

Rice: A user guide for archaeologists

From the UCL Early Rice Project.

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1. Kinds of rice

1.1. Wild rices

Asian cultivated rice, *Oryza sativa*, is diverse a complex species closely to related to, and interfertile with, two wild rices, the annual *Oryza nivara* and the perennial *Oryza rufipogon* (old synonym: *O. perennis*). It should be noted that some taxonomists/ geneticists do not recognize the separation of *O. nivara* and therefore use *O. rufipogon* in a broad sense. In addition, weedy rices are often referred to *O. rufipogon*, although *O. spontanea* is probably a better term as recent genetic evidence suggests that weedy rices are descended not directly from wild population but either from domesticated rices that have gone feral or hybrids between domesticated *O. sativa* and wild rices. This means that the weedy rices retain some adaptations for agricultural habitats that evolved during domestication but have reverted to adaptations, like seed dispersal through panicle shattering, that are shared with wild rices.

In western Africa, the domesticated *Oryza glaberrima* represents a parallel evolution of rice domestication.

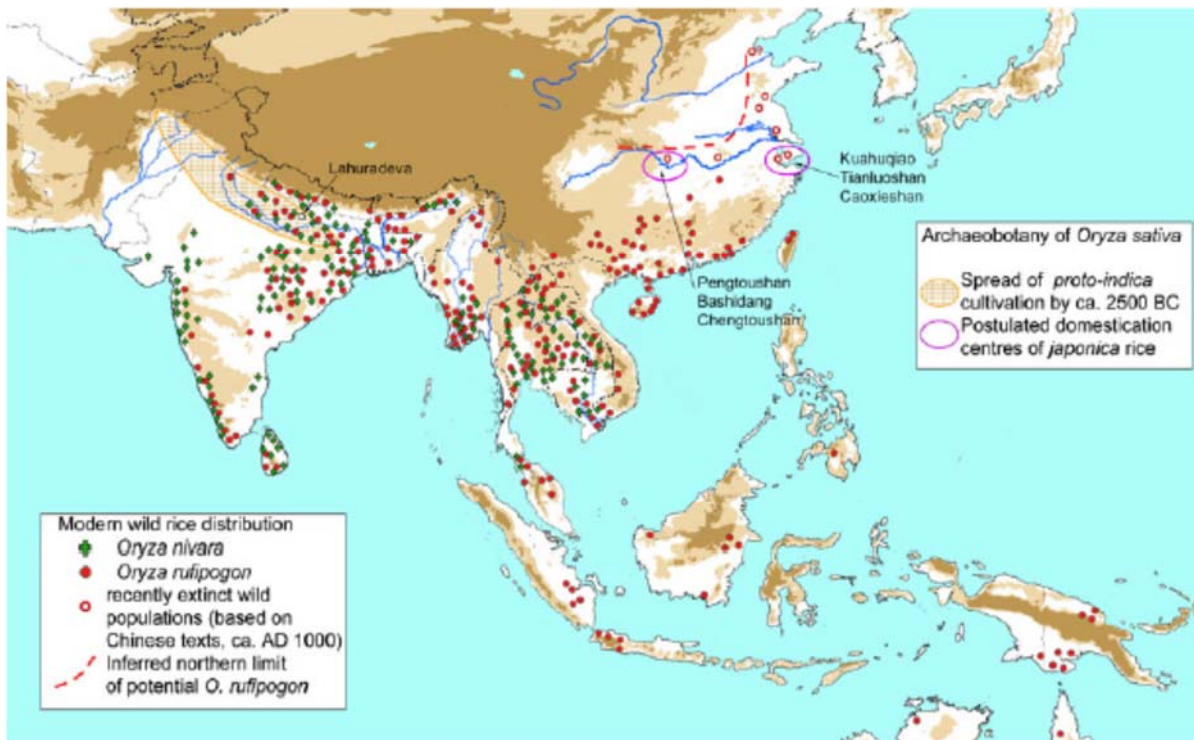
Worldwide there are 20 wild rice species, found in the tropics of South America, Africa, Australia and Asia. In Tropical Asia there are 10 wild rice species (Table 1). Most of these are perennials and grow in shady forest settings. As such they are generally poor grain producers and are unlikely to form extensive stands, and can be expected to have been rare foraged foods. The wide spread *Oryza officinalis* occurs in some more open settings, including disturbed wetland margins and might be expected to have been utilized as a forged food in some cases, and it has indeed been recovered from some archaeological sites in India and China. The only wild rices that occur primarily in full sun are the wild progenitor complex of *O. rufipogon* and *O. nivara*. Which can be expected to occur in larger grain rich stands. The annual *O. nivara* should be a prolific grain producer as it put no investment perennial organs. This made it an attractive resource for foragers.

Modern genetic data indicates that domesticated subspecies *japonica* derives perennial *O. rufipogon* in China. In addition it suggests that *O. nivara* was the main ancestor for domestication of rice in the subspecies *indica* and *aus*, although genes flow from the *japonica* subspecies was also important (Choi et al. 2017).

Table 1. Wild rices of Asia (after Vaughan 1994)

| Species | Distribution | Habitat | Growth habit and light conditions |
|--|---|--|--------------------------------------|
| <i>Oryza granulata</i> | India, Nepal, Sri Lanka, Myanmar, China, Laos, Thailand, Vietnam, Cambodia, Indonesia, Philippines | In moist deciduous forests (e.g. Indian teak forests), bamboo thickets, near water holes | Perennial, full shade |
| <i>Oryza longiglumis</i> | Papua New Guinea, Irian Jaya | Forests and swamps | Perennial, full shade |
| <i>Oryza meyeriana</i> | Thailand, Indonesia, Malaysia, Philippines | Dipterocarp forests by streams | Perennial, full shade |
| <i>Oryza minuta</i> | Philippines, Papua New Guinea | Sago swamps, or fertile alluvia | C |
| <i>Oryza nivara</i> [wild progenitor of crops] | South Asia and mainland Southeast Asia (see map below) | Shallow, seasonal water in monsoon season | Annual, full sun |
| <i>Oryza officinalis</i> | India, Nepal, Bangladesh, Myanmar, China, Thailand, Vietnam, Malaysia, Indonesia, Papua New Guinea, Philippines | Forest margins, edges of rice fields and fruit gardens, seasonally wet areas | Perennial, full sun to partial shade |
| <i>Oryza rhizomatis</i> | Sri Lanka | Tropical forest or scrub, swampy or flooded areas | Perennial, full sun to partial shade |
| <i>Oryza ridleyi</i> | Myanmar, Thailand, Cambodia, Malaysia, Indonesia, Papua New Guinea | Evergreen or dipterocarp forests, on wet soils or in marshlands | Perennial, full shade |
| <i>Oryza rufipogon</i> | South Asia, Mainland and Island Southeast Asia, China | Swamps, marshes, open ditches | Perennial, full sun |
| <i>Oryza schlechteri</i> | Irian Jaya, Papua New Guinea | Undisturbed wet forests and along rivers | Perennial, full sun to partial shade |

The modern/recent distribution of the wild progenitor complex gives some general guidance of where wild rice may have been exploited by hunter-gatherers or brought into cultivation, but it must be kept in mind that some regional populations are likely to have gone extinct (extirpation) over the course of the Holocene due to climate change and human impacts on habitat. Inferences from modern genetics and archaeobotanical evidence suggest that early cultivation leading to domestication began outside the modern distribution: the Yangtze basin for *japonica* and the upper Ganges or Indus tributaries for *indica*.



