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Department of Anthropology

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Seeds as Artifacts of Communities of Practice:

The Domestication of Erect Knotweed in Eastern North America

by

Natalie G. Mueller

A dissertation presented to
The Graduate School
of Washington University in
partial fulfillment of the
requirements for the degree
of Doctor of Philosophy

May 2017

St. Louis, Missouri

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Natalie G. Mueller

Washington University in St. Louis

May 2017

This work is dedicated to my parents, Martha and Timothy Mueller.

Thanks for reading to me.

Abstract

Seeds as Artifacts of Communities of Practice:

The Domestication of Erect Knotweed in Eastern North America

by

Natalie G. Mueller

Doctor of Philosophy in Anthropology

Washington University in St. Louis, 2017

Professor Gayle J. Fritz, Chair

Humans are the ultimate ecosystem engineers, and in transforming ecosystems we also change the selective environment for the plants and animals that live among us. The bodies and behaviors of domesticated plants and animals are thus rich artifacts of traditional ecological knowledge and practice. I study the morphology and behavior of domesticated plants as a proxy for ancient agricultural communities of practice. The transition from food procurement to food production is one of the most significant shifts in human history. I consider this process as the evolution and spread of a knowledge system. Domestication studies are usually focused on differentiating wild from domestic types, but I wanted to investigate variation under cultivation. Normally discussed in the context of contemporary or historical small-scale farming, landraces are plant varieties that have been developed to grow particularly well under local conditions or to suit local preferences. Because landraces need to be maintained across generations of both plants and people, they are reflections of communities of practice, social learning, and Traditional Ecological Knowledge systems. By undertaking a detailed case study of variation within a

single crop, I hoped to be able to use seeds in the same way that pottery, lithic tools, or iconography are used: to reveal shared traditions and connections between communities.

This dissertation is focused on the “lost crops” of Eastern North America: a suite of annual seed crops that were cultivated for thousands of years before the introduction of maize and other tropical crops through trade. These crops are referred to as the Eastern Agricultural Complex (EAC). I chose to investigate one of these, erect knotweed (*Polygonum erectum* L.), which was cultivated for its edible seeds by Indigenous people in Eastern North America for ~2,000 years. My goals were 1) to establish whether or not erect knotweed had been domesticated by ancient farmers; and 2) to document variation under cultivation that might reveal different communities of practice in Eastern North America.

This dissertation consists of five chapters:

- 1) A formal description of the domesticated sub-species of erect knotweed (*Polygonum erectum* ssp. *watsoniae* N.G. Muell.) including taxonomic background and a comparative analysis of other species of *Polygonum* native to the study area/
- 2) An overview of domestication syndrome in a desiccated assemblage of erect knotweed from the Whitney Bluff site, Arkansas, and a discussion of its implications for ancient agricultural practice in Eastern North America.
- 3) The results of field studies and experimental cultivation of erect knotweed over two growing seasons, with a discussion of the hypothesized roles of plasticity and heredity in the domestication of this species.
- 4) An experimental study of the processes that affect preservation of erect knotweed seeds and fruits, namely: carbonization (burning in anoxic conditions) and taphonomy (physical

weathering after deposition). These processes systematically bias the archaeobotanical record and need to be accounted for in domestication studies.

5) A review of the archaeological background, and a comparison of ancient erect knotweed assemblages from 14 archaeological sites spanning 2,000 years.

My concluding thoughts place this research in the context of global studies of domestication and food production. I suggest that optimal foraging models used in human behavioral ecology may consistently under-rank the seeds of small seeded annuals, and that plasticity under cultivation may have been one factor that made disturbance adapted plants attractive to ancient foragers. I argue that niche construction, food production, and delayed return strategies are all roughly synonymous terms, and that domestication is a likely, but not predetermined, outcome of such systems and behaviors. The spread of food producing economies was dependent on the spread of complex systems of knowledge through interacting communities of practice and without these systems of traditional ecological knowledge domesticated varieties could not be maintained.

1. Introduction

Humans are the ultimate ecosystem engineers, and in transforming ecosystems we also change the selective environment for the plants and animals that live among us. The bodies and behaviors of domesticated plants and animals are thus rich artifacts of traditional ecological knowledge and practice. I study the morphology and behavior of domesticated plants as a proxy for ancient agricultural communities of practice. The transition from food procurement to food production is one of the most significant shifts in human history. I consider this process as the evolution and spread of a knowledge system. I expect domesticated varieties to be sustained in locations where exchange between communities was institutionalized and intense, because whenever one community developed a new technique or a plant variety with beneficial attributes, this knowledge and material could quickly spread. Domestication studies are usually focused on differentiating wild from domestic types, but I wanted to investigate variation under cultivation. Normally discussed in the context of contemporary or historical small-scale farming, landraces are plant varieties that have been developed to grow particularly well under local conditions or to suit local preferences. Because landraces need to be maintained, they are reflections of communities of practice and of social learning (Boyd and Richerson 1988; Lavé and Wenger 1991) and of ancient Traditional Ecological Knowledge systems (Turner et. al. 2000). By undertaking a detailed case study of variation within a single crop, I hoped to be able to use seeds in the same way that pottery, lithic tools, or iconography are used: to reveal shared traditions and connections between communities.

This dissertation is focused on the “lost crops” of Eastern North America (ENA): a suite of annual seed crops that were cultivated for thousands of years before the introduction of maize

and other tropical crops through trade (Smith 2006). These crops are referred to as the Eastern Agricultural Complex (EAC). I chose to investigate one of these, erect knotweed (*Polygonum erectum* L.), which was cultivated for its edible seeds by Indigenous people in Eastern North America for ~2,000 years. In the 1980s, archaeobotanists had reported ancient assemblages of erect knotweed seeds that looked very different than the seeds of modern plants (Asch and Asch 1985; Fritz 1986). While these assemblages appeared to be a domesticated sub-species, natural variation within genus *Polygonum* was not understood well enough to be certain. My goals were 1) to establish whether or not erect knotweed had been domesticated by ancient farmers; and 2) to document variation under cultivation that might reveal different communities of practice in Eastern North America.

This dissertation consists of seven chapters¹:

- 1) This introduction, which provides a brief introduction to the archaeology of ENA, a history of research on erect knotweed, and a summary of the results of this project.
- 2) A formal description of the domesticated sub-species of erect knotweed (*Polygonum erectum* ssp. *watsoniae* N.G. Muell.) including taxonomic background and a comparative analysis of other species of *Polygonum* native to the study area (Mueller 2017a).
- 3) An overview of domestication syndrome in a desiccated assemblage of erect knotweed from the Whitney Bluff site, Arkansas, and a discussion of its implications for ancient agricultural practice in Eastern North America (Mueller 2017b).

¹ Each chapter is in a slightly different style and has a separate bibliography because they were prepared as articles to be published in different journals. Full citations for each published article can be found in the References for this Introduction, and are included as footnotes on the title page of each published Chapter (Chapters 2-5).

- 4) The results of field studies and experimental cultivation of erect knotweed over two growing seasons, with a discussion of the hypothesized roles of plasticity and heredity in the domestication of this species (Mueller 2017c).
- 5) An experimental study of the processes that affect preservation of erect knotweed seeds and fruits, namely: carbonization (burning in anoxic conditions) and taphonomy (physical weathering after deposition), as well as a probabilistic analysis of how sample size effects margin of error when using nominal variables to differentiate populations. These biases need to be accounted for in domestication studies (Mueller 2017d).
- 6) A review of the archaeological background, and a comparison of ancient erect knotweed assemblages from 14 archaeological sites spanning 2,000 years.
- 7) Concluding thoughts, which puts this research in the context of global studies of domestication and the origins of food production.

1.1 Archaeological Background

When the indigenous cuisine of ENA is invoked, most people imagine maize, beans, and squash – the triumvirate of staple foods spilling out of the archetypal Thanksgiving cornucopia. These crops are also known as the Three Sisters of eastern Native American agriculture, grown together by the Haudenosaunee and other eastern peoples in a highly productive intercropped field system (Mt. Pleasant 2006; Mt. Pleasant et al. 2010). But maize, beans, and the most iconic squash variety, the pumpkin (*Cucurbita pepo* ssp. *pepo*), were not domesticated in ENA, nor were they a part of its earliest agricultural system. These three crops were obtained through trade from Mexico, probably via the Southwest and Plains. For thousands of years before their arrival, farmers in ENA grew different crops, most of which were lost to history until archaeologists rediscovered them beginning in the 1930s. Beginning with the analysis of assemblages from dry

rockshelters and caves by Melvin Gilmore (1931), Volney Jones (1936), and Richard Yarnell (Watson and Yarnell 1966; Yarnell 1969; 1974), and intensifying with the introduction of systematic recovery of plant remains by flotation (Ford, ed. 1978; 1985), archaeologists realized that an entirely unknown agricultural system had taken shape in ENA beginning some 5,000 years ago.

The Holocene archaeological record of ENA is divided into three broad periods: Archaic, Woodland, and Mississippian (Figure 1.1). The calendar dates associated with these periods vary widely depending on the sub-region. The Mississippian is also geographically restricted to the southeastern part of ENA, with other late prehistoric archaeological cultures recognized in some sub-regions, and with “Late Woodland” continuing until the beginning of European colonization in others. For the core area of ancient EAC cultivation (Figure 1.2), the Archaic ends around 1200 BCE and the Woodland period encompasses the next two millennia, ending around at 1000 CE. The Mississippian, where it occurs, ends at or slightly before contact with Europeans (Anderson and Sassaman 2012). This dissertation spans all three eras, but does not cover all of ENA. The EAC was only cultivated within what Fritz (1993) has described as the “core area”, a region that encompasses the river valleys between the western Appalachian mountains and the Great Plains, south from the Great Lakes to roughly the confluence of the Arkansas and Mississippi Rivers (Figure 1.2). I focused on this region because EAC crops are less visible outside of the core area and were probably less important to subsistence, but it should be noted that they are sometimes also recovered from sites in the Northeast, the South, east of the Appalachian mountains and south of the Arkansas River, and the eastern Great Plains.

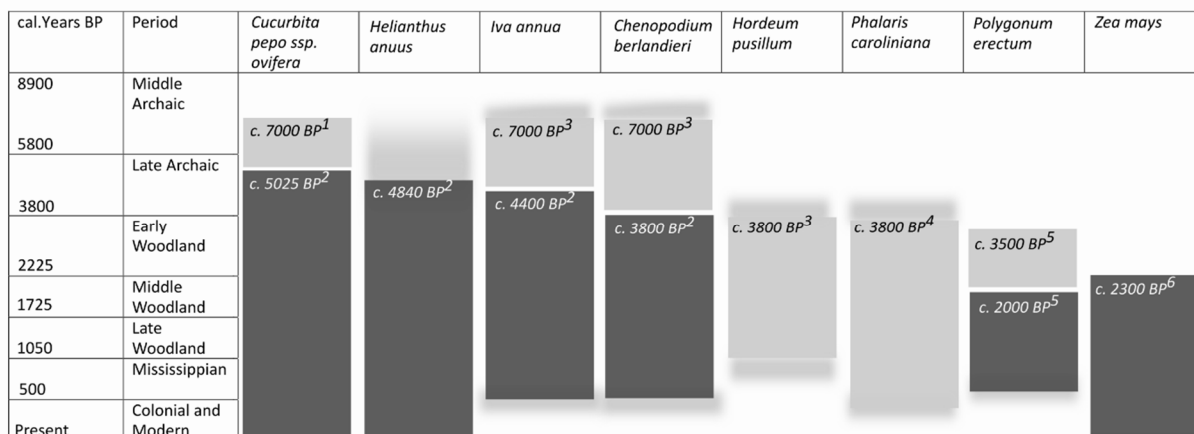


Figure 1.1. Light grey boxes indicate likely period of cultivation prior to the earliest dated assemblage that exhibits morphological indicators of domestication. Dark grey boxes indicate the period of cultivation after the first domesticated assemblage. Shaded grey boxes indicate that a direct radiocarbon data is not available for the earliest or latest reported assemblage. ¹Fritz 1999 ² Smith and Yarnell 2009 ³ Simon and Parker 2006 ⁴ Fritz 2014 ⁵ This dissertation ⁶ Hart and Lovis 2013

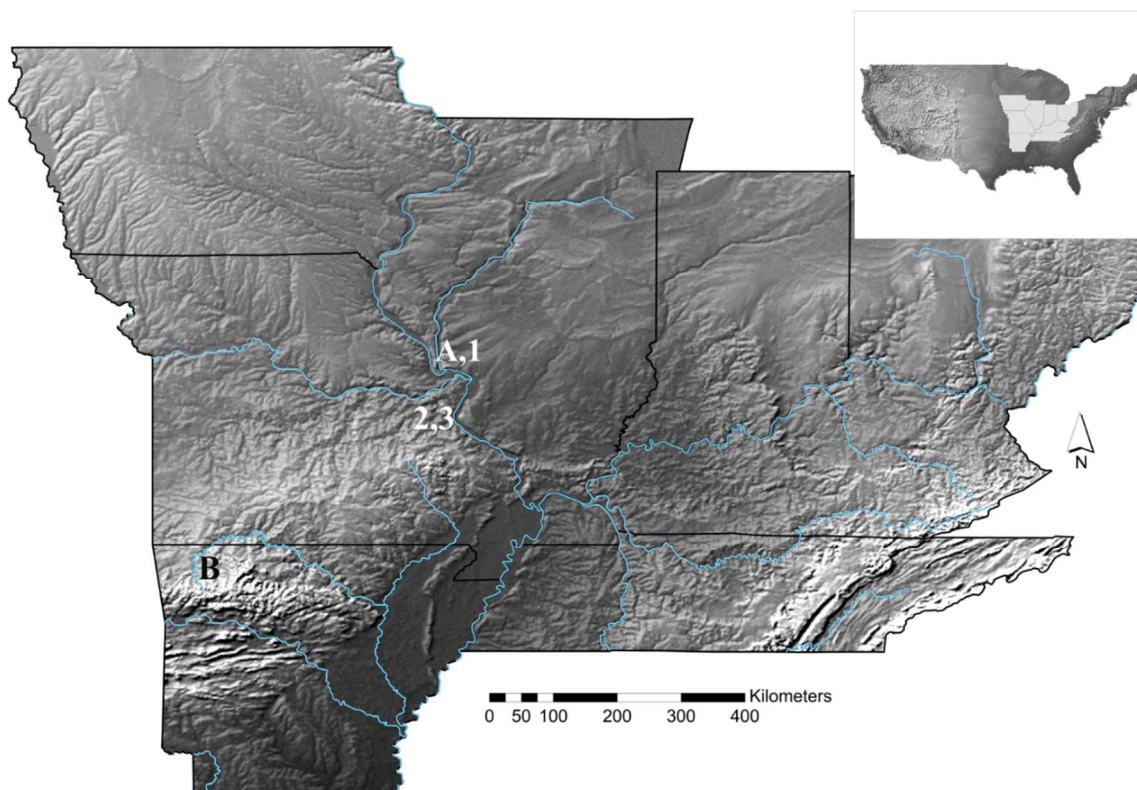


Figure 1.2: Map of the core area of the Eastern Agricultural Complex. Domesticated assemblages of erect knotweed referenced in the text: A) Hill Creek site, IL; B) Whitney Bluff site, AR; 1-3: Populations of modern erect knotweed sampled for the greenhouse experiment, described in Chapter 4.

