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ORIGINAL ARTICLE

Documenting domestication in a lost crop (*Polygonum erectum* L.): evolutionary bet-hedgers under cultivation

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Abstract This study uses morphometrics and digital image analysis to document domestication syndrome in an annual seed crop, *Polygonum erectum* L. (erect knotweed), which was cultivated by Native Americans for c. 2,500 years in eastern North America. This plant is one of several seed crops referred to as the Eastern Agricultural Complex, a pre-maize agricultural system that supported societies in a core area centred on the central Mississippi valley for millennia. The extinct domesticated subspecies *P. erectum* ssp. *watsoniae* N. G. Muell. described here, exhibits some classic markers of domestication, including larger fruits and reduced germination inhibitors in comparison to its wild progenitor. Domesticated *P. erectum* also exhibits greatly reduced germination heteromorphism. Germination heteromorphism is the classic example of evolutionary bet-hedging in plants: wild *P. erectum* sacrifices maximum fitness per generation for a reduction in fitness variance over many generations. It does so by producing two different types of fruits: ones that germinate immediately in the spring after they are produced (smooth morphs), and ones that remain in the soil seed bank for one or more growing seasons before germinating (tubercled morphs). Tubercled morphs allow populations to recover after adverse events. Under cultivation, the selective pressures that maintained this strategy were relaxed as humans saved seeds and created predictable microenvironments for seedlings, resulting in homogenous harvests and reliable germination for ancient farmers.

Keywords Domestication · Morphometrics · Eastern Agricultural Complex · Origins of agriculture · Evolutionary bet-hedging

Introduction

Human mediated selection alters the bodies and behaviours of plants and animals. This process forms the core of most definitions of domestication. Domesticated species or subspecies are described in terms of how their morphology and behaviour differs from that of their wild ancestors. For some classes of domesticated organisms, a clear syndrome of domestication exists. Cereals are the classic example. Domesticated cereals are annual grasses cultivated for their seeds that usually differ from their wild ancestors in several key respects. In comparison to their progenitors, they usually have larger seeds, reduced germination inhibitors, non-shattering seed attachments, simultaneous fruiting, and more determinate growth habits (Harlan et al. 1973). Some aspects of this domestication syndrome also appear in other small-seeded annual crops that are not grasses (Fritz 1984; Fritz and Smith 1988; Langlie et al. 2011; Smith 2014). The processes by which these changes and other unique domestication syndromes could have evolved, through both unintentional and intentional selection by cultivators, have been theorized (for example, Asouti and Fuller 2012, 2013; D'Andrea 2008; Flannery 1973; Harlan and De Wet 1965; Rindos 1984; Smith 1992) and in some cases explored experimentally (Abbo et al. 2011; Hillman and Davies 1990; Piperno et al.

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2015). A few of the key characteristics of domesticated annual seed crops are commonly observable in the archaeological record: increased seed size, reduced germination inhibitors, and more robust seed attachments. This study documents a unique domestication syndrome in an annual crop, *Polygonum erectum* L. (erect knotweed).

Beginning c. 1900 BCE, native peoples in eastern North America (ENA) began to cultivate annual seed crops. These pre-maize crops are collectively known as the Eastern Agricultural Complex (EAC) (Ford 1985; Fritz 1993; Smith 1992, 2006; Smith and Yarnell 2009; Yarnell 1993). Two cereal crops were cultivated, *Phalaris caroliniana* Walter (maygrass) and *Hordeum pusillum* Nutt. (little barley) (Fritz 2014; Hunter 1992). The domestication of *H. pusillum* is a matter of debate. Hunter (1992) found equivocal evidence for morphological changes in seeds from archaeological sites in ENA, including non-significant increases in grain size and other qualitative changes. *H. pusillum* was also grown in the southwest, where Adams (2014) has recently summarized the evidence for domestication. She argues that the predominance of hull-less charred caryopses in the archaeological record constitutes evidence of naked grains, a trait that also became predominant in Old World *Hordeum vulgare* L. (domesticated barley). No clear morphological differences have been noted between archaeological assemblages and modern plants in ENA for maygrass, but contextual evidence amply demonstrates that it was cultivated for centuries (Asch and Asch 1985b). Three EAC crops exhibit domestication syndromes: *Helianthus annuus* L. var. *macrocarpus* Cockerell (sunflower), *Chenopodium berlandieri* Moq. ssp. *jonesianum* Smith and Funk (goosefoot), and *Iva annua* L var. *macrocarpa* S.F. Blake (sumpweed) (Blake 1939; Heiser 1954; Smith and Funk 1985; Smith 2014). The domestication status of the final important crop of the EAC, *Polygonum erectum*, has remained uncertain for decades. Asch and Asch (1985a, b) first speculated that *P. erectum* may have been domesticated, based on their analysis of a Late Mississippian carbonized assemblage of knotweed fruits from the Hill Creek site in the lower Illinois valley. This assemblage exhibited curious morphological characteristics, described below, that did not resemble any modern comparative collection. Two years later, Fritz reported a similar, but desiccated, assemblage dating to approximately the same time period from the Whitney Bluff site, a rock shelter in northwestern Arkansas (Fritz 1986, p. 74).

Recognizing domestication syndrome in knotweed

Many species of *Polygonum* L. sect. *Polygonum* produce trigonal achenes, which are one-seeded fruits consisting of seeds encased in a tough fruit coat, or pericarp (Fig. 1). Some knotweeds exhibit seasonally controlled achene dimorphism; they produce two distinct fruit types in ratios that vary over the course of the growing season (Costea et al. 2005; Mueller forthcoming). Tubercled morphs have lower aspect ratios so that their major and minor axes are closer to equal, and thicker pericarps with distinctive surface textures that are often diagnostic of particular species (Fig. 1; Costea et al. 2005). During the summer and early fall, plants produce only tubercled morphs. Beginning in mid-September, plants begin to produce both tubercled and smooth morphs. Smooth morphs have higher aspect ratios with a longer major axis compared to minor axis, and thinner pericarps that lack diagnostic surface textures (Fig. 1). The ratio of smooth to tubercled morphs by late October varies from species to species, and is possibly controlled by sunlight, rainfall, or temperature such that it varies from year to year (Brenkle 1946). The two different types are sometimes referred to as *late season morphs* and *early season morphs*, but the terms *smooth morphs* and *tubercled morphs* are used here: the former terms are misleading since both morphs are produced late in the season, as detailed below.

Beginning in the 1980s, palaeoethnobotanists recognized that one species of *Polygonum* had been cultivated by ancient Native Americans in what Fritz (1993, p. 41) has called the core area of pre-maize agriculture: from western Iowa, Missouri, and Arkansas to eastern Ohio, Illinois, Indiana, Kentucky, and Tennessee. They identified the cultivated species as *P. erectum* based on the striate-tubercled surface texture and shape of archaeological tubercled morphs (Fig. 1; Asch and Asch 1985b). The ratio of smooth to tubercled morphs is not always reported, but where it is noted, archaeological assemblages almost always contain both smooth and tubercled achenes in varying proportions (for example, Asch and Asch 1985b; Powell 2000, p. 40; Simon and Parker 2006, p. 239). The morphology of smooth achenes has not been the subject of much study by either botanists or archaeologists, and these have not been considered diagnostic of particular species. *The Flora of North America* summarizes smooth achenes in *Polygonum* sect. *Polygonum* thus: “Late-season achenes in all species are hypertrophied, olivaceous, lanceolate, exserted, and smooth. They have little taxonomic significance” (Costea et al. 2005). Smooth morphs in archaeological assemblages were assumed to have come from the same plants as the diagnostic tubercled morphs that were recovered from the same contexts—that is, from *P. erectum* plants.

Speculation about a domesticated subspecies of *P. erectum* began when two curious assemblages were reported in the mid 1980s. First, Asch and Asch (1985a, b) reported a carbonized assemblage from the Late Mississippian Hill Creek site in Illinois that was composed exclusively of smooth morphs. These achenes were also larger than the *P. erectum* smooth morphs in their reference collections. To ascertain whether or not *P. erectum* was capable of producing such a harvest, Asch and Asch gathered achenes from populations in Kansas, Missouri and Illinois during three different growing seasons (Asch and Asch 1985a). Their survey suggested that *P. erectum* does not produce monomorphic harvests similar to the Hill Creek assemblage. The smooth morphs they collected were also smaller than those from the Hill Creek assemblage, even without corrections for carbonization. They concluded: "If assessments of variability in wild-type *P. erectum* are accurate, then two alternative explanations can be advanced to account for the peculiarities of the Hill Creek knotweed: (1) They are a domesticated form of erect knotweed… or; (2) The Hill Creek achenes are not erect knotweed, but some other species in the knotweed section of *Polygonum*…" (Asch and Asch 1985b, pp. 144–145). In particular, they suggested that if the Hill Creek assemblage was not *P. erectum*, it might instead belong to a closely related species, *P. ramosissimum* Michaux (Asch and Asch 1985b, p. 146), which is known to produce many smooth achenes under certain (unspecified) conditions (Mertens and Raven 1965). Fritz (1986) reported a similar nearly monomorphic assemblage of large smooth morphs from the Mississippian Whitney Bluff sites, Arkansas. These had become desiccated after being stored or otherwise deposited in a dry rock shelter and were remarkably well-preserved. But without a clearer sense of variability in seasonal achene production among modern populations of *P. erectum*, domestication remained an open question.

