



Documenting the Evolution of Agrobiodiversity in the Archaeological Record: Landraces of a Newly Described Domesticated (*Polygonum erectum*) in North America

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Abstract Relatively few farmers today actively maintain crop biodiversity, but for most of the history of agriculture this was the norm. Archaeobotanical analyses can reveal the processes that led to the evolution of crop biodiversity throughout the Holocene, an issue of critical importance in an era of climate change and agrobiodiversity loss. Indigenous eastern North Americans domesticated several annual seed crops, called the Eastern Agricultural Complex, beginning c. 1800 BC. Using population morphometrics, this paper reports new evidence for the evolution of a domesticated sub-species of one of these crops, erect knotweed (*Polygonum erectum* L.), and its subsequent diversification under cultivation. Morphometric analyses were conducted on archaeological erect knotweed populations spanning its ancient cultivated range, and these were directly dated to c. 1–1350 AD, anchoring the evolution of this crop in both time and space. Domesticated erect knotweed first appears c. 1 AD in the Middle Ohio Valley. A diachronic series of populations from western Illinois shows that this species was domesticated again c. 150–1000 AD. This study shows how agricultural knowledge and material were maintained and shared (or not) by communities during an important era in eastern North America's history: when small communities were aggregating to form the earliest urban center at Cahokia, in the American Bottom floodplain. A distinctive landrace was developed by farmers in the American Bottom which is significantly different from cultivated populations in other regions. Subsequent Mississippian assemblages (c. 1000–1350 AD) indicate divergent agricultural communities of practice, and possibly the eventual feralization of erect knotweed. Archaeobotanical studies have a vast untapped potential to reveal interaction between

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communities, or their isolation, and to investigate the evolution of crops after initial domestication.

Keywords Domestication · Landraces · Agrobiodiversity · Eastern agricultural complex · Origins of agriculture · Niche construction · Communities of practice

Introduction

“When we compare the individuals of the same variety or sub-variety of our older cultivated plants and animals, one of the first points which strikes us is, that they generally differ more from each other than do individuals of any one species or variety in a state of nature.”

–Charles Darwin, *On the Origin of Species*, Chap. 1. 1859

Morphological studies of crop seeds in the archaeological record have usually focused on identifying changes in wild species undergoing the initial process of domestication. But humans do not cease shaping domesticated plants and animals at the moment that they can be distinguished from their wild progenitors. They continue to exert selective pressure on domesticates as long as they live in association, both consciously and unconsciously adapting them to local environmental conditions and tastes, or even to the idiosyncrasies of individual fancy (Brush 2000; Nazarea 2005; Thomas *et al.* 2012; Jarvis *et al.* 2008). Since the discovery of hybrid vigor prompted the breeding of genetically homogenous crop varieties beginning in the early twentieth century, the trend within industrialized agriculture has been towards greater homogeneity in crop morphology and genetics. This trend has intensified with the addition of patentable genes to elite hybrid varieties (Kloppenburger 2005). Surrounded as many of us are by homogenous crops, it is easy to lose sight of the simple fact pointed out by Darwin in the opening chapter of *On the Origin of Species*: domestication usually creates a remarkable array of distinct types in comparison to natural selection (Darwin 1902 [1859]). In annual crops, these are called landraces: phenotypically and (sometimes) genetically recognizable varieties that have been developed at a local social and environmental scale. This enormous reservoir of crop genetic diversity was developed by farmers over the course of thousands of years, and is the source of the beneficial adaptations tapped by plant breeders to create “improved” varieties since the late nineteenth century (Zeven 1998; Brown 1989).

Because landraces are created in part by farmer seed selection, they often have seeds that are distinguishable in terms of shape and size from other landraces (Brunken *et al.* 1977; Hilu and De Wet 1976; Vavilov 1992). This circumstance renders landraces amenable to archaeobotanical study, since seeds are readily preserved at many archaeological sites. Crop genetic diversity is a priceless but threatened resource. Today, relatively few farmers select and save their own seed, but for most of the history of agriculture this was the norm. With the increasingly high resolution of the archaeobotanical record in some regions, it is now possible to study crop diversification

over hundreds or thousands of years. Archaeobotanical studies have a vast untapped potential to contribute to our understanding the conditions and practices that tend to result in the creation and maintenance of crop biodiversity.

The development and exchange of ancient landraces and the evolution of crop genetic diversity has increasingly been the subject of study within archaeology, using both ancient DNA and morphometrics (Chiou *et al.* 2014; Da Fonseca *et al.* 2015; Freitas *et al.* 2003; Jaenicke-Després and Smith 2006; Lema *et al.* 2008; Liu *et al.* 2016; Toulemonde *et al.* 2015). Meanwhile, because of their importance to maintaining food security in an era of population growth and climate change, a great deal of effort has been expended in the past quarter century elucidating how contemporary farmers maintain morphologically and functionally distinct landraces (Demissie and Bjørnstad 1996; Louette and Smale 2000; Misiko 2010; Moreno *et al.* 2006; Teshome *et al.* 1999; Tsehaye *et al.* 2006; Westengen *et al.* 2014, and many others). This body of research demonstrates that landraces are artifacts of communities of practice: a group of people participating in social learning on a given domain—in this case agriculture (Lavé and Wenger 1991). Crop varieties are direct artifacts of communally held knowledge. Since they need to be re-created on a yearly basis through seed selection and various forms of management, they cease to exist if they are not maintained within social institutions that facilitate the acquisition and practice of complex bodies of knowledge (McCullough and Matson 2016; Misiko 2010; Mueller 2018). They thus also reflect the diffusion (or lack thereof) of knowledge and material between communities (Badstue *et al.* 2006; Calvet-Mir *et al.* 2012; Kiptot *et al.* 2006; McGuire 2008; Pautasso *et al.* 2013; Perales *et al.* 2005; Thomas *et al.* 2011; Stromberg *et al.* 2010). Making the connection between distinctive landrace morphologies in the archaeological record and the myriad social dynamics they embody requires (1) a high resolution archaeobotanical record at the scale of ancient communities of practice; and (2) a morphological dataset that captures variation in ancient crop *populations*, *i.e.* measurements of large samples of seeds from well-defined archaeological contexts. These two conditions cannot yet be met in all regions, but high resolution archaeobotanical records are available from many areas, including eastern North America (ENA).

I use morphometric and experimental data on one crop species, erect knotweed (*Polygonum erectum* L.), to explore the development and spread of agricultural communities of practice in pre-Columbian ENA. This region was home to a pre-maize agricultural system based on a suite of native seed crops that was lost to history. In the late 1960s, archaeologists began to adopt methods for systematically recovering and dating plant remains from sites. As a result of this methodological revolution, it quickly became clear that ENA, long considered a backwater of agricultural development, had been home to an indigenous crop complex now called the Eastern Agricultural Complex (EAC) for thousands of years before the introduction of maize and other tropical crops from Mexico (Ford 1985; Scarry 1993; Smith 2006) (Fig. 1). Subsequently, a fortuitous combination of legal and institutional frameworks have resulted in the collection of an extremely high resolution and methodologically consistent archaeobotanical record in parts of ENA, especially in western Illinois near the confluence of the Illinois, Mississippi, and Missouri rivers. (Asch and Asch 1985b; Johannessen 1988; Simon and Parker 2006). This region is known to the archaeologists as the Lower Illinois valley (LIV) and the American Bottom (AMB), after its major floodplains (Fig. 1), and has yielded most of the samples analyzed here.