Cultivation of the EAC crops began during the Late Archaic period,² when the first indigenous domesticates evolved under the management of seasonally mobile hunter-gatherers (Smith and Yarnell 2009; Figure 1.1). Although the archaeological record is relatively thin for the Early Woodland period (c. 1200 BCE – 300 BCE), it is clear from rockshelter and cave assemblages that EAC cultivation continued during this era, and erect knotweed likely entered the crop system during the Early Woodland (Gremillion 1993). During the Middle Woodland period (c. 300 BCE – 300 CE) the abundance of crop remains increases markedly in some regions, such as the Illinois and Ohio River valleys and the American Bottom region (the floodplain of the Mississippi just south of its confluence with the Missouri River, see Figure 1.2) (Fritz 1990; 2000; Asch and Asch 1985b; Simon and Parker 2006). This is also an era characterized by intense interregional exchange. The archaeological record manifests a new set of ritual practices, artistic traditions, and trade relationships called Hopewell in many regions across ENA during the Middle Woodland. The Late Woodland era (c. 300 – 1000 CE) saw a decrease in the construction of monumental architecture and interregional trade, but a continuing intensification of agricultural production, larger settlements, and more permanent architecture (Anderson and Mainfort, eds. 2002; Emerson et al., eds. 2000). The Mississippian era is characterized by the development of stratified settlement systems with larger, often fortified, temple towns at their apex, and by a particular belief system manifested by shared iconography (Pauketat 2002; Reilly and Garber, eds. 2010). It has gradually become clear that maize was not fully integrated into the economy of ENA until relatively late. A recent re-dating of many Late Woodland maize assemblages from Illinois has shown them to be intrusive from later Mississippian phases (Simon 2014). There is evidence that maize was cultivated in the Northeast

² Cultivation of one EAC crop, squash (*Cucurbita pepo* ssp. *ovifera*) extends back even further, into the Middle Archaic (Fritz 1999).

as early as the Middle Woodland, but there is little evidence that maize became an important part of agricultural systems in the core area of EAC cultivation until after c. 900 CE (Hart and Lovis 2013; Simon 2017). Thereafter, it quickly becomes ubiquitous in the archaeological record and was adopted by previously non-agricultural people in the lower Mississippi valley and elsewhere in the Southeast. The EAC crops (other than sunflower and squash) become less common in the last centuries before colonization, but may not have completely fallen out of cultivation until the era of social upheaval and demographic collapse following the arrival of Europeans (Smith 1992). This schematic summary is only meant to orient readers unfamiliar with North American culture history for the first four chapters, which do not contain much archaeological background; a much more detailed archaeological contextualization can be found in Chapter 6.

The crops that made up EAC were part of a diverse subsistence system, including many wild plants and animals, which sustained communities in ENA for roughly 3,000 years. Most of these crops were subjected to sufficiently different conditions under cultivation that they diverged from their wild relatives –they were domesticated – but we know very little about how they were cultivated, harvested, and consumed. The EAC crops are taxonomically diverse. Some, such as goosefoot (*Chenopodium berlandieri*), little barley (*Hordeum pusillum*) and maygrass (*Phalaris caroliniana*) are closely related to important crops from elsewhere in the world: quinoa (*Chenopodium quinoa*), barley proper (*Hordeum vulgare*), and canary grass (*Phalaris canariensis*), respectively. About these, we can gain some insight into how they may have been grown, processed, and consumed, from their crop relatives. Sunflower (*Helianthus annuus*) and eastern pepo squash (*Cucurbita pepo* ssp. *ovifera* – varieties such as acorn squash) are the only EAC crops that have survived to be grown on historic and contemporary farms, and can be directly observed under cultivation. Two others, sumpweed (*Iva annua*) and erect knotweed (the

subject of this dissertation) are not closely related to any existing crop species, either contemporary or historical. Their behavior under cultivation is (or was until this study) entirely unknown.

1.2 Erect Knotweed Background

Many species of knotweed (*Polygonum* L. subsect. *Polygonum*) produce trigonal achenes, which are one-seeded fruits consisting of seeds encased in a tough fruit coat, or pericarp (see Figure 2.1). Some knotweeds, including erect knotweed, 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). Tubercled morphs have thicker pericarps and smooth morphs have thinner pericarps, a characteristic that make smooth morphs quicker to germinate and less able to remain viable in the seed bank for extended periods of time. The ratio of smooth to tubercled morphs by late October or early November, when the plant senesces, varies from species to species, and had never been subject to quantification before this study. Beginning in the 1970s, paleoethnobotanists recognized that a species of knotweed had been part of the EAC, although at first species identifications were tentative, conflicting, or absent (Munson et al. 1971; Struever and Vickery 1973; Yarnell 1974). In time, the cultivated species was identified as erect knotweed based on the striate-tubercled surface texture and shape of archaeological tubercled morphs (Asch and Asch 1985b). Tubercled morphs can be used to identify various species of knotweed, while smooth morphs have always been considered undiagnostic. Archaeological assemblages almost always contain both smooth and tubercled achenes in varying proportions, so smooth morphs in archaeological assemblages were identified by association. Just as archaeologists will date all objects in a well-defined context by association with a single radiocarbon date, the 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 erect knotweed plants.

Speculation about a domesticated subspecies of erect knotweed began when two curious assemblages were reported in the mid-1980s. First, Asch and Asch (1985a; 1985b) reported a carbonized assemblage from the Late Mississippian Hill Creek site, IL, which was composed exclusively of smooth morphs. These achenes were also larger than the erect knotweed smooth morphs in their reference collections. Fritz (1986) reported a similar assemblage of abnormally large smooth morphs from the Mississippian Whitney Bluff site, AR. There were two knotty problems. First, without any tubercled morphs in these assemblages, the achenes had to be considered undiagnostic to the level of species – in other words, they might come from one of several species of knotweed with similar smooth morphs. Since archaeobotanists had focused on erect knotweed, they did not have a clear idea of the range of variability in the size of achenes in closely related species: it was possible that some species missing from archaeobotanical comparative collections might have very large smooth achenes like the ones from Whitney Bluff and Hill Creek. The second problem was that no one had made a careful study of fruit dimorphism in erect knotweed and its close relatives. Botanists had reported that one species in particular (*Polygonum ramosissimum*) produced a lot of smooth morphs under certain (unspecified) conditions (Mertens and Raven 1965), and alluded to the fact that dimorphism was to some degree plastic (Brenkle 1946), but floristic treatments are otherwise silent on the proportions of smooth and tubercled morphs typical of each species. Asch and Asch (1985b:144-5), after outlining these problems, posed two alternative explanations that helped structure the first part of this research: “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*...”

To my knowledge, Asch and Asch (1985b) and Murray and Sheehan (1984) are the only archaeobotanists to have studied living erect knotweed plants before this study. Asch and Asch made a series of seed collections in the late 1970s and early 1980s and made two pertinent observations. One of their key arguments that erect knotweed was cultivated, rather than simply harvested from wild stands, was that it is a rare species, and it was especially difficult to find stands dense enough to yield a sizeable harvest. Second, they observed that erect knotweed does produce more smooth morphs at the end of the growing season, but they did not observe any plants or populations that produced *only* smooth morphs. Murray and Sheehan made a survey of several species of what was then genus *Polygonum* (including several smartweeds, now *Persicaria* sp.) in Indiana. They found that processing erect knotweed was time consuming and laborious because it was difficult to separate the seeds from the plant, and difficult to break the pericarp.

Several pieces of research by botanists and ecologists also provide pertinent background. Yurtseva (2001) clarified the structure of the dimorphic pericarps in a study of two closely related Eurasian subspecies: tubercled morphs have thicker pericarps because they are fortified with layers of wax. These guard against waterlogging, desiccation, and pathogens, allowing the tubercled morph to remain viable in seed bank for longer than the smooth morph. Certain experimental studies of related species suggested that a pronounced germination heteromorphism might exist between the two morphs, although this had never been tested *per se* (Metzger 1992; Sultan 1996). Plants exhibiting germination heteromorphism produce two or more different seed types that have different necessary conditions for germination. Previous studies suggested that

the tubercled morphs might remain in the seed bank for longer than smooth morphs before germinating. The germination behavior of smooth morphs was unknown, but given their thinner pericarps and less robust defenses against pathogens and moisture, I hypothesized that they would germinate more readily. These previous studies helped structure the study of living erect knotweed populations and plants presented in Chapter 4.

1.3 Summary of Results

In order to understand variation under cultivation, a solid foundation of data describing natural variation is needed. Erect knotweed belongs to a notoriously plastic genus which has been the subject of conflicting taxonomic treatments for almost a century. The first step of this research was to understand the phylogeny of knotweed (*Polygonum* sp.) and closely related genera, and then to screen all species that were native to the study area and produced similar size and shaped fruits to those recovered from archaeological sites. Only four native species were similar enough to warrant morphometric comparison to archaeological specimens. These species were compared to a desiccated assemblage from the Whitney Bluff site, Arkansas, which dates to c. 800 BP. This assemblage was selected for the first comparative analysis because it is the only large assemblage that was preserved via desiccation, and thus is not subject to the distortions and biases caused by carbonization (Chapter 5). The Whitney Bluff achenes are identified as a domesticated sub-species, *P. erectum* ssp. *watsoniae* N.G. Muell., which has significantly larger achenes (fruits) and reduced achene dimorphism (Chapter 2). These results are discussed in the context of domestication studies and evolutionary bet-hedging theory in Chapter 3.

Surveys of erect knotweed populations in Missouri and Illinois support the observation of Asch and Asch that this species is rare, but contrary to their experience I found that in some cases it will form dense stands in the wild. I found that the majority of seeds “wait for the

harvester,” and that it is extremely easy to hand strip seeds from completely senesced plants. In my late October to early November harvests, the proportion of smooth morphs varied considerably, but was never more than 72% smooth morphs. I separated the results of these harvests into batches of smooth and tubercled morphs for greenhouse experiments. My first finding was that neither morph will germinate without first being subjected to simulated winter conditions in the seed bank, a process that horticulturists called *seed stratification*. After spending six weeks in cold mud, the germination rate of smooth morphs was much higher than that of tubercled morphs. I also found that under greenhouse conditions with never-varying 12 hours of sunlight per day, erect knotweed plants do not produce any smooth morphs. This finding supports results of experiments on a related species of *Persicaria*, which suggested that pericarp production is a plastic response to available sunlight (plants produce seeds with thin pericarps in low light conditions) (Sultan 1996). I also found that yields can be greatly increased by growing plants at lower densities than occur naturally. I discuss the implications of all of these findings for ancient agricultural practice in ENA in Chapter 4.

Before analyzing the other archaeological assemblages, I first needed to consider the effects of carbonization, preservation bias, and sampling bias. I conducted two carbonization experiments and found that erect knotweed achenes shrink and change shape when burned and that complete achenes will only be preserved if burned at very low temperatures. I also found evidence for differential preservation: tubercled achenes shrink more than smooth achenes and are more likely to survive carbonization intact. I used these findings to develop carbonization corrections for use in the analyses of archaeological assemblages. One of the characteristics of domestication syndrome in erect knotweed is a decrease in achene dimorphism (a higher percentage of smooth morphs than in wild populations). I examined the probabilistic relationship

between sample size and estimates of population proportion and developed criteria for determining if the sample size is large enough to be confident that the population it came from exhibited decreased achene dimorphism. These analyses and results are presented in Chapter 5.

Chapter 6 reports new radiocarbon dates for all but one of the analyzed assemblages and gives an archaeological overview of each of the sites in the context of broader social and agricultural trends. Size and population proportion of smooth morphs are reported for each site, and three unusual looking assemblages are also subjected to multispecies morphometric comparison. The earliest assemblage of erect knotweed to exhibit domestication syndrome comes from an early Middle Woodland sub-mound cremation burial in Kentucky (the Walker Noe site). Slightly later Middle Woodland assemblages from western Illinois and the American Bottom do not show signs of domestication, so it is unclear how widespread domesticated erect knotweed was during the Middle Woodland. The *in situ* evolution of domesticated erect knotweed is demonstrated in the American Bottom region, with wild morphology at the Middle Woodland Meridian Hills site and increasing fruit size and proportions of smooth morphs at several sequential Late Woodland sites, culminating in a domesticated landrace by the Mississippian era. Meanwhile, nearby Late Woodland communities in the Lower Missouri River valley continued to cultivate wild erect knotweed. In the Mississippian era, different landraces of domesticated erect knotweed are visible at three different sites in Illinois, Missouri, and Arkansas, while Fort Ancient farmers in the Ohio River valley evidently did not have access to the same seed stock and agricultural knowledge. I discuss some of the agricultural practices that might explain the variability in the archaeological record with reference to my experiments and survey of modern populations, and suggest directions for further research.

My concluding thoughts place this research in the context of global studies of domestication and food production. I suggest that optimal foraging models used in human behavioral ecology may consistently under-rank the seeds of small seeded annuals, and that plasticity under cultivation may have been one factor that made disturbance adapted plants attractive to ancient foragers. I argue that niche construction (Odling-Smee et al. 2003), food production, and delayed return strategies (Woodburn 1982) are all roughly synonymous terms, and that domestication is a likely, but not predetermined, outcome of such systems and behaviors. The spread of food producing economies was dependent on the spread of complex systems of knowledge through interacting communities of practice and without these systems of traditional ecological knowledge domesticated varieties could not be maintained.

1.4 References

Anderson, David G. and Robert C. Mainfort (editors)

2002 *The Woodland Southeast*. University of Alabama Press, Tuscaloosa.

Anderson, David G. and Kenneth E. Sassaman

2012 *Recent Developments in Southeastern Archaeology*. SAA Press, Washington, DC.

Asch, David L. and Nancy B. Asch

1985a Archaeobotany. In *The Hill Creek Homestead and the Late Mississippian Settlement in the Lower Illinois River Valley*, edited by Michael D. Conner, pp. 115-170. Kampsville Archaeological Center. vol. 1. The Center for American Archaeology, Kampsville, IL.

1985b Prehistoric Plant Cultivation in West Central Illinois. In *Prehistoric Food Production in North America*, edited by Richard I. Ford, pp. 149-203.

Anthropology Papers No.75, Museum of Anthropolog. University of Michigan,
Ann Arbor.

Boyd, Robert and Peter J. Richerson

1988 *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.

Brenkle, Jacob F.

1946 Notes on Avicularia II. *Phytologia* 2(5):169-171.

Costea, Mihai, François J. Tardif and Harold H. Hinds

2005 *Polygonum* L. In *Flora of North America North of Mexico*, edited by Flora of
North America Editorial Committee. vol. 5. eFloras.org, New York and Oxford.

Emerson, Thomas E., Dale L. McElrath and Andrew C. Fortier (editors)

2000 *Late Woodland Societies: Tradition and Transformation across the Midcontinent*.
University of Nebraska Press, Lincoln.

Ford, Richard A. (editor)

1978 *The Nature and Status of Ethnobotany*. Anthropology Papers No.67, Museum of
Anthropology, University of Michigan, Ann Arbor.

Ford, Richard I. (editor)

1985 *Prehistoric Food Production in North America*. Anthropology Papers No.75,
Museum of Anthropology. University of Michigan, Ann Arbor.

Fritz, Gayle J.

- 1986 Prehistoric Ozark Agriculture: The University of Arkansas Rockshelter Collections. Dissertation, Anthropology, University of North Carolina, Chapel Hill.
- 1990 Multiple Pathways to Farming in Precontact Eastern North America. *Journal of World Prehistory* 4(4):387-435.
- 1993 Early and Middle Woodland Period Paleoethnobotany. In *Foraging and Farming in the Eastern Woodlands*, edited by C. Margaret Scarry, pp. 39-56. University Press of Florida, Gainesville.
- 1999 Gender and the Early Cultivation of Gourds in Eastern North America. *American Antiquity* 64(3):417-429.
- 2000 Native Farming Systems and Ecosystems in the Mississippi River Valley. In *Imperfect Balance: Landscape Transformations in the Precolumbian Americas*, edited by David L. Lentz, pp. 224-249. Columbia University Press, New York.

Gilmore, Melvin R.

- 1931 Vegetal Remains of the Ozark Bluff-Dweller Culture. *Papers of the Michigan Academy of Sciences, Arts, and Letters* 14:83-102.

Gremillion, Kristen J.

- 1993 Plant Husbandry at the Archaic/Woodland Transition: Evidence from the Cold Oak Shelter, Kentucky. *Midcontinental Journal of Archaeology* 18:161-189.

Hart, John P. and William A. Lovis

2013 Reevaluating What We Know About the Histories of Maize in Northeastern North America: A Review of Current Evidence. *Journal of Archaeological Research* 21(2):175-216.

