Alpoim Guedes J, Jiang M, He K, Wu X, Jiang Z (2013) Site of Baodun yields earliest evidence for the spread of rice and foxtail millet agriculture to south-west China. Antiquity 87:758-771

d'Alpoim Guedes J, Lu H, Li Y, Spengler RN, Wu X, Aldenderfer M (2014) Moving agriculture onto the Tibetan plateau: the archaeobotanical evidence. Archaeol Anthropol Sci 6:255-269

d'Alpoim Guedes JA, Lu H, Hein AM, Schmidt AH (2015) Early evidence for the use of wheat and barley as staple crops on the margins of the Tibetan Plateau. Proc Natl Acad Sci USA 112:5625-5630

de Klerk P, Couwenberg J, Joosten H (2015) Pollen and macrofossils attributable to *Fagopyrum* in western Eurasia prior to the Late Medieval: An intercontinental mystery. Palaeogeogr Palaeoclimatol Palaeoecol 440:1-21

Dempewolf H, Hodgins KA, Rummell SE, Ellstrand NC, Rieseberg LH (2012) Reproductive isolation during domestication. Plant Cell 24:2710-2717

Faegri K, Iversen J (1989) Textbook of pollen analysis. 4th edn (Faegri K, Kaland PE, Krzywinski K, eds). John Wiley & Sons Ltd, Chichester, pp 3-328

Fuller DQ, Zhang Y, Weisskopf A, Qin L (in press) Assembling Chinese Domestications: multi-focal agricultural origins. In: Kaner S, Janik L, Yano K (eds) Origins of Agriculture: Challenging old orthodoxies, championing new perspectives. McDonald Institute for Archaeological Research, Cambridge

Glémin S, Bataillon T (2009) A comparative view of the evolution of grasses under domestication. New Phytol 183:273-290

Janik, L (2002) Wandering weed: the journey of buckwheat (*Fagopyrum* sp.) as an indicator of human movement in Russia. In: Ancient Interactions: East and West in Eurasia (eds Boyle K, Renfrew C, Levine M). McDonald Institute for Archaeological Research, Cambridge, pp. 299–308

Jia PW, Betts A, Wu X (2011) New evidence for Bronze Age agricultural settlements in the Zhunge'er (Junggar) Basin, China. J Field Archaeol 36:269-280

Jia X (2012) Cultural evolution process and plant remains during Neolithic- Bronze Age in Northeast Qinghai Province (Qing Hai Sheng Dong Bei Bu Di Qu Xin Shi Qi – Qing Tong Shi Dai Wen Hua Yan Jin Guo Cheng Yu Zhi Wu Yi Cun Yan Jiu). PhD Dissertation, Lanzhou University. In Chinese

Jiang H, Li X, Li C (2007) Cereal remains from Yanghai Tomb in Turpan, Xinjiang and their palaeoenvironmental significance. In Chinese with English abstract. J Palaeogeogr 9:551–558

Jiang H, Wu Y, Wang H, Ferguson DK, Li C-S (2013) Ancient plant use at the site of Yuergou, Xinjiang, China: implications from desiccated and charred plant remains. Veg Hist Archaeobot 22:129-140

Jones MK (2004) Between fertile crescents: minor grain crops and agricultural origins. In: Jones MK (ed) Traces of ancestry: studies in honour of Colin Renfrew. Oxbow Books, Cambridge, pp 127-135

Jones MK, Hunt HV, Lightfoot E, Lister DL, Liu X, Motuzaite-Matuzeviciute G (2011) Food globalization in prehistory. World Archaeol 43:665–675

Katz NJ, Katz SV Kipiani MG (1965) Atlas and keys of fruits and seeds occurring in the Quaternary deposits of the USSR. Academy of Sciences of the USSR, Moscow

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T (2007) Importance of pollinators in changing landscapes for world crops. Proc R Soc Lond B Biol Sci 274:303-313

Knörzer K-H (2000) 3000 years of agriculture in a valley of the High Himalayas. Veg Hist Archaeobot 9:219-222

Konishi T, Ohnishi O (2007) Close genetic relationship between cultivated and natural populations of common buckwheat in the Sanjiang area is not due to recent gene flow between them - an analysis using microsatellite markers. Genes Genet Syst 82:53-64

Konishi T, Yasuo Y, Ohnishi O (2005) Original birthplace of cultivated common buckwheat inferred from genetic relationships among cultivated populations and natural populations of wild common buckwheat revealed by AFLP analysis. Genes Genet Syst 80:113-119