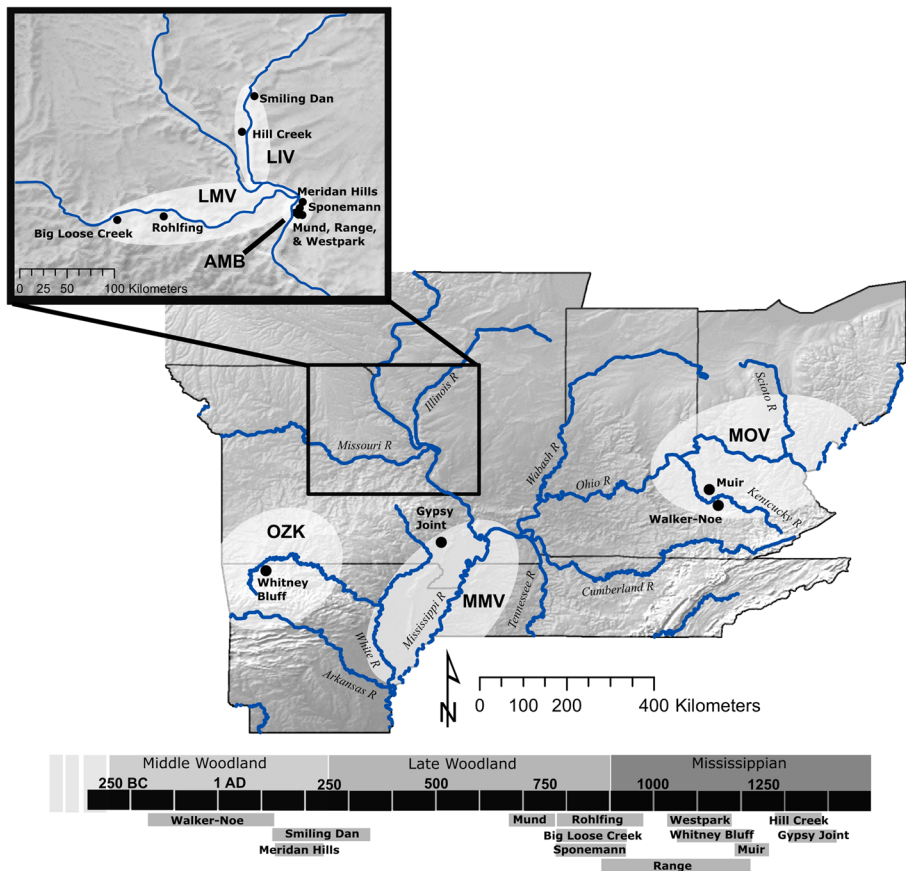


Fig. 1 Map of study area showing sites included in this analysis. Regions mentioned in the text are represented approximately by shaded white ovals: American Bottom (AMB), Lower Illinois Valley (LIV), Lower Missouri Valley (LMV), Middle Mississippi Valley (MMV), Middle Ohio Valley (MOV), and Ozarks (OZK). The timeline represents the calibrated ages of each assemblage of erect knotweed (95.5%) based on dated achenes, not the entire occupation of the site. Radiocarbon dates are reported in Table 1

Erect knotweed is an annual herbaceous plant that was cultivated for its edible seeds, which are somewhat similar to those of buckwheat (*Fagopyrum esculentum* Moench) (both are in the family Polygonaceae; Fig. 2). Like buckwheat and some other non-cereal crops, such as sunflowers, erect knotweed produces *achenes*, which are one seeded fruits with hard pericarps (fruit coats). It may have been harvested as a seed crop as early as 1500 BC, and is abundant and ubiquitous at many archaeological sites dating to the Middle Woodland – Mississippian periods, c. 250 BC–1400 AD, in the region shown in Fig. 1 (Mueller 2017e). A comparative analysis of several knotweed species native to the study area and the Whitney Bluff assemblage (c. AD 1100; Table 1) resulted in the formal description of a domesticated sub-species, *Polygonum erectum* ssp. *watsoniae* N.G. Muell., with the Whitney Bluff assemblage as the type specimen for the new taxon (Mueller 2017d).

In comparison to wild erect knotweed, *P. erectum* ssp. *watsoniae* has larger seeds and reduced achene dimorphism. The latter criteria requires some explanation. Wild

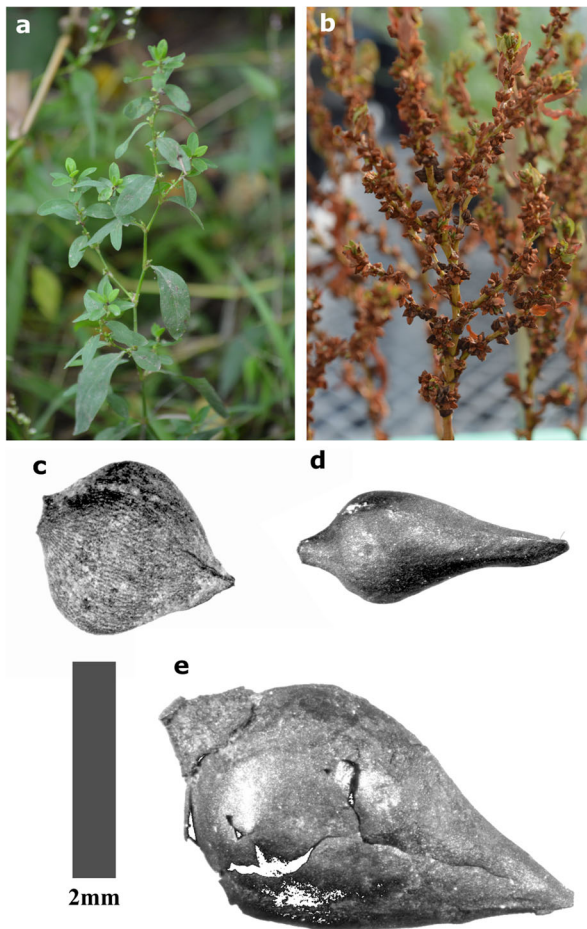


Fig. 2 Erect knotweed morphology. **a** Erect knotweed plant in late summer, with flowers and early achenes developing in the axils of its branches; **b** senesced plant in late October, covered in achenes that are easily hand-stripped; **c** tubercled morph achene from a modern plant, experimentally carbonized; **d** smooth morph achene from a modern plant, experimentally carbonized; and **e** domesticated size carbonized achenes from the Hill Creek site, for comparison. These microphotographs are representative of those analyzed to generate the morphometric datasets represented in Figs. 3 and 4 and Table 2

erect knotweed produces two achene morphs: tubercled morphs that have a thicker, more durable fruit coat and greater innate dormancy, and smooth morphs that have a thinner, more permeable fruit coat and germinate more readily (Fig. 2). From a farmer's perspective, this means smooth morphs can be counted on to germinate reliably when planted the spring after they are harvested, and tubercled morphs cannot. From the plant's perspective, tubercled morphs are a means of bet-hedging in an unpredictable environment (Childs *et al.* 2010; Cohen 1966). They can remain viable in the seed bank for several generations and allow a population to regenerate if an entire generation is lost to flood, drought, or predation. I have argued that humans relieved the selective pressures that maintain such strategies in wild plants by moving erect knotweed seedlings to more predictable habitats and by storing seeds, providing an alternative to survival in the soil seed bank in bad years (Mueller 2017b, 2017c). Seedlings sprung

Table 1 Dates, context, sample sizes, sample proportions

| Site name & number | Contexts sampled | Age | Error | NOSAMS # or source | Calibrated age range (94.5%) | Median | N, Morphometric analysis ¹ | N, Total achenes ² | % Smooth ³ |
|--------------------------|---|------|-------|---------------------------------|---------------------------------|---------|--|----------------------------------|-----------------------|
| Walker-Noe 15GD56 | Unit 9, Z2 L2 Feature 2 Sub-mound burial | 2000 | 60 | Pollack <i>et al.</i> 2006:67-8 | 167 BCE – CE 125 | 8 BCE | 3 | 24 | *100 |
| | F242 (Pit) | 1950 | 25 | 134355 | 21 BCE – CE 125 | CE 52 | 8 | 16 | *94 |
| | F194 (Pit) | 1840 | 20 | 134362 | CE 125–238 | CE 176 | 22 | 43 | 23 |
| | F110 (Pit) | 1750 | 20 | 134363 | CE 236–347 | CE293 | 2 | 14 | 0 |
| | F164 (Pit) | | | | | | 14 | 40 | 28 |
| | F205 (Pit) | | | | | | 34 | 79 | 37 |
| | F92 (Pit) | | | | | | 15 | 35 | 34 |
| Meridian Hills 11MS1258 | F55 (Pit) | 1830 | 20 | 134359 | CE 130–237 | CE 182 | 13 | 30 | 43 |
| Mund 11S435 | Feature 90 (Pit) | 1280 | 20 | 134357 | CE 672–770 | CE 717 | 28 | 31 | 6 |
| Big Loose Creek 23OS1208 | F32 (Pit) | | | | | | 45 | 124 | *100 |
| | F19 (Pit) | 1170 | 20 | 136215 | CE 774–943 | CE 845 | 10 | 11 | 82 |
| Sponemann 11MS517 | F592 (Pit) | 1160 | 15 | 134358 | CE 776–950 | CE 878 | 56 | 97 | 22 |
| Rohlfing 23FR525 | F7, Z4 (Pit) | | | | | | 79 | 123 | 24 |
| | F7 (contents of vessel in pit) | 1140 | 20 | 134365 | CE 777–977 | CE 924 | 46 | 54 | 57 |
| Range 11S47 | F501 (Pit) | 1010 | 75 | Kelly 2007:470 | CE 880–1213 | CE 1029 | 3 | 11 | 82 |
| Westpark 11MO86 | Feature 300 (Pit) | 910 | 20 | 134,356 | CE 1037–1183 | CE 1094 | 70 | 137 | *80 |
| Whitney Bluff 3BE20 | 32-57-5 (Pit) | 885 | 20 | 134366 | CE 1046–1217 | CE 1163 | 100 | 500 | *78 |
| | 32-57-3 (Pit) | | | | | | 81 | 706 | *100 |
| Muir 15JS86 | F22 (Pit) | 825 | 15 | 134361 | CE 1180–1260 | CE 1223 | 120 | 601 | *100 |
| Hill Creek 11PK525 | Feature 1 (Pit) | 680 | 15 | 136214 | CE 1277–1383 | CE 1291 | 19 | 65 | 14 |
| Gypsy Joint 23RI101a | F5b (Pit) | 575 | 20 | 134351 | CE 1310–1415 | CE 1345 | 146 | 400 | *100 |
| | | | | | | | 140 | 1043 | *87 |