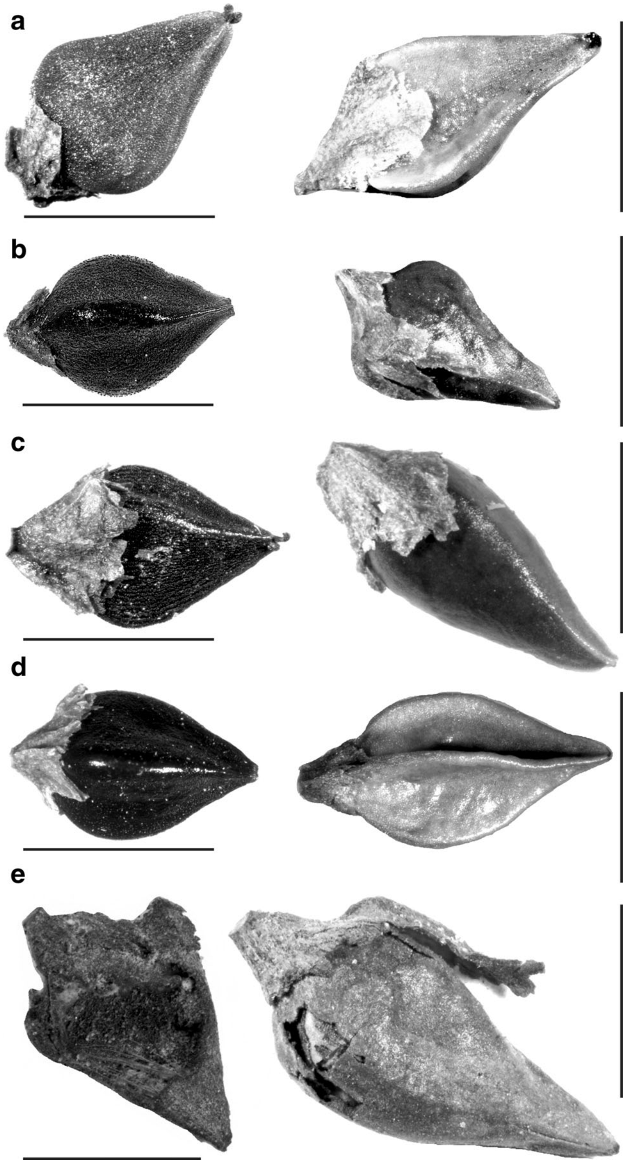

Fig. 1 Examples of the dimorphic achenes of the four species considered in this analysis and the newly described domesticated subspecies—tubercled morphs (the most common surface texture of each species) *on the left*, smooth morphs *on the right*. Perianths have been removed from modern achenes (see Fig. 2 for examples with perianth). **a** *P. achoreum*, uniformly tubercled; **b** *P. aviculare* ssp. *buxiforme*, coarsely striate-tubercled; **c** *P. erectum*, striate-tubercled; **d** *P. ramosissimum*, obscurely tubercled; **e** *P. erectum* ssp. *watsoniae* (Whitney Bluff assemblage, lacking perianths), striate-tubercled. Examples of *P. ramosissimum* and *P. achoreum* achenes shown here are deflated. On the *P. achoreum* smooth morph pictured here, the central ridge is entirely slumped over, obscuring one of its sub-equal faces, while on the *P. ramosissimum* smooth morph achene pictured here the central ridge protrudes upward, but the two sub-equal faces are markedly concave. Smooth morphs of *P. aviculare* ssp. *buxiforme*, *P. erectum*, and *P. erectum* ssp. *watsoniae* pictured here are not deflated. This is a rare morphology for *P. aviculare* ssp. *buxiforme*, and a common one for both ssp. of *P. erectum* (ESM Table 3); *scale bars* 2 mm

The hypothetical effects of human mediated selection on fruit heteromorphism

Variability in pericarp texture and thickness are important beyond esoteric taxonomic purposes. These fruit characteristics bear on questions of agricultural practice and domestication in ENA. Several species of *Polygonum* (taxonomy reviewed in Mueller forthcoming) produce two different types of fruits as a form of risk reduction. The smooth morphs will germinate and grow quickly the spring after they are produced. The thin, smooth pericarp is too insubstantial to allow for long-term preservation in soil. The relatively large endosperm further promotes fast growth. If these plants are killed off by bad weather or some other disturbance, then the tubercled morphs will renew the population when conditions improve. Tubercled achenes do not just have thicker walls and cuticles, they also have layers of wax that prevent or slow the penetration of fungi and pathogens, and guard against both waterlogging and desiccation, allowing the seed to remain healthy and viable in the soil over several years (Yurtseva 2001, pp. 524–525). Experiments in two closely related species have shown that the pericarp also mechanically restricts the embryo, thus controlling the timing of germination (Courtney 1968; Metzger 1992). Other studies have shown that achenes with thicker pericarps germinate more slowly (Sultan 1996).

Achene dimorphism in knotweeds is a form of diversification bet-hedging (Childs et al. 2010; Cohen 1966; Slatkin 1974). Bet-hedging as an evolutionary strategy was first defined mathematically by Dan Cohen (1966) to explain how populations can achieve greater reproductive success over the long-term even while employing strategies that do not maximize fitness within a given reproductive cycle. His model organism was a hypothetical annual plant that can either produce dormant seeds, seeds that germinate immediately, or some combination of the two. Cohen's model showed that in environments where the probability of total reproductive failure within a given year is high, long-term population growth is optimized when plants produce a combination of seeds that germinate immediately and seeds that are dormant, provided that the dormant seeds are well-protected enough to remain viable for more than one year. In more stable environments, where the risk of total reproductive failure in a given year is low, a high proportion of dormant seeds are detrimental to long-term population growth. The longer a seed remains in the seed bank, the more likely it is to fall victim to decay or predation before it is able to reproduce itself (Cohen 1966, p. 128). I hypothesize that human mediated selection acted on *P. erectum* fruit heteromorphism—specifically, that humans created less risky environments for populations of *P. erectum*. A domesticated erect knotweed with homogenous, thin-pericarp fruits would produce seed stock that germinates more reliably, a desirable characteristic from the point of view of a farmer. But this germination strategy could only evolve in a stable, predictable environment where tubercled morphs were no longer needed to protect populations from extinction in bad years.

The hypothetical effects of human mediated selection on fruit or seed size

Fruit or seed size increase in annual plants is a classic (although by no means universal) indicator of selection in human created environments. Harlan et al. (1973) hypothesized that larger seeds may have evolved in annual seed crops because of conscious selection of larger seedlings. Farmers and gardeners often remove smaller seedlings early in the season to give the strongest plants more room to grow. Harlan and colleagues suggested that this process of thinning favours the offspring of plants that produce large seeds, because large seeds produce seedlings that grow faster (for example, Boyd et al. 1971; Clements and Latter 1974; Rogler 1954). The perisperm or endosperm contained within the seed is the metaphorical lunch that the mother plant packs for its offspring: the bigger the lunch, the faster the seedling can grow, all other things being equal. Planting methods may also have selected for larger seeds. Without humans, seeds fall to the ground and are only occasionally buried by sediment deposition or animal dispersal. The greater success of large seeds compared to small seeds increases with the depth of planting (Rogler 1954), so planting at any depth greater than would naturally occur also confers an advantage on large-seeded plants (Harlan et al. 1973, p. 318).

There may also have been more general agro-ecological effects on seed size. Dozens of experiments and ecological studies have shown that larger seeds have greater success in establishment relative to smaller seeds under a variety of environmental stresses, from shade to drought (Leishman et al. 2000). Bigger seeds are better under many different conditions, but this advantage is usually counterbalanced in nature by an imperative to produce many seeds. Size of offspring and number of offspring cannot be simultaneously maximized given that finite resources are available to the mother plant (Smith and Fretwell 1974). Under cultivation, the plant's imperative to produce many seeds is reduced because farmers are attempting to protect both plants and their seeds from disturbance and predation. Additionally, the resources available to the mother plant are usually increased in various ways compared to their relatives outside of cultivation. Farmers may reduce competition from other species, create sunnier environments, provide more water, or enrich soils, among many other possible improvements. Agro-ecosytems in general are less risky and richer environments, where the production of larger seeds is both possible and evolutionarily advantageous.