Map of modern/recent rice wild progenitors (Fuller et al. 2010)

1.2 Domesticated rices: subspecies and varieties

In Asian domesticated rice there are three distinct groups, or evolutionary lineages, that are well supported by modern genetics, *japonica*, *indica* and *aus* (Schatz et al 2014; Choi et al 2017). Traditional subspecies taxonomy has long separated *indica* from *japonica*, but *aus* has only been recognized as distinct from *indica* in the past decade or so (since 2005), and does not yet have a formally recognized subspecies name. These three lineages have partly evolved separately, i.e. with potentially independent processes of early cultivation and domestication or partial domestication, but they have also hybridized. Genetic data suggest that *japonica* evolved many domestication traits that were later loaned to the other subspecies through hybridization. This implies that *japonica* rices were fully domesticated earlier and dispersed to other regions, but it also means that people were using and probably managing local wild rices before domesticated *japonica* diffused to the regions of *indica* and *aus* origins. The leads to the idea that there was non-domestication cultivation or pre-domestication cultivation of *proto-indica* rices in India, and presumably of *proto-aus* rices, perhaps in the Assam region? (see Fuller et al 2010; Castillo et al 2016)

A subspecies division is officially recognized between *japonica* and *indica*, although both subspecies are grown in most regions of Asian today. These have traditionally been recognized through grain shape, and although this is never 100% reliable it remains useful (see below) As implied by genetic *aus* rices fall within *indica* morphological diversity but have a separate history that remains largely unknown. Within *japonica* temperate and tropical subgroups are often recognized. Temperate *japonica* is adapted to higher latitudes and cold winter regions, where its cultivation is restricted to hot summer months. It is hypothesized to have evolved sometime after the Longshan period (post 2000 BC) in Northern China (Fuller et al 2016). The original forms of domesticated rice in the Yangtze basin would be closer to modern tropical *japonica*. Aromatic rice (e.g. Thai Jasmine) as are *japonica* rices, but appear to have evolved from the temperate group.

The main divisions in *Oryza sativa*

A. *Japonica*

- a. Temperate japonica = ch. jing 粳稻 (e.g. short-grained rices, sushi rice)
- b. Fragrant rices group (e.g. basmati, Thai jasmine)
- c. Tropical japonica [includes *javanica*]

B. *Indica* = ch. Xian 籼稻

- a. (ancient) Proto-Indica
- b. (modern) *indica*

C. *Aus* = ch. Xian 籼稻, huang lu 黄陆

- a. Proto-Aus
- b. (Modern) Aus (focused on Assam, Bangladesh, Burma(?), some upland rices of SE/ East Asia, including the “Champa rice” introduced to Fujian in 1012 AD)

D. *Oryza spontanea* – weedy rices. These share shattering with wild rices, and are often placed in *Oryza rufipogon*, but genetic analyses indicate that they evolved from domesticated rice and acquired new mutations that conferred some wild-type adaptations. Morphologically, spikelet bases will look wild, and grains are somewhat smaller than crops, but it is unclear how many other domestication related traits have really reverted to wild type (e.g. among phytoliths, etc.)

Within these groups there are many regional and local varieties. The table below (from Fuller and Castillo 2016) is an attempt to compile and simplify some of this variation. A thorough understanding of this diversity, however, will require lots more archaeological and historical research and further genetic work.

Table 2. A summary of Asian rice variation in terms of ecotypes, cultivar groups and subspecies

| Clade/ taxon | Cultivar group/ ecotype | Geography | Water Conditions | Photoperiod PPD=sensitive ppd=insensitive | Comments |
|--|---|---|---|---|---|
| Subspecies Indica | | | | | |
| <i>indica</i> group | <i>Aman</i> | Bengal/ Bangladesh | Deep water. Upland & irrigated, long seasons (Mar-Nov) | PPD, strong | |
| | <i>Rayada</i> group | Bengal/ Bangladesh. Similar types in Southeast Asia | Floating rices, deepwater | PPD, strong | Early Elongation Ability in intercalary meristems, controlled by one major gene from <i>rufipogon</i> (Hattori et al. 2007). |
| | <i>Cereh / Tjereh</i> | Indonesia | Lowland rainfed | PPD, strong | Usually red pericarp . Note some 'gundil varieties fall here (Oka 1988: 151) |
| | Typical <i>Indica</i> of Southeast Asia, "10th-month rice" of Vietnam | southeast Asian plains | lowland | PPD | Incl. <i>rare</i> Black-pericarp glutinous <i>indica</i> (in Laos & Thailand: Prathepha 2007) |
| | Chinese xian <i>籼</i> rice, some Japanese upland rice | China, Korea, Japan | Upland, shortseason, | <i>ppd</i> to weak PPD | Introduction events unknown, likely multiple |
| | 1 st cropped rice | Taiwan | Lowland. Sown winter and harvested by summer. | <i>ppd</i> | Related to above(?); |
| <i>aus</i> group | <i>aus</i> , dry, short season (Mar-July) | Bengal to Assam, Bangladesh | Lowland, dry | <i>ppd</i> | Centre of diversity: Bangladesh |
| | <i>Boro</i> , irrigated, winter (Oct.-Jan.) | Bengal, Bangladesh | Lowland, dry | <i>ppd</i> | |
| | Deepwater <i>aus</i> , <i>Ashwina</i> group | Bangladesh, Bengal, Manipur | Deepwater rice, offseason. Grown in stagnant permanent water. | <i>ppd</i> | See Oka 1988: 151 |
| | <i>Champa</i> rice, "fifth-month rice" | Vietnam, Thailand | Lowland, dry, rainfed, short season | <i>ppd</i> | introduced to China c. 1100 AD from S. Vietnam (Barker 2011) |
| | Some upland <i>indica</i> types of China, Taiwan, Japan. | China, Taiwan, Japan | Dry/upland, shortseason | <i>ppd</i> | Heritage from Champa rices (above) (cf. Ishikawa et al. 2002). These are included in traditional Chinese xian <i>籼</i> rice |
| Subsp. Japonica | | | | | |
| Tropical <i>japonica</i> group (syn. <i>javanica</i>) | Basic "tropical japonica" | | Probably lowland, floodplains, rainfed | Originally PPD ? | Probably close the original rices of the Lower Yangtze. Includes glutinous (<i>wx</i>) types that evolved secondarily |
| | <i>bulu</i> (=javanica) | Indonesia, Philippines | Lowland, dry (rainfed) | <i>ppd</i> | Awned (<i>bulu</i> means "hair") |
| | <i>gundil</i> (= <i>javanica</i>) | Indonesia | Lowland, dry (rainfed) | <i>ppd</i> | Awnless |
| | <i>nuda</i> | SW China | Dry, lowland or upland | <i>ppd</i> | Awnless |
| | American Long-grain | Mississippi basin | Lowland, irrigated | Mainly <i>ppd</i> | Awnless |
| | African upland | West Africa | Upland, rainfed | Mainly <i>ppd</i> | Awnless; distinct from African rice , <i>Oryza glabberima</i> |
| | Black rice, Lao <i>khao kam</i> | Laos, Vietnam, Thailand | Upland rainfed | <i>ppd</i> [?] | Black-pericarp glutinous (<i>wx</i>) |
| Temperate <i>japonica</i> group (syn. <i>sinica</i>) | Chinese <i>jing</i> <i>粳</i> rice | China, Korea, Japan | Lowland, usually irrigated | PPD | Included many glutinous (<i>wx</i>) and some non-glutinous (<i>Wx</i>). |
| | Short-grained California rice | California | Lowland, irrigated | PPD | |
| | Risotto, paella rices | Mediterranean Europe | Lowland, irrigated | Mainly <i>ppd</i> | Italian Arborio is a glutinous (<i>wx</i>) type; Carnaloni is non-sticky (<i>Wx</i>). (cf. Cortois et al. 2011) |
| | Dian-Chi Lake deepwater rice | Yunnan | deepwater | PPD (?) | Recently extinct (Oka 1988: 217) |
| Aromatic group [=frag] | e.g. Indian <i>basmati</i> , Iran <i>sadri</i> , Thai jasmine, <i>hom</i> rices of Laos | SE Asia, South Asia, Iran | Mostly Lowland, irrigated | PPD or <i>ppd</i> | Mainly derived from temperate <i>japonica</i> <i>BADH2</i> mutation group (Kovach et al 2009). Lao fragrant rices include waxy and non-waxy (Appa Rao et al. 2006a) |