Jones, Volney H.

1936 The Vegetal Remains of Newt Kash Hollow Shelter. In *Rock Shelters in Menifee County, Kentucky*, edited by W.S. Webb and W.D. Funkhouser, pp. 147-167. University of Kentucky Press, Lexington.

Kent, Reilly. F. and James F. Garber (editors)

2010 *Ancient Objects and Sacred Realms: Interpretations of Mississippian Iconography*. University of Texas Press, Austin.

Lavé, Jean and Etienne Wenger

1991 *Situated learning: Legitimate peripheral participation*. Cambridge University Press, Cambridge.

Mertens, Thomas R. and Peter H. Raven

1965 Taxonomy of *Polygonum*, section *Polygonum* (Avicularia) in North America. *Madrono* 18(3):85-92.

Metzger, James D.

1992 Physiological Basis of Achene Dormancy in *Polygonum convovulus* (Polygonaceae). *American Journal of Botany* 79(8):882-886.

Mt Pleasant, Jane

2006 The Science Behind the ‘Three Sisters’ Mound System: An Agronomic Assessment of an Indigenous Agricultural System in the Northeast. In *Histories of Maize: Multidisciplinary Approaches to the Prehistory, Linguistics, Biogeography, Domestication, and Evolution of Maize*, edited by John E. Staller, Robert H. Tykot and Bruce F. Benz, pp. 529-538. Left Coast Press, New York.

Mt. Pleasant, Jane and Robert F. Burt

2010 Estimation Productivity of Traditional Iroquoian Cropping Systems from Field Experiments and Historical Literature. *Journal of Ethnobiology* 30(1):52-79.

Mueller, Natalie G.

2017a An Extinct Domesticated Subspecies of Erect Knotweed in Eastern North America: *Polygonum erectum* L. ssp. *watsoniae* (POLYGONACEAE). *Novon* 25(2).

2017b Documenting domestication in a lost crop (*Polygonum erectum* L.): evolutionary bet-hedgers under cultivation. *Vegetation History and Archaeobotany* 26(3):313-327.

2017c Evolutionary “Bet-Hedgers” under Cultivation: Investigating the Domestication of Erect Knotweed (*Polygonum erectum* L.) using Growth Experiments. *Human Ecology* 45(2):189-203.

2017d Carbonization, Differential Preservation, and Sampling Bias in Domestication Studies: An Erect Knotweed (*Polygonum erectum* L.) Case Study. *Journal of Archaeological Science: Reports* 13:303-311.

Munson, Patrick J., Paul W. Parmalee and Richard A. Yarnell

- 1971 Subsistence Ecology of Scovill, a Terminal Middle Woodland Village. *American Antiquity* 36(4):410-431.

Murray, Priscilla M. and Mark C. Sheehan

- 1984 Prehistoric Polygonum Use in the Midwestern United States. In *Experiments and Observations on Aboriginal Wild Plant Food Utilization in Eastern North America*, edited by Patrick J. Munson. Prehistory Research Series. vol. VI. Indiana Historical Society, Indianapolis.

Odling-Smee, John F., Kevin N. Laland and Marcus W. Feldman

- 2003 *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.

Pauketat, Timothy R

- 2002 A Fourth-Generation Synthesis of Cahokia and Mississippianization. *Midcontinental Journal of Archaeology* 27(2):149-170.

Simon, Mary L.

- 2014 Reevaluating the Introduction of Maize into the American Bottom and Western Illinois. *Occasional Papers of the Midwest Archaeological Conference* 1(1):97-134.
- 2017 Reevaluating the Evidence for Middle Woodland Maize from the Holding Site. *American Antiquity* 82(1):140-150.

Simon, Mary L. and Kathryn E. Parker

- 2006 Prehistoric Plant Use in the American Bottom: New Thoughts and Interpretations.
Southeastern Archaeology 25(2):212-257.

Smith, Bruce D.

- 1992 *Rivers of Change: Essays on Early Agriculture in Eastern North America*.
Smithsonian Institution Press, Washington.
- 2006 Eastern North America as an Independent Center of Plant Domestication.
Proceedings of the National Academy of Sciences 103(33):12223-12228.

Smith, Bruce D. and Richard A. Yarnell

- 2009 Initial Formation of an Indigenous Crop Complex in Eastern North America at
3800 B.P. *Proceedings of the National Academy of Sciences* 106(16):6561-6566.

Struever, Stuart and Kent D. Vickery

- 1973 The Beginnings of Cultivation in the Midwest-Riverine Area of the United States.
American Anthropologist 75(5):1197-1220.

Sultan, Sonia E.

- 1996 Phenotypic Plasticity for Offspring Traits in *Polygonum persicaria*. *Ecology*
77(6):1791-1807.

Turner, Nancy J. , Marianne Boelscher Ignace and Ronald Ignace

- 2000 Traditional Ecological Knowledge and Wisdom of Aboriginal Peoples in British
Columbia. *Ecological Applications* 10(5):1275-1287.

Watson, Patty Jo and Richard A. Yarnell

- 1966 Archaeological and Paleoethnobotanical Investigations in Salts Cave, Mammoth Cave National Park, Kentucky. *American Antiquity* 31(6):842-849.

Woodburn, James

- 1982 Egalitarian Societies. *Man, New Series* 17(3):431-451.

Yarnell, Richard A.

- 1969 Contents of human paleofeces. In *The Prehistory of Salts Cave, Kentucky*, edited by Patty Jo Watson, pp. 41-54. Reports of Investigations. vol. 16. Illinois State Museum, Springfield, IL.
- 1974 Plant food and cultivation of the Salts Cavers. In *The Archaeology of the Mammoth Cave Area*, edited by Patty Jo Watson, pp. 113-122. Academic Press, New York.

Yurtseva, O.V.

- 2001 Ultrasculpture of Achene Surface in *Polygonum* section *Polygonum* (Polygonaceae) in Russia. *Nordic Journal of Botany* 21(4):513-528.

2. An Extinct Domesticated Subspecies of Erect Knotweed in Eastern North America: *Polygonum erectum* L. subsp. *watsoniae* (Polygonaceae)³

2.1 Abstract

This paper provides a description of an extinct domesticated subspecies of erect knotweed (*Polygonum erectum* L.). Masses of erect knotweed (*Polygonum erectum* L.) achenes are often recovered from archaeological sites in Eastern North America dating to c. 3000–600 BP. Several paleoethnobotanical assemblages from the later part of this era (c. 1000–600 BP) contain achenes that are outside the range of natural variation for erect knotweed. The most well preserved of these archaeological assemblages, a desiccated cache of achenes from the Whitney Bluff site, Arkansas (c. 900 BP), is compared to four closely related taxa of *Polygonum*. The Whitney Bluff achenes are most similar to those of *P. erectum*, but differ from modern fruits of this species in three respects: 1) fruits are larger; 2) average pericarp thickness is reduced; and 3) fruit dimorphism is greatly reduced. These differences are typical of domestication syndrome in annual seed crops. The Whitney Bluff assemblage is described as the type specimen of a domesticated sub-species, *Polygonum erectum* subsp. *watsoniae* N.G. Muell.

2.2 Introduction

From c. 3900–600 BP, a suite of native seed crops known as the Eastern Agricultural Complex (EAC) was cultivated in Eastern North America (Smith and Yarnell 2009). Previous studies have documented changes in seed shape and size to demonstrate that two of these crops

³ 2017, *Novon* 25(2):166-179.

were domesticated: *Iva annua* L. var. *macrocarpa* Blake and *Chenopodium berlandieri* Moq. subsp. *jonesianum* B. Smith (Blake 1939; Smith and Funk 1985). The domestication of little barley (*Hordeum pusillum* Nutt.) has also been suggested based on differences in seed morphology between archaeological specimens and modern plants (Hunter 1992; Adams 2014). Erect knotweed (*Polygonum erectum* L.) was cultivated alongside these lost domesticates for hundreds of years. It has been found in hearths, storage pits, and human feces at archaeological sites across the Midwest dating from c. 3000–600 BP (Asch and Asch 1985b; Faulkner 1991; Powell 2000; Gremillion 2004; Simon and Parker 2006).

Polygonum erectum and many species within *Polygonum* L. sect. *Polygonum* exhibit seasonal achene dimorphism. Native or naturalized North American species that exhibit seasonal achene dimorphism include: *P. achoreum* (S.F. Blake) R.C. Jacks, *P. aviculare* L. complex (sensu Costea and Tardif 2004), *P. glaucum* Nutt., *P. erectum*, *P. marinense* T.R. Mertens and P.H. Raven, *P. patulum* M. Bieb., *P. plebeium* R. Brown, *P. ramosissimum* Michx., and *P. striatulum* B.L. Robinson. These species produce two different fruit morphs, referred to by pericarp texture. Tubercled morphs have lower aspect ratios (i.e. a shorter length compared to width) and thicker pericarps with a variety of textures that are diagnostic of different species (Costea et al. 2005). Smooth morphs have a higher aspect ratio (i.e. a longer length compared width) and thinner pericarps (Figure 2.1). Tubercled morphs have layers of cuticle and wax in their pericarps that slow the penetration of moisture and pathogens, allowing seeds to remain viable for several seasons (Yurtseva 2001). Smooth morphs germinate much more readily the spring after they are produced (Chapter 4). Plants produce tubercled morphs throughout the growing season, and begin to produce smooth morphs in mid-September.

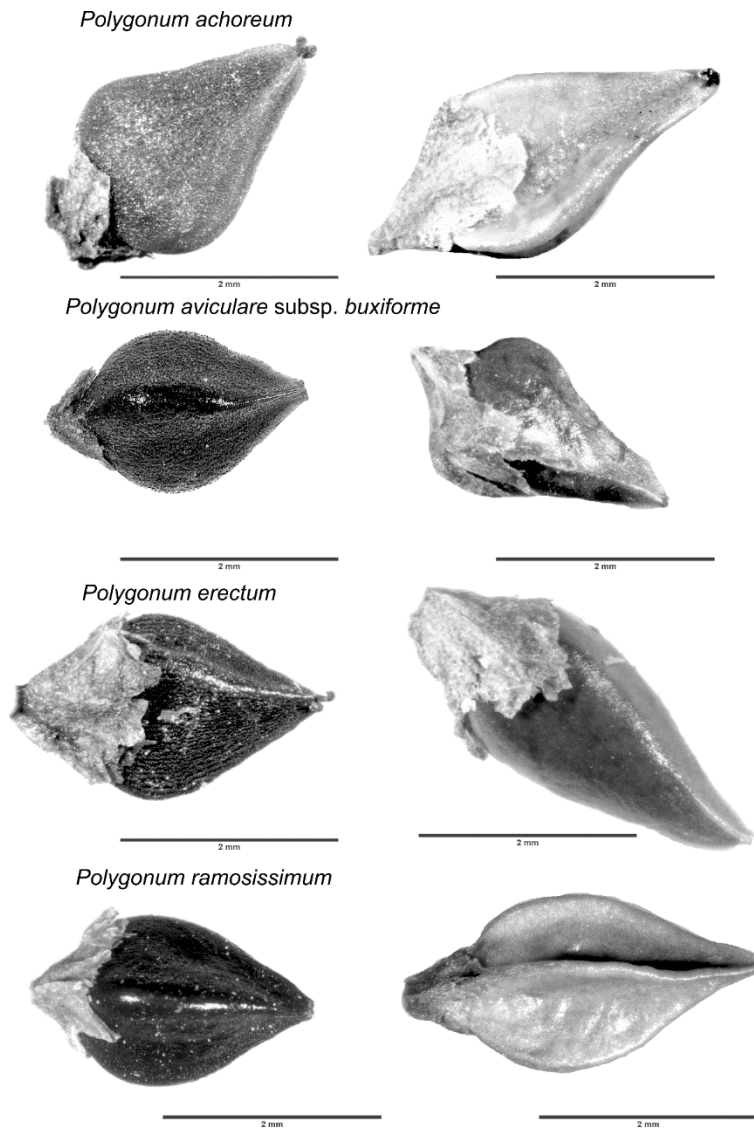


Figure 2.1: Examples of the dimorphic achenes of the four species considered in this analysis. Perianths have been removed. Left: Tubercled morphs with typical surface textures, shape, and size for each species. *P. achoreum* achenes are usually uniformly tubercled, *P. aviculare* subsp. *buxiforme* achenes are coarsely tubercled, *P. erectum* achenes are striate-tubercled – compare to those from Whitney Bluff. The *P. ramosissimum* achene pictured here is roughened, but surface texture varies within this species. Right: Smooth morphs of typical shape and size for each species. *P. erectum* and *P. aviculare* subsp. *buxiforme* achenes pictured here have convex faces, which gives them a plump appearance. This is a rare morphology for *P. aviculare* subsp. *buxiforme*, and a very common one for *P. erectum* (see Table 2.3). *P. ramosissimum* and *P. achoreum* smooth morph achenes have concave faces and a deflated appearance. This *P. achoreum* smooth morph is an example where the central ridge has slumped over so one face is completely obscured, whereas the *P. ramosissimum* smooth morph has a sunken central ridge.

Beginning in the 1980s, the achenes found in abundance at archaeological sites were identified by paleoethnobotanists as *Polygonum erectum* on the basis of their surface texture

(striate-tubercled) and the distinctive shape of their tubercled achenes (Martin 1954). Smooth achenes also occurred in most archaeological samples, and were assumed to also come from *P. erectum* plants, although their morphology has not been considered diagnostic to species by botanists or paleoethnobotanists (Asch and Asch 1985a; Costea et.al. 2005).

Speculation about a domesticated subspecies of erect knotweed began in the mid-1980s, when two strange assemblages were reported. At the Late Mississippian (c. 700 BP) Hill Creek site, IL, thousands of carbonized smooth morph achenes were recovered from a large storage pit – no tubercled morphs were present (Asch and Asch 1985a). The Hill Creek achenes were also larger than the erect knotweed smooth morphs in available reference collections. To ascertain whether or not erect knotweed was capable of producing such a harvest, Asch and Asch gathered achenes from *P. erectum* populations in Kansas, Missouri and Illinois during three different growing seasons (Asch and Asch 1985a). This survey suggested that erect knotweed does not produce monomorphic harvests: tubercled morphs were always present. Asch and Asch (1985a:144-5) 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*....” In particular, Asch and Asch (1985b) suggested *P. ramosissimum*, which was known to produce many smooth late season achenes (Mertens and Raven 1965). Fritz (1986) reported a similar near-monomorphic assemblage of large, smooth morph achenes from the Mississippian Whitney Bluff site, AR. These were desiccated in a dry rockshelter and were remarkably well-preserved. But without a clearer sense of variability in seasonal achene

production within and among species of *Polygonum*, erect knotweed domestication remained an open question.

The Whitney Bluff site was one of 80 Ozarks rockshelters excavated during the 1920s and 1930s by the University of Arkansas Museum. The results of these excavations were never published but are documented in field notes and photographs on file at the University of Arkansas Museum. The well-preserved plant remains from the rockshelters were first examined by Melvin Gilmore and Volney Jones (Gilmore 1931). Since then, many scholars have examined parts of these important collections (see Fritz 1986). The crop plant remains from 19 rockshelters, including Whitney Bluff, were analyzed and reported by Gayle Fritz (1986), who also synthesized field and laboratory notes for those 19 sites to reconstruct as much of the archaeological context as possible. The exact location of the Whitney Bluff site is one important piece of information missing from the original field reports, but excavation notes indicate that it is located in Benton County, AR, on the banks of the White River. Materials recovered from Whitney Bluff include a woven bag, baskets, string, mussel shell, stone tools, one potsherd, cane tools, turkey bones, a smashed gourd bowl, and plant foods (Fritz 1986).