Materials and methods

The archaeological photosample

An analysis of the Hill Creek assemblage requires various corrections for carbonization and imperfect preservation which have been developed experimentally and will be reported elsewhere, along with analyses of other carbonized assemblages of *P. erectum* that show evidence of domestication syndrome. Here, the analysis focuses on the Whitney Bluff assemblage, which can be directly compared to modern achenes because of its near perfect preservation.

During the 1920s and 1930s a team from the University of Arkansas Museum excavated the Whitney Bluff site, along with 80 other Ozark rockshelters. Although the results of these excavations were never fully published, the uncommonly well-preserved plant remains were examined by early researchers of ancient agriculture in ENA (Gilmore 1931; see Fritz 1986, p. 6). The crop plant remains from 19 rock shelters, including Whitney Bluff, were analysed and reported by Gayle Fritz (1986), who also synthesized field and laboratory notes on file at the University of Arkansas Museum to reconstruct as much of the archaeological context as possible. Original excavation notes indicate that the site is located in Benton Co., Arkansas, on the banks of the White River. Other materials recovered from Whitney Bluff include a woven bag, baskets, string, mussel shell, stone tools, one potsherd, cane tools, turkey bones, and plant foods (Fritz 1986, p. 20).

Two large samples of *Polygonum* were recovered from this site (University of Arkansas Museum accession #s 32-57-3a and 32-57-5c). Both came from a "cache" that also contained a broken gourd bowl and a drawstring bag. It is unknown whether they were two distinct samples each from their own container, or mixed in a single context (Fritz 1986, pp. 107, 92). Domesticated *Chenopodium berlandieri* ssp. *jonesianum* was also recovered from this context (Fritz 1986, pp. 91–92). I concur with Fritz' observation that the two samples of *Polygonum* are very similar and probably did not come from distinct contexts (Fritz 1986, pp. 107–108). They are treated as a single sample in this analysis. A fragment of the gourd from this context was dated by Fritz to 785 ± 75 uncal BP (1986, p. 74), or cal AD 1040–1386. A recent direct date from one of the knotweed achenes returned a date of 885 ± 20 uncal BP, or cal AD 1046-1217 (NOSAMS #134366, calibrated using IntCal 13, Reimer et al. 2013).

The morphometric analysis was performed using digital images of a photosample, a subsample of an entire archaeobotanical assemblage that only includes fruits whose entire pericarp are intact. The Whitney Bluff assemblage was well-preserved enough to observe pericarp texture on all achenes, but some appear to have been gnawed by rodents and were not complete enough to include in the morphometric analysis. As with the sampling protocol for the larger study, where >100 intact achenes were present, the size of the photosample was determined by the weight of the entire assemblage: 1 photograph per 0.01 g. I chose to sub-sample by weight rather than count in order not to bias the sample against poorly preserved carbonized assemblages where fewer measurable achenes were present as a percentage of the total identifiable knotweed. In most archaeological assemblages, the vast majority of identifiable knotweed is in the form of seeds (kernels), the pericarp having popped and disintegrated during carbonization. For Whitney Bluff, this sampling strategy dictated a photosample of 80 achenes from 32-57-3a and 120 from 32-57-5c. Many of the Whitney Bluff achenes retained some or all of their perianth parts, as discussed below. The presence of the perianth or parts of the perianth may somewhat inflate area and width measurements and slightly distort shape descriptors, but perianths are generally tightly conforming to the shape of the underlying fruit (Fig. 2). Of the 1,307 achenes examined, all but two were smooth morphs. The two tubercled morphs are described below and the more complete of the two is pictured in Fig. 1. Measurements of length and width reported here are very similar to those reported by Fritz on two different sub-samples of 100 achenes (Fritz 1986, pp. 108).

The herbarium photosample

A total of 73 individual herbarium specimens from the Missouri Botanical Garden and National Herbarium were examined. Achenes were taken from 51 of these for morphometric analysis (ESM Table 1). These will be referred to as the herbarium photosample. Four species of *Polygonum* sect. *Polygonum* that could have been cultivated by pre-Contact Native Americans and were native to the Midwest were sampled: *P. erectum* L., native *P. aviculare* L. ssp. *buxiforme* (Small) Costea & Tardif (prostrate knotweed), *P. achoreum* S. F. Blake (Blake's knotweed), and *P. ramosissimum* Michaux (bushy knotweed). The relevant taxonomic background that informed the sampling strategy, along with a list of all herbarium specimens examined for this study are reported elsewhere (Mueller forthcoming). Only loose fruits were removed from the herbarium sheet packets on specimens collected since 1950, as per the sampling regulations of the Missouri Botanical Garden and National Herbarium. By drawing on samples from herbarium specimens, I was able to take plasticity into account by including plants from many different seasons and years. This is important because some observers have suggested that achene dimorphism may vary from year to year, with certain conditions favouring the production of smooth morphs (Brenkle 1946), and achene dimorphism is known to vary throughout the growing season.

Sample size is not uniform because the amount of loose fruits available depends on the age-at-death of the specimen and the time of year when it was collected. Plants collected from June–August have very few mature fruits, and those tend to adhere more tightly to the specimen. On the other hand, there were more of these specimens available for study than those collected in the fall, because botanists prefer to collect plants with both fruits and flowers for herbarium specimens, not dead or dying plants

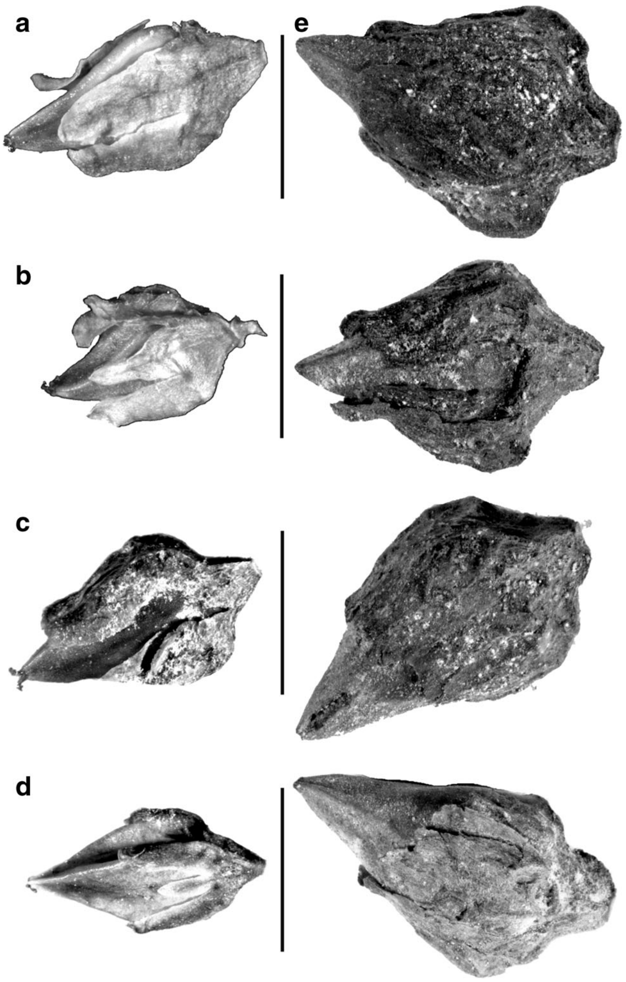

Fig. 2 Examples of the smooth morph achenes with perianth adhering. *Left column* representative achenes from the herbarium photosample, **a** *P. achoreum*; **b** *P. aviculare* ssp. *buxiforme*; **c** *P. erectum*; **d** *P. ramosissimum.* The example of *P. ramosissimum* shown here is about half exserted (protruding) from its perianth—most are even more exserted. The other three species in the *left column* are mostly enclosed in their perianths, like the achenes from Whitney Bluff (**e** *P. erectum* ssp. *watsoniae*, *right column*); *scale bars* 2 mm

at the end of their life cycle. Plants collected in late September and October sometimes have hundreds of fruits, and they are also more likely to dehisce and be stored in the loose materials packet. Late fall samples were especially important for clearing up the question of monomorphic assemblages, but they were also rare. This explains the very small sample of late fall *P. achoreum*. In this case, the visual inspection of the much larger sample of fruits adhering to *P. achoreum* herbarium specimens supports the conclusions drawn from the photographed fruits. After completing the analysis of the sampled fruits, I returned to the Missouri Botanical Garden herbarium several times to observe more specimens and verify that the criteria outlined below were representative of the species as a whole.