2. Cultivated or Domesticated? Agriculture? Definitions and potential indicators

Domestication = morphological (genetic) change in plants. **A status of the plant.** A similar “domestication syndrome” across many crops (as recognized by Karl Hammer 1984; Harlan et al 1973; see Fuller 2007). This is a population process, evolves to fixation across alleles and traits

This includes Changes in **seed dispersal & germination** processes which can leave markers in archaeobotanical evidence in terms of **spikelet bases, grain shape, and husk phytoliths.**

Most important is reliance of humans for seed dispersal, which comes about through changes in the **spikelet base** that make plant easier to harvest and reliant on human harvesters.

Other changes take place to growth habit: taller, more erect plants; annual instead of perennial. These are less readily seed archaeobotanically, but may affect leaf size and leaf maturation cycles, that in turn may manifest in changes on **bulliform phytoliths** from the leaves. But this is still poorly understood in terms of the role of genetic changes and environmental influence. Changes in habit have also been inferred from evidence for field systems that appear best suited to erect rather than spreading plants in the archaeological sequence of the Lower Yangtze (see Fuller and Qin 2009; Weisskopf et al 2015; Fuller et al 2016)

Cultivation = human practices, including soil clearance, tillage, planting, weeding, harvesting. **A behavioural repertoire of human society.** This may be small scale, and it may involve cultivation of morphologically wild plants. In the beginning all cultivation is *pre-domestication cultivation*. Current archaeological data suggest that domestication traits evolved in crops over a period 2000-4000 years (Fuller et al 2014). The main evidence for inferring pre-domestication cultivation does not come from any trait of the crops, but from evidence for associated arable weed flora, large scale storage, tillage tools, or other indirect inferences. Morphologically domestication species, especially non-shattering cereal require cultivation and therefore the present of domesticated rice implies cultivation, but cultivation does not necessarily imply domestication.

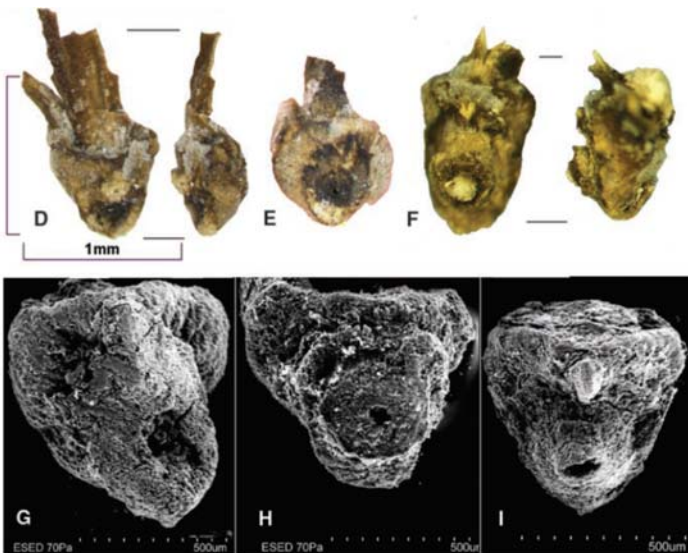
Cultivation may be small scale and economically unimportant. Therefore it is useful to think of **agriculture** as something distinct, i.e. cultivation on a larger scale, with major economic reliance on the cultivated species. This notion was clarified through the writings of David Harris (e.g. Harris 1989; Harris and Fuller 2014). **Agriculture** usually is focused on already domesticated species. Thus the ultimate transition from foraging economies to agricultural economies may be much later than the start of cultivation, and even later than domestication (see discussion in Fuller et al 2014; Stevens and Fuller 2017). Agriculture represents transformations to the economy and at the landscape scale. Early cultivation before agriculture is often discussed in terms of “low level food production” (Smith 2001).

3. Spikelet bases

These are the most diagnostic remains in terms of domestication status. They also are a routine dehusking waste and therefore provide information on crop-processing. For recovery, flotation through 0.3 or 0.25mm mesh is recommended, although most will be found in sorting the >0.5mm fraction.



Top to bottom: Domesticated, wild, “immature” (green-harvested OR domesticated but probably temperate japonica with *sh1* mutation). (From Fuller and Qin 2008)

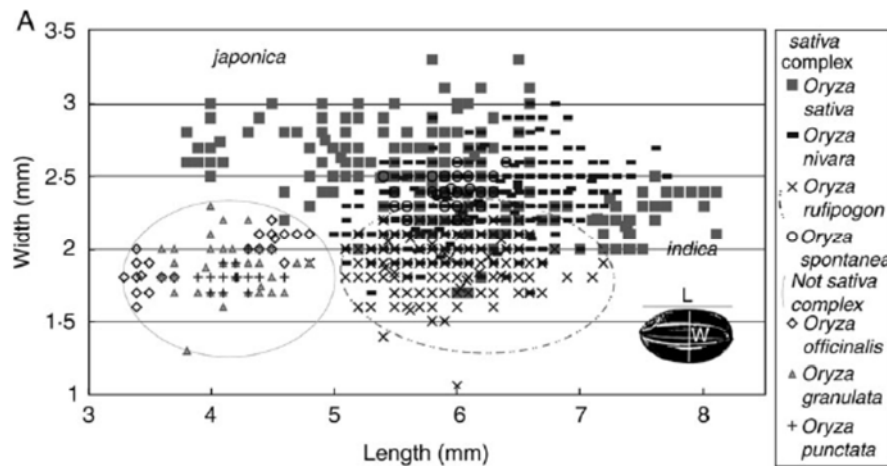


Left to right: domesticated, wild, immature (from Fuller et al 2009)