Table 1 (continued)

| Site name & number | Contexts sampled | Age | Error | NOSAMS # or source | Calibrated age range (94.5%) | Median | N, Morphometric analysis ¹ | N, Total achenes ² | % Smooth ³ |
|-------------------------|------------------|-----|-------|-----------------------|---------------------------------|-----------------|--|----------------------------------|-----------------------|
| Belews Creek Missouri | | | | | | CE 2014–2015 | 140 | 140 | 29 |
| Crawford Creek Illinois | | | | | | CE 2014–2105 | 87 | 87 | 24 |
| Herbarium specimens | | | | | | CE 1950–Present | 48 | 48 | 27 |

¹ Reports the number of achenes that were well-preserved enough to take size and shape measurements, which are represented in Figs. 3 and 4, with summary statistics presented in Table 1

² Reports the number of specimens that had enough preserved pericarp to classify as either smooth or tubercled morphs, many of which were not well-preserved enough to measure

³ Reports the percentage of “Total achenes” that were smooth morphs

*indicates a sample proportion that is significantly higher than the natural range of variation (and thus indicative of domestication), given sample size

from smooth morphs also develop more rapidly in the 5 weeks after germination, which likely led to their greater success in fields and gardens if people were thinning out cultivated patches. Experiments show that thinning would have noticeably increased yield, and it also would tend to select for larger seeds (Mueller 2017b, c). Direct evidence for this practice comes from the domestication syndrome itself: both an increase in seed size and a decrease in the percentage of tubercled morphs are characteristic of domesticated populations.

Having established that domesticated erect knotweed did exist by AD 1100, the goals of the subsequent analyses reported here were (1) to determine when and where erect knotweed was domesticated; and (2) to document variation within and between cultivated populations that might reveal different communities of practice. I analyzed concentrations of erect knotweed achenes from 13 archaeological sites, then obtained direct dates for each assemblage (Table 1; Fig. 1). The assemblages date c. 1–1350 AD and span the region where erect knotweed was cultivated in ancient times. This approach allows for a preliminary reconstruction of erect knotweed's entire evolutionary history as a crop, including both its domestication and its subsequent diversification. It also allows me to use the morphology of populations of erect knotweed as an artifact of agricultural practice, one that can be used to understand the spread of knowledge and seed stock between communities, or their isolation.

The following review is meant to put the botanical assemblages selected for this study in context and introduce key moments and trends in the development of agriculture in ENA. Special attention is given to evidence for the development of practices that are known to create and maintain crop biodiversity: field diversity (in terms of altitude, available moisture, soil type, *etc.*) (Teshome *et al.* 1999), farmer seed selection (Louette and Smale 2000; Moreno *et al.* 2006; Tsehaye *et al.* 2006), and seed exchange networks (Thomas *et al.* 2011).

The Development of Agriculture in Eastern North America

ENA is one of the independent centers of plant domestication, where the domestication of annual plants began c. 3000 BC, during the Late Archaic period (see Fig. 1 for a schematic timeline of ENA archaeological periods). The earliest domesticates were squash (*Cucurbita pepo* ssp. *ovifera* D.S. Decker), sumpweed (also referred to as marshelder; *Iva annua* L.), sunflower (*Helianthus annuus* L.), and goosefoot (*Chenopodium berlandieri* Moq.). The domesticated forms of sunflower (*Helianthus annuus* L. var. *macrocarpus* Cockerell) and sumpweed (*Iva annua* L. var. *macrocarpa* S.F. Blake) are recognized archaeologically by an increase in achene (fruit) or kernel (seed) size compared to wild progenitors (Blake 1939; Heiser 1954; Smith 2014; Yarnell 1972). Domesticated goosefoot (*Chenopodium berlandieri* Moq. subsp. *jonesianum* Smith and Funk) is recognized on the basis of a thin, smooth seed coat (testa) and an increase in seed volume associated with a change in the shape of the seed margin (Fritz and Smith 1988; Gremillion 1993a, Smith and Funk 1985). For squash, domestication is recognized by an increase in seed size and an increase in rind thickness (Cowan and Smith 1993; Fritz 1999; Kay *et al.* 1980). Ancient DNA analyses have confirmed that although both squashes and goosefoot were also domesticated in Mexico, they were independently domesticated in eastern

North America (Kistler *et al.* 2015; Kistler and Shapiro 2011). Bottle gourds (*Lagenaria siceraria* (Molina) Standl.) were also cultivated during the Archaic (Doran *et al.* 1990; Kay *et al.* 1980). These most likely floated across the Atlantic Ocean from their native Africa and were probably spread by both humans and megafauna in the New World (Kistler *et al.* 2014).

The earliest evidence for domestication in ENA comes from the Phillips Spring site in south-central Missouri and consists of abnormally large squash seeds directly dated to 3000 BC (B. D. Smith and Yarnell 2009). But the presence of domesticated squashes and gourds does not necessarily imply the beginnings of food producing economies: some have argued that squashes and gourds (like dogs) could easily be domesticated by highly mobile hunters and gatherers, and were probably initially both consumed (seeds, flowers) and used to make tools, such as cups, bowls, dippers, and fish net floats. Squash remains of a similar age from Maine, outside the possible wild range of squashes and in a region that remained agriculture-free until the Colonial era, further demonstrate that hunter-gatherers were extending the range of squashes and gourds, at the very least (Fritz 1999).

A few centuries later, domesticated sunflower made its first appearance at the Hayes site on the Duck River in Tennessee (Crites 1993; Smith and Yarnell 2009). Throughout the 3rd millennium BC, some societies in ENA began to invest more energy in cultivating annual seed crops. The inhabitants of Napoleon Hollow in the Lower Illinois valley, had domesticated sumpweed by c. 2200 BC: 44 abnormally large sumpweed achenes come from the Late Archaic strata of this site. Unlike the isolated squash and gourd remains at Phillips Spring and the domesticated sunflower achenes at the Hayes site, the domesticated sumpweed at Napoleon Hollow was accompanied by the remains of other plants that were destined to become part of the EAC, including squash, goosefoot, and sunflower (Asch and Asch 1986). By c.1800 BC, the inhabitants of the Riverton site on the Wabash River in Illinois were cultivating bottle gourd, squash, domesticated sunflower, domesticated sumpweed, and both domesticated and wild/weedy goosefoot. Little barley (*Hordeum pusillum* Nutt.), which became an important crop during the Middle and Late Woodland periods, was also present in small amounts at Riverton (Smith and Yarnell 2009).

Clearly by this time, certain communities in the river valleys of the midcontinent were invested in the cultivation of annual seed crops and were experimenting with a variety of different plants. However, it is unlikely that Late Archaic communities were primarily farmers of small-seeded annual plants. At all of the sites mentioned above, nuts, especially hickory (*Carya* sp.), were overwhelming abundant, and EAC crops were represented by small amounts of seeds in comparison to later sites. At the contemporary shell-mound Archaic sites of the Green River, Kentucky, early small-seeded crops are almost invisible and riverine and nut resources were obviously the focus of subsistence activities (Crawford 1982; Marquardt and Watson 2005). Nevertheless, some communities of hunter-gatherers developed and maintained domesticated populations of at least five different plants (gourds, squashes, sunflower, goosefoot, and sumpweed). According to classic theories of domestication, this means that they were subjecting cultivated plants to a set of selective pressures different from those faced by their wild ancestors, and thus developing genetically distinct populations over many generations (de Wet and Harlan 1975). New evidence from experimental cultivation of the EAC crops suggests that some of the morphological changes documented by

archaeobotanists may have happened rapidly (over the course of only few growing seasons) as a result of developmental plasticity in garden ecosystems (Mueller *et al.* 2017)—but either way changes in seed morphology reflects human ecosystem engineering and the development of consistent cultivation practices during the Late Archaic.

During this early era, there is little evidence that erect knotweed was cultivated. Simon and Parker (2006) review several Late Archaic sites in the American Bottom where erect knotweed was recovered alongside other members of the EAC, but in very small amounts. In west-central Kentucky and southeastern Ohio, a few knotweed seeds, species unknown, have been recovered from Late Archaic sites (Patton and Curran 2016; Crawford 1982). Given the weedy nature of these species, a few seeds may simply represent the local vegetation (Simon 2009), and its frequent incidental presence around houses and camps and along trails might have been what first brought it to humans' attention. Even though erect knotweed was probably not cultivated yet, the foundations of agricultural knowledge and practice built during the Late Archaic shaped the development of the Woodland and Mississippian EAC, which are the subject of this study.

The Early Woodland period begins with migrations into uplands in many regions of ENA, a phenomenon that was likely caused by increased flood frequency or severity in the Mississippi River and its tributaries (Kidder 2006). The most abundant evidence for Early Woodland food production comes from the upland rockshelters, especially in eastern Kentucky and Tennessee (Gremillion 1993b, 2004). This is likely only partially caused by preservation or sampling bias: Significant clearance of upland forest, most likely by anthropogenic fire, indicates that cultivation also moved out of the floodplain and onto previously forested upland terraces (Delcourt *et al.* 1986; Delcourt and Delcourt 2004; Delcourt *et al.* 1998; Abrams *et al.* 2014). The suite of plants recovered from Early Woodland rockshelters usually includes all of the Archaic crops discussed above, with the addition of maygrass (*Phalaris caroliniana* Walt.), a spring maturing annual grass that was cultivated in ENA for ~2500 years (Fritz 2014). Erect knotweed is also sometimes recovered from storage contexts at rockshelters and caves dating to the Early Woodland (Gremillion 1993b; Yarnell 1974), and this is the first clear evidence for its cultivation. I have argued that upland farmers on the eastern margin of the core area pioneered new agricultural methods, especially the use of altitudinal variation in field placement, to mitigate risk, which resulted in the domestication of erect knotweed in the Ohio valley by 1 AD (Mueller 2018).