In *Polygonum*, the perianth adheres to the fruit even after it is mature, forming a papery shell. The perianth was removed using a razor under a dissecting microscope. Samples from each species with their perianth intact were also examined for comparison with the Whitney Bluff achenes, many of which retain some or all of their perianth (Fig. 2). Each fruit's receptacle (the thickened part of the stem that attaches to the fruit) was left intact for comparison with the Whitney Bluff achenes, which universally retain their receptacles. Grey scale photographs of each fruit were taken in the same orientation with the widest of their three sides facing downwards (Figs. 1, 2). While photographing, the texture of each fruit's pericarp was recorded as "smooth" or "tubercled." Then several shape factors, area, length, and width were measured, using ImageJ (ESM Table 2). In order to take measurements, the object to be measured must be thresholded (differentiated from the background on the basis of colour or shade). With solid objects like seeds on a white or black background it is usually easy to select all non-white or non-black pixels, but it is sometimes necessary to manually trace the outline of fruits that are similar in colour to the background.

Morphometrics and non-metric criteria

An assessment of some aspect of morphology is at the heart of most plant domestication studies in archaeobotany, but the use of morphometric approaches is still quite rare. In recent years, researchers studying cereal domestication have preferred to use non-metric, descriptive criteria to identify domesticated cereals, recognizing that grain size is variable and affected by carbonization in ways that are still imperfectly understood (Braadbaart and Wright 2007). For example, details of the morphology of the abscission scars on the spikelet bases of wheat, barley, and rice indicate the evolution of non-shattering varieties, and are the state-of-the-art indicator of domestication in these taxa (Fuller et al. 2009; Tanno and Willcox 2012). When metric criteria *are* used in domestication studies, they are usually point-to-point distances, such as length, width, and thickness (Zach and Klee 2003; Smith 2014; Yarnell 1978). These are taken using a micrometer in the eyepiece of a microscope. One drawback of taking measurements this way is that the data are immediately disconnected from the specimen that they describe.

Morphometric analysis uses two-dimensional digital images to quantitatively assess size and shape (Table 2; reviewed in Rovner and Gyulai 2006). The distribution of measurement values within a population has been used to successfully distinguish between wild and domesticated seeds (Rovner and Gyulai 2006) and to correctly classify hundreds of different weed species (Granitto et al. 2004). Morphometric measurements can be taken quickly and consistently on thousands of specimens, and are uniform and repeatable. Images and the data derived from them remain linked through a unique name so that further studies can be conducted on the same assemblage and outliers can be re-examined. Because the raw material of a morphometric analysis is an image, it is possible to use area, rather than length and width, as a proxy for size, and to track changes in shape (Dahlberg and Wasylikowa 1996).

Size

At the outset of this study, I attempted to quantify height using the microscope's z-stepping motor to calculate the distances between the microscope stage and the highest point on each fruit. Unfortunately, it proved impossible to systematically measure the height of trigonal achenes, particularly carbonized ones that would not lie flat due to puffing. As this measurement obscured more than it illuminated, it is not included in the following morphometric analyses. Until 3D imaging of very small objects becomes less expensive and more accurate, it will remain difficult to accurately *quantify* seed volume, although it is possible to create robust qualitative criteria for assessing volume, as when margin configuration is used to recognize change in chenopod seed morphology (Fritz 1984; Gremillion 1993; Langlie et al. 2011; Smith and Funk 1985). This was the approach ultimately adopted for identifying smooth morphs to species using the criterion *fruit deflation*, described below, which is rough approximation of volume.

Shape

Formulae used to assess shape by ImageJ are listed in ESM Table 2. Roundness and aspect ratio are roughly inversely-related shape descriptors, but roundness is more sensitive than aspect ratio because roundness is a function of *area* and major axis, whereas aspect ratio is determined by two vectors: major axis and minor axis. Circularity is the most sensitive shape measure of the three because it is a function of area and perimeter. I hoped to develop shape criteria for distinguishing between species based on their smooth morphs alone, and to quantify the differences in tubercled morph shape referred to in taxonomic treatments.

Non-metric characters

Tubercled morph pericarp texture is a key diagnostic character for identifying species of *Polygonum* (Costea et al. 2005). The distinctive striate-tubercled texture of archaeological fruits was the key criterion originally used to identify them as *P. erectum.* While this surface texture has been considered diagnostic of *P. erectum*, other species also sometimes produce achenes with this surface texture (ESM Table 3; Mueller forthcoming). Useful non-metric characters for differentiating between species using smooth morphs are perianth morphology and deflation, described below (see also Figs. 1, 2).

Statistics

For this study, tubercled morphs are not compared statistically, because there is only one measurable tubercled morph from Whitney Bluff. For the smooth morphs, Levene's test revealed that the samples had significantly different variances for all metric variables (area, length, width, aspect ratio, roundness and circularity). For this reason, Welch's *t* test for unequal variances was used to compare each species to the Whitney Bluff assemblage.

Results

Seasonal variability

ESM Table 1 shows the total number of achenes of each morph from each species aggregated by season of harvest. Visual inspection of fruits adhering to herbarium specimens confirmed the impression given by the photosample—with only two exceptions, plants of all four species exhibited fruit dimorphism no matter in what season they were collected.

Even with only a small photosample of 5–20 seeds from each plant, there were only two instances of uniformly smooth morph photosamples. This indicates that smooth morphs rarely predominate. Even late in the season, tubercled morphs are always present even in a small random sample of fruits. The two exceptions were both *P. ramosissimum* specimens. One was collected on September 22 and the other was collected on October 23. After analysing the photosamples from these plants (n = 12 and n = 14, respectively), I returned to the herbarium to ascertain whether or not the plants in question had really produced *only* smooth morphs. All of the observable achenes on both of these specimens were smooth morphs. Thus *P. ramosissimum* does occasionally produce monomorphic assemblages of smooth morph achenes, but not necessarily in late fall. Further study of this species is necessary to determine what conditions produce this effect.

The possibility of monomorphic harvests from wild plants was what made earlier researchers hesitate to designate the Hill Creek and Whitney Bluff assemblages as domesticated *P. erectum*. Asch and Asch wrote: “If the knotweed species at the Hill Creek site is not *P. erectum*…then it is probably *P. ramosissimum*” (1985b, p. 146). This species commonly produces smooth morph achenes according to most treatments, and its late season fruits are so different from its summer fruits that specimens