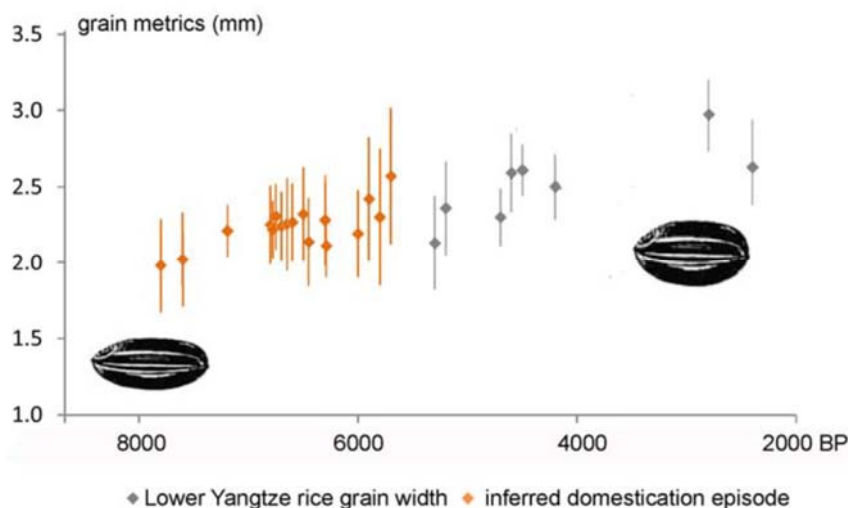
Note that some authors (e.g. Zheng et al 2007) included the “immature” type with domesticates, but this appear to be based on a mis-understanding of the underlying genetics by attributing these to the temperate japonica *qsh1* mutation, evolved long after domestication in a subset of east Asian rices (see Castillo et al 2016; Ishikawa et al 2017).

4. Grain metrics

Grain metrics are probably the most widely reported and easiest to collection quantitative data on rice. However, calibration based on the magnification level is important to avoid inaccurate results (some of which exist in the literature). Grain measurements change during domestication, with grains tending to get larger, especially wider and thicker. Grain shape, indexed by Length-to-Width ratio also tend to differ between wild and domesticated and between subspecies of domesticated rice. Metrics, however, always present a range and therefore comparison need to be made on an assemblage basis and judged keeping in mind potential overlap and therefore some proportion of false assignments.

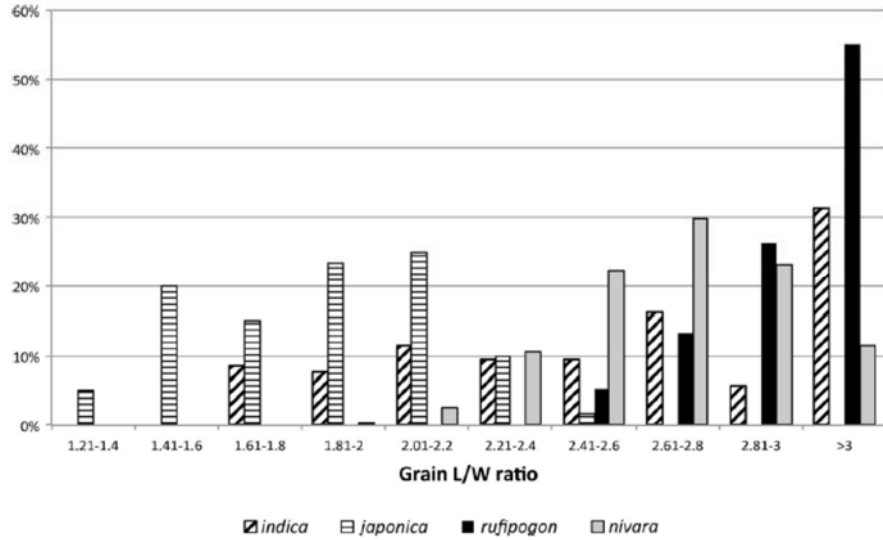


Plot of length and width measurements on reference material of domesticated and wild rices (Fuller et al. 2007). The above graph demonstrated that wild rices outside the complex of *sativa* and its wild progenitors are readily separated, and that domesticated rices tend to be larger, usually wider and occasionally longer than their wild progenitors.

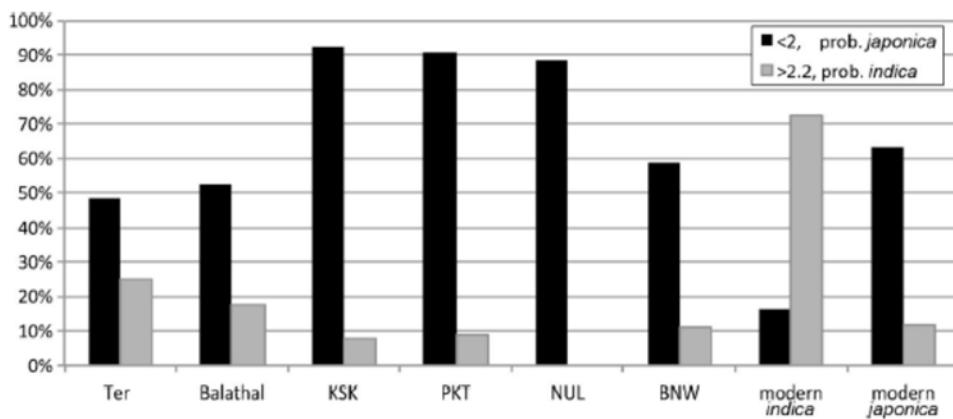


Size change during rice domestication illustrated with grain breadth on charred grains (average and standard deviation). (From Stevens and Fuller 2017). This graph shows that early cultivated rice, prior to be domesticated average around 2mm grain width or less (after charring), whereas fully domesticated rice have averages or substantial proportion of the population >2.4mm wide (after charring)

Fig. 8 Comparison of L/W ratios of domesticated rice (*indica* and *japonica*) and wild rice (*rufipogon* and *nivara*). Modern reference material after Fuller et al. 2007, but *indica/japonica* assignment reassessed based on latest IRRRI data; *aus* population excluded



The above plot of grain L/W ratios demonstrated that domesticated *japonica* subspecies tends to be short and fat (<2.2), whereas subspecies *indica* is longer (>2), with some overlap. Wild rices also have very high L/W ratios as domestication has favoured grain fatness (Fig. 8 from Castillo et al 2016).