Two large samples of *Polygonum* achenes were recovered from this site (University of Arkansas Museum accession numbers 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 1986:107; 1986:92). Domesticated *Chenopodium berlandieri* subsp. *jonesianum* was also recovered from this context (Fritz 1986). A fragment of the gourd from the cache was dated to 785 +/-75 BP (cal. A.D. 1042 –1386; Fritz 1986). The *Polygonum* itself yielded a date of 885 +/- 20 BP (cal. AD 1046–1217; NOSAMS sample number 123466). These two samples are comprised of 1307

achenes. Fritz (1986) measured the length and width of 200 achenes and noted that they were larger than available reference collections of *P. erectum*, and were all smooth morphs.

This study was designed to compare the Hill Creek and Whitney Bluff assemblages (among the 40 other archaeological assemblages that I analyzed in the course of a larger study) to erect knotweed and several other species from which they could possibly be derived. Two possibilities are considered here: 1) all archaeological assemblages, including those from Hill Creek and Whitney Bluff, fall within the range of natural variability for some species native to the study area; or 2) the archaeological assemblages from Hill Creek and Whitney Bluff exhibit domestication syndrome as a result of hundreds of years of cultivation. In either case, the first step is to determine which species is represented at these sites. All but one of the available archaeological assemblages have been distorted by carbonization, and require careful correction before they can be compared to uncarbonized fruits. The Whitney Bluff assemblage, on the other hand, was not subject to distortion because it was preserved via desiccation.

2.3 Polygonaceae Systematics and Potential Progenitor Taxa

Species were considered as possible progenitors of the Whitney Bluff assemblage if 1) they had similar fruit and perianth morphology; 2) they were native to pre-Columbian North America; and 3) they occur in the region where ancient knotweed cultivation is documented (parts of modern day Arkansas, Illinois, Indiana, Iowa, Kentucky, Missouri, Ohio, and Tennessee). The relationships among species of *Polygonum* and between it and related genera have been debated and revised repeatedly for decades, so it was necessary to carefully review the bases for current taxonomies in order to make sure there were not species in other clades that should be considered, and to double check the identifications of all specimens sampled for this study.

Polygonum belongs to the family Polygonaceae, a monophyletic group (Cuénoud et al. 2002) characterized by several synapomorphies, including ocrea (sheathing stipules), orthotropous ovules, and quincunial aestivation. Many members have trigonous achenes, while others have lenticular biconvex or discoid fruits. Older taxonomic treatments recognized three or four distinct subfamilies, but more recently specialists have mainly dealt with two sub-families separated on the basis of molecular and morphological characters: Eriogonoideae and Polygonoideae (Sanchez and Chron 2008; Burke and Sanchez 2011). As currently circumscribed, monophyletic Polygonoideae remains a fairly distinctive clade. Members are herbs, shrubs, or lianas with ocrea, swollen nodes, flowers subtended by bracteoles, lenticular or trigonous achenes, and lobed or entire endosperm (Sanchez et al. 2011).

Within Polygonoideae, three tribes contain species native to Eastern North America: Persicarieae (smartweeds), Polygoneae (knotweeds), and Rumiceae (docks). Within Rumiceae, only species in *Rumex* L. are native to the study area (*Rumex altissimus* Alph., *Rumex hastatulus* Baldw., *Rumex maritimus* L., *Rumex salicifolius* Weinm., and *Rumex verticillatus* L.) Their achenes are trigonous but are easily distinguished from archaeological specimens by their more acute angles in cross-sectional view, and their symmetrical, ovoid shape in plan-view (i.e. when viewed from above, see illustrations in Martin 1954:514). Their tepals, which give the flowers a winged appearance (or in the case of *R. maritimus*, toothed, bristle-like tepals), are very different from the perianths preserved on many desiccated archaeological specimens from Whitney Bluff (Figure 2.2), so a native species of *Rumex* can be positively ruled out.

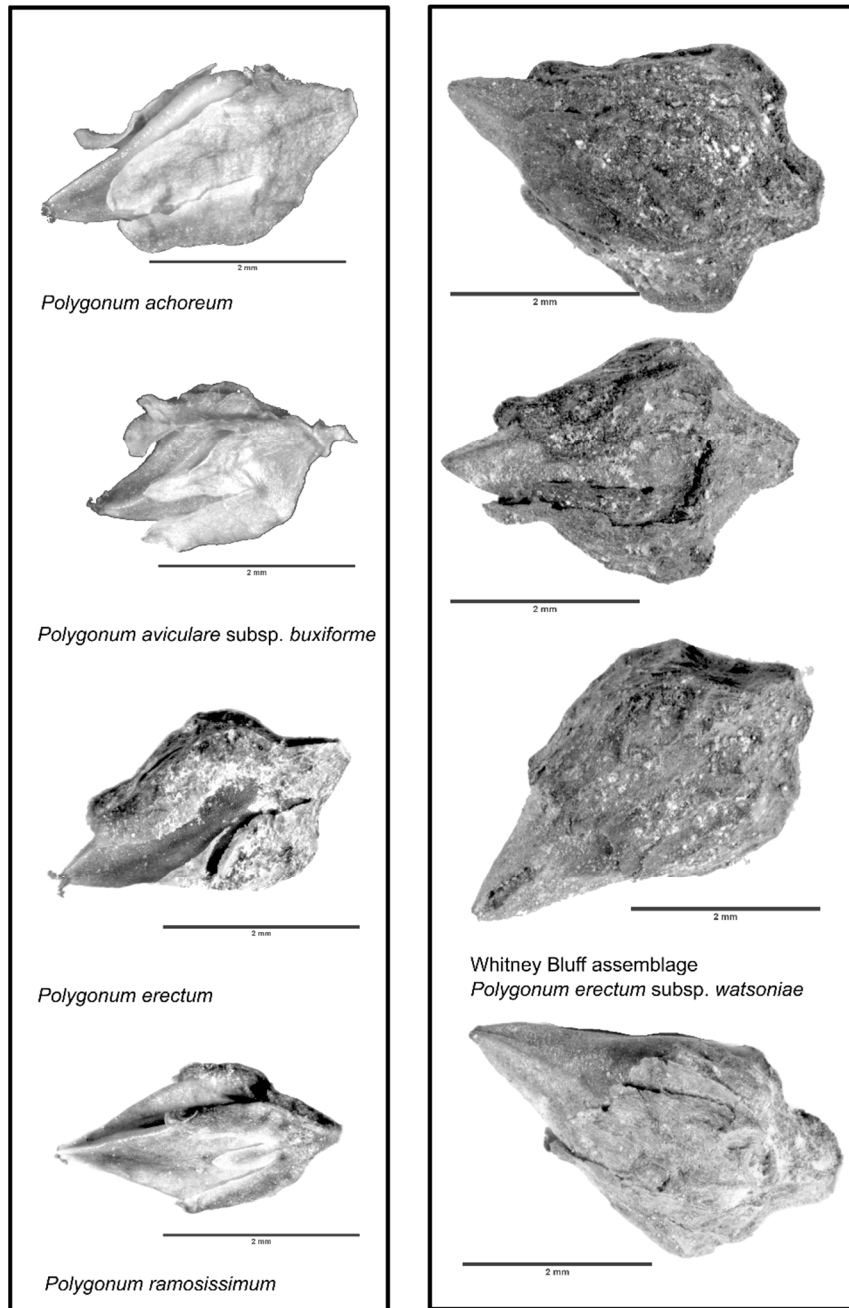


Figure 2.2: Left: Examples of the smooth morph achenes for each of the four species with perianth adhering. *P. ramosissimum* is significantly more exserted from its perianth than the other three species. Right: Examples of Whitney Bluff achenes, to scale with those from modern species. Convex faces are almost universal within this assemblage, as within *P. erectum* (see Figure 2.1; Table 2.3).

Several of the smartweeds (*Persicaria* Miller) that are native to the study area produce biconvex or discoid achenes and can easily be eliminated (*P. amphibia* (L.) Gray, *P. arifolia* (L.)

Haroldson, *P. careyi* (Olney) Greene, *P. glabra* (Willd.) M. Gomez, and *P. pensylvanica* (L.) M. Gomez). Three others, *P. bicornis* Rafinesque, *P. hydropiper* (L.) Spach, and *P. lapathifolia* (L.) Gray, produce mostly biconvex or discoid achenes and rarely produce trigonous achenes, so archaeological assemblages that are composed entirely of trigonous achenes cannot come from these species. Five other smartweeds native to the study area produce only or primarily trigonous achenes somewhat similar to those found archaeologically (*P. hydropiperoides* Michx., *P. punctata* (Elliott) Small, *P. sagittata* (L.) H. Gross, *P. setacea* (Baldwin) Small, *P. virginiana* (L.) Gaertn.). These were also examined but were found to be easily distinguishable from archaeological specimens. The achenes I observed at the Missouri Botanical Garden herbarium conform to the illustrations of Martin (1954) for several of these species (at the time, they were all considered to be members of *Polygonum*). In plan-view, in comparison to the Whitney Bluff achenes, the achenes of these species are variously 1) more symmetrical and ovoid (*P. punctatum*); 2) more ovoid, with a sharper point at the apex (*P. hydropiperoides*), or; 3) lack clear faces and are only vaguely trigonous (*P. virginianum*). *P. sagittata* and *P. setaceum* have achenes that somewhat resemble the *tubercled morphs* recovered from archaeological sites in shape, but they have a smooth pericarp texture (the latter species also has much smaller achenes than any recovered archaeologically). Even more obviously (with the exception of *P. virginianum*), the adhering campanulate perianths of these species do not resemble those of the Whitney Bluff specimens (Figure 2.2). In addition, within these species of *Persicaria*, the perianth almost always completely encloses the mature achene, whereas the Whitney Bluff achenes are partially exserted.

Polygoneae has recently gone through a major revision based on molecular data. As currently circumscribed, Polygoneae are monophyletic and include *Atraphaxis* L., *Duma* T.M. Schust,

Fallopia Adans., *Knorringia* (Czukav) Tzvelev, *Muehlenbeckia* Meisn. (incl. *Homalocladium* (F.Muell.) L.H.Bailey), *Polygonum* L. (incl. *Polygonella* Michx.), and *Reynoutria* Houtt. (Schuster et al. 2011). Besides the members of *Polygonum* in the strict sense sampled for this study (discussed below), there are only two species native to the study area in these genera: *Fallopia cilinodis* (Michx.) Holub, and *Fallopia scandens* (L.) Holub. These can be distinguished from archaeological specimens based on the shape of their achenes (ovoid in plan-view) and, in the case of *F. scandens*, by its distinctive winged tepals.

Within *Polygonum* in the strict sense, Schuster and colleagues (2011) found molecular support for three sections corresponding to the treatment of Ronse De Craene et al. (2004).

1. Species in *Polygonum* sect. *Pseudomollia* Boiss. are mostly restricted to Central Asia and the Middle East, and do not occur in North America at all (Schuster et al. 2011:1661).
2. *Polygonum* sect. *Duravia* S. Watson is composed of two geographically distinct North American clades, subsect. *Duravia* (S. Watson) Ronse De Craene & S.-P. Hong of western North America, and subsect. *Polygonella* (Michx.) Ronse De Craene & S.-P. Hong of southeastern North America. The same close relationship between these two subgroups had previously been recovered using cladistic analyses of morphological characters (Ronse De Craene et al. 2000) and is further supported by the fact that *Polygonum* sect. *Duravia* (including *Polygonella* Michx.) does not share the pollen morphology common to all other members of *Polygonum* (Hong et al. 2005), but *Polygonella* is still treated as a distinct genus in the *Flora of North America* (Freeman 2005) All but one member of subsect. *Duravia* occur only in the western United States. One is very common in the Midwest (*Polygonum tenue* Michx.), but is easily ruled out by its elliptic to oblong fruits. Two species of subsect. *Polygonella* occur in the study area

(most are restricted to the Gulf Coast states). One of these is a perennial shrub (*Polygonum americanum* (Fisch. & C.A.Mey.) T.M. Schust. & Reveal), and the other is an annual herb (*Polygonum articulatum* (L.) Meisn.) that grows on sand dunes and lakeshores. Both have flowers that do not resemble those preserved on archaeological specimens (having distinct rather than connate tepals) and fruits that in cross section have acute angles like those of *Rumex* species.

3. By process of elimination, only species within *Polygonum* sect. *Polygonum* remain for consideration.

Unfortunately, within *Polygonum* sect. *Polygonum* there are some unresolved taxonomic issues at the specific level. This is especially true of the common species *Polygonum aviculare* L. sensu stricto and its closely related taxa, which are now treated as the *Polygonum aviculare* complex by the *Flora of North America* (Costea and Tardif 2004; Costea et al. 2005). Members of this complex are found all over the world as cosmopolitan weeds. The *P. aviculare* complex encompasses numerous taxa that were treated as separate species in overlapping and conflicting taxonomies for centuries (*P. aviculare* L. sensu stricto; *P. depressum* Meisn. = *P. arenastrum* Boreau; *P. neglectum* Besser; and *P. buxiforme* Small). Costea and Tardif (2004) merged what had previously been five species into one because the previously recognized species could not be separated by chromosome number or be reliably differentiated morphologically. They also considered it likely that hybridization is frequent within the *P. aviculare* complex. Of the recognized subspecies, only *P. aviculare* subsp. *buxiforme* (Small) Costea and Tardif is native to North America (Costea and Tardif 2004).

Specimens of *P. aviculare* subsp. *buxiforme* recently re-examined by Costea et. al. (2005) for the *Flora of North America*, or by Yaskievych (2013) for the *Flora of Missouri*, were

included in this study. Three other native species within *Polygonum* subsect. *Polygonum* occur in the study area: *P. erectum*, *P. ramosissimum*, and *P. achoreum*. All of the other species of *Polygonum* that occur in the study area are introduced from the Eastern Hemisphere.

2.3 Achene Morphology and Dimorphism

There is a long history of attempts to distinguish among species of *Polygonum* based on achene morphology (e.g. Martin 1954; Mertens and Raven 1965; Wolf and McNeill 1986). Surface texture, relative width of the three faces, convexity of the faces and edges, and color of tubercled achenes have all been used in taxonomies to distinguish species, yet these treatments frequently contradict one another. For example, while tubercled morph surface texture is sometimes diagnostic of species, it can also be variable within species. In *The Flora of North America* (Costea et al. 2005), *P. erectum* tubercled morphs are described as “striate-tubercled,” i.e. the tubercles are arranged in rows. The specimens I examined confirm this, and most treatments agree. But other species are not so consistent. *P. ramosissimum* tubercled achenes are described in *The Flora of North America* 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. Wolf and McNeill (1986:478) describe *P. ramosissimum* achenes as “smooth (rarely roughened),” not recognizing any tubercled achenes for this species. Of the 59 *P. ramosissimum* tubercled achenes in my photosample, all four of these textures are present in addition to seven achenes that are distinctly striate-tubercled, a texture not mentioned by either treatment and considered by paleoethnobotanists to be diagnostic of *P. erectum*. *P. achoreum* achenes are described as uniformly tubercled in most treatments. The majority do fit that description, but ten out of 51 tubercled achenes in the photosample are striate-tubercled. *P.*

aviculare subsp. *buxiforme* achenes are described in the *Flora of North America* as “coarsely striate-tubercled to obscurely tubercled” – about a quarter of those in my photosample are coarsely striate-tubercled (Costea et al. 2005; Figure 1). In other words, all four taxa produce the striate-tubercled achenes that most paleoethnobotanists consider diagnostic of *P. erectum*, but at different frequencies (Table 2.3). Martin (1954) recognized that the identification of *Polygonum* seeds to species required consideration of multiple characters including shape, size, and surface characteristics. Even taking into account all of these, Martin (1954:514) conceded: “the process is not always easy and sure,” citing variability within a species and even between the fruits on a single plant.