Kvavadze E (2007) Pollen analysis report. In: Narimanishvili G, Amiranashvili J, Davlianidze R, Murvanidze B, Shanshashvili N, Kvachadze M (eds) Archaeological Investigations at Site IV-156, Saphar-Kharaba, KP120, Tsalka District. Otar Lordkipanidze Centre of Archaeology of the Georgian National Museum, Tbilisi, pp 42-48 + appendices

Li J-F, Abuduresule I, Hueber FM, Li W-Y, Hu X-J, Li Y-Z, Li C-S (2013) Buried in Sands: Environmental Analysis at the Archaeological Site of Xiaohe Cemetery, Xinjiang, China. PLoS One 8:e68957

Li MQ, Yang XY, Wang H, Wang Q, Jia X, Ge QS (2010) Starch grains from dental calculus reveal ancient plant foodstuffs at Chenqimogou site, Gansu Province. (Gan Su Lin Tan

Chen Qi Mo Gou Yi Zhi Ren Ya Jie Shi Zhong Dian Fen Fan Ying De Gu Ren Lei Zhi Wu Xing Shi Wu). Sci China Ser D Earth Sci 40: 486-492. In Chinese

Li X, Shang X, Dodson J, Zhou X (2009) Holocene agriculture in the Guanzhong basin in NW China indicated by pollen and charcoal evidence. Holocene 19:1213-1220

Li X, Zhou X, Zhou J, Dodson J, Zhang H, Shang X (2007) The earliest archaeobiological evidence of the broadening agriculture in China recorded at Xishanping site in Gansu Province. Sci China Ser D Earth Sci 50:1707-1714

Li Y (1979) Brief report on the excavation of Maquan West Han Dynasty Tomb of Shaanxi Xianyang. Kao Gu 2:125-135

Li YY, Willis KJ, Zhou LP, H.T. C (2006) The impact of ancient civilization on the northeastern Chinese landscape: palaeoecological evidence from the Western Liaohe River Basin, Inner Mongolia. Holocene 16:1109-1121

Liu H et al. (2016) Human settlements and plant utilization since the late prehistoric period in the Nujiang River valley, Southeast Tibetan Plateau. Archaeol Res Asia 5:63-71

Makohonienko M, Kitagawa H, Fujiki T, Liu X, Yasuda Y, Yin H (2008) Late Holocene vegetation changes and human impact in the Changbai Mountains area, Northeast China. Quat Int 184:94–108

Makohonienko M et al. (2004) Late-Holocene natural and anthropogenic vegetation changes in the Dongbei Pingyuan (Manchurian Plain), northeastern China. Quat Int 123-125:71–88

Miras Y (2009) L'étude des relations entre végétation et pluie pollinique actuelle sur le plateau de Millevaches (Limousin, France): outil pour une meilleure caractérisation pollenanalytique des formes paysagères et des pratiques agrosylvopastorales. Rev Sci Nat Auvergne 73: 71–104

Monfreda C, Ramankutty N, Foley JA (2008). Farming the planet. Part 2: Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. Global Biogeochemical Cycles 22, GB1022, doi:10.1029/2007GB002947.

Moore PD, Webb JA, Collison ME (1991) Pollen analysis. Blackwell scientific publications, Oxford

Murai M, Ohnishi O (1996) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. X. Diffusion routes revealed by RAPD markers. Genes Genet Syst 71:211-218

Ni J, Cao X, Jeltsch F, Herzschuh U (2014) Biome distribution over the last 22,000 yr in China. Palaeogeogr Palaeoclimatol Palaeoecol 409:33-47

Ohnishi O (1991) Discovery of the wild ancestor of common buckwheat. Fagopyrum 11:5-10

Ohnishi O (1993a) A memorandum on the distribution of buckwheat species in Tibet and the Himalayan hills: has buckwheat crossed the Himalayas? Fagopyrum 13:3-10

Ohnishi O (1993b) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. IX. Concluding remarks on worldwide survey of allozyme variability. Jpn J Genet 68:317-326

Ohnishi O (1993c) Population genetics of cultivated common buckwheat, *Fagopyrum esculentum* Moench. VIII. Local differentiation of landraces in Europe and the silk road. Jpn J Genet 68:303-316

Ohnishi O (1994) Buckwheat in Karakoram and the Hindukush. Fagopyrum 14:17-25

Ohnishi O (1998a) Search for the Wild Ancestor of Buckwheat I. Description of new *Fagopyrum* (Polygonaceae) species and their distribution in China and the Himalayan hills. Fagopyrum 15:18- 28

Ohnishi O (1998b) Search for the wild ancestor of buckwheat III. The wild ancestor of cultivated common buckwheat, and of Tartary buckwheat. Econ Bot 52:123-133