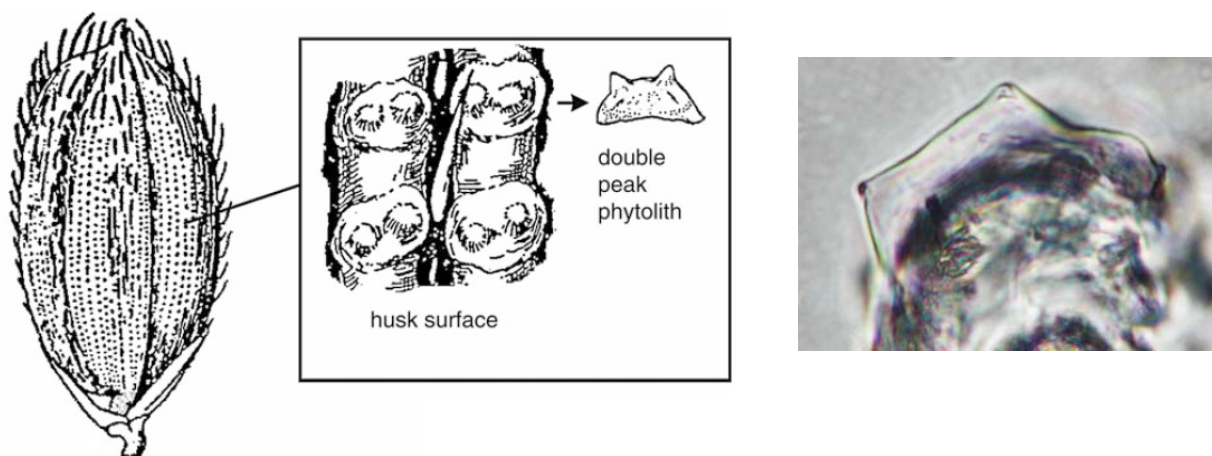


The chart above (from Castillo et al 2016) illustrated how assemblage may be assessed by compiling grain L/W ratios, ignoring those between 2 and 2.2 (the core overlap zone) and considering just those <2 or >2.2. The application on modern material suggests that we can expect correct classification about 85% of the time. Thus Southeast Asian assemblages (KSK, PKT, NUL, BNW) suggest more or less pure *japonica*. Assemblages like those from Ter and Balathal suggest a mixture of *indica* and *japonica*. These grain metric results are very close to those derived from ancient chloroplast DNA from the same assemblages.

5. Husk phytoliths

The husks of rice are full of silica and often all the cells of silicified. The rows of cells on the rice husk include trapezoidal phytoliths the upper corners of which often form into peaks, as in the image below. These are diagnostic of the genus *Oryza*, although a few similar forms may occur more rarely in other grasses. These are often the most frequent form of rice phytolith. Because these derive from husk, disposed of after dehusking, they are an indicator of dehusking waste and useful in crop-processing studies. (See Harvey and Fuller 2005)

Size and shape of these varies and has been suggested to be useful in tracking domestication through measurements on populations (Zhao et al 1998), although these are not definitive because of large degrees of overlap and because cell size is also impacted by environmental conditions. An explanatory mechanism for how these change during domestication has never been satisfactorily elaborated, although some relationship to grain size change seem plausible.



The proposed method for looking at double peak cells and domestication uses 5 measurement on each phytolith as defined below, left (from Zhao et al 1998)- note that H is measured twice on each side of the phytolith. Some of these are then used in squared form. These are combined in discriminant functions that are meant to assign individual phytoliths to like domesticated or wild (i.e. if the domesticated score is greater than the wild score: formula at right)

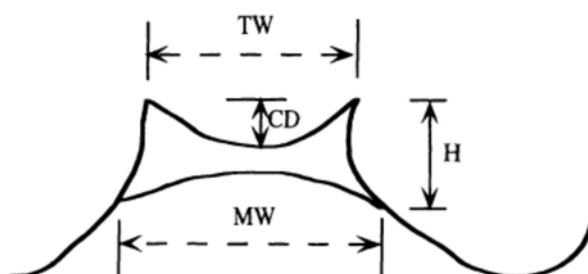


Fig. 2. Double-peaked glume cell measurements.

Prediction of domestic rice

$$= -19.027 - 0.129(TW) + 0.116(MW) + 0.676(H1) + 3.101(H2) + 0.921(CD) - 0.028(H1^2) - 0.079(H2^2) - 0.047(CD^2)$$

Prediction of wild rice

$$= -14.124 - 0.085(TW) + 0.113(MW) + 0.7(H1) + 2.288(H2) + 1.338(CD) - 0.021(H1^2) - 0.066(H2^2) - 0.067(CD^2)$$

As originally developed, Zhao et al (1998) reported correct classification in their modern reference set was correct in >70% of test cases. The formulae were developed by taking Bayesian approach to discriminant function analysis. In an attempt to employ and extend this work, we attempted to

replicate this in London with modern rice accessions, but found a correct identification in only 44% of cases (Harvey 2006). In addition measurements on phytoliths from Chalcolithic sites in Orissa (Gopalpur and Golbai Sassan) predicted a majority wild rice and on 39% domesticated. However these sites (dating 1500-1000 BC) have spikelets bases that indicate fully domesticated rice (100% non-shattering at Gopalpur and ~70% at Golbai out of a small sample size: unpublished UCL data from Kingwell-Banham 2015). This indicates that this phytolith discrimination method is unlikely to work in India, raising questions about what biogeographic contexts it would be useful in, if at all. One problem is that some of the variation in ancient cultivars may not be well represented in modern landraces. Indeed some of the measurements on archaeological phytoliths from Orissa fell outside the range of modern material, both wild and domesticated.

Also, against this method are two applications in China that have yielded results that are illogical with regards to what is known about rice domestication.

- 1) As applied by Zhao (1998) to Diaotonghuan cave in Jiangxi and change from predicted wild in pre-ceramic layers and predicted domesticated dominance in early ceramic layers was found. At the time Zhao wrote this it was assumed that the advent of pottery was Neolithic and sometime in the early Holocene, but recent dating work on nearby Xianrendong and another South Chinese cave, Yuchanyuan, indicate the ceramics began to be produced around the Last Glacial Maximum or just after 18,000-16,000 BP. The ceramics at Diaotonghuan are comparable and thus this would re-date the alleged rice domesticated to ~18,000-16,000 BP, nearly 10,000 years earlier than potential sedentary, agricultural villages. A more plausible alternative explanation is that rice husk cells (and grains) change shape in response to the major and rapid change in climate and atmospheric carbon dioxide levels that took place after the LGM
- 2) As applied by Itzein-Davey et al (2007) in the Lower Yangtze region to a stratigraphic sequence of Qingpu rice bulliforms dating between 2300 BP and 1800 BO (i.e. Warring State through Han Dynasty era), they found the majority of double peaks were predicted as wild, often as much as 80% in some samples. Rice was certainly morphologically domesticated in the Lower Yangtze long before this and we would expect fairly intensive rice agriculture during Han times. These results also call into question this index.

Nevertheless plotting double peak measurements over a time series may provide a line of evidence for rice that is changing and evolving morphologically. This has recently been applied in South America to argue for a lost rice domestication in the Amazon (Hilbert et al 2017).

In the context of Chinese rice domestication the study of Wu et al (2014) demonstrated both that wild and domesticated predictions are very mixed on sites of early cultivation but also that there is a trend for more double peak cells to fall towards the apparently domesticated end of the spectrum through time.

The bottom line: Variation in husk phytoliths exists but its significance in terms of domestication, varietal changes, cultivation ecology remains unclear and deserves further study.

6. Bulliform phytoliths

Fan shaped bulliform phytoliths form along the veins of rice leaves. Rice (genus *Oryza*) has a distinctive shape although some fanlike bulliforms do occur in other grasses, but with different shapes. These are also sometimes referred to “motor cells” as these cells function, when alive, to fold and unfold the leaf and thus to control sunlight exposure, which in turn relates to amounts of photosynthesis and water evaporation from the leaf. Once they are silicified and have become phytoliths they stop functioning so this tend to mean that the phytoliths come from older rather than younger leaves.