All of this variability is exhibited by the ostensibly *diagnostic* tubercled achenes – the smooth, late season achenes have not previously been considered systematically. As noted above, knotweeds exhibit seasonal achene dimorphism: they produce two distinct fruit types in ratios that vary over the course of the growing season. In the past, taxonomists have considered smooth morphs to be undiagnostic. For example, the in *Flora of North America* smooth achenes in *Polygonum* sect. *Polygonum* are summarized thus: “Late-season [smooth] achenes in all species are hypertrophied, olivaceous, lanceolate, exserted, and smooth. They have little taxonomic significance” (Costea et al. 2005). Wolf and McNeill (1986) and Mertens and Raven (1965) deal with late season achenes only to note that they are more common on some species than others, and to point out that plants bearing such fruits have been mistaken for separate species in the past. This study by necessity asks whether or not the morphology of smooth achenes is diagnostic of particular species, since the goal here is to identify archaeological assemblages composed mostly, or occasionally exclusively, of smooth achenes.

2.4 Materials and Methods

I concur with Fritz' (1986) observation that the two samples of *Polygonum* from Whitney Bluff are very similar and probably came from the same context. They are treated as a single sample in this analysis. The morphometric analysis of achenes was performed using digital images of a photosample. The Whitney Bluff assemblage is only one of 40 archaeological assemblages that I analyzed as part of a larger study of pre-Columbian agricultural practice. Per sampling protocol for the larger study, the size of the photosample was determined by the weight of the entire assemblage. I photographed 1 achene per 0.01g. 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. Although the Whitney Bluff *Polygonum* was not carbonized, I adhered this sampling strategy for the sake of consistency. I randomly selected a photosample of 80 achenes from 32-57-3a and 120 from 32-57-5c. Many of the Whitney Bluff achenes retain some or all of their perianth parts. The presence of the perianth or parts of the perianth may somewhat inflate area and width measurements, but the perianths of the Whitney Bluff achenes generally tightly conform to the shape of the underlying fruit (Figure 2.2). Of the 1307 achenes in the two samples, *all but two* were smooth morphs. The two tubercled morphs were also photographed and measured, and are described below (Figure 2.3). Measurements of length and width reported here are very similar to those reported by Fritz (1986) on two different subsamples of 100 achenes.

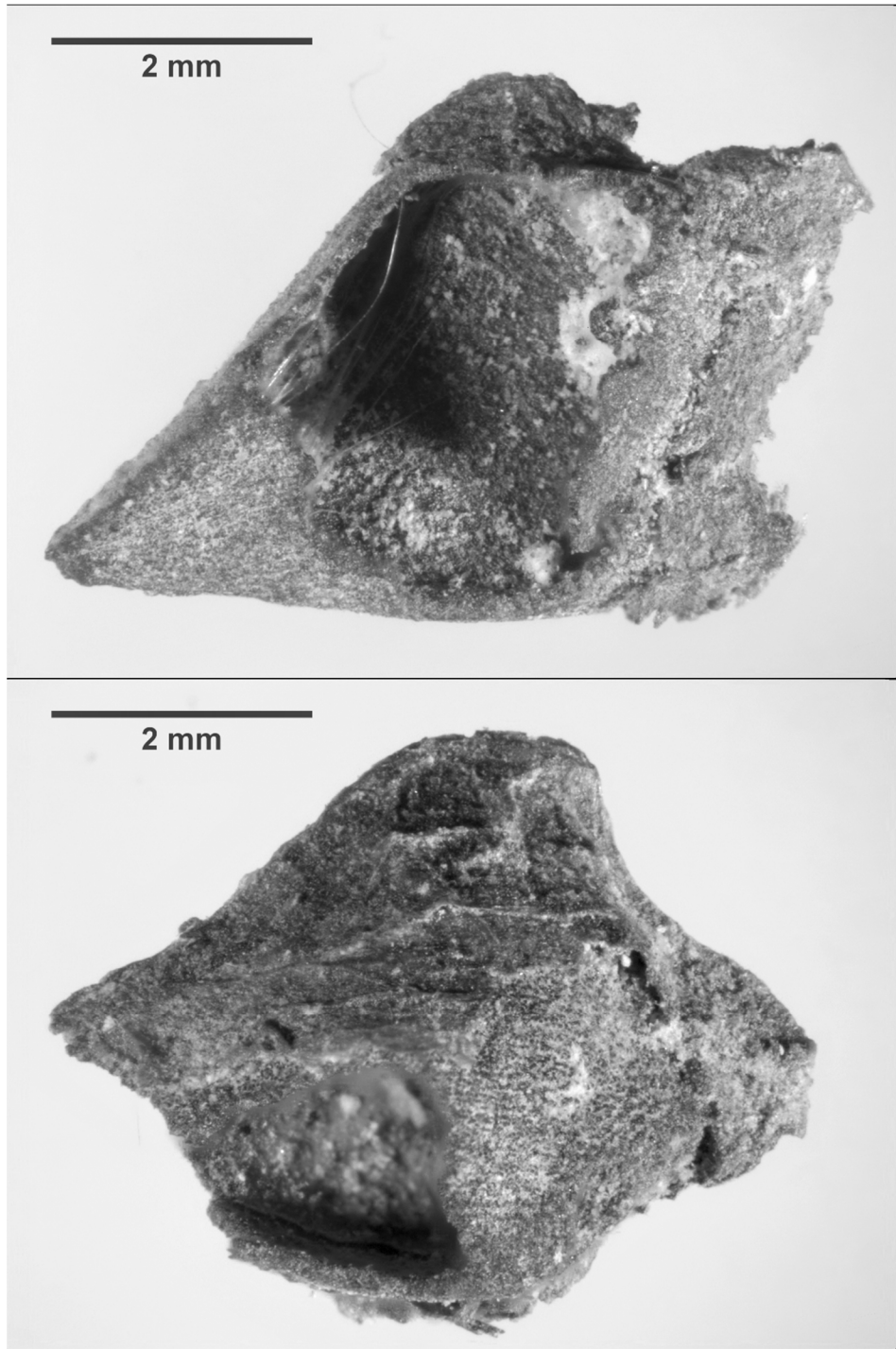


Figure 2.3: Whitney Bluff tubercled morphs, with striate-tubercled surface texture. Compare to tubercled morphs in Figure 1.

A total of 73 herbarium specimens of *P. achoreum*, *P. aviculare* subsp. *buxiforme*, *P. erectum*, and *P. ramosissimum* from the Missouri Botanical Garden and National Herbarium were examined (Appendix 1). The photosample used for morphometric analysis was taken from 51 of these (Table 2.1). These species were sampled because 1) they had fruit and perianth morphology similar enough to that of the Whitney Bluff assemblage to warrant comparison, 2) they were native to pre-Columbian North America and; 3) they occur in the region where ancient knotweed cultivation is documented. I considered *P. erectum* and *P. achoreum* as two different species (Mertens and Raven 1965; Löve and Löve 1982; Wolf and McNeill 1986; Costea et al. 2005; Yatskievych 2013). I did not consider specimens of *P. aviculare* other than *P. aviculare* subsp. *buxiforme*, although given the messy taxonomic history, many of these specimens may be native plants or hybridized with native plants. Only loose fruits were removed from the herbarium sheet packets on specimens collected since 1950, per the sampling regulations of the Missouri Botanical Garden and National Herbarium. These loose fruits comprise the photosample, whose morphology is described in detail below. Because taxonomy within *Polygonum* has varied greatly over the past century, whenever possible I only used samples that had been examined for the latest treatments in the *Flora of North America* and/or the *Flora of Missouri* (Costea et al. 2005; Yatskievych 2013). Where I had to use specimens that were not examined for these treatments, I double-checked the identification myself using keys from those treatments.

I took grayscale photographs of each fruit selected for the photosample in the same orientation with the widest of their three sides down (Figures 2.1 and 2.2) using a Zeiss SV11 microscope fitted with a manual stage, z-stepping motor, and an AxioCam MRC5 digital camera. I recorded the texture of each pericarp as “Smooth” or “Tuberled.” Using ImageJ open source

software, I measured several shape factors and area, length, and width. In order to take area and shape measurements, the object to be measured must be thresholded (differentiated from the background on the basis of color or shade). With solid objects such as 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 color to the background. The shape factors collected for each achene are aspect ratio, roundness, and circularity. Formulas for each are given in Table 2.2. Length and width are the two longest perpendicular straight line distances across the image of the achene. All morphometric measurements were taken using ImageJ.

Table 2.1: Herbarium Photosample Summary				
Species	# of plants sampled		# of achenes	
<i>P. erectum</i>	21		153	
<i>P. achoreum</i>	10		60	
<i>P. ramosissimum</i>	11		100	
<i>P. aviculare</i> subsp. <i>buxiforme</i>	10		92	
Total	52		405	
Collection season				
	# of achenes: Total (Tubercled / Smooth / Indeterminate)			
	<i>P. erectum</i>	<i>P. achoreum</i>	<i>P. ramosissimum</i>	<i>P. aviculare</i> subsp. <i>buxiforme</i>
June 1- August 31	16 (14/0/2)	23 (21/1/1)	34 (34/0/0)	30 (25/5/0)
September	70 (66/4/0)	24 (24/0/0)	14 (0/14/0)	34 (31/3/0)
October 1- November 24	67 (51/16/0)	13 (6/7/0)	52 (25/27/0)	28 (6/20/2)

Table 2.1: Achenes for the photosample were taken from the loose materials packets of the herbarium specimens listed in Appendix 1. If many fruits were in the packet, a sample of 20 was photographed. Otherwise, all loose fruits were photographed. The measurements and observations reported in Table 2.3 are drawn from this photosample.

Table 2.2: Morphometric Measurements		
Measurements	Description	Procedure/Formula
Area	# of pixels within the margins of object	Select image of achene, area measured in mm ²
Length	#of pixels along major axis of selected object	Draw line to measure length in mm
Width	Number of pixels along minor axis of selected object	Draw line to measure length in mm
Shape Factors		
Aspect Ratio	Degree of elongation; major axis divided by (mean of) minor axis (axes). Axes derived from an ellipse fitted around the selected object.	[Major axis]/[Minor axis]
Roundness	Roughly inverse of aspect ratio, a measure of elongation of the major axis with respect to the object's area. Axis derived from an ellipse fitted around the selected object.	$4 \times ([Area]/(\pi \times [Major \ axis]))$
Circularity	Relationship between perimeter and area; degree of departure from a circle. 1.0 is a perfect circle, 0.0 is a straight line.	$4\pi \times [Area]/[Perimeter]^2$

Table 2.2: Gives the formulas used to generate the morphometric measures reported in Table 2.3. All image analysis was completed using ImageJ open source image analysis software.

2.5 Results and Discussion

The Whitney Bluff assemblage is most obviously different from a normal harvest of erect knotweed achenes in that it is very nearly monomorphic: smooth morph achenes are overwhelmingly predominant. In the recent herbarium specimens examined for this study, the ratio of smooth to tubercled morphs varies from species to species, among individuals of the same species, and according to the season (Table 2.1). Seasonality is certainly a factor for all four species: smooth achenes are rare before the middle of the September. But even with only a small photosample of 5–20 seeds from each plant, there were only two instances of uniformly smooth morph photosamples from any one plant. This indicates that smooth morphs rarely predominate in *any* of the four species: even late in the season, tubercled morphs are present even in a small random sample of fruits. The two exceptions were both *P. ramosissimum* specimens, one collected on September 22 and the other on October 23. After analyzing the

photosamples from these plants (n=12 and n=14, respectively), I checked whether the plants in question had really produced *only* smooth morphs. All of the hundreds of observable achenes on both specimens were smooth morphs. Thus *P. ramosissimum* does occasionally produce monomorphic assemblages of smooth morph achenes. Further study of this species is necessary to determine what conditions produce this effect. However, the Whitney Bluff achenes are easily distinguished from those of *P. ramosissimum*. Smooth achenes of *P. ramosissimum* are almost completely exserted from their perianth. Indeed, plants with this fruit morphology were once thought to be a different species, *P. exsertum* Small, but are now considered a variant of *P. ramosissimum* (Mertens and Raven 1965:85). In contrast, Whitney Bluff smooth achenes are more enclosed in their perianths, similar to those of the other three species examined (Figure 2.2).

The Whitney Bluff assemblage resembles *P. erectum*, as opposed to any of the other three species, in having smooth morph achenes with convex rather than plane or concave faces. This criterion refers to the degree of fruit concavity as observed on the two subequal faces of the achene (see Figures 1 and 2). When these faces are markedly concave, the achene becomes flattened, with the central ridge sunken or sometimes slumped over to one side. Mertens and Raven (1965:85) 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* subsp. *buxiforme* and *P. achoreum* observed for this study, but not to those of *P. erectum*. *Polygonum erectum* smooth achenes, like the Whitney Bluff achenes, almost always have convex faces when mature, giving them a plump appearance in comparison to the other species (Figure 2.1; Table 2.3). *Polygonum erectum* is the only species that produces a majority of plump

smooth morphs, although a small minority of smooth *P. aviculare* subsp. *buxiforme* achenes were also relatively convex.

Table 2.3: Summary statistics for size and other characters by species compared to the Whitney Bluff assemblage					
Smooth morphs					
	<i>achoreum</i>	<i>buxiforme</i>	<i>erectum</i>	<i>ramosissimum</i>	Whitney Bluff
Area	3.38 +/- 0.257*	2.28 +/- 0.349*	3.22 +/- 0.780*	4.21 +/- 1.338*	5.66 +/- 0.683
Length	3.20 +/-0.222*	2.69+/-0.270*	3.23+/-0.329*	3.64+/-0.609*	4.16+/-0.243
Width	1.70+/-0.095*	1.35+/-0.163*	1.63+/-0.190*	1.78+/-0.366*	2.30+/-0.257
Circularity	0.54+/-0.137	0.52+/-0.154	0.44+/-0.126	0.49+/-0.091	0.46+/-0.073
Aspect Ratio	1.89+/-0.126*	2.00+/-0.434*	1.95+/-0.279*	2.03+/-0.283*	1.76+/-0.227
Roundness	0.53+/-0.034*	0.52+/-0.108*	0.52+/-0.072*	0.50+/-0.07*	0.58+/-0.069
Deflated/total	9/9	12/15	41/41	1/20	3/200
Tubercled morphs					
	<i>achoreum</i>	<i>buxiforme</i>	<i>erectum</i>	<i>ramosissimum</i>	Whitney Bluff
Area	3.34 +/-0.651	2.37 +/-0.354	3.49+/-0.528	2.99+/-0.761	4.15
Length	2.85+/-0.309	2.40+/-0.197	2.92+/-0.202	2.79+/-0.433	3.40
Width	1.88+/-0.222	1.55+/-0.171	1.88+/-0.208	1.63+/-0.181	2.23
Circularity	0.64+/-0.199	0.65+/-0.515	0.56+/-0.104	0.56+/-0.086	0.55
Aspect Ratio	1.47+/-0.125	1.52+/-0.156	1.51+/-0.147	1.65+/-0.192	1.51
Roundness	0.69+/-0.058	0.66+/-0.063	0.67+/-0.065	0.61+/-0.067	0.66
Striate-tubercled/total	10/51	14/62	131/131	7/59	1/1

Table 2.3: Summary of the morphometric analysis and non-metric characteristics of the photosample summarized in Table 2.1. Smooth morphs: * indicates a significant difference in the mean for that measure between a given species and the Whitney Bluff assemblage (the type specimen for domesticated *P. erectum* ssp. *watsoniae*), according to Welch’s unequal variance t-test. See Figures 1 and *Results* section for discussion of the non-metric character *Deflation*. Tubercled morphs: Mean values for each species are compared to the one measureable tubercled morph from Whitney Bluff, pictured in Figure 1. A sample of one is not adequate for statistical comparison, so none were made. See Figure 1 and *Results* for examples and descriptions of surface textures, including striate-tubercled.

The Whitney Bluff smooth morphs are significantly different from all four modern species in terms of size, whether measured by area, length, or width, as expected of a domesticated plant (Table 2.3). Although the differences are not significant, fruit circularity indicates that the Whitney Bluff assemblage, *P. erectum*, and *P. ramosissimum* form a similar

group in terms of shape, and that *P. aviculare* subsp. *buxiforme* and *P. achoreum* are different (Table 2.3).