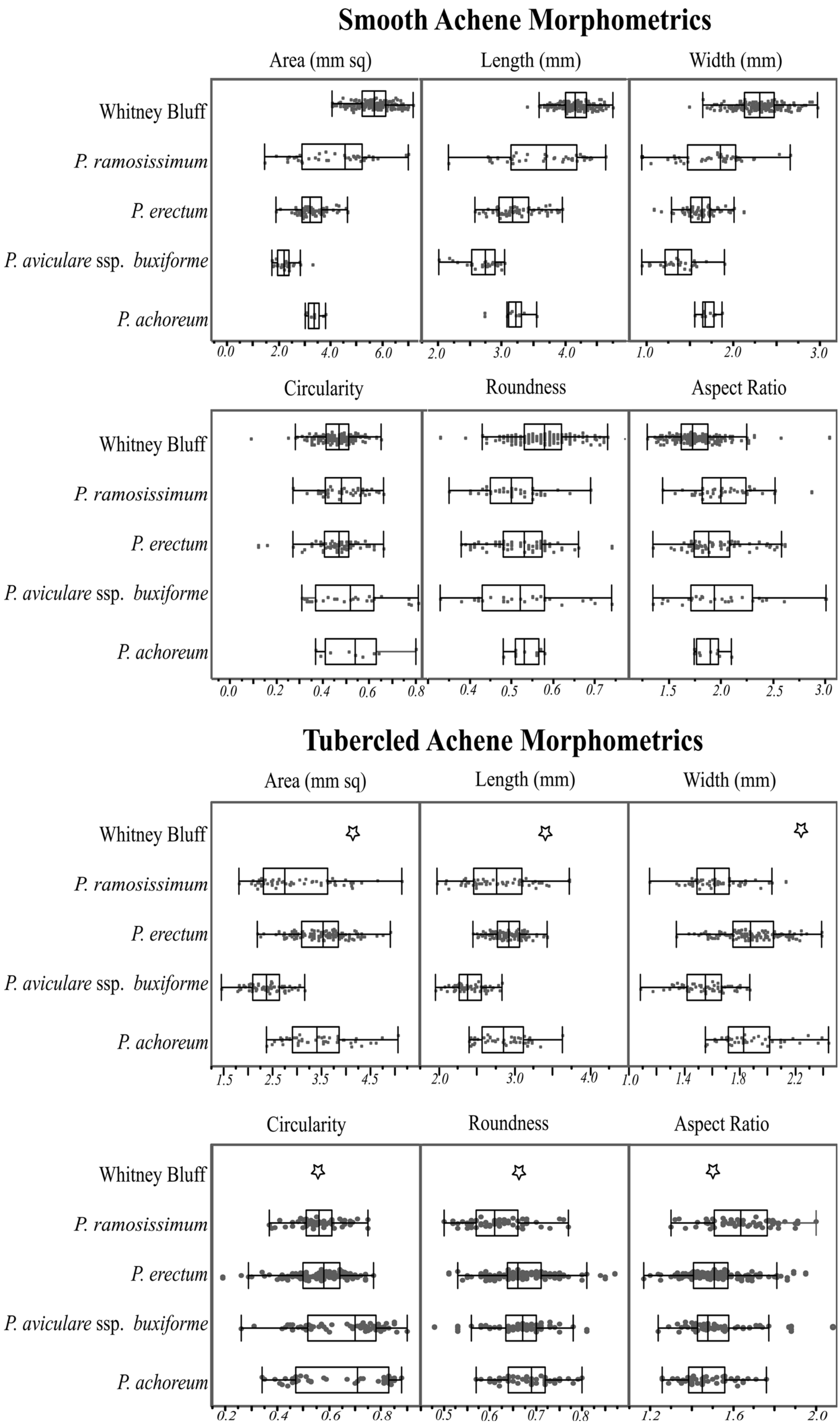

Fig. 3 Box plots visualizing the range of values for morphometric measurements of each population. Vertical line is the median value, boxes represent 1st–3rd quartiles. Whiskers extend from the end of the box to the outermost data point that falls within (3rd or 1st quartile + 1.5*interquartile range), and any values that fall outside of that range are represented as outliers by dots. For the tubercled morph plots, the star represents the value for the one measurable tubercled morph from Whitney Bluff

bearing mostly smooth morphs were long mistaken for a different species (Mertens and Raven 1965, pp. 85–86). The possibility that the Whitney Bluff assemblage is *P. ramosissimum* is explored below.

Smooth morph size

The Whitney Bluff achenes are larger than the smooth morphs of any existing species, by any measure (ESM Table 3; Fig. 3). The difference between Whitney Bluff and all species in terms of size is highly significant (Welch's *t* test for unequal variance, <0.001). The four extant species' smooth morphs are also significantly different from each other in terms of size, with one exception—*P. achoreum* was not significantly different from *P. erectum*. Given the small sample size for *P. achoreum*, that is not surprising. It may be that these species, too, can be differentiated using smooth morph size if a larger sample is collected. This result is contrary to previous treatments of these species, which have not found smooth morph size be taxonomically significant (reviewed in Mueller forthcoming).

Smooth morph shape

No significant differences in circularity between the Whitney Bluff smooth morphs and the modern species were found using Welch's *t* test for unequal variances. However, the mean circularity of the Whitney Bluff assemblage is most similar to that of the smooth morphs of *P. erectum*. These two samples have very similar mean circularities of 0.44 and 0.46 respectively. *P. achoreum* and *P. aviculare* ssp. *buxiforme,* with mean circularities of 0.52 and 0.54 respectively, form a subtly different cluster according to this shape factor, with *P. ramosissimum* in the middle with a mean circularity of 0.49 (ESM Table 3; Fig. 3). All four species were significantly different from the Whitney Bluff achenes in terms of aspect ratio and roundness ($p < 0.01$; ESM Table 3). The Whitney Bluff assemblage has the lowest aspect ratio of any of the samples and the highest roundness, meaning that the Whitney Bluff smooth morphs tend to be less elongated than those of the other species. The morphometric analysis confirmed the prevailing wisdom that there is much less variation in the shape of smooth morphs between species than there is for tubercled morphs (Fig. 3).

Non-metric characters of smooth morphs

Perianth morphology

The preserved perianths of the Whitney Bluff specimens leave little doubt that they are not *P. ramosissimum* (Fig. 2). Smooth morphs of *P. ramosissimum* are extremely exserted (protruding) from their perianths (plants with this fruit morphology were once designated *P. exsertum* Small), with the preserved outer flower parts covering, maximally, half the length of the mature fruit, and often much less. The other three species' smooth morphs and the Whitney Bluff achenes with preserved perianths are not so exserted: their perianth usually extends to just short of the tip of the achene. Representative examples of achenes with adhering perianths are shown in Fig. 2. While this criterion will not be useful in analysing carbonized assemblages (where perianths are very rarely preserved), it does provide strong evidence that the Whitney Bluff assemblage, at least, did not come from *P. ramosissimum* plants.

Deflation

This criterion refers to the degree of fruit deflation as observed on the two subequal faces of the achene (Fig. 1). When these faces are markedly concave, the achene becomes flattened, with the central ridge sometimes slumped over to one side (Fig. 1). Mertens and Raven (1965, p. 85) described the late season achenes of *P. ramosissimum* as "flattened and wrinkled." This description is apt, and also applies to most of the smooth morphs of *P. aviculare* ssp. *buxiforme* and *P. achoreum* observed in this study, but not to those of *P. erectum*, the smooth morphs of which, like those of the Whitney Bluff achenes, almost always have convex faces, giving them a plump appearance in comparison to the other species (Fig. 1). This characteristic was also noted by Fritz (1986, p. 109), who described the Whitney Bluff achenes as "faintly trigonous, but rounded except at the distal tip where three angles are manifested."

Tubercled morphs

Of the 1,307 achenes with observable pericarps in this assemblage, only *two* were tubercled morphs. These both exhibit the striate-tubercled morphology typical of *P. erectum* (Fig. 1). Only one is complete enough to be measured, and its measurements are indicated by a star in comparison to box plots for extant species tubercled morphs in Fig. 3. The Whitney Bluff tubercled morph is large, but there is only one complete specimen and it falls within the natural range of three out of four of the species (Fig. 3). Likewise, in terms of shape, the lone Whitney Bluff tubercled morph could just as easily have come from any of the four species.

Isolating this single tubercled achene from the rest of the Whitney Bluff assemblage reveals an unfortunate truth about this ancient crop: any morphological analysis of knotweed requires *populations*. Very little can be said about a single *Polygonum* achene of either morph—it cannot even be confidently identified to species. While tubercled morph surface texture *is* diagnostic of species, it is also variable. Taxonomic treatments reflect this: they vary slightly from flora to flora, probably depending on which specimens were examined by the writer. Taking *The Flora of North America* (Costea et al. 2005) as an example, *P. erectum* tubercled morphs are described as "striate-tubercled," that is, the tubercles are arranged in rows (see Fig. 1 for examples of surface textures). The specimens examined confirm this. All *P. erectum* tubercled morphs are always striate-tubercled, but other species are more variable. *P. ramosissimum* tubercled achenes are described as "smooth to roughened, sometimes uniformly or obscurely tubercled." Uniformly tubercled achenes have dense tubercles with no rows discernible, while obscurely tubercled achenes have tubercles that are inconspicuous or restricted to certain areas of the achene. Of the 59 tubercled morphs of *P. ramosissimum* in the photosample, all four of these textures are present in addition to seven achenes that are distinctly striate-tubercled. *P. achoreum's* achenes are described as uniformly tubercled. The majority do fit that description, but ten out of 51 tubercled achenes in the photosample are striate-tubercled. *P. aviculare* ssp. *buxiforme*'s achenes are described as "coarsely striate-tubercled to obscurely tubercled"—about a quarter of those in the photosample are striate-tubercled, but these have coarse tubercles, which differ from those on the other three species (Fig. 1; Costea et al. 2005). In other words, all four species produce striate-tubercled achenes, but at different frequencies (ESM Table 3).

As with smooth morphs, size is useful for distinguishing between species. Mean area can be used to reliably distinguish *P. ramosissimum* and *P. aviculare* ssp. *buxiforme* from the other species, but *P. erectum* and *P. achoreum* have similarly sized tubercled achenes (ESM Table 3; Fig. 3). Circularity seems to sort the species into two groups: *P. ramosissimum* and *P. erectum* form one group, *P. aviculare* ssp. *buxiforme* and *P. achoreum* form another, both in terms of mean values and distribution of values (normal vs. bimodal; ESM Table 3; Fig. 3). Using a combination of metric and non-metric criteria, small assemblages of tubercled morphs can be more confidently assigned to species. Large assemblages of knotweed where *all* of the tubercled morphs are striate-tubercled morphs can still be confidently identified as *P. erectum* without conducting a morphometric analysis, since this is the only species that consistently produces achenes with this surface texture, because it is highly unlikely that a random sample of achenes from any of the other species would *all* be striate-tubercled.