Ohnishi O (2000) Geographical distribution of allozymes in natural populations of wild Tartary buckwheat. Fagopyrum 17:29-34

Ohnishi O (2009) On the origin of common buckwheat based on allozyme analyses of cultivated and wild populations of common buckwheat. Fagopyrum 26:3-9

Ohnishi O, Konishi T (2001) Cultivated and wild buckwheat species in eastern Tibet. Fagopyrum 18:3-8

Ohnishi O, Matsuoka Y (1996) Search for the wild ancestor of common buckwheat II. Taxonomy of *Fagopyrum* (Polygonaceae) species based on morphology, isozymes and cpDNA variability. Genes GenetSyst 71:383-390

Ohnishi O, Tomiyoshi M (2005) Distribution of cultivated and wild buckwheat species in the Nu river valley of southwestern China. Fagopyrum 22:1-5

Ohnishi O, Yasui Y (1998) Search for wild buckwheat species in high mountain regions of Yunnan and Sichuan provinces of China. Fagopyrum 15:8-17

Okuda M et al. (2003) Late Holocene vegetation and environment at Cauduntou, west of Yangtze Delta,SW Jiangsu Province,East China. Quat Int 105:39-47

Pidek IA (2009) Palinologiczny zapis sukcesji wtórnej na Roztoczu Środkowym. Środowisko Kultura 6: 127–128. In Polish

Qiao H (2014) Qinghai prehistorical and archaeological analysis (Qing Hai Shi Qian Kao Gu Yan Jiu Tan Xi). Chaidamu Kaifa Yanjiu 2 26-29. In Chinese

Ramankutty N, Foley JA (1999). Estimating historical changes in global land cover: croplands from 1700 to 1992. Global Biogeochemical Cycles 13:997-1027

Shang X, Li X (2010) Holocene vegetation characteristics of the southern Loess Plateau in the Weihe River valley in China. Rev Palaeobot Palynol 160:46-52

Shi X (1977) Brief report on the excavation of Yangjiawan Han Dynasty Tomb of Xianyang City (Xian Yang Yang Jia Wan Han Mu Fa Jue Jian Bao). Wen Wu 10:10-21. In Chinese

Spengler RN, Cerasetti B, Tengberg M, Cattani M, Rouse LM (2014a) Agriculturalists and pastoralists: Bronze Age economy of the Murghab alluvial fan, southern Central Asia. Veg Hist Archaeobot 23:805-820

Spengler RN, Chang C, Tourtellotte PA (2013) Agricultural production in the Central Asian mountains: Tuzusai, Kazakhstan (410–150 B.C.) J Field Archaeol 38:68-85

Spengler RN, Frachetti M, Domani P (2014b) Late Bronze Age agriculture at Tasbas in the Dzhungar Mountains of eastern Kazakhstan. Quat Int 348:147-157

Spengler RN, Frachetti M, Doumani P, Rouse LM, Cerasetti B, Bullion E, Mar'yashev A (2014c) Early agriculture and crop transmission among Bronze Age mobile pastoralists of Central Eurasia. Proc R Soc Lond Ser B 281:20133382

Spengler RN, Willcox G (2013) Archaeobotanical results from Sarazm, Tajikistan, an Early Bronze Age settlement on the edge: agriculture and exchange. J Env Archaeol 18:211-221

Sun Y (2013) Archaeobotanical analysis of Bayantala Site of Liao Dynasty (Ba Yan Ta La Liao Dai Yi Zhi Zhi Wu Yi Cun Ji Xiang Guan Wen Ti Yan Jiu). Journal of Chifeng University (Social Sciences) 34:7-10. In Chinese

Tsuji K, Ohnishi O (2000) Origiin of cultivated Tartary buckwheat (*Fagopyrum tataricum* Gaertn.) revealed by RAPD analyses. Genet Resour Crop Evol 47:431-438

Tsuji K, Ohnishi O (2001) Phylogenetic relationships among wild and cultivated Tartary buckwheat (*Fagopyrum tataricum* Gaert.) populations revealed by AFLP analyses. Genes Genet Syst 76:47-52

Van Leeuven P, Punt W, Hoen PP (1988) The Northwest European Pollen Flora, 43 (Polygonaceae). Rev Palaeobot Palynol 57:81-151

Wang FX, Qian NF, Zhang YL, Yang HQ (1995) Chinese floral pollen morphology (Zhong Guo Zhi Wu Hua Fen Xing Tai). Science Press, Beijing. In Chinese

Wang Q (2014) Plant Macrofossil Analysis of Xueshan Site in Chengjiang County of Yunnan Province (Yun Nan Cheng Jiang Xue Shan Yi Zhi Da Zhi Wu Fen Xi). MPhil dissertation, Shandong University. In Chinese