Another unique source of data about Early Woodland subsistence comes from the paleofeces of mineral miners in the Salts and Mammoth Cave systems of eastern Kentucky (Yarnell 1969) and Big Bone cave in eastern Tennessee (Faulkner 1991), in addition to the intestinal and colon contents of one mummy, a young boy who died in Mammoth cave (Robbins 1974; Yarnell 1974a). This direct evidence for consumption supports the impression given by the archaeobotanical record in general: nuts (especially hickory) were very important foods, but small-seeded annuals (especially sumpweed and goosefoot) were a ubiquitous part of the human diets. The achenes of erect knotweed were found in three different paleofecal specimens from Big Bone cave dating to the later part of the Early Woodland period, c. 200 BC (Faulker 1991) and “knotweed or smartweed” was recovered from several of the Salts and Mammoth cave paleofeces (Yarnell 1969).

Though erect knotweed was cultivated in the east during the Early Woodland, is was probably not yet a crop on the western margin of the core area. One remarkable assemblage from the Ozarks (OZK), Marble Bluff, includes a carbonized assemblage of three fragmentary bags full of domesticated goosefoot seeds. A mixed assemblage from a nearby context contained wild or weedy type goosefoot, a member of the mint family (Lamiaceae), ragweed, sunflower, amaranth (*Amaranthus* sp.), gourd or squash, sumpweed, and maygrass—in addition to several seeds identified by Fritz (1997:51) as “knotweed (*Polygonum* sp., but probably not *Polygonum erectum*)” (Fritz 1986). The knotweed from Marble Bluff, as Fritz suspected, is not erect knotweed. According to the latest taxonomies, it is not a member of the same genus: it is a species of smartweed (*Persicaria* sp.) (Mueller 2017e). However, this fascinating assemblage provides evidence for the selection and separation of superior seed stock for planting. The bags of domesticated goosefoot may have been seed sock, while the lower quality seed stored nearby was for food.

At the end of the Early Woodland period, the appearance of Adena/Hopewell sites in the Ohio River valley signals the beginning of Middle Woodland trends: long distance trade, increasing interregional interaction, and the construction of monumental architecture, coincident with increasing visibility and variability of EAC crops. The Archaic crops are supplemented by maygrass, erect knotweed, and little barely (*Hordeum pusillum* Nutt.), which became increasingly important throughout the Woodland period in the Middle Ohio valley (MOV) (Wymer 1996, 2009; Wymer and Abrams 2003), the Lower Illinois valley (Asch and Asch 1985b), the American Bottom (Simon and Parker 2006), central Tennessee (Crites 1987), northwestern Arkansas (Fritz 1986), and in the central Mississippian valley (Fritz 1993, 2000). Localized evidence for land clearance and erosion is present for at least one large Middle Woodland earthwork (McLauchlan 2003). I have suggested elsewhere that exchange at Middle Woodland mound centers and earthworks may have included the seeds of superior seed stock (Mueller 2013, 2018). In this scenario, the increased intensity and tempo of exchange in general during the Middle Woodland period contributed to the spread of agricultural materials and knowledge in particular, and resulted in the solidification of food producing economies. At the same time, gathered plant resources continue to be very visible parts of archaeobotanical assemblages, creating an overall impression of a diverse food system that relied on a patchy landscape of cultivated fields, open woodlands, and marshes. The Middle Woodland is the earliest era for which there are large concentrations of archaeological erect knotweed available for analysis.

Three Middle Woodland assemblages of erect knotweed were analyzed for this analysis: Walker-Noe (MOV), Smiling Dan (LIV), and Meridian Hills (AMB) (Fig. 1). Walker-Noe is an Adena/Hopewell mound located at a large quarry site complex on a tributary of the Kentucky River. Unlike any of the other analyzed assemblages, this one comes from a ritual context. It was interred with a series of cremation burials (Pollack *et al.* 2005). The other two Middle Woodland assemblages come from storage pits at period-typical hamlets, consisting of a few small houses and associated pits and middens (Williams 1993; Stafford and Sant 1985).

The timing and social dynamics of the introduction of maize (*Zea mays* L.) into Woodland economies remain topics of active research. Evidence for Middle Woodland maize cultivation is scanty, scattered and has recently been called into question. Direct dates on macrobotanical remains from the American Bottom (Riley *et al.* 1994), eastern

Tennessee (Chapman and Crites 1987), and southern Ohio (Crawford *et al.* 1997) seemed to suggest that maize was present, although not widely cultivated, during Middle Woodland times. However, recent isotopic analysis of the dated specimens from the American Bottom revealed that they were not actually maize, and that other early occurrences of maize in that region were either not maize or intrusive from later periods (Simon 2014, 2017). Mysteriously, despite the fact that maize probably came to ENA from the Southwest *via* the southern Great Plains, the earliest dates on maize (from residues containing phytoliths and starch, as early as 200 BC) come from the Northeast (Hart *et al.* 2007; Hart and Lovis 2013; Thompson *et al.* 2004). At present it is not clear what these enigmatic Middle Woodland maize remains signify, but Simon's (2014:120) suggestion that we view Middle Woodland maize in the context of "sociocultural systems that included long-distance trade networks of exotic items" seems reasonable. Maize may have been one such item, but it was not widely cultivated during the Middle Woodland.

Late Woodland societies continued and intensified the food production system of Middle Woodland times, with its characteristic diversity of crops and continuing reliance on wild resources. In the American Bottom, populations were gradually coalescing into the more nucleated and complex predecessors of Mississippian towns (Kelly 1990, 2002), leaving behind increasingly abundant evidence of EAC cultivation (Simon and Parker 2006), and integrating maize into their fields by 900 CE (Simon 2014). Meanwhile, along the Lower Missouri river (LMV), EAC cultivation continued and maize cultivation was picked up patchily, with evidence of maize cultivation at some sites also around 900 CE (Lopinot and Powell 2015; Wright and Shaffer 2014). By the end of the Late Woodland period, societies in the American Bottom and western Illinois had integrated maize into the EAC (Simon 2014) but further south in the Mississippi valley (south of the Arkansas River) this did not occur until hundreds of years later (Fritz and Kidder 1993; Nassaney 1994).

During the Late Woodland period, erect knotweed was an important and highly visible crop across the core area of EAC cultivation. A diachronic series of Late Woodland assemblages from five different sites in the American Bottom and nearby Lower Missouri valley were analyzed for this analysis in order to document spatially and temporally related populations (Fig. 1). I focused on obtaining several diachronic samples from this time period in a single region because previous research indicated that the Late Woodland was the period of interest for the domestication of erect knotweed. Asch and Asch (1985a, b) and Fritz (1986) had documented Mississippian assemblages of erect knotweed with distinctive morphologies, and other researchers (Lopinot *et al.* 1991; Powell 2000) had suggested that there might be others in the American Bottom dating to the Terminal Late Woodland or early Mississippian. My goal was to document changes in morphology over time, from an Early or Middle Woodland wild-type baseline to a domesticated sub-species by Mississippian times.

The three sites from the American Bottom (Mund, Sponemann, and Range) are all large, multicomponent sites that were occupied for hundreds of years. Although they vary in the details of their microtopographic placement within the floodplain and cultural-historical associations, all three assemblages came from storage pits at large villages that were engaged in farming, fishing, hunting, and gathering in an unusually rich and varied environment (Fortier and Finney 1983; Fortier *et al.* 1991; Kelly *et al.* 2007). The two assemblages from the Lower Missouri valley (Big Loose Creek,

Rohlfing) both come from storage contexts at smaller villages with shorter occupations (Grantham 2010; Herdon 2006). They are contemporaneous with each other and with the analyzed assemblage from Sponemann.