Summary

The morphometric analysis clearly shows that the Whitney Bluff assemblage is outside the range of variation for any extant species in terms of achene size, and has differently shaped smooth morph achenes than any extant species (ESM Table 3; Fig. 3; and see Mueller forthcoming for an exhaustive review of achene characteristics in closely related species and genera not treated in this paper). As we do not find achenes the size and shape of the Whitney Bluff achenes on any extant species, this assemblage warrants taxonomic treatment. It is possible that the Whitney Bluff assemblage represents an entirely different species—perhaps one that is now extinct. But since there is abundant archaeological evidence demonstrating that *Polygonum* was cultivated by ancient societies, and since the differences between the Whitney Bluff assemblage and extant species are exactly what we would expect to result from cultivation, the most parsimonious explanation is that the Whitney Bluff assemblage represents a domesticated subspecies.

It should be stated at the outset that circumstantial evidence strongly supports the hypothesis that the Whitney Bluff assemblage is a domesticated form of *P. erectum*: Its remains begin to appear at archaeological sites c. 1,500 years before the Ozark Bluff Dwellers left part of their harvest in the Whitney Bluff rock shelter, both in Arkansas and across the core area of EAC cultivation (Fritz 1986; Gremillion 1998; Simon and Parker 2006; Wymer and Abrams 2003). At Late Woodland and Mississippian sites, masses of *P. erectum* achenes are routinely recovered from storage pits in several different sub-regions (Fritz 1986; Powell 2000; Simon and Parker 2006). There is no evidence that any other species was ever cultivated. But strong evidence is required to argue for an extinct domesticate, and other possible explanations must be ruled out.

The sum of the morphological evidence presented here also points to *P. erectum* as the most likely species designation for the Whitney Bluff assemblage. The evidence is summarized in ESM Table 4. Of the four species, only *P. ramosissimum* is known to produce monomorphic harvests of smooth morph achenes, a strong indication that it should be considered a contender. Shape factor analysis was inconclusive, since the Whitney Bluff assemblage is significantly different in terms of aspect ratio and roundness from all extant species. In terms of circularity, which is the most sensitive of the three shape factors, the Whitney Bluff achenes are more similar to *P. erectum* than they are to the other three species, even if these differences do not rise to the level of statistical significance. Perianth morphology indicates that the Whitney Bluff assemblage is not *P. ramosissimum*, since Whitney Bluff achenes are not nearly as exerted from their perianths as the smooth morphs of that species. *P. erectum* is the only species that routinely produces non-deflated (plump) smooth achenes, like those of the Whitney Bluff assemblage. The two tubercled morphs from Whitney Bluff also provide tentative support for the designation of the Whitney Bluff assemblage as a subspecies of *P. erectum*, as they have striate-tubercled pericarps.

Although the archaeological specimens from Whitney Bluff which were designated *P. erectum* ssp. *watsoniae* (Mueller forthcoming) are most similar to *P. erectum*, they differ from modern *P. erectum* in three ways. Average size for *P. erectum* ssp. *watsoniae* achenes is greater, whether measured by area, length, or width (ESM Table 3; Fig. 3). A great reduction of achene dimorphism is also diagnostic of *P. erectum* ssp. *watsoniae*. Of the 21 *P. erectum* herbarium specimens sampled, collected from 13 different states over a span of 100 years, and hundreds of wild-growing plants observed during the course of this study, none produced a monomorphic harvest. Even in late October and early November, *P. erectum* plants often still produce a *majority* of tubercled morph fruits. Because assemblages of *P. erectum* ssp. *watsoniae* have very few or no tubercled morphs, with their thicker pericarps, average pericarp thickness is much less than that from any given harvest of wild erect knotweed (Mueller forthcoming). Both the increase in fruit size and the reduction of germination inhibitors exhibited by *P. erectum* ssp. *watsoniae* are classic indicators of domestication syndrome in annual seed crops. The reduction or elimination of fruit dimorphism in itself should also be considered a symptom of domestication that is perhaps unique to *P. erectum*. To understand why, it is necessary to briefly explore how fruit dimorphism evolves and is maintained outside of cultivation.

Discussion

Fruit dimorphism as diversification bet-hedging

Evolutionary bet-hedging refers to situations in which organisms sacrifice maximum fitness per generation for a reduction in fitness variance over time (Slatkin 1974; Childs et al. 2010). Germination heteromorphism is the quintessential and most well understood bet-hedging strategy, and has evolved in many different plant families (Venable 1985; Imbert 2002). Plants that exhibit germination heteromorphism produce two or more different types of seeds with different inherent dormancy characteristics. Some, like *P. erectum* and its relatives, produce one morph that is non-dormant, usually with a thin seed or fruit coat that is more permeable to water and/or sunlight than that of the dormant morphs. Dormancy heteromorphism is thought to evolve in response to temporal variation—unpredictable or frequently disturbed habitats—such that neither morph is consistently successful (Cohen 1966; Venable 1985; Childs et al. 2010). Fitness is a multiplicative, rather than additive, process: the number of offspring in each generation is a factor of the number of individuals in the previous generation which survived to reproduce. This means that the average fitness of a population over many generations is sensitive to even sporadic to low values. An occasion of zero fitness (no surviving offspring) can lead to extinction, at least locally. Dormancy heteromorphism "allows cohorts of individuals of the same genotype to sample a range of different environments through time" (Childs et al. 2010, p. 2).

An anecdote from own observations serves as an apt illustration of the mathematical models behind bet-hedging theory. During the growing season of 2014, three populations of *P. erectum* in the vicinity of St. Louis, Missouri, were regularly visited while tracking their growth and reproduction. That year, all three populations survived until the first snow in early November, cumulatively producing tens of thousands of seeds. The following year, *all three* populations were wiped out by floods in June, before they had begun to reproduce. In all three cases, when the populations were visited after the floods had receded, there were no living seedlings. In greenhouse experiments using the achenes collected from these populations before their demise, 60–100 % of smooth morph fruits subjected to six weeks of stratification in cold, moist soil germinated. I infer that most of the smooth morphs produced in 2014 had germinated by the time the floods killed these populations in 2015. Tubercled morphs, on the other hand, are protected from moisture and pathogens (Yurtseva 2001) and are able to remain in the seedbank. In greenhouse experiments, 0–35 % of tubercled morphs germinated after the same cold treatment applied to the smooth morphs, meaning that many tubercled morphs probably do not germinate immediately in the spring of the year after they were produced. In the spring of 2016, I returned to find robust populations of *P. erectum* at two of the study sites where all plants had been wiped out the year before. The surviving population is now made up almost entirely of seedlings sprung from tubercled morphs, which were able to survive the adverse growing season of 2015 in the seed bank. Sequences of events like this maintain dormancy heteromorphism where it arises, despite the fact that in many years the quicker germination and faster early growth of smooth morphs probably contributes to their greater fitness, especially in a microenvironment where there is usually intense competition from siblings and other weedy annuals.

Discussing the evolution of seed heteromorphism in general, Silvertown (1984, p. 9) summarized: "Dormancy [is a means of] avoiding unfavourable periods *by escape in time*…Dispersal is a means of avoiding unfavourable periods *by escape in space* and can be considered an alternative to dormancy" (emphasis added). *P. erectum* seeds may be naturally dispersed by various means, including floods and possibly birds, but most seeds fall to the ground within a few centimetres of the parent plant. Dormancy heteromorphism evolved in response to events like the early summer floods of 2015. By producing two different types of achenes, *P. erectum* plants can escape population extinction *in time.* But ancient farmers relaxed this source of natural selection on *P. erectum* plants under cultivation by providing an escape *in space*—a new dispersal mechanism. Farmers save seeds, providing an alternative to the soil seed bank and ensuring that some seeds will survive adverse events (assuming that farmers carefully manage their seed stock). They may also either (1) protect plants from floods and droughts through landscape modification and cultivation or; (2) plant crops in a variety of topographic locations so that the entire population is rarely wiped out by a single event. Under the protection of farmers, monomorphic harvests of fruits that germinate and grow quickly are less risky. Plants that produce such harvests are more likely to contribute to the next generation of plants under cultivation, but would quickly go extinct outside of cultivation.