Winton AL, Winton KB (1932). The structure and composition of foods. John Wiley and Sons; Chapman & Hall, New York; London

Xue Y (2010) Study of Plant Remains from Haimenkou Site in Jianchuan County, Yunnan Province. (Yun Nan Jian Chuan Hai Men Kou Yi Zhi Zhi Wu Yi Cun Chu Bu Yan Jiu). MPhil dissertation, Peking University. In Chinese

Yamane K, Yasuo Y, Ohnishi O (2003) Intraspecific cpDNA variations of diploid and tetraploid perennial buckwheat, *Fagopyrum cymosum* (Polygonaceae). Am J Bot 90:339-346

Yang C, Xu K, Zhao Z (2010) Report of Flotation of Sunchangqing Site from Jilin, Baicheng County. Bei Fang Wen Wu 4:48-51

Yao Y, Guo D, Li C (2013) Palynological analysis, paleovegetation and paleoclimate at Jininglu Archaeological site, Inner Mongolia (Nei Meng Gu Ji Ning Lu Cheng Yi Zhi Bao Fen Fen Xi Yu Gu Zhi Bei, Gu Qi Hou Chu Tan). Chinese Science Bulletin 58 (Supplement I): 90-96. In Chinese

Yao YF, Song XY, Wortley AH, Blackmore S, Li CS (2015) A 22,570-year record of vegetational and climatic change from Wenhai Lake in the Hengduan Mountains biodiversity hotspot, Yunnan, Southwest China. Biogeosciences 12:1525–1535

Yi S, Saito Y, Oshim H, Zhou Y, Wei H (2003a) Holocene environmental history inferred from pollen assemblages in the Huanghe (Yellow River) delta, China: climatic change and human impact. Quat Sci Rev 22:609–628

Yi S, Saito Y, Zhao Q, Wang P (2003b) Vegetation and climate changes in the Changjiang (Yangtze River) Delta, China, during the past 13,000 years inferred from pollen records. Quat Sci Rev 22:1501–1519

Zhang S (2015) Climate-vegetation changes and human activity history of Gonghai Lake in Shanxi Province during the last 2000 years (2000 Nian Yi Lai Shanxi Ning Wu Gong Hai Di Qu Qi Hou- Zhi Bei Bian Hua Yu Ren Lei Huo Dong). MPhil Dissertation, Hebei Normal University. In Chinese

Zhao Z (2008) Archaeobotanical analysis of Dingjiawa site (Ding Jia Wa Yi Zhi Fu Xuan Jie Guo Fen Xi Bao Gao). In: Archaeological Excavation Report of Beijing (Bei Jing Duan Kao Gu Fa Jue Bao Gao Ji). Scientific Press, Beijing, pp 229-237. In Chinese

Zhao Z (2011) New Archaeobotanic Data for the Study of the Origins of Agriculture in China. Curr Anthropol 52:S295-S306

Zhou ZZ, Zhao ZC,Wang XY, Xu RX, Li YC (2003) Pollen morphology, tepal and fruit microcharacteristics of the genus *Fagopyrum* Mill. from China. Acta Phytotaxon Sin 41: 63–78

Zhu A (2011) Brief report on the excavation of Muozuizi Han Dynasty Tomb of Gansu Wuwei (Gan Su Wu Wei Mo Zui Zi Han Mu Fa Jue Jian Bao). Wen Wu 6:4-11. In Chinese

Table 1

No.	Sample type	Sediment type (pollen cores)	Site/section name	Province	Taxonomic identification	Dating method	Dating result	Reference
1	Pollen sequence	Loess-palaeosol	Xindian section (新店)	Shaanxi	*Fagopyrum*. sp	AMS 14C and OSL	from 5500 cal BP	Li et al. 2009
2	Pollen sequence	Loess-palaeosol	Beizhuangcun section (北庄村)	Shaanxi	*Fagopyrum*. sp	Stratigraphic comparison	from 5000 cal BP	Shang and Li 2010
3	Pollen sequence	Alluvial sediment	Wangxianggou site (王乡沟)	Inner Mongolia	*Fagopyrum*. sp	AMS 14C	from 4700 cal BP	Li et al. 2006
4	Pollen sequence	Loess-palaeosol with cultural layers	Xishanping site (西山坪)	Gansu	*Fagopyrum*. sp	AMS 14C	from 4600 cal BP	Li et al. 2007
5	Pollen sequence	Alluvial sediment	CM97 (Chongming island, 崇明岛)	Shanghai	*Fagopyrum*. sp	AMS 14C	4500 cal BP	Yi et al. 2003b
6	Pollen sequence	Loess-palaeosol	Jingbian section (靖边)	Shaanxi	*Fagopyrum*. sp	Stratigraphic comparison	4000 cal BP	Cheng and Jiang 2011
7	Pollen sequence	Loess-palaeosol	Fuxian section (富县)	Shaanxi	*Fagopyrum*. sp	Stratigraphic comparison	4000 cal BP	Cheng and Jiang 2011
8	Pollen	Alluvial	Cauduntou	Jiangsu	*Fagopyrum*.	AMS 14C	2500-2700 cal	Okuda et al.