These are relatively large for single celled phytoliths (28-40 μm) and therefore fairly easy to recover and to spot in phytolith slides.

Bulliforms have suggested to be useful for tracking domestication, separating subspecies *japonica* and *indica*, and for studying crop processing. Identification approaches relies on measurements and/or counting variation in the number of chips along the scalloped edge of the fan.

In terms of crop-processing they are an indicators of leaf presence (i.e. straw), i.e from harvested rice and/or threshing by-production as opposed to husk phytoliths that represent

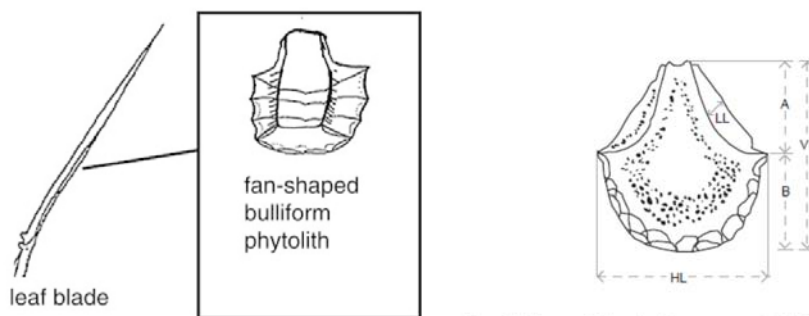
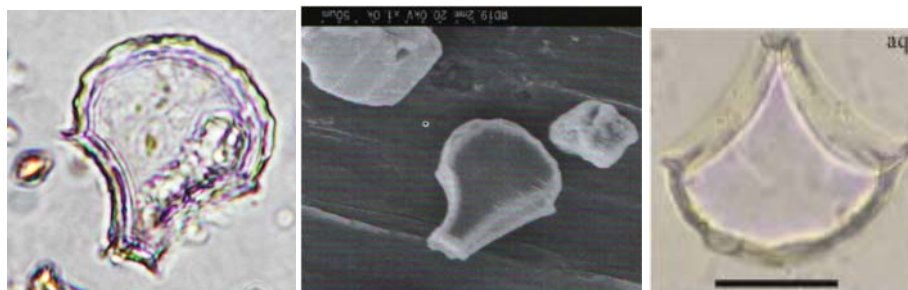


Figure 6.5: Diagram of Fujiwara bulliform measurements (after Fujiwara et al. 1993).

Research pioneered by Fujiwara in Japan identified a spectrum of shapes in these bulliforms suggesting that the narrow “handle” of the fan is relatively longer and then fan shorter in domesticated *japonica* than in wild rice or subspecies *indica*, i.e. the b/a ratio is smaller in *japonica*. They have proposed a discriminant function on the basis of 5 measurements for separating *indica* and *japonica* (Wang et al 1996), below right.

$$Z (PO) = -0.4947VL + 0.2994HL - 0.1357LL + 3.8154b/a + 8.9567$$

(Z (PO) > 0, *indica*; Z (PO) ≤ 0, *japonica*)



Left: Bulliform phytoliths from Neolithic Mahagara, India (from Harvey & Fuller 2005), on the *indica* end of the spectrum; middle: bulliform from Lower Yangtze Nanhebang, China (from Zheng et al 2003a), on the *japonica* end; right modern *japonica* type bulliform from Gu et al 2013

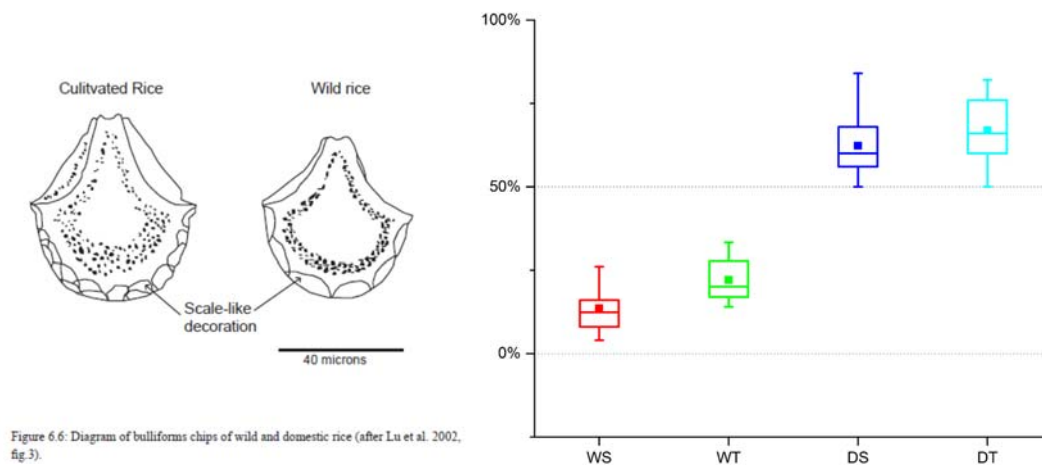
A study of bulliforms from Lower Yangtze archaeological sites suggest that they became large and more pronounced in their *japonica* morphological metrics over time, 5000 and 2000 BC, over the period when domestication was completed and grain size increased (Zheng et al 2003a)

Measurements on controlled experimental crosses indicate the bulliform shape is influenced by numerous genes, with 16 genes (QTLs) suggested, but these QTLs only explain somewhere between 37% and 54% of the variation, suggesting the environment (growing conditions) play a major role (Zheng et al 2003b). No QTLs were correlated with the b/a ratio suggesting this may be largely environmental.

Bottom line on metrics: May be useful for separating *indica* from *japonica* when it can be assumed that rice fully domesticated; and trend may be found alongside domestication. Further work is needed, especially on aus and more variation found in South Asia and more tropical varieties in Southeast Asia.

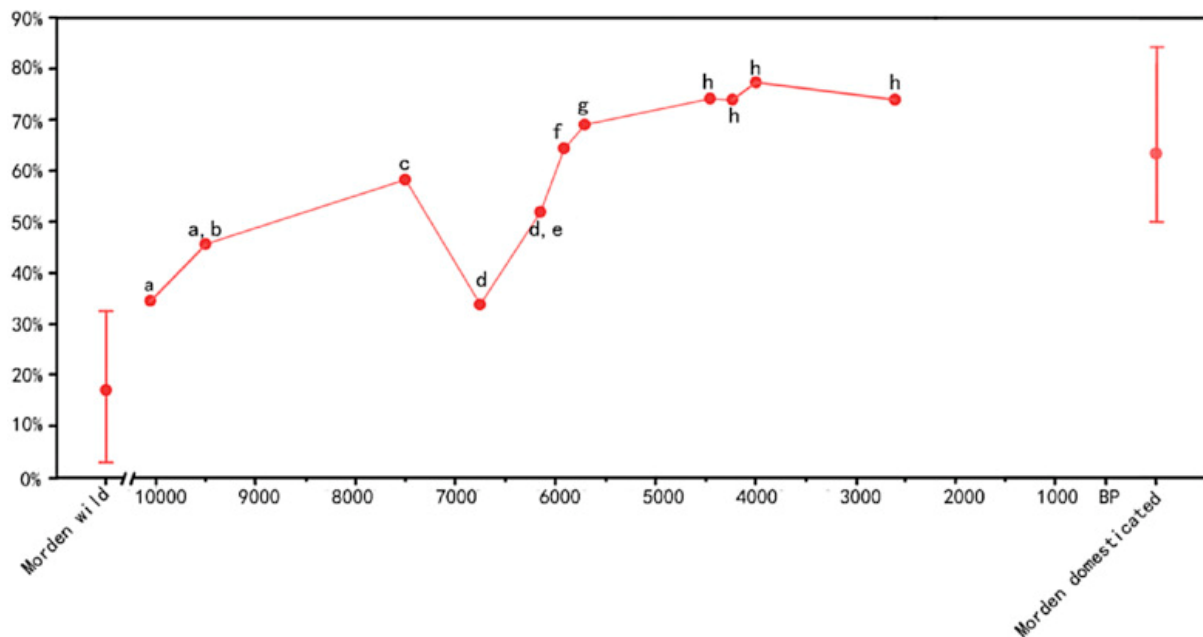
Bulliform scalloped margin: scale counts and domestication