Of the 1307 achenes with observable pericarps in the Whitney Bluff assemblage, two were tubercled morphs. Both exhibit the striate-tubercled surface texture and shape typical of *P. erectum* tubercled morphs (Figure 2.3, compare with Figure 2.1). All four species sometimes produce striate-tubercled achenes, but only *P. erectum* produces a majority of this type (Table 2.3). Only one is complete enough to be measured, and it is compared to the tubercled morphs from the herbarium samples in Table 2.3. Similar to the smooth morphs, the Whitney Bluff tubercled achene is also uncommonly large and groups by circularity with *P. erectum* and *P. ramosissimum*. The two tubercled achenes from Whitney Bluff are thus most parsimoniously identified as *P. erectum*.

This study suggests that the morphology of smooth morph (late season) achenes within *Polygonum* sect. *Polygonum*, which has long been considered taxonomically useless, does vary systematically. Both the size and shape of smooth morphs differ among the four species considered here (Table 2.3), suggesting that further studies of smooth achene morphology may be taxonomically fruitful. These results also suggest that paleoethnobotanists should be more cautious when using pericarp surface texture to identify assemblages to species. Tubercled morph surface texture cannot be used to positively determine the species when only a few achenes are preserved (as often occurs with archaeological assemblages) because all four of the species examined here occasionally produce striate-tubercled achenes. As with smooth morphs, both area and circularity are useful for distinguishing between species. Mean area can be used to reliably distinguish *P. ramosissimum* and *P. aviculare* subsp. *buxiforme* from the other species, but *P. erectum* and *P. achoreum* have similarly sized tubercled achenes (Table 2.3). In terms of

circularity, for both tubercled and smooth morphs, *P. ramosissimum* and *P. erectum* form one group, *P. aviculare* subsp. *buxiforme* and *P. achoreum* form another (Table 2.3). Using a combination of metric and non-metric criteria, small assemblages of tubercled morphs or even single achenes can be more confidently assigned to species. For example, the Whitney Bluff tubercled achene groups with *P. erectum* and *P. ramosissimum* in terms of circularity and its surface texture indicates that it is more likely to belong to the former. Since it is much larger than normal for any of the species, area is not helpful in this case.

The Whitney Bluff achenes are identified as a subspecies of *P. erectum*, rather than one of the other possible species, on the weight of several lines of evidence. Circumstantial evidence strongly supports the hypothesis that the Whitney Bluff achenes came from erect knotweed plants: *P. erectum* was cultivated for c. 1500 years, it is documented in clear storage, cooking, and consumption contexts at hundreds of sites, and there is no evidence that any other species of knotweed was ever cultivated. But strong evidence is required to argue for an extinct domesticate, and other possible explanations must be ruled out. Of the four species of *Polygonum* native to the study area, only *P. ramosissimum* occasionally produces monomorphic harvests of smooth achenes. But the Whitney Bluff achenes are distinguishable from *P. ramosissimum* smooth morphs on the basis of two clear characters: they are not nearly as exerted from their perianths and they do not have concave faces. The latter character also differentiates the Whitney Bluff achenes from those of *P. achoreum* and *P. aviculare* subsp. *buxiforme*, which in any case are shaped quite differently, being much more circular in plan-view (Table 2.3). The two tubercled morphs from Whitney Bluff, with their striate-tubercled surface texture, also support the designation of the Whitney Bluff assemblage as a subspecies of *P. erectum*.

This conclusion could be further strengthened by extracting DNA from the Whitney Bluff achenes and comparing it to that of modern species. Ancient DNA could also help answer questions about how the process of domestication unfolded. It is probable that aDNA is preserved in the Whitney Bluff *Polygonum* achenes: two previous projects have successfully extracted DNA from *Chenopodium berlandieri* seeds (Kistler and Shapiro 2011) and *Cucurbita* seeds (Kistler et. al. 2015) from nearby rockshelters that are the same age or older than the *Polygonum* cache at Whitney Bluff. Although permission has been granted to attempt aDNA extraction from the Whitney Bluff *Polygonum*, this project is hampered by the fact that information about genetic variation within *Polygonum* is very low-resolution. An initial attempt to use plastid genome variation to characterize the four species analyzed here was a failure: plastid genome variability was found to be too low (Logan Kistler, personal communication). Assembly of a nuclear genome for *P. erectum* is the next step in this project, and is currently underway.

Although the archaeological specimens described here are most similar to *P. erectum*, they differ from modern *P. erectum* in three ways. Average size for the Whitney Bluff achenes is greater than that of any of the four modern species, whether measured by area (as determined from photographs), length, or width (Table 2.3). They are also distinguished by a great reduction in achene dimorphism. Of the 32 *P. erectum* herbarium specimens and hundreds of wild-growing plants I observed during the course of this study, none produced a monomorphic harvest. Even in late October and early November, *P. erectum* plants still usually produce a majority of tubercled morph fruits. Preliminary data indicates that a typical late October/early November harvest of a population of *P. erectum* plants will yield a proportion of smooth morphs between 30-70% (Chapter 4). Both the Whitney Bluff assemblage and the Hill Creek assemblage are thus far

outside the normal range of variation. Because the plant represented in these assemblages produces fewer tubercled morphs, which have thicker pericarps, than *P. erectum* subsp. *erectum*, average pericarp thickness would be greatly reduced for any given harvest from the former. Both the increase in fruit size and the reduction of germination inhibitors are classic indicators of domestication syndrome in annual seed crops. Considering the extensive contextual evidence for cultivation from archaeological sites, this material should be considered an extinct domesticate. It is therefore recognized herein as a new subspecies of *P. erectum*. The probable selective pressures that caused the evolution of the domesticated subspecies documented in this study have been explored experimentally and archaeologically (Chapters 3-6).

2.6 Taxonomic Treatment

Polygonum erectum L. subsp. *watsoniae* N.G. Muell., subsp. nov. TYPE: U.S.A. Arkansas:

Benton County, Whitney Bluff rockshelter (3BE20). 1932. *W. Henbest and C. Finger Jr. 32-57-5c* (holotype, UARK No. 20121!; isotype, Arkansas Museum)

2.6.1. Diagnosis. *Polygonum erectum* subsp. *watsoniae* most closely resembles *Polygonum erectum* subsp. *erectum*, but can be distinguished from it by greatly reduced achene dimorphism: almost all achenes have smooth pericarps, 30–70 μ thick, with very few exceptions having striate-tubercled pericarps 120–150 μ thick; smooth achenes are larger than those of *Polygonum erectum* subsp. *erectum*, averaging 4.2 mm \times 2.3 mm, and are shaped differently, having a lower aspect ratio (mean 1.76); they also differ from smooth achenes of *Polygonum ramosissimum* Michx. in having a plump appearance caused by convex sub-equal faces, unwrinkled pericarps, and retained perianths that cover >50% of the length of the achene.

2.6.2 Discussion. Assemblages of *Polygonum erectum* subsp. *watsoniae* have been found in excavations of Native American sites in Arkansas and Illinois dating to c. AD 1000–1400, along

with the seeds and fruits of other plants cultivated by the ancestors of Native Americans. This domesticated subspecies is now believed to be extinct. Its name commemorates archaeologist Patty Jo Watson, whose pioneering research was instrumental to the recognition of the Eastern Agricultural Complex.

The holotype preserved at UARK is a subsample taken from one of the two large samples of Whitney Bluff achenes that are preserved at the Arkansas Museum; the remainder of that sample constitutes an isotype.

Paratype. U.S.A. **Arkansas:** Benton County, Whitney Bluff rockshelter (3BE20). 1932. *Wayne Henbest and Charles Finger Jr. 32-57-3a* (Arkansas Museum).

2.7 References

- Adams, K. R. 2014. Little barley grass (*Hordeum pusillum* Nutt.): A Prehispanic New World domesticate lost to history. Pp. 139--179 in Minnis, P.E., ed, *New Lives for Ancient and Extinct Crops*. The University of Arizona Press, Tucson, AZ.
- Asch, D. L. & N. B. Asch. 1985a. Archaeobotany. Pp. 115--170 in Conner, M. D. (ed), *The Hill Creek Homestead and the Late Mississippian Settlement in the Lower Illinois River Valley*. The Center for American Archaeology, Kampsville, IL.
- Asch, D. L. & N. B. Asch. 1985b. Prehistoric plant cultivation in West Central Illinois. Pp. 149--203 in: Ford, R.I., ed, *Prehistoric Food Production in North America*. Museum of Anthropology, University of Michigan, Ann Arbor, MI.
- Blake, S. F. 1939. A new variety of *Iva ciliata* from Indian rock shelters in the south-central United States. *Rhodora* 41: 81--86.

- Burke, J. M. & A. Sanchez. 2011. Revised sub-family classification for Polygonaceae, with tribal classification for Eriogonoideae. *Brittonia* 63: 510--520.
- Costea, M. & F. J. Tardif. 2004. The biology of Canadian weeds: *Polygonum aviculare* L. *Canad. J. Pl. Sci.* 131: 481--506.
- Costea, M., F. J. Tardif & H. H. Hinds. 2005. *Polygonum* L. Pp. 547--571 in: Flora of North America Editorial Committee, ed, Flora of North America North of Mexico, vol. 5. Oxford University Press, New York.
- Cuénoud, P., V. Savolainen, L. W. Chatrou, M. Powell, R. J. Grayer & M. W. Chase. 2002. Molecular phylogenetics of Caryophyllales based on nuclear 18S rDNA and plastid *rbcl*, *atpB*, and *matK* DNA sequences. *Amer. J. Bot.* 89: 132--144.
- Faulkner, C. T. 1991. Prehistoric diet and parasitic infection in Tennessee: Evidence from the analysis of desiccated human paleofeces. *Amer. Antiquity* 56: 687--700.
- Freeman, C. C. 2005. *Polygonella* Michaux. Pp. 534--540 in: Committee, Flora of North America Editorial Committee ed, Flora of North America North of Mexico, vol. 5. Oxford University Press, New York.
- Fritz, G. J. 1986. Prehistoric Ozark Agriculture: The University of Arkansas Rockshelter Collections. Doctoral Dissertation. University of North Carolina, Chapel Hill, NC.
- Gilmore, M. R. 1931. Vegetal remains of the Ozark Bluff-Dweller Culture. *Pap. Mich. Acad. Sci., Arts Lett.* 14: 83--102.
- Gremillion, K. J. 2004. Seed processing and the origins of food production in Eastern North America. *Amer. Antiquity* 69: 215--233.
- Harlan, J. R., J. M. J. De Wet & E. G. Price. 1973. Comparative evolution of cereals. *Evolution* 27: 311--325.

- Hong, S.-P., I. C. Oh & L. P. Ronse De Craene. 2005. Pollen morphology of the genera *Polygonum* s. str. and *Polygonella* (Polygoneae: Polygonaceae). *Pl. Syst. Evol.* 254: 13--30.
- Hunter, A. A. 1992. Utilization of *Hordeum pusillum* (Little Barley) in the Midwest United States: Applying Rindos' Co-Evolutionary Model of Domestication. Doctoral Dissertation. University of Missouri, Columbia, MO.
- Kistler, L., L.A. Newsom, T.M. Ryan, A.C. Clarke, B.D. Smith, & G.H. Perry. 2015. Gourds and squashes (*Cucurbita* spp.) adapted to megafaunal extinction and ecological anachronism through domestication. *Proc. Natl. Acad. Sci. U.S.A.* 112:15107-15112
- Kistler, L., & B. Shapiro. 2011. Ancient DNA confirms a local origin of domesticated chenopod in eastern North America. *J. Archaeol. Sci.* 28: 3549-3554
- Löve, Á and D. Löve. 1982. Chromosome Number Report LXXIV. *Taxon* 31: 119--128.
- Martin, A. C. 1954. Identifying *Polygonum* seeds. *J. Wildl. Manage.* 18: 514--520.
- Mertens, T. R. & P. H. Raven. 1965. Taxonomy of *Polygonum*, section *Polygonum* (Avicularia) in North America. *Madrono*: 85--92.
- Powell, G. 2000. Charred, non-maize seed concentrations in the American Bottom area: Examples from the Westpark Site (11-MO-96), Monroe County, Illinois. *Midcontinental Journal of Archaeology* 25: 27--48.
- Ronse De Craene, L.P., S.-P. Hong & E. Smets. 2000. Systematic significance of fruit morphology and anatomy in tribes Persicarieae and Polygoneae (Polygonaceae). *Bot. J. Linn. Soc.* 134: 301--371.
- Ronse De Craene, L.P., S.-P. Hong & D.F. Smets. 2004. What is the taxonomic status of *Polygonella*? Evidence of floral morphology. *Ann. Missouri Bot. Gard.* 91: 320--345.

- Sanchez, A. & K. A. Kron. 2008. Taxonomy of Polygonoideae (Polygonaceae): A new tribal classification. *Taxon* 60: 151--160.
- Sanchez, A., T. M. Schuster & K. A. Kron. 2009. A large scale phylogeny of Polygonaceae based on molecular data. *Int. J. Pl. Sci.* 170: 1044--1055.
- Sanchez, A., T. M. Schuster, J.M. Burke, & K.A. Kron. 2011. Taxonomy of Polygonoideae (Polygonaceae): A New Tribal Classification. *Taxon* 60: 151-160
- Schuster, T. M., J. L. Reveal & K. A. Kron. 2011. Phylogeny of Polygoneae (Polygonaceae:Polygonoideae). *Taxon* 60: 1653--1666.
- Simon, M. L. & K. E. Parker. 2006. Prehistoric plant use in the American Bottom: New thoughts and interpretations. *Southeast. Archaeol.* 25: 212--257.
- Smith, B. D. & V. A. Funk. 1985. A newly described subfossil cultivar of *Chenopodium* (Chenopodiaceae). *Phytologia* 57: 445--448.
- Smith, B. D. & R. A. Yarnell. 2009. Initial formation of an indigenous crop complex in eastern North America at 3800 B.P. *Proc. Natl. Acad. Sci. U.S.A.* 106: 6561--6566.
- Wolf, S. J. & J. McNeill. 1986. Synopsis and achene morphology of *Polygonum* section *Polygonum* (Polygonaceae) in Canada. *Rhodora* 88: 457--479.
- Yatskievych, G. 2013. Steyermark's Flora of Missouri, Revised, vol. 3. Missouri Botanical Garden Press, St. Louis, MO.
- Yurtseva, O. V. 2001. Ultrasculpture of the achene surface in *Polygonum* section *Polygonum* (Polygonaceae) in Russia. *Nordic J. Bot.* 21: 513—528.

3. Documenting Domestication in a Lost Crop (*Polygonum erectum* L.): Evolutionary Bet-Hedgers under Cultivation⁴

3.1 Abstract

This study uses morphometrics and digital image analysis to document domestication syndrome in an annual seed crop, erect knotweed (*Polygonum erectum* L.), which was cultivated by Native Americans for c. 2500 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 centered on the Central Mississippi Valley for millennia. The extinct domesticated subspecies of erect knotweed described here (*Polygonum erectum* subsp. *watsoniae* N.G.Muell.), exhibits some classic markers of domestication, including larger fruits and reduced germination inhibitors in comparison to its wild progenitor. Domesticated erect knotweed also exhibits greatly reduced germination heteromorphism. Germination heteromorphism is the classic example of evolutionary bet-hedging in plants: wild erect knotweed 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 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 maintain this strategy were relaxed as humans saved seeds and created predictable microenvironments for seedlings, resulting in homogenous harvests and reliable germination for ancient farmers.

⁴ 2017, *Vegetation History and Archaeobotany* 26(3):313-327.

3.2 Introduction

Human mediated selection alters the bodies and behaviors 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 behavior 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 (e.g., Asouti and Fuller 2012; Asouti and Fuller 2013; D’Andrea 2008; Flannery 1973; Harlan and deWet 1965; Rindos 1984; Smith 1992) and in some cases explored experimentally (Abbo et al. 2011; Hillman and Davies 1990; Piperno et. al. 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, erect knotweed (*Polygonum erectum* L.).