	sequence	sediment	(朝墩头)		sp		BP	2003
9	Pollen sequence	Lake core	Wenhai Lake core (文海湖)	Yunnan	Polygonaceae pollen (likely to be *Fagopyrum*)	AMS 14C	2400 cal BP	Yao et al. 2015
10	Pollen sequence	Alluvial sediment	H9602	Shandong	*Fagopyrum*. sp	AMS 14C	1300 cal BP	Yi et al. 2003a
11	Pollen sequence	Alluvial sediment	Jinchuan site/ (金川)	Jilin	*Fagopyrum esculentum*	AMS 14C	1100 cal BP	Makohonienko et al. 2008
12	Pollen sequence	Peat	Muchang site/ (牧场)	Dongbei pingyuan	*Fagopyrum*. sp	AMS 14C	1050 cal BP	Makohonienko et al. 2004
13	Pollen sequence	Lake core	GH09B (公海)	Shanxi	*Fagopyrum*. sp	AMS 14C, 137Cs and 215Pb	1040-680 cal BP	Zhang 2015
14	Pollen sequence	Cultural layers	Lucheng site (路城)	Inner Mongolia	*Fagopyrum esculentum*	Archaeological culture	700-600 cal BP	Yao et al. 2013
15	Starch grains		Chenqimogou site (陈旗磨沟)	Gansu	*Fagopyrum esculentum*	Archaeological culture	4000 cal BP	Li et al. 2010
16	Starch grains		Changning site (长宁)	Qinghai	Buckwheat (qiaomai)	Archaeological culture	4000 cal BP	Qiao 2014
17	Charred		Dingjiawa site	Beijing	*Fagopyrum*	Archaeological	2720-2420	Zhao 2008

	seeds		(丁家洼)		*sagittatum*	culture	cal BP	
18	Charred seeds		Haimenkou site (海门口)	Yunnan	*Fagopyrum esculentum*	AMS 14C	2720-2170 cal BP	Xue 2010
19	Charred seeds		Xueshan site (学山)	Yunnan	*Fagopyrum esculentum*	Archaeological culture	2430-1940 cal BP	Wang 2014
20	Charred seeds		Yingpandi site (营盘地)	Qinghai	Buckwheat (qiaomai)	AMS 14C	2250 cal BP	Jia 2012
21	Charred seeds		Yangjiawan Han Dynasty tomb (杨家湾汉墓)	Shaanxi	Buckwheat (qiaomai)	Archaeological culture	2150-1940 cal BP	Shi 1977
22	Charred seeds		Maquan Han Dynasty tomb (马泉汉墓)	Shaanxi	Buckwheat (qiaomai)	Archaeological culture	2150-1940 cal BP	Li 1979
23	Charred seeds		Mozuizi site (磨嘴子)	Gansu	Buckwheat (qiaomai)	Archaeological culture	2150-1930 cal BP	Zhu 2011
24	Charred seeds		Kyung-lung Mesa	Tibet	*Fagopyrum* sp.	AMS 14C	1256-1070 cal BP	d'Alpoim Guedes et al. 2014
25	Charred seeds		Bayantala site (巴彦塔拉)	Inner Mongolia	*Fagopyrum esculentum*	Archaeological culture	1040-830 cal BP	Sun 2013
26	Charred		Sunchangqing	Jilin	*Fagopyrum*	Archaeological	1030-720	Yang et al.

	seeds		site(孙长青)		*esculentum*	culture	cal BP	2010

Table 1. Sites and pollen sections in China with identifications of *Fagopyrum*/buckwheat.

Figure 1. Diagrams of *Fagopyrum* pollen percentage in China.
A: 8 pollen diagrams with a relatively high amount of *Fagopyrum* pollen, which show two expansions of buckwheat in China during the Holocene (Li 2007; Li, 2009; Shang, 2010; Li, 2006; Makohonienko, 2008; Zhang, 2013; Yi, 2006; Yao, 2013). The grey shadow represents the first expansion of buckwheat during 5000-4000 aBP; the hollow area represents the second expansion of buckwheat during 1600-1000 a BP in China.
B: 6 pollen diagrams with a low percentage of *Fagopyrum* pollen (Cheng, 2011; Okuda, 2003; Yao, 2015; Makohonienko, 2004; Yi, 2003). Pollen diagrams reproduced from the references above with kind permission of the original authors, editors and publishers.