Another approach to documenting bulliforms is to count the “scale-like” facets along the rounded edge of the “fan”. The fans in domesticated rices tend to have more facets. Initially Lu et al (2002) proposed that phytoliths with 9 or more facets are likely domesticated, while less than 9 are wild. This has been backed up by field comparisons of wild and cultivated rices in South China (Huan et al 2015) These studies indicate that example with less than 9 facets occur in cultivated rice and more than 8 occur in wild rice but the frequency differences are substantial (see below).



Left: illustration of rice bulliform and facets (“scale-like”) ((Lu et al 2002). Right: % of ≥9 scale-like facets in modern Chinese populations of wild rice (*O. rufipogon*) subtropical (WS), wild rice tropical (WT), domesticated rice subtropical, domesticated rice tropical (after Huan et al 2015)

This means in in time series data assemblages can be use to track changes over time. This is nicely demonstrated in a time series through the Early and Middle Holocene for the Lower Yangtze by Ma et al (2016). It should be noted also that current approach of Ma et al (2016) exclude from counts any assymmetric phytoliths.



Time series of rice bulliform facet counts (% of ≥ 9) from Lower Yangtze sites (Ma et al 2016).

These data show a direction of travel over time that is similar to non-shattering, grain size increase and other indicators. However, much variation is hidden by the fact that difference between 8 facets (very common in wild rices) and 9 facets (probably the most common value in domesticated rices).

In addition, an explanatory mechanism is not yet firmly established, unlike established domestication traits such as non-shattering and seed size. While ~ 16 genes may affect bulliform shape, environmental factors are also essential, and domestication is ultimately about genetic changes that differentiate domesticates from their wild ancestors. Therefore it is essential to understand how much of this shift phenotypic response to environmental conditions as opposed to evolution. Huan et al (2015) suggest that the increase faceting in domesticated rice is due to increased use of leaf folding to control evaporation from leaves. They hypothesize that the erect growth habit of rice and drier growing conditions than wild rice would lead to increased faceting. If this is merely a phenotypic response then it becomes a less useful *domestication* indicator. But this can also be questioned, as ecological indices (see below) suggest that early rice in China was grown under wet, wild-like conditions (at least at Tianluoshan) and that erect growth habit and drier conditions occurred only from the later Majiabang period, and then returned to very wet conditions (Weisskopf et al 2015). So further work is needed to understand genetic and phylogenetic signal in bulliform facet variation as opposed to difference due to habitat.

The bottom line: on the whole this looks like a promising and worthwhile complementary dataset, but it remains no substitute for morphological domestication data from macro-remains, as other environmental factors seem to be at play.

In addition it is worth noting some studies that question the reliability of this approach.

Applications in India that raise questions over the universal applicability of this approach.

- 1) Harvey (2006) counted this chips on bulliforms from Chalcolithic sites in Orissa (Golbai Sassan and Gopalpur, dating 1500-1000 BC), both of which have domesticated rice (based on spikelet base data), and wet field ecology (further work by Kingwell-Banham 2015). In this material the average number of chips is 8.6 and "wild" chip counts (< 9) outnumber those with 9 or more, and thus bulliforms predict 56% wild (a higher level than any of the reference domesticated

rice samples in China by Huan et al. 2015). This is out of agreement with the non-shattering spikelet base data, weed flora and large village context all of which indicate fully domesticated, wet-rice based agricultural economies.

- 2) Saxena et al (2006) applied this to phytoliths from the lake sedimentary sequence at Lahuradewa, next to a Neolithic site in the Ganges plain of the same name. They reported both wild and domesticated bulliforms through the core in roughly equal proportions between 8600 and 3500 BP after which wild forms declined. While Lahuradewa is often discussed as an early site of rice cultivation in India, critical review suggests this was primarily wild rice gathering prior to ca. 2000 BC or so after domesticated rice became available through hybridization with japonica (the proto-indica hypothesis) (Fuller and Qin 2009; Fuller 2011; Murphy and Fuller 2017). Thus the phytolith data here appear out of agreement with macroremains and rice genetics.

Applications in Southeast Asia and China that raise questions over the universal applicability of this approach.

- 3) The initial introduction of this approach (Lu et al 2002) included a dataset on a sea floor core between China and Taiwan, an area that would have been flooded after the Last Glacial. This palaeoenvironmental sequence produced rice phytoliths- and rice would be expected in fresh water wetlands in such areas when they were above sea level. However, this included substantial numbers of the “domesticated” type. Is it realistic to believe that domesticated rice was already cultivated in flooded regions of Southeast China during the Last Glacial (LGM)? If so, then it must have been a dead-end experiment, as the evolution of domesticated rice is documented over the course of the Early and Middle Holocene, starting anew apparently. However, if the bulliform faceting is responding to environmental conditions this LGM population may have nothing to do with human selection and domestication
- 4) The Loagan Bonut pollen core on Borneo near Niah Cave produced substantial quantities of rice bulliforms with high facet counts (i.e. “domesticated”) around 8000-7500 BP, but not later (Hunt and Premathilake 2012). Is this also to be interpreted as a lost domestication of rice? Or could this be a particular situation in terms of environmental conditions that encouraged wild rice and more leaf folding and bulliform faceting?

Cases 2-4 have all been presented as cases of early farming, which would represent “stealth domestication” without other clear indicators for cultivation over millennia leading to these. In all cases phenotypic plasticity in response to environmental change needs to be considered.