Plasticity

The precise ratio of smooth/tubercled morphs produced each year by *P. erectum* may also be partially, or even primarily, controlled by adaptive transgenerational plasticity—an epigenetic effect whereby "parent individuals alter specific developmental traits in their progeny in response to particular environmental stresses, and these alterations may enhance offspring growth and success under those same stresses" (Herman and Sultan 2011, p. 1). Adaptive transgenerational plasticity specifically refers to effects that enhance, rather than reduce, the fitness of offspring. Examples of deleterious parental effects are well-known, and include reduced seed provisioning (smaller seeds) and reduced seed production (fewer seeds overall) in response to low light, poor soils, or drought (Roach and Wulff 1987), but adaptive parental effects are now also being explored. One of the key early pieces of research on adaptive transgenerational plasticity in plants was serendipitously conducted on *Persicaria maculosa* Gray, a species that, until recent taxonomic treatments, belonged to the same genus as *P. erectum* (it was formerly called *P. persicaria* L.; Mueller forthcoming). Sultan (1996) grew achenes from cloned parents under varying conditions. Among other inherited responses to environmental constraints, she observed that plants grown under low light were able to maintain seed provisioning by sacrificing pericarp production. These plants produced achenes that were the same weight as those produced by plants in full sun, but with pericarps reduced by >40 % (Sultan 1996, p. 1795). Like *P. erectum* smooth morphs, these thin pericarp offspring germinated sooner and grew more quickly—an adaptive response to the shady (in nature: crowded) environment experienced by their parents.

In *P. erectum*, thin pericarp achenes are only produced from mid September on, suggesting that their production may also be a response to low light. Preliminary data from my own greenhouse experiments indicates that erect knotweed grown under artificial light (12 h/day) only produces tubercled achenes. I expect that early generations of cultivated *P. erectum* would actually have produced *more* tubercled morphs and *less* smooth morphs due to plastic responses to light. As farmers created full-sun environments and reduced competition, *P. erectum* plants would have been able to allocate resources to both seed provisioning and pericarp production for more of the season. Domesticated assemblages do not appear until several hundred years after cultivation began, so it seems that it took many generations for the increased fitness of cultivated plants producing harvests of predominately smooth morphs to swamp this plastic effect. The effect of low light on achene growth demonstrated for *P. maculosa* needs to be replicated for *P. erectum*, and there may be other environmental factors that govern the ratio of tubercled morph to smooth morph production. Sultan's (1996) results are an invitation to explore the interaction of knotweed plasticity with various forms of human cultivation—thinning, irrigation, fertilization, and so on.

Plasticity may have played a large role in attracting farmers to particular plants in the first place. It cannot always be assumed that the characteristics of a progenitor in modern environments are the same as those which attracted gatherers to its ancestors. The various forms that wild progenitors may have taken should be a subject of investigation for all domesticated plants (Gremillion and Piperno 2009; Piperno et al. 2015). A plant's immediate plasticity or capacity for rapid adaptive transgenerational plasticity may have been traits in and of themselves that attracted the attention of early farmers, because in highly plastic plants the effects of cultivation would have been immediately apparent. Smartweeds, close relatives of knotweeds, have been the subject of decades of research on the evolutionary effects of plasticity (Sultan 1996, 2001, 2003; Sultan et al. 2013). While it is beyond the scope of this discussion to enumerate the many findings of this research, in general Sultan and colleagues have demonstrated that some smartweeds are capable of drastically altering their morphology in response to environmental conditions (immediate plasticity) (Sultan 2001), and of rapidly evolving new morphologies to take advantage of new habitats (adaptive transgenerational plasticity) (Sultan et al. 2013).

The remarkable plasticity of knotweeds is memorialized by the many now-defunct species names within the genus; *Polygonum* has been a “knotty problem” for plant taxonomists for decades (Mertens 1968; Mueller forthcoming). From the perspective of domestication studies, it is easy to view plasticity as an annoyance because it needs to be considered as an alternative explanation to artificial selection for any change in the morphology of crop plants. But the great plasticity of *P. erectum* actually provides an opportunity to recover ancient agriculture practice. Because knotweeds respond so quickly and easily to their environments, the morphology of a knotweed plant (or even just a cache of burned achenes) could be used as a key to reconstruct that environment, when plastic responses are better understood. If future studies reveal that monomorphic achene production, like that evidenced by the Whitney Bluff and Hill Creek assemblages, can be induced in *P. erectum* under certain conditions *without* invoking generations of selection under cultivation, that insight will still tell us something about how Mississippian farmers were interacting with their crops and shaping their environment.

Conclusions

Morphologically distinct assemblages of knotweed have been recovered from some Mississippian sites. The most well-preserved of these comes from the Whitney Bluff site, Arkansas. This desiccated assemblage was compared to several modern species of knotweed native to the area of ancient cultivation. The possibility that these assemblages represent natural variation within erect knotweed or a closely related species has been ruled out, and a domesticated subspecies has been described (Mueller forthcoming). *P. erectum* ssp. *watsoniae* differs from its wild ancestor in three ways: its fruits are larger, average pericarp thickness is reduced, and fruit heteromorphism is reduced. With reference to the classic domestication syndrome in cereals, larger seeds may have been selected both intentionally and automatically, through the culling of slow growing seedlings (Harlan et al. 1973), deep planting (Rogler 1954), and the creation of stable and enriched agroecosystems (Leishman et al. 2000; Smith and Fretwell 1974). Evolutionary bet-hedging theory (Childs et al. 2010; Cohen 1966; Imbert 2002; Slatkin 1974; Venable 1985) suggests mechanisms for the reduction of fruit dimorphism and average pericarp thickness under cultivation. Over the course of hundreds of years of cultivation, farmers relaxed the selective pressures that maintained germination heteromorphism by acting as seed dispersers (Silvertown 1984), moving erect knotweed seeds into more stable environments and saving seeds outside of the seed bank.

On the time scale of a single season, however, knotweed’s plastic response to full-sun environments might actually have led to the production of more tubercled morphs, not less. This adaptive transgenerational plasticity, thoroughly documented in *Persicaria maculosa* (Herman and Sultan 2011; Sultan 1996) and suggested by my own experiments for erect knotweed, makes the existence of assemblages like the one from Whitney Bluff even more remarkable. Rather than contributing to the domestication syndrome observed in *P. erectum*, this particular plastic response probably worked against its development. Nevertheless, by Mississippian times, some communities had developed a domesticated form of *P. erectum*. Analysis of other *P. erectum* assemblages from older and contemporaneous sites, observations of wild-growing *P. erectum*, and experimental cultivation are ongoing, and will provide more insights into how this lost crop evolved in pre-Columbian agroecosystems.

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References

Abbo S, Rachamim E, Zehavi Y, Zezak I, Lev-Yadun S, Gopher A (2011) Experimental growing of wild pea in Israel and its bearing on Near Eastern plant domestication. Ann Bot 107:1,399–1,404

Adams KR (2014) Little barley grass (*Hordeum pusillum* Nutt.): A Prehispanic New World domesticate lost to history. In: Minnis PE (ed) New lives for ancient and extinct crops. The University of Arizona Press, Tuscon, pp 139–179

Asch DL, Asch NB (1985a) Archaeobotany. In: Conner MD (ed) The Hill Creek homestead and the Late Mississippian settlement in the lower Illinois River valley, vol 1. Kampsville Archaeological Center. The Center for American Archaeology, Kampsville, pp 115–170

Asch DL, Asch NB (1985b) Prehistoric plant cultivation in West Central Illinois. In: Ford RI (ed) Prehistoric food production in North America, vol 75., Museum of AnthropologyUniversity of Michigan, Ann Arbor, MI, pp 149–203

Asouti E, Fuller DQ (2012) From foraging to farming in the southern Levant: the development of epipalaeolithic and pre-pottery neolithic plant management strategies. Veget Hist Archaeobot 21:149–162

Asouti E, Fuller DQ (2013) A contextual approach to the emergence of agriculture in southwest Asia. Curr Anthropol 54:299–345

Blake SF (1939) A new variety of *Iva ciliata* from Indian rock shelters in the south-central United States. Rhodora 41:81–86

Boyd WJR, Gordon AG, LaCroix LJ (1971) Seed size, germination resistance, and seedling vigor in barley. Can J Plant Sci 51:93–99

Braadbaart F, Wright PJ (2007) Changes in mass and dimensions of sunflower (*Helianthus annuus* L.) achenes and seeds due to carbonization. Econ Bot 61:137–153

Brenkle JF (1946) Notes on Avicularia II. Phytologia 2:169–171

Childs DZ, Metcalf CJE, Rees M (2010) Evolutionary bet-hedging in the Real World: empirical evidence and challenges revealed by plants. Proc R Soc Lond B 277:3055–3064

Clements RJ, Latter BDH (1974) Responses to selection for seed weight and seedling vigour in *Phalaris*. Crop Pasture Sci 25:33–44

Cohen D (1966) Optimizing reproduction in a randomly varying environment. J Theor Biol 12:119–129

Costea M, Tardif FJ, Hinds HH (2005) *Polygonum* L. In: Committee FoNAE (ed) Flora of North America north of Mexico, vol 5. http://www.eFloras.org, New York and Oxford

Courtney AD (1968) Seed dormancy and field emergence in *Polygonum aviculare*. J Appl Ecol 5:675–684

D'Andrea AC (2008) T'ef (*Eragrostis tef*) in ancient agricultural systems of highland Ethiopia. Econ Bot 62:547–566