Figure 2. Location of sites and sections within modern-day China with identifications of *Fagopyrum*/buckwheat. a) pre-4000 cal BP; b) 4000-2000 cal BP; c) post-2000 cal BP. Sample types: ▲ charred seeds; ■ starch grains; ⬢ pollen sequence.

Figure 3. Approximate distribution of the wild subspecies *F. esculentum* subsp. *ancestralis* and *F. tataricum* subsp. *potanini*, in relation to Chinese provinces and rivers mentioned in the text. The Sanjiang area inferred by Konishi et al. 2005, Konishi and Ohnishi 2007 and Ohnishi 2009 as the centre of origin of domesticated *F.*

esculentum is also shown. Rivers in the Sanjiang area shown as initials on the map: Jinsha (J), Lancang (L), Nu (N). Based on Ohnishi (1998a) and Tsuji et al. (1999).

Figure 4. Distribution of buckwheat cultivation in relation to potential natural vegetation. Buckwheat cultivation data represent total crop production in metric tons; darker colour represents higher production. Data from http://www.earthstat.org/data-download/ (last accessed 03 April 2017), based on data in Monfreda et al. 2008, which contains full data description. Potential natural vegetation data from http://www.earthstat.org/data-download/ (last accessed 03 April 2017), based on Ramankutty and Foley 1999 which contains full data description.