The end of the Late Woodland period and the beginning of the Mississippian period is marked by the coalescence of the first and only urban society in pre-Columbian ENA, at Cahokia in the American Bottom. Cahokia was built rapidly around 1050 AD in an event that archaeologists refer to as the “Big Bang.” At its height, it was home to at least 15,000 people inhabiting the urban core and several thousand more living in Greater Cahokia, which stretched from the uplands east of the ceremonial precinct across the floodplain to the Mississippi river and into what is now St. Louis, Missouri (Pauketat 2002, 2003). As with all cases of nascent urbanism, the underlying food production system has been a subject of great interest. Researchers once assumed that Mississippian agriculture, in its earliest manifestation at Cahokia, must have been distinct from Woodland agriculture, either in intensity or its focus on maize as a staple crop. In this formulation, intensive maize agriculture was either the impetus for or outcome of the social stratification and nascent urbanism evident at Cahokia. This focus on maize as the enabler of civilization was reviewed and critiqued as “zeacentrism” (Fritz and Lopinot 2007). These researchers and others (Simon and Parker 2006) present abundant evidence that EAC crops continued to be ubiquitous in both mundane and special contexts in the American Bottom throughout the occupation of Cahokia. In more recent years, Cahokian agriculture has been less often characterized as the enabler of civilization than as a liability. In these narratives, whatever Cahokians were doing to make a living was unstable with respect to the unprecedented population density of the Mississippian American Bottom. It was thus vulnerable to both drought (Benson *et al.* 2009) and floods (Munoz *et al.* 2014), perturbations that led to the abandonment of the American Bottom. There are dissenters to the agricultural collapse narrative of Cahokia’s abandonment (Emerson and Hedman 2014), but overall, the change in agricultural practice coincident with the rise of Cahokia has been given a remarkable amount of both credit and blame. Recent work demonstrating that maize was only widely adopted in the American Bottom in the century preceding the coalescence of Cahokia is sure to reignite this debate (Simon 2014, 2017). One early Mississippian assemblage from the American Bottom (Westpark) is included in the analysis.

Westpark is a multicomponent site that was occupied from at least the Late Woodland—early Mississippian (650–1200 CE) (Powell 2000). Over 200 features including 28 structures were mapped and excavated, but the site probably is much more extensive as it was excavated quickly and incompletely ahead of development (Lopinot *et al.* 1991), and includes an unexcavated Mississippian component to the north of the excavations (John Kelly, pers. comm. 2016). The analyzed assemblage comes from the bottom 2–5 cm of a pit that contained a homogenous mass of erect knotweed kernels and achenes (Powell 2000). This feature was one of four pits that each contained thousands of erect knotweed kernels and achenes. Lopinot *et al.* (1991) estimated that just one of these contained 63 l of erect knotweed achenes and kernels. Westpark is used to investigate whether or not erect knotweed evolution continued on the same trajectory across the hypothetical agricultural boundary between Late Woodland and Mississippian agricultural practice in the American Bottom.

During the Mississippian era, maize agriculture was practiced by most communities in ENA, although regional variations existed and some EAC crops continued to be

cultivated right up until contact with Europeans (Asch and Asch 1977). My goal for this part of the analysis was to document differences between cultivated and/or domesticated populations, if they existed. Five Mississippian assemblages are included in this analysis: Westpark (AMB), Whitney Bluff (OZK), Muir (MOV), Hill Creek (LIV), and Gypsy Joint (Middle Mississippi valley, MMV) (Fig. 1). The importance of the earliest assemblage, Westpark, for understanding changes in agricultural practice associated with nascent urbanism at Cahokia has already been discussed.

During the twelfth century, when the Whitney Bluff assemblage was deposited in a shallow pit within a dry rockshelter on the White River, the bluff shelters of the Ozarks were on the periphery of the Caddo region. Mississippian towns in the larger river valleys of the Ozark highlands are similar in structure to those of the Arkansas valley Caddo, and the bluff shelters were most likely part of the same settlement system (Fritz 1984; Sabo 1986; Trubowitz 1983). Maize was probably integrated into the economy of northwestern Arkansas around the same time that it was adopted in the American Bottom: the end of the Late Woodland period, c. AD 900–1000. Meanwhile, as at Cahokia, the older EAC crops were still being cultivated (Fritz 1986).

The Hill Creek assemblage is slightly later, dating to the mid-1300s (Table 1), and comes from a small homestead in the Lower Illinois valley (Conner 1985). Although it is not located in the American Bottom, it may be one endpoint of the line of American Bottom landraces tracked though the Late Woodland and early Mississippian in this analysis because it is likely that the farmers at Hill Creek either came from the American Bottom or were in regular contact with farmers there. The nature of interaction between the American Bottom and the Lower Illinois valley during the Mississippian period has been widely debated for several decades. The Lower Illinois valley may have been a resource procurement area for Cahokia – populated by immigrant homesteaders who provided surplus agricultural products to town-dwellers to the north and south (Conner 1985; Goldstein 1980). Others have argued that Late Woodland populations remained in place and gradually integrated Mississippian material culture and institutions into their way of life (Delaney-Rivera 2004; Farnsworth *et al.* 1991). Either way, it is possible that the erect knotweed at Hill Creek originated in the American Bottom and was either brought to the Lower Illinois valley by immigrant farmers or obtained by locals through trade. On the other hand, it may also have evolved in the Lower Illinois valley, where erect knotweed was one of the most important EAC crops throughout the Middle and Late Woodland periods.

While a variety of crops continued to be important to the livelihoods of farmers in the Middle Mississippian and Caddo regions until c. AD 1400, Mississippian agriculture in the Middle Ohio valley developed along different lines (Wagner 1987). The older EAC crops are seldom recovered from Mississippian sites in this region, which are referred to as Fort Ancient, and maize was a clear staple crop even at the earliest Fort Ancient sites (Rossen 1988; Wagner 1987). The early Fort Ancient Muir site is no exception, but in addition to abundant evidence for maize cultivation, several hundred erect knotweed achenes were recovered (Turnbow and Sharp 1988). This assemblage is included in the analysis as an outlier: what was happening to EAC crops under cultivation by farmers who were so focused on maize agriculture?

Despite the importance of EAC crops in some Mississippian economies, they did eventually fall out of cultivation in the last centuries before the colonial era (with the exception of squash, sunflower, and possibly goosefoot and sumpweed). The processes

involved in these abandonments are unclear. It is possible that EAC crops fell out of cultivation abruptly, with domesticated varieties suddenly disappearing from the archaeological record. It is also possible that communities gradually invested less energy in cultivation and seed selection, which would result in a process of feralization. In this scenario, a decrease in the quality of seed stock may be apparent before the crop disappears from the record all together. If so, the latest assemblages might be more similar to modern wild plants than to earlier domesticated populations. The final Mississippian assemblage comes from a hamlet in the Middle Mississippi valley (Smith 1987). It is the latest known large concentration of erect knotweed, and so represents a tentative endpoint in this crop's evolutionary history.

Materials and Methods

Only assemblages from discrete, well-defined contexts (all but one were pits, the exception was from a sub-mound burial feature) that contained *at least* 10 measureable achenes were considered. Such assemblages are rare, but this sampling strategy was adopted because concentrations of seeds from a well-defined contexts are more likely to represent a living population than scattered seeds taken from across a site. The validity of this assumption was supported by the fact that whenever I obtained a new date for a previously dated context the two were in agreement (Asch and Asch 1985a; Fritz 1986; Pollack *et al.* 2005; Table 1). For sites where more than one context is listed in Table 1, the contexts were subsequently determined by the excavators to be continuous and thus achenes recovered from them are treated as a single population. There is one exception: the Smiling Dan site. To simplify this analysis, I combined morphometric data from several distinct contexts for this site. However, the individual group means for shape and size were very similar and considering them as separate samples would not alter the results presented here (Mueller 2018). I took microphotographs of each well-preserved achene and subjected them to morphometric analysis using ImageJ (Mueller 2017b), then corrected for carbonization and other taphonomic differences using experimentally derived correction factors (Mueller 2017a). The resulting measurements are compared to those from a modern sample of erect knotweed achenes from herbarium specimens and two populations growing in Illinois and Missouri (Mueller 2017c; Table 1). These were measured using the same procedure.

Analysis 1: Domestication

Domesticated erect knotweed differs from its wild progenitor in two ways: it has larger achenes and achene dimorphism is reduced or eliminated (see *Introduction*). Area is used as a measure of size because it is a more accurate approximation of volume than length or width, but length times width is also reported in Table 2 to facilitate comparison with earlier studies “Significantly different” indicates a p value of < 0.05 using a Welch's t tests for unequal variances. The percentage of each assemblage made up of smooth morphs is also considered. In modern wild populations, this percentage does not exceed 75%, but in fully domesticated assemblages in the archaeological record it is up to 100%. Determining whether or not an assemblage is outside of the