Beginning c. 1900 BCE, Native peoples in Eastern North America (ENA) began to cultivate native annual seed crops. These pre-maize crops are collectively known as the Eastern Agricultural Complex (EAC) (Ford, ed. 1985; Fritz 1993; Smith 1992; Smith 2006; Smith and

Yarnell 2009; Yarnell 1993). Two cereal crops were cultivated, maygrass (*Phalaris caroliniana* Walter) and little barley (*Hordeum pusillum* Nutt.) (Fritz 2014; Hunter 1992). No clear morphological differences have been noted between archaeological assemblages and modern plants in ENA for these crops⁵, but contextual evidence amply demonstrates that they were cultivated for centuries (Asch and Asch 1985b). Three EAC annual seed crops exhibit domestication syndromes: sunflower (*Helianthus annuus* L. var. *macrocarpus* Cockerell), goosefoot (*Chenopodium berlandieri* Moq. subsp. *jonesianum* Smith and Funk), and sumpweed (*Iva annua* L var. *macrocarpa* S.F. Blake) (Blake 1939; Heiser 1954; Smith and Funk 1985; Smith 2014). The domestication status of the final important crop of the EAC, erect knotweed, has remained uncertain for decades. Asch and Asch (1985a; 1985b) first speculated that erect knotweed 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 (1986) reported a similar, but desiccated, assemblage dating to approximately the same time period (Fritz 1986:74) from the Whitney Bluff site, a rockshelter in northwestern Arkansas.

3.3 Recognizing domestication syndrome in knotweed

Many species of knotweed (*Polygonum* L. subsect. *Polygonum*) produce trigonal achenes, which are one-seeded fruits consisting of seeds encased in a tough fruit coat, or pericarp (Figure 2.2.1). Some knotweeds exhibit seasonally controlled achene dimorphism; they produce

⁵ The domestication of little barley 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. Little barley 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 predominate in Old World domesticated barley (*Hordeum vulgare* L.).

two distinct fruit types in ratios that vary over the course of the growing season (Costea et al. 2005; Chapter 2). Tubercled morphs have lower aspect ratios (i.e., their major and minor axes are closer to equal) and thicker pericarps with distinctive surface textures that are often diagnostic of particular species (Costea et al. 2005; Figure 2.2.1). 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 ratio (i.e., a longer major axis compared to minor axis) and thinner pericarps that lack diagnostic surface textures (Figure 2.2.1). 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 (Brenckle 1946). The two different types are sometimes referred to as *late season morphs* and *early season morphs*, but I will use *smooth morphs* and *tubercled morphs* here: the former terms are misleading since both morphs are produced late in the season, as detailed below.

Beginning in the 1980s, paleoethnobotanists recognized that one species of knotweed had been cultivated by ancient Native Americans in what Fritz (1993:41) 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 erect knotweed based on the striate-tubercled surface texture and shape of archaeological tubercled morphs (Asch and Asch 1985b; Figure 2.2.1). 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 (e.g., Asch and Asch 1985b; Powell 2000:40; Simon and Park 2006:239). 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, exerted, 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 erect knotweed plants.

Speculation about a domesticated subspecies of erect knotweed began when two curious assemblages were reported in the mid-1980s. First, Asch and Asch (1985a; 1985b) reported a carbonized assemblage from the Late Mississippian Hill Creek site, IL that was composed exclusively of smooth morphs. These achenes were also larger than the erect knotweed smooth morphs in their reference collections. To ascertain whether or not erect knotweed 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 erect knotweed 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. Asch and Asch (1985b:144-5) 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*...” In particular, Asch and Asch (1985b:146) suggested that if the Hill Creek assemblage was not erect knotweed, it might instead belong to a closely related species, *Polygonum ramosissimum* Michaux, which is known to produce many smooth achenes under certain (unspecified) conditions (Mertens and Raven 1965). Two years later, Fritz (1986) reported a similar nearly

monomorphic assemblage of large smooth morphs from the Mississippian Whitney Bluff sites, AR. These had become desiccated after being stored or otherwise deposited in a dry rockshelter and were remarkably well-preserved. But without a clearer sense of variability in seasonal achene production among modern populations, erect knotweed domestication remained an open question.

3.4 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 knotweed (taxonomy reviewed in Chapter 2) 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 (Chapter 4). 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 cuticle, they also have layers of wax that prevent or slow the penetration of fungi and pathogens, guard against both waterlogging and desiccation, allowing the seed to remain healthy and viable in the soil over several years (Yurtseva 2001:524-5). Experiments have shown that the pericarp also mechanically restricts the embryo, thus controlling the timing of germination, in two closely related species (Courtney 1968; Metzger 1992). Other studies have shown that achenes with thicker pericarps germinate more slowly (Chapter 4; 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 was high, long-term population growth was optimized when plants produced 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 1966:128). I hypothesize that human mediated selection acted on erect knotweed fruit heteromorphism – specifically, that humans created less risky environments for populations of erect knotweed. 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 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.

3.5 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 and colleagues (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 favors the offspring of plants that produce large seeds, because large seeds produce seedlings that grow faster (e.g., Boyd et al 1971; Clements and Latter 1973; 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. 1973:318).

There may also have been more general agroecological 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 1975). Under cultivation, the plant's imperative to produce many seed 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. Agroecosystems in general are less risky and richer environments, where the production of larger seeds is both possible and evolutionarily advantageous.

3.6 Materials and Methods

3.6.1. 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 erect knotweed 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 1986:6). The crop plant remains from 19 rockshelters, including Whitney Bluff, were analyzed 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 1986:20).

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 1986:107; 1986:92).

Domesticated *Chenopodium berlandieri* subsp. *jonesianum* was also recovered from this context (Fritz 1986: 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 1986:107-8). They are treated as a single sample in this analysis. A fragment of the gourd from this context was dated by Fritz to uncal 785 +/-75 BP (1986:74), or cal A.D. 1040-1386. A recent direct date from one of the knotweed achenes returned a date of uncal 885 +/- 20 BP, or cal A.D. 1046-1217 (NOSAMS #134366).⁶

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. Per sampling protocol for the larger study, where > 100 intact achenes were present, the size of the photosample was determined by the weight of entire assemblage: 1 photograph per 0.01g. I chose to sub-sample by weight rather than count in order not to bias the sample against poorly preserved carbonized assemblages where fewer measureable achenes were present as a percentage of the total identifiable knotweed⁷. 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 retain some or all of their perianth parts, as discussed below. The presence of the perianth or parts of the perianth may

⁶ Calibrated using IntCal 13 (Reimer et al. 2013)

⁷ 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.

somewhat inflate area and width measurements and slightly distort shape descriptors, but perianths are generally tightly conforming to the shape of the underlying fruit (Figure 2.2). Of the 1307 achenes I examined, all but two were smooth morphs. The two tubercled morphs are described below and the more complete of the two is pictured in Figure 2.2.1. Measurements of length and width reported here are very similar to those reported by Fritz on two different subsamples of 100 achenes (Fritz 1986:108).

3.6.2 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 (Figure 2.1). These will be referred to as the herbarium photosample. Four species of knotweed (*Polygonum* subsect. *Polygonum*) that could have been cultivated by pre-Contact Native Americans (i.e., are native to the Midwest) were sampled: erect knotweed (*Polygonum erectum* L.), native prostrate knotweed (*Polygonum aviculare* L. subsp. *buxiforme* (Small) Costea & Tardif), Blake's knotweed (*Polygonum achoreum* S. F. Blake), and bushy knotweed (*Polygonum ramosissimum* Michaux). The relevant taxonomic background that informed the sampling strategy, along with a list of all herbarium specimens examined for this study are reported elsewhere (Chapter 2). Only loose fruits were removed from the herbarium sheet packets on specimens collected since 1950, 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 favoring the production of smooth morphs (Brenckle 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 that 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 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, my 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 knotweed, the perianth adheres to the fruit even after it is mature, forming a papery shell. I removed the perianth using a razor under a dissecting microscope. I also examined samples from each species with their perianth intact for comparison with Whitney Bluff achenes, many of which retain their some or all of their perianth (Figure 2.2). I left each fruit's receptacle (the thickened part of the stem that attaches to the fruit) intact for comparison with the Whitney Bluff achenes, which universally retain their receptacles. I took grayscale photographs of each fruit in the same orientation with the widest of their three sides down (see Figures 1 and 2). While photographing, I recorded the texture of each fruit's pericarp as "Smooth" or "Tubercled." I then measured several shape factors and area, length, and width using ImageJ (Figure 2.2). In

order to take measurements, the object to be measured must be thresholded (differentiated from the background on the basis of color 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 color to the background.

3.6.3 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 (e.g., Zach and Klee 2003; Smith 2014; Yarnell 1978). These are taken using micrometers in the eye piece 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 is a technique which uses two-dimensional digital images to quantitatively assess size and shape (reviewed in Rovner and Gyulai 2006; Figure 2.2). 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.

1. Size

Seed *volume* is the property that we would ideally measure in domestication studies. Whether people intentionally select larger seeds to increase food production or unintentionally select larger seeds by culling slow-growing seedlings or deep planting, an increase in seed volume is the result. But volume is not easily measured for objects as small as seeds. Instead, it is customary to report length and width, and sometimes to calculate length X width as a size index (Yarnell 1978). Length and width are easy and quick to measure, but fail to capture all size increases due to changes in shape. By becoming more circular, an object can have a greater area (as viewed from above) and volume without the maximum perpendicular distances from edge to edge changing at all. Some researchers have used morphometric methods to capture area and perimeter instead of using length and width (Dahlberg and Wasylkova 1996) – the approach adopted in this study. Length and width are also reported to facilitate comparison with other studies.

Changes in volume have also sometimes been used to characterize domesticates using non-metric criteria. Quinoa (*Chenopodium quinoa* Willd.) and EAC domesticated *Chenopodium berlandieri* subsp. *jonesianum* are examples. Seed margin configuration is scored based on an assessment of shape (Fritz and Smith 1988; Langlie et al. 2011). Seed margin affects the thickness of the seed, and thus its volume. For some Old World grains thickness is a standard measurement alongside length and width (e.g., Zach and Klee 2003). Where thickness is used to

quantify change in volume, the same problem arises as with length and width – namely, this metric only captures changes in size along a single axis.

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. I decided that this measurement obscured more than it illuminated, and 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.

2. Shape

Formulae used to assess shape by ImageJ are listed in Figure 2.2. 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.

3. Non-metric characters

Tubercled morph pericarp texture. Tubercled morph pericarp texture is a key diagnostic character for identifying species of knotweed (Costea et al. 2005). The distinctive striate-tubercled texture of archaeological fruits was the key criterion originally used to identify them as erect knotweed. While this surface texture has been considered diagnostic of *P. erectum*, other species also sometimes produce achenes with this surface texture (Figure 2.3; Chapter 2).

Smooth morphs. Useful non-metric characters for differentiating between species using smooth morphs are *perianth morphology* and *deflation*, described below (see also Figures 2.1 and 2.2).

4. 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.

3.7 Results

1. Seasonal variability

Figure 2.1 reports 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 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 analyzing 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 erect knotweed. Asch and Asch wrote: “If the knotweed species at the Hill Creek site is not *P. erectum*...then it is probably *P. ramosissimum*” (1985b: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 bearing mostly smooth morphs were long mistaken for a different species (Mertens and Raven 1965:85-6). The possibility that the Whitney Bluff assemblage is *P. ramosissimum* is explored below.

2. Smooth Morph Size

The Whitney Bluff achenes are larger than the smooth morphs of any existing species, by any measure (Figure 2.3; Figure 3.1). 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 Chapter 2).

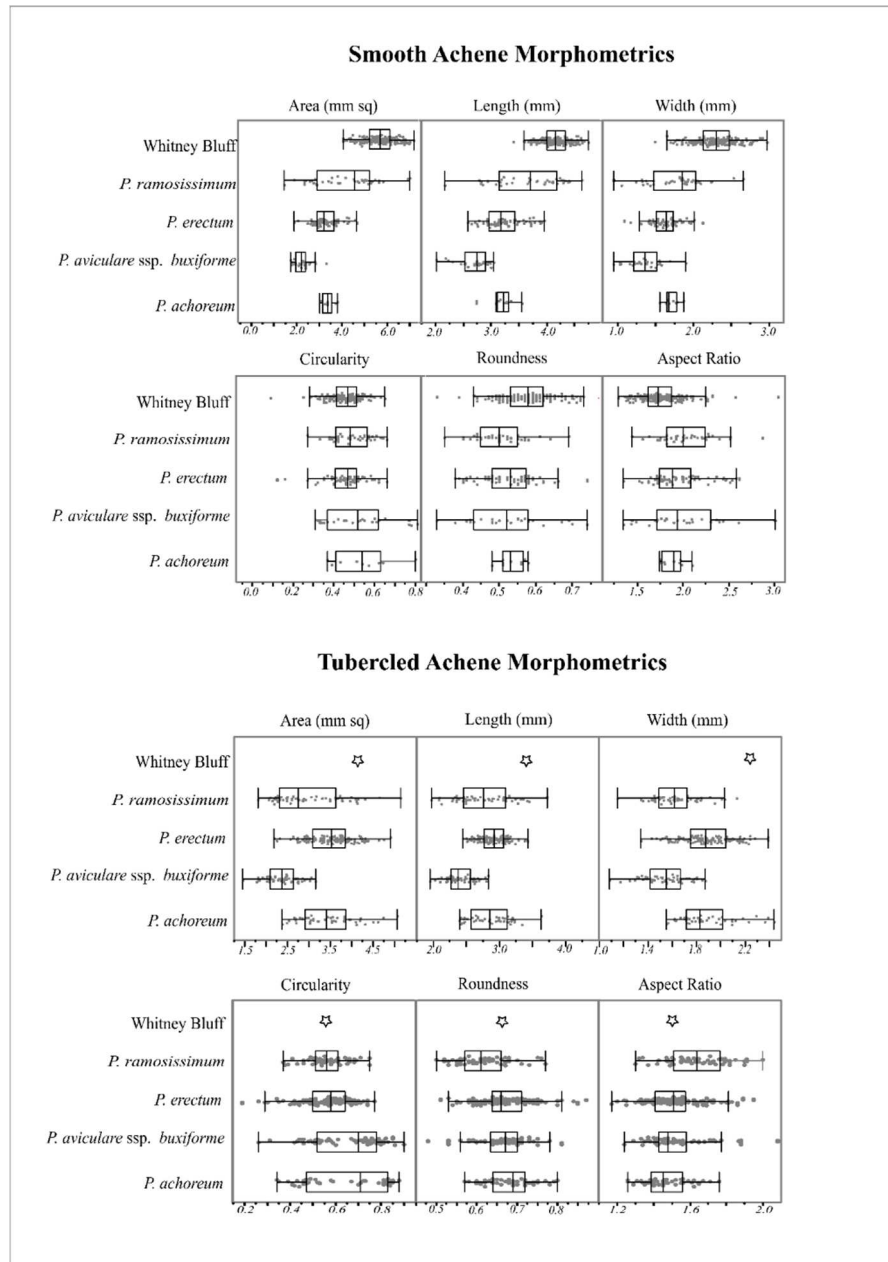


Figure 3.1: Box plots visualizing the range of values for morphometric measurements of each population. Vertical line is the median value, boxes represent 1st- 3rd quartiles. Whiskers extend from the end of the box to the outermost data point that falls within [3rd or 1st quartile + 1.5 * interquartile 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.

3. 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* subsp. *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 (Figure 2.3; Figure 3.1). All four species were significantly different from the Whitney Bluff achenes in terms of Aspect Ratio and Roundness ($p > 0.01$; Figure 2.3). 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 (Figure 3.1).

4. Non-metric characters of smooth morphs

Perianth morphology. The preserved perianths of the Whitney Bluff specimens leave little doubt that it is not *P. ramosissimum* (Figure 2.2). Smooth morphs of *P. ramosissimum* are extremely exserted from their perianths (plants with this fruit morphology were once designated *Polygonum 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 Figure 2.2. While this criteria will not be useful in analyzing 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 (Figure 2.2.1). When these faces are markedly concave, the achene becomes flattened, with the central ridge sometimes slumped over to one side (Figure 2.2.1). Mertens and Raven (1965:85) 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* subsp. *buxiforme* and *P. achoreum* observed in this study, but not to those of *P. erectum*. *P. erectum* smooth morphs, like those of the Whitney Bluff achenes, almost always have convex faces, giving them a plump appearance in comparison to the other species (Figure 2.2.1). This characteristic was also noted by Fritz (1986:109), who described the Whitney Bluff achenes as “faintly trigonous, but rounded except at the distal tip where three angles are manifested.”