Figure 1

Click here to download Figure Fig_1_HVH210717_flat.tif

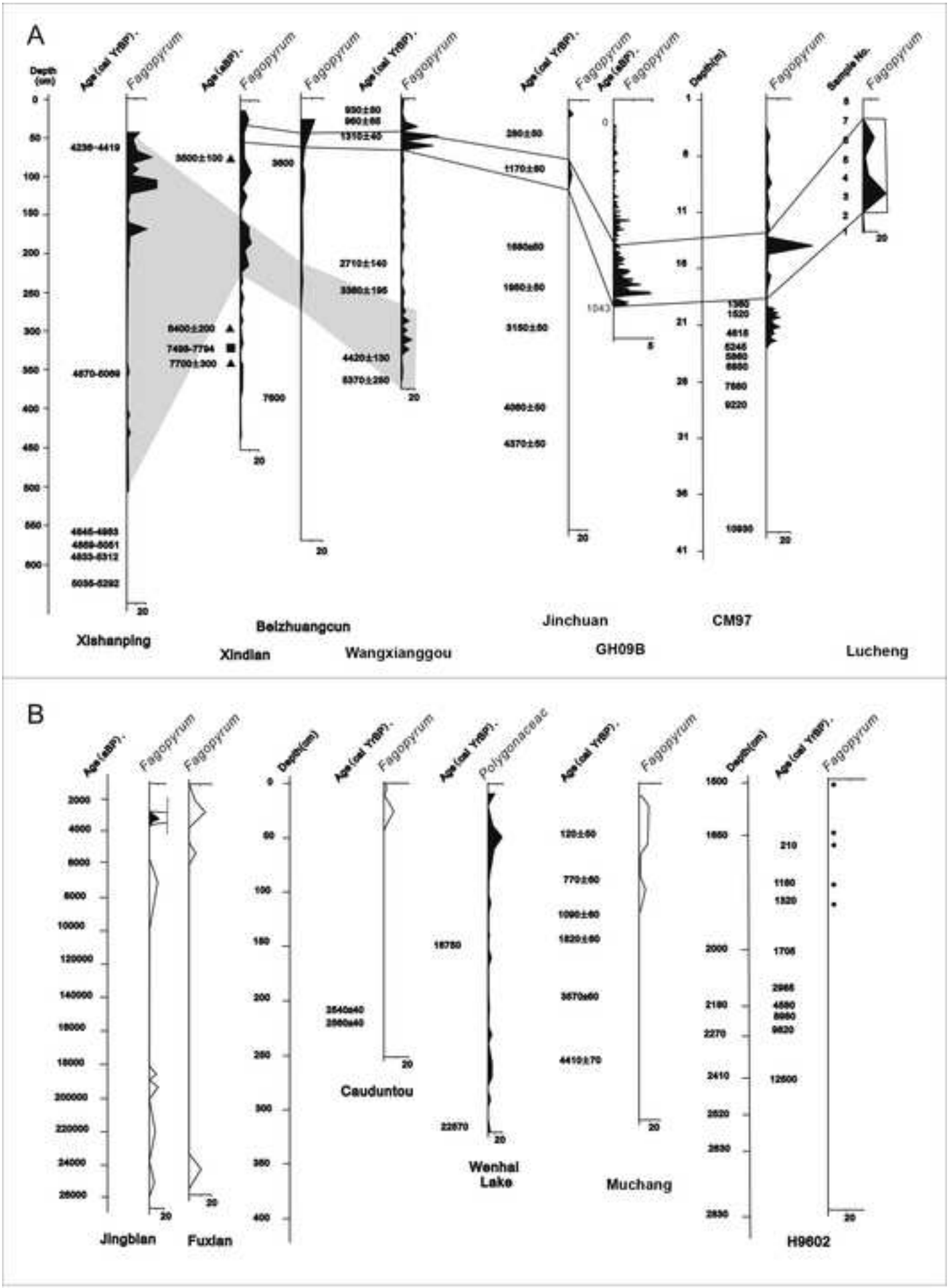

Figure 2

Click here to download Figure Fig_2revised_HVH210717.tif