Table 2 Summary statistics for morphometric analysis

| Period | Site | Texture | N | Area | | Length X Width | | Circularity | | |
|---------------|------------------|-----------------|-----------|------|---------|----------------|---------|-------------|---------|------|
| | | | | Mean | Std Dev | Mean | Std Dev | Mean | Std Dev | |
| MOD | Bellews Creek | Smooth | 40 | 2.77 | 0.31 | 4.7 | 0.49 | 0.36 | 0.09 | |
| | | Tubercled | 100 | 3.16 | 0.51 | 5.04 | 0.75 | 0.53 | 0.11 | |
| | Crawford Creek | Smooth | 21 | 3.69 | 0.47 | 6.3 | 0.77 | 0.39 | 0.16 | |
| | | Tubercled | 66 | 3.03 | 0.41 | 4.75 | 0.73 | 0.45 | 0.11 | |
| | Herbarium sample | Smooth | 13 | 3.9 | 0.38 | 6.16 | 0.69 | 0.49 | 0.08 | |
| | | Tubercled | 35 | 3.51 | 0.51 | 5.71 | 0.84 | 0.6 | 0.09 | |
| MW | Walker Noe | Smooth | 9 | 4.49 | 0.8 | 7.15 | 1.36 | 0.46 | 0.1 | |
| | | Tubercled | 1 | 4.04 | . | 6.48 | . | 0.39 | . | |
| | Smiling Dan | Smooth | 23 | 3.43 | 0.78 | 5.6 | 1.46 | 0.44 | 0.08 | |
| | | Tubercled | 60 | 3.29 | 0.59 | 5.4 | 1.18 | 0.34 | 0.09 | |
| | Meridian Hills | Smooth | 2 | 4.26 | 0.63 | 6.85 | 0.87 | 0.43 | 0.09 | |
| | | Tubercled | 26 | 3.46 | 0.57 | 5.58 | 1 | 0.41 | 0.09 | |
| LW | Mund | Smooth | 44 | 2.46 | 0.48 | 3.96 | 0.85 | 0.49 | 0.07 | |
| | | Big Loose Creek | Smooth | 8 | 3.38 | 1.11 | 5.4 | 1.59 | 0.4 | 0.06 |
| | | | Tubercled | 53 | 2.98 | 0.59 | 4.73 | 0.88 | 0.31 | 0.07 |
| | Sponemann | Smooth | 10 | 4.45 | 0.69 | 7.68 | 1.25 | 0.48 | 0.05 | |
| | | Tubercled | 54 | 3.44 | 0.5 | 5.55 | 0.83 | 0.35 | 0.09 | |
| | Rohlfing | Smooth | 14 | 3.04 | 0.47 | 4.84 | 0.66 | 0.39 | 0.06 | |
| | | Tubercled | 19 | 2.88 | 0.47 | 4.61 | 0.72 | 0.32 | 0.07 | |
| | Range | Smooth | 31 | 4.3 | 0.53 | 7.22 | 0.98 | 0.49 | 0.07 | |
| | | Tubercled | 10 | 3.79 | 0.4 | 6.21 | 0.5 | 0.42 | 0.08 | |
| | MIS | Westpark | Smooth | 70 | 5.04 | 0.82 | 8.45 | 1.54 | 0.48 | 0.08 |
| Tubercled | | | 16 | 4.79 | 0.87 | 8.38 | 1.7 | 0.5 | 0.08 | |
| Whitney Bluff | | Smooth | 195 | 5.67 | 0.68 | 9.58 | 1.18 | 0.46 | 0.07 | |
| | | Tubercled | 1 | 4.15 | . | 7.58 | . | 0.55 | . | |
| Muir | | Smooth | 1 | 3 | . | 4.55 | . | 0.47 | . | |
| | | Tubercled | 18 | 2.4 | 0.36 | 3.64 | 0.62 | 0.42 | 0.08 | |
| Hill Creek | | Smooth | 95 | 5.39 | 0.96 | 9.08 | 1.67 | 0.52 | 0.08 | |
| Gypsy Joint | | Smooth | 83 | 4.12 | 0.55 | 6.9 | 1.01 | 0.44 | 0.05 | |
| | | Tubercled | 40 | 3.5 | 0.4 | 5.73 | 0.67 | 0.32 | 0.06 | |

natural range of variation for this parameter is a function of sample size and sample proportion, but as a rule of thumb, for large assemblages sample proportions of > 85% can be considered out of the ordinary, especially because smooth morphs are more likely to be destroyed by carbonization (Mueller 2017a). The number of achenes in each assemblage for which fruit coat texture could be observed (“Total achenes” in Table 1) was always greater than the number that were well-preserved enough to be measured (“Morphometric analysis,” in Table 1) so both sample sizes are reported in Table 1. For the total achenes count, only fragments > 50% of a complete achene were counted, to avoid double counting.

Analysis 2: Recognizing Landraces

I used the shape factor circularity ($4\pi \times [\text{Area}]/[\text{Perimeter}]^2$) to assess differences in shape between the assemblages that might be associated with the development of characteristic landraces. Measures of circularity vary between 0 and 1, with 1 being a perfect circle and values approaching 0 indicating an elongated shape. I predicted that if distinctive landraces were evolving, then assemblages that were from the same region would be more similar in shape than those from different regions, even if the assemblages were roughly contemporaneous. I excluded tubercled morphs in this analysis, because several domesticated assemblages have too few (or no) tubercled morphs for a comparison, and the two fruit types have distinctly different shapes (Table 1; Fig. 2). The assemblages from Meridian Hills and Muir, which only have 1–2 measureable smooth morphs each, thus had to be excluded from this analysis.

Results

Summary statistics on assemblage size and shape are reported in Table 2.

Analysis 1: Domestication

Middle Woodland The earliest analyzed assemblage, from a burial context at the Adena/Hopewell Walker-Noe site, unexpectedly has significantly larger seeds than the modern comparative sample, and a percentage of smooth morphs outside the range of variation for wild erect knotweed. This makes Walker-Noe the earliest known assemblage of domesticated erect knotweed by almost a millennium. The other two Middle Woodland assemblages are not domesticated, although Meridian Hills does have significantly larger achenes than the modern comparative sample, perhaps indicating the beginnings of selection under human cultivation (Fig. 3). These assemblages and their implications for the development of agriculture in ENA are discussed in greater detail elsewhere (Mueller 2018).

Late Woodland In the American Bottom, the diachronic series comprised of (in chronological order) Meridian Hills, Mund, Sponemann, Range, and Westpark shows domestication occurring *in situ* within this floodplain (Fig. 3). Early Late Woodland Mund is an unusual assemblage in that its achenes are actually significantly smaller than the modern comparative sample and it is comprised exclusively of smooth morphs. The circumstances that may explain this combination of characteristics are discussed below. The other four assemblages from the American Bottom perfectly fit expectations for an evolving domesticated sub-species: each successive assemblage has a higher proportion of smooth morphs and larger achenes, culminating in the fully domesticated early Mississippian Westpark assemblage. The two Late Woodland assemblages from the nearby Lower Missouri valley (Big Loose Creek and Rohlfing) show no signs of domestication (Fig. 3).

Mississippian Of the five Mississippian sites, all but one have significantly larger achenes and a significantly higher percentage of smooth morphs than wild erect

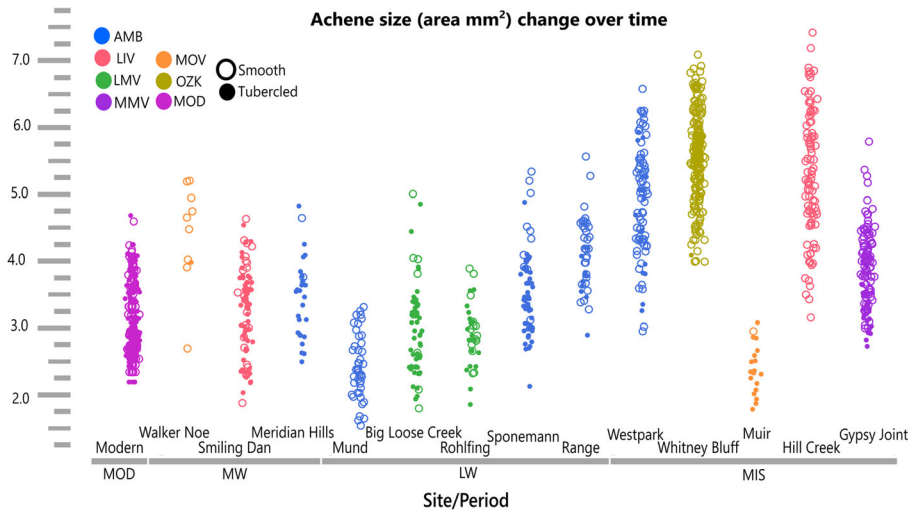


Fig. 3 Evidence for the domestication of erect knotweed in ENA. The domestication syndrome of erect knotweed is recognized by an increase in achene size and an increase in the proportion of smooth morphs (which have little innate dormancy) (Mueller 2017d, 2017b, 2017c). This figure represents change in achene size over time. Means and standard deviations can be found in Table 2. Sites are arranged in chronological order based on median calibrated dates (Table 1) and are colored by region (Fig. 1) to show local trends more clearly. Area measurements for all carbonized achenes were individually corrected using experimentally derived factors (Mueller 2017a). The proportion of smooth morphs is graphically represented here with open circles for each achene of that type. Sample size for the morphometric analysis, provenience of the modern comparative sample (MOD), and the proportion of smooth morphs in each assemblage can be found in Table 1. The following assemblages can be considered domesticated because they exhibit significant increases in seed size and proportion of smooth morphs: Walker-Noe, Range, Westpark, Whitney Bluff, Hill Creek, and Gypsy Joint

knotweed, indicating that they are domesticated. The knotweed achenes from the early For Ancient Muir site are certainly not domesticated: this assemblage consists of abnormally small tubercled morphs (Fig. 3). The circumstances that may have created this unique assemblage are considered below. The latest assemblage, Gypsy Joint, while still a domesticated assemblage, shows some signs of feralization (significantly smaller achenes and a lower proportion of smooth morphs than earlier domesticated assemblages).