Dahlberg JA, Wasylikowa K (1996) Image and statistical analyses of early *Sorghum* remains (8000 BP) from the Nabta Playa archaeological site in the Western Desert, southern Egypt. Veget Hist Archaeobot 5:293–299

Flannery KV (1973) The origins of agriculture. Ann Rev Anthropol 2:271–310

Ford RI (ed) (1985) Prehistoric food production in North America, vol 75., Anthropological PapersMuseum of Anthropology, University of Michigan, Ann Arbor

Fritz GJ (1984) Identification of cultigen amaranth and chenopod from rockshelter sites in Northwest Arkansas. Am Antiq 49:558–572

Fritz GJ (1986) Prehistoric Ozark agriculture: The University of Arkansas rockshelter collections. Dissertation, University of North Carolina

Fritz GJ (1993) Early and Middle Woodland period palaeoethnobotany. In: Scarry CM (ed) Foraging and farming in the Eastern Woodlands. University Press of Florida, Gainesville, pp 39–56

Fritz GJ (2014) Maygrass: Its role and significance in native Eastern North American. In: Minnis PE (ed) New lives for ancient and extinct crop. Universtiy of Arizona Press, Tuscon, pp 12–43

Fritz GJ, Smith BD (1988) Old collections and new technology: documenting the domestication of *Chenopodium* in Eastern North America. Midcont J Archaeol 13:3–27

Fuller DQ, Qin L, Zheng Y, Zhao Z, Chen X, Hosoya LA, Sun G-P (2009) The domestication process and domestication rate in rice: spikelet bases from the Lower Yangtze. Science 323:1,607–1,610

Gilmore MR (1931) Vegetal remains of the Ozark Bluff-Dweller Culture. Pap Mich Acad Sci Arts Lett 14:83–102

Granitto PM, Verdes PF, Ceccatto HA (2004) Large-scale investigation of weed seed identification by machine vision. Comput Electron Agric 47:15–24

Gremillion KJ (1993) The evolution of seed morphology in domesticated *Chenopodium*: an archaeological case study. J Ethnobiol 13:149–169

Gremillion KJ (1998) Changing roles of wild and cultivated plant resources among early farmers of eastern Kentucky. Southeast. Archaeol 17:140–157

Gremillion KJ, Piperno DR (2009) Human behavioral ecology, phenotypic (developmental) plasticity, and agricultural origins. Curr Anthropol 50:615–619

Harlan JR, De Wet JMJ (1965) Some thoughts about weeds. Econ Bot 19:16–24

Harlan JR, De Wet JMJ, Price EG (1973) Comparative evolution of cereals. Evol 27:311–325

Heiser CB Jr (1954) Variation and subspeciation in the common sunflower, *Helianthus annuus*. Am Midl Nat 51:287–305

Herman JJ, Sultan SE (2011) Adaptive transgenerational plasticity in plants: case studies, mechanisms, and implications for natural populations. Front Plant Sci 2:1–10

Hillman GC, Davies MS (1990) Measured domestication rates in wild wheats and barley under primitive cultivation, and their archaeological implications. J World Prehist 4:157–222

Hunter AA (1992) Utilization of *Hordeum pusillum* (Little Barley) in the Midwest United States: Applying Rindos' Co-evolutionary model of domestication. Dissertation, University of Missouri-Columbia

Imbert E (2002) Ecological consequences and ontogeny of seed heteromorphism. Perspect Plant Ecol Evol Syst 5:13–36

Langlie BS, Hastorf CA, Bruno MC, Bermann M, Bonzani RM, Condarco WC (2011) Diversity in Andean *Chenopodium* domestication: describing a new morphological type from La Barca, Bolivia 1,300–1,250 BC. J Ethnobiol 31:72–88

Leishman MR, Wright IJ, Moles AT, Westoby M (2000) The evolutionary ecology of seed size. In: Fenner M (ed) Seeds: the ecology of regeneration in plant communities, pp 31–57

Mertens TR (1968) *Polygonum*: A knotty problem in plant taxonomy. Am Biol Teach 30:832–840

Mertens TR, Raven PH (1965) Taxonomy of *Polygonum*, section *Polygonum* (Avicularia) in North America. Madrono 18:85–92

Metzger JD (1992) Physiological basis of achene dormancy in *Polygonum convovulus* (Polygonaceae). Am J Bot 79:882–886

Mueller NG (forthcoming) An extinct domesticated subspecies of erect knotweed in eastern North America: *Polygonum erectum* L. ssp. *watsoniae* (POLYGONACEAE). Novon 25 (2)

Piperno DR, Holst I, Winter K, McMillan O (2015) Teosinte before domestication: experimental study of growth and phenotypic variability in late pleistocene and early Holocene environments. Quat Int 363:65–77

Powell G (2000) Charred, non-maize seed concentrations in the American bottom area: examples from the Westpark site (11-MO-96), Monroe County, Illinois. Midcont J Archaeol 25:27–48

Reimer PJ et al. (2013) IntCal13 and marine13 radiocarbon age calibration curves 0–50,000 years cal BP. Radiocarbon 55:1,869–1,887

K-i Tanno, Willcox G (2012) Distinguishing wild and domestic wheat and barley spikelets from early Holocene sites in the Near East. Veget Hist Archaeobot 21:107–115

Rindos D (1984) The origins of agriculture: an evolutionary perspective. Academic Press, Orlando

Roach DA, Wulff RD (1987) Maternal effects in plants. Ann Rev Ecol Syst 18:209–235

Rogler GA (1954) Seed size and seedling vigor in crested wheatgrass. Agron. J 46:216–220

Rovner I, Gyulai F (2006) Computer-assisted morphometry: a new method for assessing and distinguishing mophological variation in wild and domestic seed populations. Econ Bot 61:154–172

Silvertown JW (1984) Phenotypic variety in seed germination behavior: the ontogeny and evolution of somatic polymorphism in seeds. Am Nat 124:1–16

Simon ML, Parker KE (2006) Prehistoric plant use in the American bottom: new thoughts and interpretations. Southeast. Archaeol 25:212–257

Slatkin M (1974) Hedging one's evolutionary bets. Nature 250:704–705

Smith BD (1992) Rivers of change: essays on early agriculture in eastern North America. Smithsonian Institution Press, Washington

Smith BD (2006) Eastern North America as an independent center of plant domestication. Proc Nat Acad Sci 103:12,223–12,228

Smith BD (2014) The domestication of *Helianthus annuus* L. (Sunflower). Veget Hist Archaeobot 23:57–74

Smith CC, Fretwell SD (1974) The optimal balance between size and number of offspring. Am Nat 108:499–506

Smith BD, Funk VA (1985) A newly described subfossil cultivar of *Chenopodium* (Chenopodiaceae). Phytologia 57:445–448

Smith BD, Yarnell RA (2009) Initial formation of an indigenous crop complex in eastern North America at 3800 BP. Proc Nat Acad Sci 106:6,561–6,566

Sultan SE (1996) Phenotypic plasticity for offspring traits in *Polygonum persicaria.* Ecology 77:1,791–1,807

Sultan SE (2001) Phenotypic plasticity for fitness components in Polygonum species of contrasting ecological breadth. Ecology 82:328–343

Sultan SE (2003) Phenotypic plasticity in plants: a case study in ecological development. Evol Dev 5:25–33

Sultan SE, Horgan-Kobelski T, Nichols LM, Riggs CE, Waples RK (2013) A resurrection study reveals rapid adaptive evolution within populations of an invasive plant. Evol Appl 6:266–278

Venable DL (1985) The evolutionary ecology of seed heteromorphism. Am Nat 126:577–595

Wymer DA, Abrams E (2003) Early woodland plant use and gardening: evidence from an adena hamlet in southeastern Ohio. Midcont J Archaeol 28:175–194

Yarnell RA (1978) Domestication of sunflower and sumpweed in eastern North America. In: Ford RA (ed) The nature and status of ethnobotany. Anthropological Papers No. 67. Museum of Anthropology, University of Michigan, Ann Arbor, MI, pp 289–299

Yarnell RA (1993) The importance of native crops during the late Archaic and Woodland periods. In: Scarry CM (ed) Foraging and farming in the Eastern Woodlands. University Press of Florida, Gainesville, pp 13–26

Yurtseva OV (2001) Ultrasculpture of achene surface in *Polygonum* section *Polygonum* (Polygonaceae) in Russia. Nord. J Bot 21:513–528

Zach B, Klee M (2003) Four thousand years of plant exploitation in the Chad Basin of NE Nigeria II: discussion on the morphology of caryopses of domesticated *Pennisetum* and complete catalogue of the fruits and seeds of Kursakata. Veget Hist Archaeobot 12:187–204