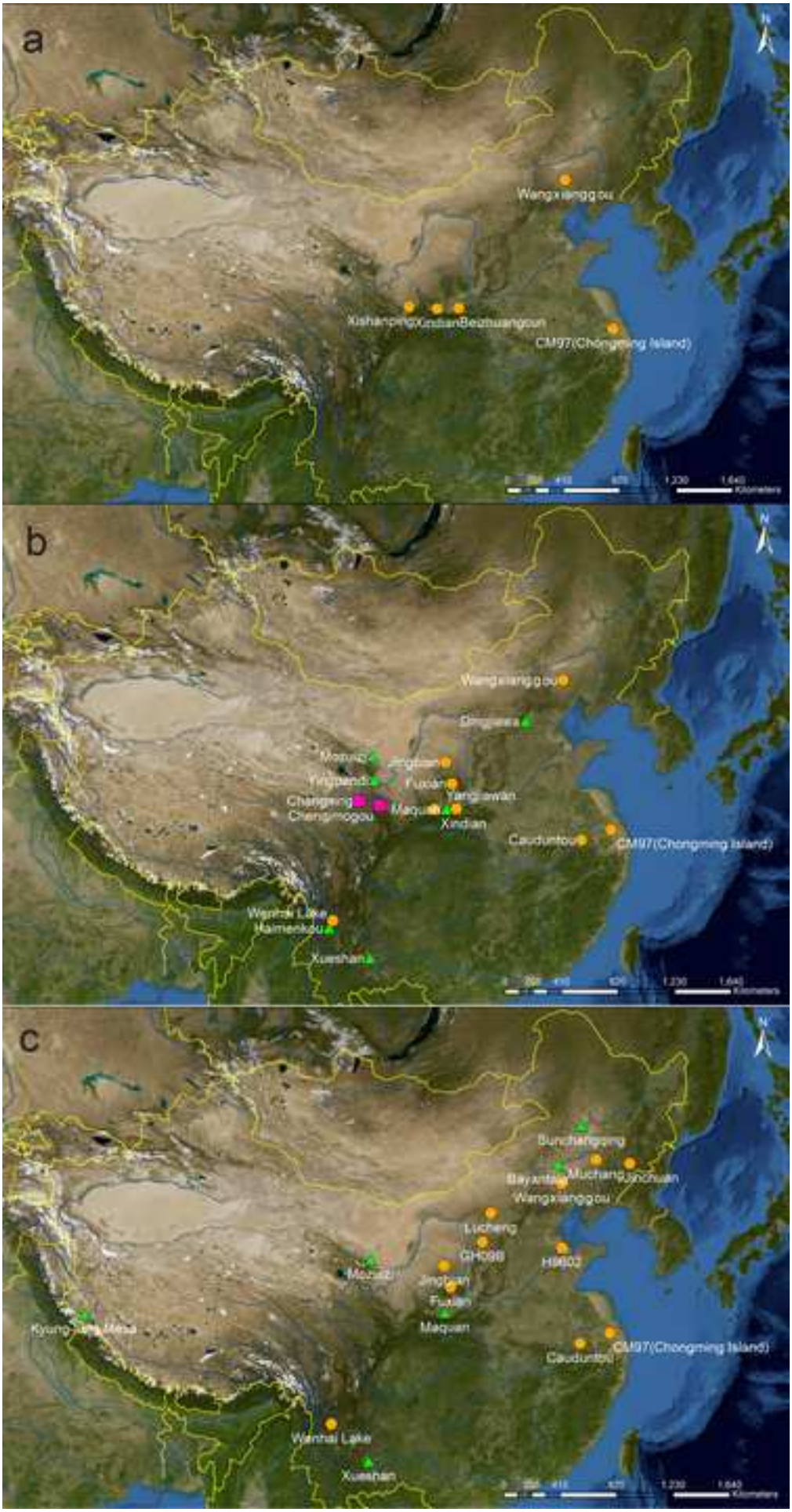

Figure 3

Click here to download Figure BuckwheatGeneralcol_Fig3flat.tif

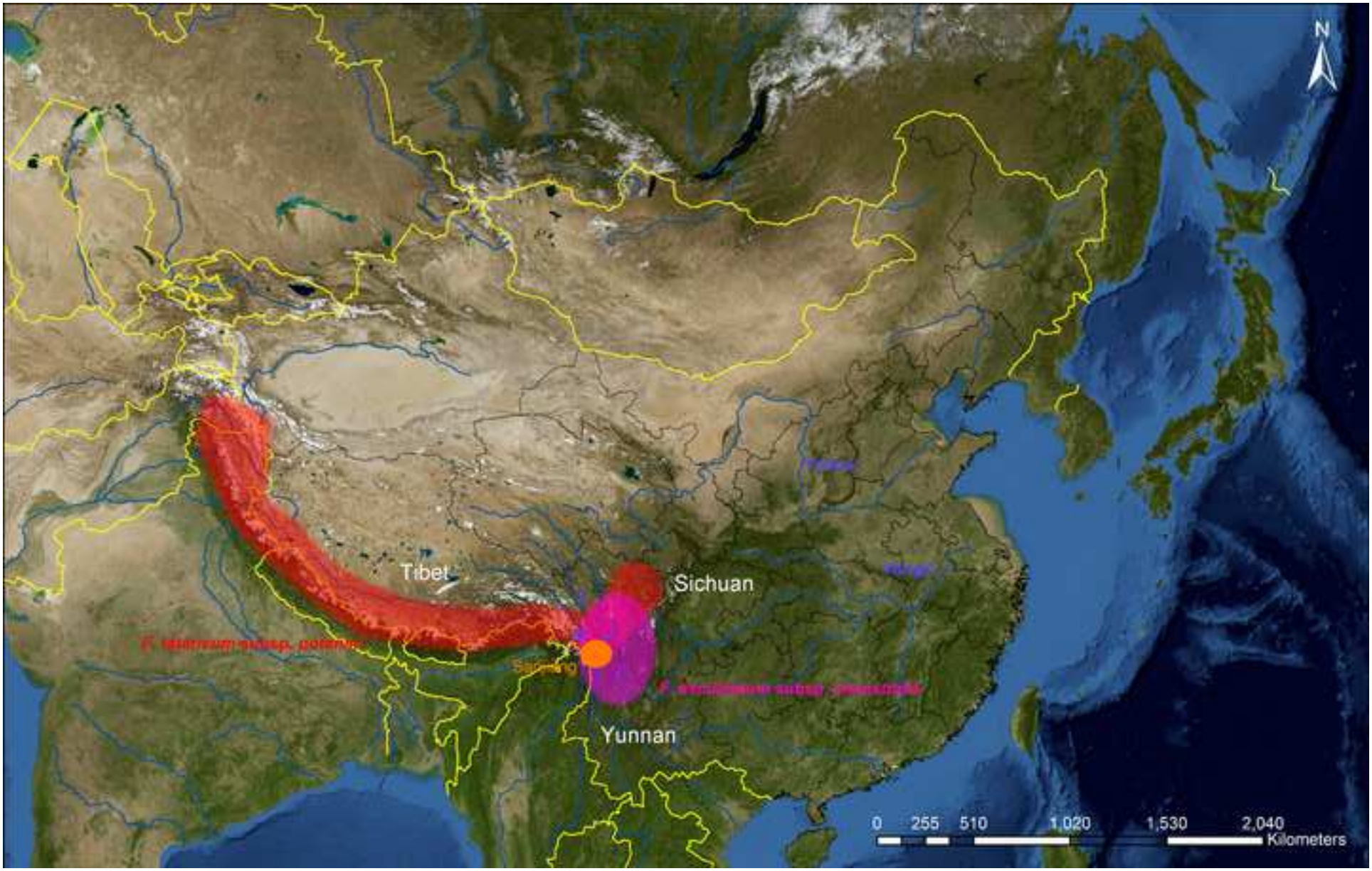

Figure 4

Click here to download Figure Fig_4flat.tif