Analysis 2: Recognizing Landraces

Modern Wild Erect Knotweed There is notable variation in shape among the three different modern samples, especially between the herbarium specimens and those collected recently (Fig. 4). These results show that, either because of genetic differences between populations or plastic responses to the environment, erect knotweed smooth morphs produced by wild populations in their natural habitat can be quite variable in shape. Whatever its cause, the variability exhibited in the wild populations makes the homogeneity of shape between the American Bottom and Hill Creek assemblages (discussed below) all the more remarkable.

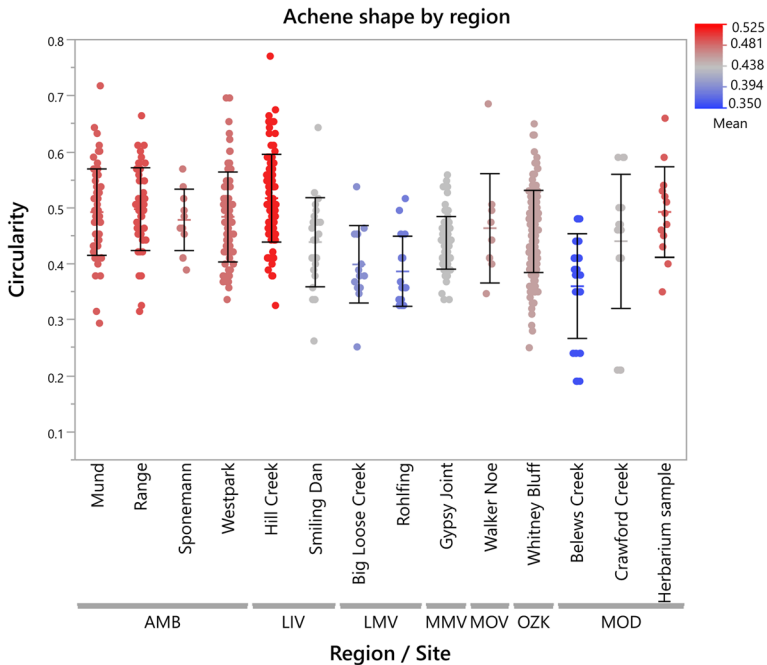


Fig. 4 Evidence for the development of distinct landraces of erect knotweed. This figure represents the shape of all smooth morph achenes (Fig. 2) from each site in terms of circularity ($(4\pi \times [\text{Area}]/[\text{Perimeter}]^2)$) derived from microphotographs. Meridian Hills and Muir had to be excluded because they lack a sufficient number of smooth morphs for statistical comparison. Each assemblage is color coded according to its mean circularity (bars represent standard deviation). The sites are arranged by region, rather than chronologically, to show the similarity of the assemblages from the American Bottom and the Hill Creek assemblage more clearly. The modern sample is separated here by source to show the variability in achene shape characteristic of modern populations of erect knotweed. The four assemblages from the American Bottom and the Hill Creek assemblage are significantly different in terms of shape from the modern comparative sample and from the other archaeological assemblages. I argue that these five assemblages represent a distinct landrace of domesticated erect knotweed. Means and standard deviations of circularity for each assemblages can be found in Table 2

Regional Variation in Cultivated Populations The two Middle Woodland assemblages that could be compared (Walker-Noe and Smiling Dan) are very similar in shape, although they come from regions separated by hundreds of miles (Fig. 4). This may be a coincidental similarity, as both hover near the mean for all modern populations. There is not yet enough data from this early period of cultivation and domestication to recognize distinct varieties, if they existed.

The four sites from the Late Woodland – Mississippian American Bottom (Mund, Range, Sponemann, and Westpark) are all very similar in shape (Fig. 4). As a group, they are significantly different from the two assemblages from the neighboring Lower Missouri valley, from the modern comparative sample, and from the other domesticated assemblages except for Hill Creek. The Hill Creek assemblage exhibits an even more extreme form of the distinctive shape of the American Bottom assemblages, whereas the domesticated assemblages from other regions (Whitney Bluff and Gypsy Joint) have significantly different shapes (Fig. 4).

Discussion

The earliest assemblages are the most enigmatic, and raise more questions than they can answer. Walker-Noe, the earliest assemblage of all those analyzed is also fully domesticated, a wholly unexpected results. More assemblages of similar age need to be analyzed to ascertain how widespread this domesticated variety was, but it evidently did not reach western Illinois, where farmers at Smiling Dan were growing what appears to be wild-type erect knotweed about 150 years later. The Meridian Hills assemblage is the earliest in the series from the American Bottom, and it may show the very beginnings of human selection, in that it has significantly larger achenes than the modern comparative sample (Mueller 2018). Unfortunately, it did not contain enough smooth morphs to determine whether the distinctive seed shape of later assemblages from the American Bottom had already appeared during the Middle Woodland.

The morphology of the next assemblage from the American Bottom sequence, from Mund, is extraordinary in two respects. Only smooth achenes are represented. With a total of 124 achenes with pericarp texture observable, this cannot be attributed to sampling error (Mueller 2017a). While this is part of the domestication syndrome of erect knotweed, the Mund smooth morphs are much smaller than modern erect knotweed smooth morphs – not larger, as is the case with other domesticated assemblages. The Mund achenes have a unique morphology. Although they do not exactly match any extant species, including erect knotweed, in terms of shape and size, they are very similar to immature smooth morphs of erect knotweed (Mueller 2017e). Ancient farmers at Mund may have harvested erect knotweed in early October, when most of the achenes were still maturing. This would prevent the inevitable seed loss that occurs when achenes become loose after the plant senesces, as well as predation by birds and insects, although it is much more difficult and time consuming than harvesting from senesced plants (Mueller 2017c). In the Old World, this very strategy is thought to have delayed the evolution of the non-shattering trait in rice for several centuries (Fuller 2007).

Both analyses indicate that farmers in the American Bottom developed a distinctive domesticated landrace between c. 150–1100 AD. Not only is there a progression over time towards a more clear expression of both aspects of the domestication syndrome of erect knotweed at Mund, Sponemann, Range, and Westpark, but these assemblages also have a distinctive shape, with consistently high circularity values, which is unlike modern erect knotweed, earlier archaeological erect knotweed, contemporary Late Woodland assemblages from the Lower Missouri valley, or later Mississippian assemblages from the Middle Mississippi valley and Ozarks (Fig. 4). These are all multi-component village sites that were occupied throughout the Late Woodland and Mississippian eras. They have provided some of the key evidence for the population nucleation that gave rise to urbanism in the American Bottom (Kelly *et al.* 2007; Fortier *et al.* 1991; Kelly 2000). How did increasing population density and the rapid adoption of maize in the American Bottom around 900 CE impact the evolution of earlier EAC crops? The American Bottom communities at Range and Westpark, who had recently integrated maize into their economies at the time when the analyzed assemblages were deposited, were also continuing to improve erect knotweed. This circumstance offers further proof that the adoption of maize did not spell doom for the cultivation of older EAC crops. Further, the same distinctive erect knotweed landrace

seen at early Mississippian Westpark was still being cultivated two centuries later at Hill Creek. This indicates that, for at least one EAC crop, the details of agricultural practice that maintain distinctive landraces (field placement and preparation and seed selection) were consistent from the Late Woodland into the Mississippian era.

This analysis provides evidence for the exchange of knowledge and material between some communities, and the isolation of others. For example, the Hill Creek assemblage from the Lower Illinois valley has the most extreme form of the characteristic shape exhibited by the American Bottom assemblages (Fig. 4). This supports the assertions of earlier researchers that farmers in the Lower Illinois valley during the Mississippian period were either immigrants from the American Bottom, or heavily influenced by their neighbors to the south. This assemblage provides direct evidence that communities in these adjacent floodplains were sharing agricultural knowledge and seed stock. The Late Woodland assemblages from the Lower Missouri valley demonstrate the opposite. Their wild-type morphology suggests that farmers in this nearby river valley were not sharing in the same community of practice as those in the American Bottom.

The Lower Missouri valley assemblages are also important for another reason. Because they come from the same latitude and time period as some of the American Bottom assemblages (Fig. 1), they provide preliminary evidence that the differences in seed shape and size documented in this analysis are not caused by plastic responses to climatic conditions. The extent to which achene morphology is the result of developmental plasticity in response to environmental variables can only be fully understood with further study of living plants. Erect knotweed and its relatives are incredibly plastic organisms (Costea and Tardif 2004; Mueller 2017d; Sultan 2001). A more nuanced understanding of developmental plasticity in erect knotweed could lead to better and more detailed inferences about agricultural practices and paleoenvironments (Mueller *et al.* 2017; Piperno *et al.* 2015; Zeder 2016; Piperno 2017). Studies of EAC crop plasticity are currently underway, and should allow us to better differentiate between the multigenerational hereditary effects of cultivation and the immediate plastic responses to cultivation techniques, field location, and climate change.