7. Ecology: Wet or Dry?

Rice can be grown along a spectrum in terms of wetness and labour investment. Dry rice is still comparatively wet compared to other crops, requiring rainfalls of at least 800 mm during the growing season. In contrast barley and various drought tolerant millets are routinely grown with 300-400 mm of rainfall. Wet rice tends to require more labour but also to provide increased yields. A good yield in rainfed rice would be 1 ton per hectare, and probably less. Whereas one would expect 1.5-3 or even much more on wet rice on traditional methods

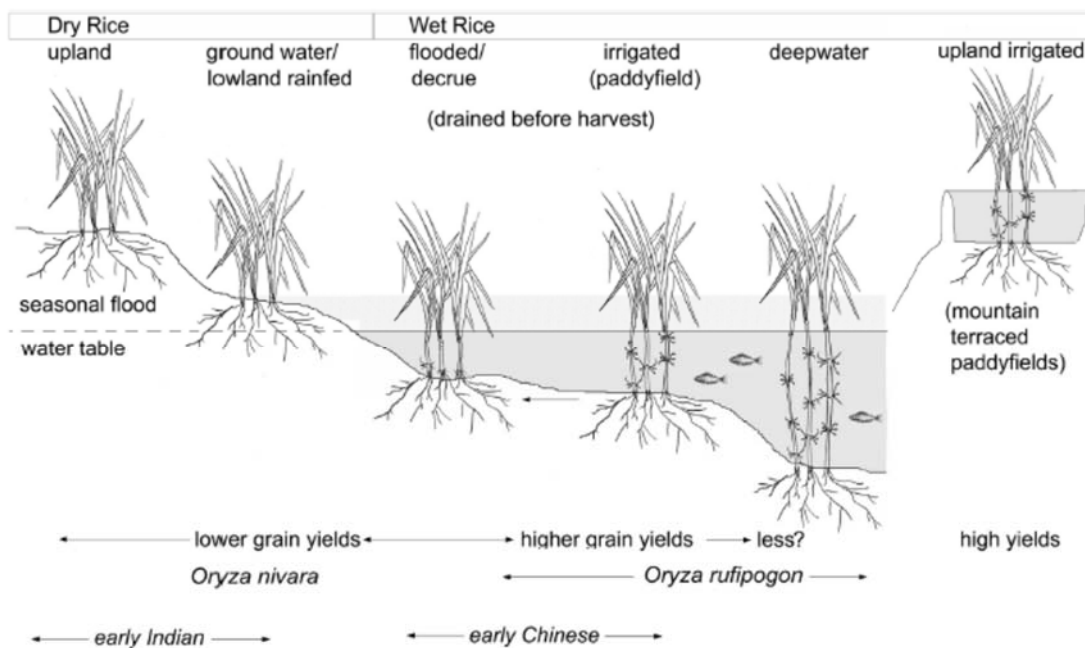


Fig. 1. Rice cultivation systems.

Schematic spectrum of dry to wet rice ecologies (Weisskopf et al 2014).

One of the major aims of the UCL Early rice project has been to improve methods for distinguishing cultivation ecologies along this spectrum through the ecology of the weed flora represented through archaeobotanical seed assemblages and/or phytolith assemblages (Fuller and Weisskopf 2011), and the chart the distribution of these through space and time (Fuller et al 2011).

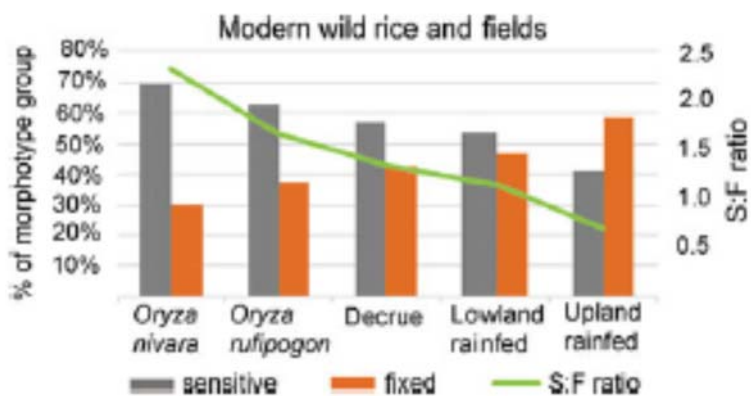
9. Phytolith assemblages and ecology

While weed flora is represented in phytolith assemblages it rare that once can identify phytoliths below very broad families (e.g. Commenlinaceae, Cyperaceae) or subfamilies (panicoid vs chloridoid grasses). Therefore we have looked other more physiologically based indices.

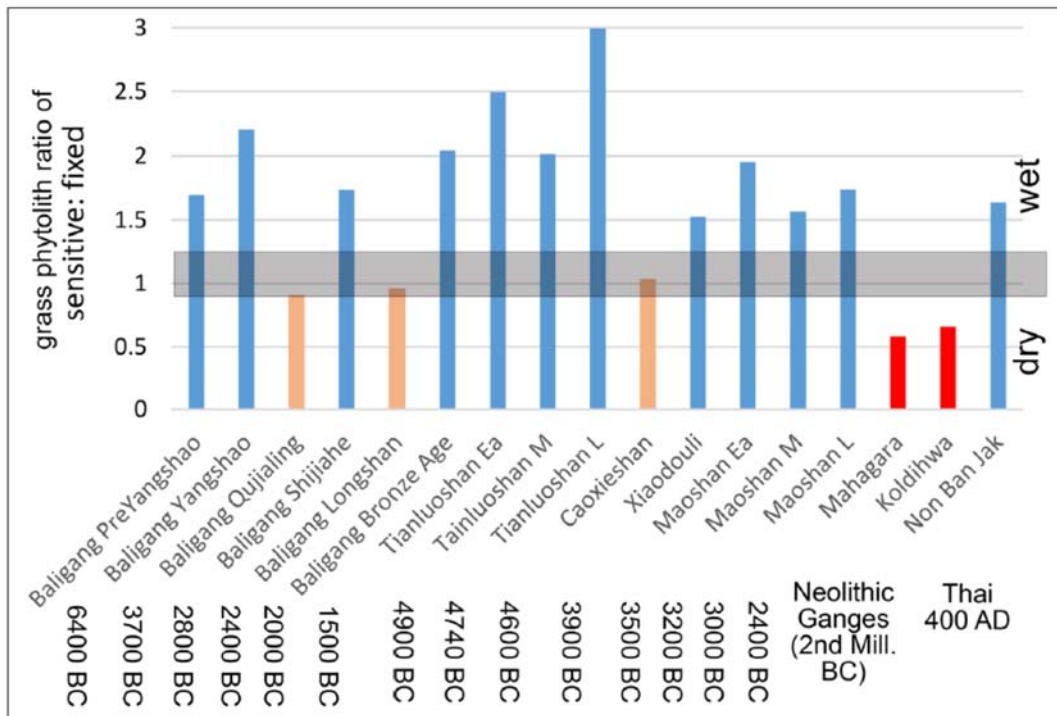
One particularly promising index is the sensitive:fixed ratio among grass phytoliths. In this the taxonomic identity of the grass is not important, but instead the source of the phytolith in terms of part of the plant tissue of the plant, separating those which normally always silicify and those which only silicify later in the plant life cycle or under an excess of evaporation, which comes about due to excessive water.

The table below divides grass phytolith types into these two classes (Weisskopf et al 2015)

| Dry or fixed, passive (short grass cells) | Wet or sensitive, active (long grass cells and stomata) |
|---|---|
| Rondel | Long smooth |
| Round rondel (<i>Stipa</i> type) | Long sinuate |
| Saddle | Long polyhedral |
| Bilobate | Long echinate |
| Scooped bilobate | Stomata |
| Square bilobate (<i>Setaria</i> type) | |
| Cross | |
| Collapsed saddle | |



Sensitive vs. Fixed occurrences in modern soils associated with different rice systems or wild rice in India (Weisskopf et al 2015).



The sensitive: fixed grass ratio at various sites/phases averages across all phytolith samples in the phase (after Fuller et al 2016).

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