The other domesticated Mississippian assemblages provide further evidence that the American Bottom – Hill Creek sequence is in fact a distinct landrace. Domesticated erect knotweed was not homogeneous across its ancient range of cultivation. The fact that farmers in the Ozarks and Middle Mississippi valley had different varieties of domesticated erect knotweed than those in the American Bottom is perhaps not surprising: such crop diversity is the norm in societies where seeds cannot be procured from centralized markets. A recent ground-breaking study of ancient sunflower chloroplast DNA demonstrated that farmers at Eden's Bluff, in the Ozarks, were maintaining two different landraces of sunflowers over the course of about 2000 years. The same study also demonstrates yet again how much diversity is not represented in our most common modern cultivars. Much more genetic diversity was present only a century ago, before many Indigenous landraces fell out of cultivation (Wales *et al.* 2018). An investigation of earlier Ozark and Middle Mississippi valley erect knotweed assemblages could shed light on the evolutionary origins of the Whitney Bluff and Gypsy Joint populations, and show whether or not there were also consistent landraces in those regions over time.

Both the Muir and Gypsy Joint assemblages give some insight into how the lost crops were lost. The Muir erect knotweed is the only Mississippian period population that is not domesticated, supporting previous claims that there were important differences in agricultural practice between Fort Ancient communities in the Middle Ohio valley and Mississippian communities further west and south (Wagner 1987). The Muir achenes are actually significantly smaller than the modern comparative sample. The most likely explanation for the morphology of the Muir knotweed is that Fort Ancient people harvested erect knotweed plants in late summer or early fall, when most tubercled morphs are immature and relatively small, and smooth morphs are absent or rare (Mueller 2017e). If they were harvesting for food, they would have gotten less of it and exerted more effort than if they had waited until the plant senesced. If they were harvesting for seed stock, they would have been met with an even more complete failure: immature tubercled morphs have a germination rate of 2% (Mueller 2017c). Whoever harvested the Muir knotweed was not well-informed about how best to manage this plant for either food or seed stock, and likely was not impressed with the results of her experiment. Knowledge loss or loss of access to seed networks may have precipitated the rapid abandonment of EAC crops seen in Fort Ancient communities. The Gypsy Joint assemblage, with its less pronounced domesticated syndrome, suggests another possible scenario. If cultivation and seed selection practices gradually changed, then EAC crops might have undergone a process of feralization even as they were still harvested for food. More analyses of late EAC assemblages are needed to test this hypothesis.

Conclusions

Domesticated plants and animals are not *faits accomplis*. They cannot be maintained in a consistent form without an equally consistent management and selection regime. For example, dingoes (*Canis lupus ssp. dingo*) diverged from their domesticated dog progenitors when they were brought to Australia some 4000 years ago. At this point, they entered into a different kind of relationship with humans than that experienced by most domesticated dogs, one where the majority of the population was feral, with only the occasional puppy becoming a tame camp dingo (Smith and Litchfield 2009). This relationship did not cause dingoes to become wolves – they retain key traits of domesticated animals such as diminished brain and body size compared to their wild ancestor (Kruska 2005)– but it did cause them to evolve into a behaviorally and morphologically distinct subspecies. They are now evolving again, as they interbreed with domesticated dogs introduced by European settlers, and increasingly forgo hunting to scavenge in towns and cities (Newsome *et al.* 2014). The form of domesticated plants or animals at any given archaeological site is thus an artifact of that community's management practices up until that time.

This analysis has shown considerable morphological variability in time and space between assemblages of erect knotweed under cultivation. Some of this variability can be explained with reference to the classic theory of domestication. The American Bottom sequence shows a progression of increasingly domesticated assemblages through time. Seed size increased, and germination inhibitors were reduced through decreasing fruit dimorphism. Both of these changes are classic signals of domestication

(Harlan *et al.* 1973). The morphological changes in erect knotweed are a result of human niche construction. Niche construction theory contends that all species modify their environments, subtly changing the selective pressures that act upon them. Niche constructing behaviors need not be biologically inherited; often they are learned (Odling-Smee *et al.* 2003). Thus the complex knowledge systems of humans can be fully integrated into evolutionary theory, not just as the results of natural selection (as in sociobiology), but as evolutionary drivers, modifying the selective pressures that affect humans and other organisms in their environments. The specific niche constructing practices involved in erect knotweed domestication based on experimental cultivation and field studies have been extensively reviewed elsewhere (Mueller 2017b, 2017c, 2018), but two of them are also relevant to the evolution of crop biodiversity and so bear repeating here. First, farmers altered the selective environment acting on erect knotweed by removing it from the unpredictable, flood-prone habitats where it naturally occurs. Diversity in field placement is a means of mitigating risk, but it can also result in the evolution of different landraces adapted to different agroecosystems. Second, saving seeds for replanting rather than relying on the soil seed bank was a critical practice that led to the domestication of erect knotweed, and is also key to the creation of distinctive landraces, especially those that can be recognized in the archaeological record based on gross morphological differences in seed shape and size.

The transition from food procurement to food production has long been seen as contingent upon domesticates. I would like to argue that this causal relationship is reversed. Central to this argument is an understanding of food production as a traditional ecological knowledge system. A traditional ecological knowledge system is composed of information, organizing principles or beliefs, expertise, and institutions that structure practice and the transmission of knowledge (Turner *et al.* 2000), and is thus also situated within a community of practice. The niche constructing activities of humans will not result in domestication unless they are maintained over many generations and applied consistently to the same populations of would-be domesticates. This statement is not meant to imply that foragers were *trying* to domesticate plants and animals. The conscious goals of their activities may have been diverse. Some might fit well into the cost-benefit analysis of an optimal foraging model, including enhancing the productivity or abundance of species they relied on for food, increasing the predictability of their access to important resources, or decreasing the necessity for travel. Other motivations may be obscure to us, relating to cultural norms about the proper treatment of plants and animals, the propitiation of spiritual forces, or the rights and responsibilities of groups and individuals. Regardless of what motivated humans to embed niche constructing activities in their traditional ecological knowledge systems, both domestication and the subsequent diversification of domesticates into distinctive varieties or breeds result from the consistent application of human mediated selection to plants and animals.

If the seeds of domesticated erect knotweed seed were gifted or traded into a community that lacked the traditional ecological knowledge to maintain it, they could not reproduce themselves. Domesticates do not enable the spread of food producing economies unless they are accompanied by knowledgeable people, and those people are positioned socially so that others can learn from them (Henrich 2001; Rogers 2003; Mueller 2018). Lavé and Wenger (1991) proposed the concept of communities of practice to explain how a novice becomes a master in a social context, a process that

involves the creation and maintenance of knowledge within a community. The rich ethnographic and historical record of the agricultural practices of descendent communities in ENA suggests that gendered institutions played an important role in this process. Historically, women were the seed keepers and were responsible for most skilled agricultural tasks (Watson and Kennedy 1991). Institutions such as sacred bundle societies, age grade societies, intercommunity gambling, and menstrual seclusion likely all played a role in the development of agricultural communities of practice (Mueller and Fritz 2016). Matrilocal and patrilocal each offer different advantages for the development of agricultural communities of practice: the former facilitating *in situ* learning between multiple generations of related women (Hart 2001), and the latter favoring the spread of crops and traditional ecological knowledge among communities. When the morphologies of ancient landraces are better resolved, we may be able to see the boundaries of communities of practice and the zones of interaction between them in the archaeological record.

This analysis illustrates the utility of crop seeds as artifacts. Like lithic tools, ceramic vessels, or works of art, the bodies of domesticated plants and animals are expressions of human social intelligence. They are developed within institutions, maintained through multi-generational communities of practice, and consciously shaped to meet the changing needs and desires of communities. Their potential as sources of inference about the human past is vast. Crop seeds are most useful as artifacts when there is extensive experimental or traditional knowledge linking their distinct morphologies to particular practices and histories. The kind of analysis employed here on a lost crop could be much more easily and fruitfully applied to more well-known crops. In particular, for crops whose extant landraces have been described in detail, it may be possible to trace these distinctive types, with all of their cultural, culinary, and historical significance, back into the archaeological record.

Today, anthropologists and agronomists who are hoping to understand the social dynamics that create and maintain agrobiodiversity have relatively few options. The proportion of the world's farmers who keep their own seed stock or rely on community institutions for seed is dwindling, and is concentrated in a few regions, mostly in the Global South or in regions that are economically peripheral. Agrobiodiversity is frequently described as a priceless resource by international organizations, hoarded in massive seed banks around the world (but especially in the Global North), and tapped by plant breeders and biotechnologists to create new (sometimes patentable) commercial varieties. Yet the labor and knowledge of the people responsible for this diversity is *explicitly not valued*. As Kloppenburg (2005:169) succinctly put it, "Plant genetic resources leave the periphery as a common – and costless—heritage of mankind, and return as a commodity – private property with exchange value." As long as traditional landraces are legally considered to be the common inheritance of all people, and thus without commercial value, we can expect communities who face economic strain to abandon their maintenance, since it constitutes a form of unpaid labor. The United Nations formally acknowledged this problem in 2007, when they declared their support for the right of Indigenous peoples to hold intellectual property rights over plant genetic resources (United Nations 2007). While we may hope and work for a reversal of the global economic trend towards industrialization and homogenization in agriculture, in the meantime the archaeological record could provide a broad and

deep view of the social processes underlying agrobiodiversity. Reconstructing the deep shared histories of communities and their crops could help us strategize to protect and expand remaining reservoirs of local agricultural knowledge and agrobiodiversity.

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