5. Tubercled morphs

Of the 1307 achenes with observable pericarps in this assemblage, only *two* were tubercled morphs. These both exhibit the striate-tubercled morphology typical of *P. erectum* (Figure 2.2.1). 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 Figure 3.1. 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 (Figure 3.1). 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 can't 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,” *i.e.*, the tubercles are arranged in rows (see Figure 2.2.1 for examples of surface textures). The specimens I 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 discernable, 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* subsp. *buxiforme*'s achenes are described as “coarsely striate-tubercled to obscurely tubercled” – about a quarter of those in my photosample are striate-tubercled, but these have coarse tubercles, which differ from those on the other three species (Costea et al. 2005; Figure 2.2.1). In other words, all four species produce striate-tubercled achenes, but at different frequencies (Figure 2.3).

As with smooth morphs, size is useful for distinguishing between species. Mean area can be used to reliably distinguish *P. ramosissimum* and *P. aviculare* subsp. *buxiforme* from the

other species, but *P. erectum* and *P. achoreum* have similarly sized tubercled achenes (Figure 2.3; Figure 3.1). Circularity seems to sort the species into two groups: *P. ramosissimum* and *P. erectum* form one group, *P. aviculare* subsp. *buxiforme* and *P. achoreum* form another, both in terms of mean values and distribution of values (normal vs. bimodal; Figure 2.3; Figure 3.1). 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, i.e., it highly is unlikely that a random sample of achenes from any of the other species would *all* be striate-tubercled.

6. 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 (Figure 2.3; Figure 3.1; and see Chapter 2 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 knotweed 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 of one of these taxa.

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*: *P. erectum* begins to appear at archaeological sites c. 1500 years before the Ozark Bluff Dwellers left part of their harvest in the Whitney Bluff rockshelter, 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 erect knotweed achenes are routinely recovered from storage pits in several different sub-regions (Fritz 1986; Powell 2000; Simon and Parker 2006; Smith and Wetterstrom 1978). 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 Table 3.1. 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, 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 exserted 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.

Table 3.1: Summary of evidence for designation of Whitney Bluff assemblage as a subspecies of <i>P. erectum</i>				
Whitney Bluff	<i>P. erectum</i>	<i>P. ramosissimum</i>	<i>P. aviculare</i> ssp. <i>buxiforme</i>	<i>P. achoreum</i>
Seasonality	-1	0	-1	-1
Smooth morph				
Area	-1	-1	-1	-1
Circularity	0	0	0	0
Roundness	-1	-1	-1	-1
Aspect ratio	-1	-1	-1	-1
Perianth morphology	0	-1	0	0
Fruit deflation	0	-1	-1	-1
Total	-3	-4	-4	-4

Table 3.1: Summary of evidence demonstrating that a) the Whitney Bluff assemblage is significantly different from any existing species; and b) despite these differences, it is most parsimoniously designated as a subspecies of *P. erectum*, rather than some other species. 0 denotes a non-significant difference. -1 denotes a statistically significant difference, except in the cases of perianth morphology and fruit deflation, which are non-metric characteristics that consistently segregate by species. Additional circumstantial evidence that the Whitney Bluff assemblage is a subspecies of erect knotweed: 1) the two tubercled achenes recovered from Whitney Bluff are striate-tubercled, a surface texture most common in *P. erectum*; 2) *P. erectum* has been recovered from hundreds of archaeological sites – there is no evidence that any other species was cultivated.

Although the archaeological specimens from Whitney Bluff, designated *Polygonum erectum* subsp. *watsoniae* (Chapter 2), are most similar to *P. erectum*, they differ from modern *P. erectum* in three ways. Average size for *Polygonum erectum* subsp. *watsoniae* achenes is greater, whether measured by area, length, or width (Figure 2.3; Figure 3.1). A great reduction of achene dimorphism is also diagnostic of *Polygonum erectum* subsp. *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 I have 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 *Polygonum erectum* subsp. *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 (Chapter 2). Both the increase in fruit size and the reduction of germination inhibitors exhibited by *Polygonum erectum* subsp. *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 erect knotweed. To understand why, it is necessary to briefly explore how fruit dimorphism evolves and is maintained outside of cultivation.

3.8 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 who survived to reproduce. This means that the average fitness of a population over many generations is sensitive to even sporadic 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. 2010:2).

An anecdote from my own observations serves as an apt illustration of the mathematical models behind bet-hedging theory. During the growing season of 2014, I regularly visited three populations of *P. erectum* in the vicinity of St. Louis, Missouri, 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 I visited the populations 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 are produced. In the spring of 2016, I returned to find a robust population of erect knotweed at one the study sites where all plants had been wiped out the year before.⁸ This 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

⁸ The fate of one of the other study populations was apparently sealed when 0.5 meters of sediment was dumped on top of the seed bank by landowners repairing a dirt road after the 2015 floods. I have not observed any erect knotweeds at this location in 2016, and have not had the opportunity to revisit the third population this year.

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 (1984:9) summarized: “Dormancy [is a means of] avoiding unfavorable periods *by escape in time*... Dispersal is a means of avoiding unfavorable 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 centimeters 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 2011:1). 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 (less 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 erect knotweed (it was formerly called *Polygonum persicaria* L.; Chapter 2). 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. Plants grown under low-light produced achenes that were the same weight as those produced by plants in full sun, but with pericarps reduced by >40% (Sultan 1996:1795). 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 maternal response to low-light. Preliminary data from my own greenhouse experiments indicates that erect knotweed grown under artificial light (12 hours/day) only produces tubercled achenes (Chapter 4). 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 can't 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; Sultan 2001; Sultan 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; Chapter 2). 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 erect knotweed 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 erect knotweed 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.

3.9 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, AR. 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 (Chapter 2). *Polygonum erectum* subsp. *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 maintain germination heteromorphism by acting as seed dispersers (Silverton 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 erect knotweed, this particular plastic response probably worked against its development. Nevertheless, by Mississippian times, some communities had developed a domesticated form of erect knotweed. Analysis of other erect knotweed assemblages from older and contemporaneous sites, observations of wild-growing erect knotweed, and experimental cultivation are ongoing, and will provide more insights into how this lost crop evolved in pre-Columbian agroecosystems.

3.10 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.

Annals of Botany 107:1399-1404

- Adams KR (2014) Little Barley Grass (*Hordeum pusillum* Nutt.): A Prehispanic New World Domesticated 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, IL, 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 Anthropology, University 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. *Vegetation History and Archaeobotany* 21:149-162
- Asouti E, Fuller DQ (2013) A Contextual Approach to the Emergence of Agriculture in Southwest Asia. *Current Anthropology* 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. *Canadian Journal of Plant Science* 51:93-99
- Braadbaart F, Wright PJ (2007) Changes in Mass and Dimensions of Sunflower (*Helianthus annuus* L.) Achenes and Aeds Due to Carbonization. *Economic Botany* 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. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20100707:1-10
- Clements R, J., Latter BDH (1974) Responses to Selection for Seed Weight and Seedling Vigour in *Phalaris*. *Crop and Pasture Science* 25:33-44
- Cohen D (1966) Optimizing Reproduction in a Randomly Varying Environment. *Journal of Theoretical Biology* 12:119-129
- Costea M, Tardif FJ, Hinds HH (2005) *Polygonum* L. In: Committee FoNAE (ed) *Flor of North America North of Mexico*, vol 5. eFloras.org, New York and Oxford,
- Courtney AD (1968) Seed Dormancy and Field Emergence in *Polygonum aviculare*. *Journal of Applied Ecology* 5:675-684
- D'Andrea AC (2008) T'ef (*Eragrostis tef*) in Ancient Agricultural Aystems of Highland Ethiopia. *Economic Botany* 62:547-566
- Dahlberg JA, Wasylkova K (1996) Image and Statistical Analyses of Early Sorghum Remains (8000 BP) from the Nabta Playa Archaeological Site in the Western Desert, Southern Egypt. *Vegetation History and Archaeobotany* 5:293-299
- Flannery KV (1973) The Origins of Agriculture. *Annual Review of Anthropology* 2:271-310
doi:10.2307/2949273
- Ford RI (ed) (1985) Prehistoric Food Production in North America vol 75. *Anthropological Papers*. Museum of Anthropology, University of Michigan, Ann Arbor
- Fritz GJ (1984) Identification of Cultigen Amaranth and Chenopod from Rockshelter Sites in Northwest Arkansas. *American Antiquity* 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 Paleoethnobotany. 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 America In: Minnis PE (ed) New Lives for Ancient and Extinct Crops. University of Arizona Press, Tucson, AZ, pp 12-43
- Fritz GJ, Smith BD (1988) Old Collections and New Technology: Documenting the Domestication of *Chenopodium* in Eastern North America. Midcontinental Journal of Archaeology 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 323:1607-1610
- Gilmore MR (1931) Vegetal Remains of the Ozark Bluff-Dweller Culture. Papers of the Michigan Academy of Sciences, Arts, and Letters 14:83-102
- Granitto PM, Verdes PF, Ceccatto HA (2004) Large-scale Investigation of Weed Seed Identification by Machine Vision. Computers and Electronics in Agriculture 47:15-24
- Gremillion KJ (1993) The Evolution of Seed Morphology in Domesticated *Chenopodium*: An Archaeological Case Study. Journal of Ethnobiology. 13:149-169
- Gremillion KJ (1998) Changing Roles of Wild and Cultivated Plant Resources Among Early Farmers of Eastern Kentucky. Southeastern Archaeology 17:140-157

- Gremillion KJ, Piperno DR (2009) Human Behavioral Ecology, Phenotypic (Developmental) Plasticity, and Agricultural Origins. *Current Anthropology* 50:615-619
- Harlan JR, De Wet JMJ (1965) Some Thoughts about Weeds. *Economic Botany* 19:16-24
- Harlan JR, De Wet JMJ, Price EG (1973) Comparative Evolution of Cereals. *Evolution* 27:311-325
- Heiser Jr CB (1954) Variation and Subspeciation in the Common Sunflower, *Helianthus annuus*. *American Midland Naturalist* 51:287-305
- Herman JJ, Sultan SE (2011) Adaptive Transgenerational Plasticity in Plants: Case Studies, Mechanisms, and Implications for Natural Populations. *Frontiers in Plant Science* 2:1-10
- Hillman GC, Davies MS (1990) Measured Domestication Rates in Wild Wheats and Barley under Primitive Cultivation, and their Archaeological Implications. *Journal of World Prehistory* 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. *Perspectives in Plant Ecology, Evolution and Systematics* 5:13-36
- Langlie BS, Hastorf CA, Bruno MC, Bermann M, M. BR, Condarco WC (2011) Diversity In Andean *Chenopodium* Domestication: Describing A New Morphological Type From La Barca, Bolivia 1300-1250 B.C. *Journal of Ethnobiology* 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. *The American Biology Teacher* 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). *American Journal of Botany* 79:882-886
- Mueller NG (2017) An Extinct Domesticated Subspecies of Erect Knotweed in Eastern North America: *Polygonum erectum* L. ssp. *watsoniae* (POLYGONACEAE). *Novon* 25:xx-xx
- Mueller NG (in press) Bet-Hedgers Under Cultivation: Germination Heteromorphism and Domestication Syndrome in Erect Knotweed (*Polygonum erectum* L.), Insights from the Field and the Greenhouse. *Human Ecology*.
- 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. *Quaternary International* 363:65-77
doi:<http://dx.doi.org/10.1016/j.quaint.2013.12.049>
- Powell G (2000) Charred, Non-Maize Seed Concentrations in the American Bottom Area: Examples from the Westpark Site (11-MO-96), Monroe County, Illinois. *Midcontinental Journal of Archaeology* 25:27-48
- Reimer PJ et al. (2013) IntCal13 and Marine13 Radiocarbon Age Calibration Curves 0-50,000 Years cal BP. *Radiocarbon* 55:1869-1887
- Rindos D (1984) *The Origins of Agriculture: An Evolutionary Perspective*. Academic Press, Orlando

- Roach DA, Wulff RD (1987) Maternal Effects in Plants. *Annual Review of Ecology and Systematics* 18:209-235
- Rogler GA (1954) Seed Size and Seedling Vigor in Crested Wheatgrass. *Agronomy Journal* 46:216-220
- Rovner I, Gyulai F (2006) Computer-Assisted Morphometry: A New Method for Assessing and Distinguishing Morphological Variation in Wild and Domestic Seed Populations. *Economic Botany* 61:154-172
- Silvertown JW (1984) Phenotypic Variety in Seed Germination Behavior: The Ontogeny and Evolution of Somatic Polymorphism in Seeds. *American Naturalist* 124:1-16
- Simon ML, Parker KE (2006) Prehistoric Plant Use in the American Bottom: New Thoughts and Interpretations. *Southeastern Archaeology* 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. *Proceedings of the National Academy of Sciences* 103:12223-12228
- Smith BD (2014) The domestication of *Helianthus annuus* L. (Sunflower). *Vegetation History and Archaeobotany* 23:57-74
- 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 B.P. *Proceedings of the National Academy of Sciences* 106:6561-6566

- Smith CC, Fretwell SD (1974) The Optimal Balance Between Size and Number of Offspring. *American Naturalist* 108:499-506
- Sultan SE (1996) Phenotypic Plasticity for Offspring Traits in *Polygonum persicaria*. *Ecology* 77:1791-1807
- 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. *Evolution & Development* 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. *Evolutionary Applications* 6:266-278
- Tanno K-i, Willcox G (2012) Distinguishing Wild and Domestic Wheat and Barley Spikelets from Early Holocene Sites in the Near East. *Vegetation History and Archaeobotany* 21:107-115
- Venable DL (1985) The Evolutionary Ecology of Seed Heteromorphism. *American Naturalist* 126:577-595
- Wymer DA, Abrams E (2003) Early Woodland Plant Use and Gardening: Evidence from an Adena Hamlet in Southeastern Ohio. *Midcontinental Journal of Archaeology* 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. *Nordic Journal of Botany* 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. *Vegetation History and Archaeobotany* 12:187-204

4. Evolutionary Bet-Hedgers under Cultivation: Investigating the Domestication of Erect Knotweed (*Polygonum erectum* L.) using Growth Experiments⁹

4.1 Abstract

Evolutionary bet-hedging refers to situations in which organisms sacrifice mean fitness for a reduction in fitness variance over time. Germination heteromorphism is the quintessential and most well understood bet-hedging strategy. It has evolved in many different plants, including the wild progenitors of some crops. Erect knotweed (*Polygonum erectum* L.), an annual seed crop, was cultivated in Eastern North America between c. 3000–600 BP. By c. 900 BP, cultivation had produced a domesticated subspecies with greatly reduced germination heteromorphism. Field observations and greenhouse experiments suggest that cultivation eliminated the selective pressures that maintain the bet-hedging strategy in erect knotweed, while humans also directly selected for seeds that germinated reliably and for seedlings with rapid early growth.. The protection provided to erect knotweed under cultivation explains the domestication syndrome that has been observed in some archaeological assemblages. Dormancy provides seeds a means of escaping adverse conditions in time, while dispersal provides an escape in space. Farmers relaxed selective pressures that maintained dormancy in erect knotweed by acting as seed dispersers, spreading disturbance-adapted plants to predictable and protected environments, and by saving and exchanging seed stock. Experimental data also indicate that adaptive transgenerational plasticity may have been working against the expression of domestication syndrome in this case.

⁹ 2017, Human Ecology 45(2):189-203.

4.2 Introduction

Ancient farmers in Eastern North America (ENA) cultivated a suite of native seed crops beginning in the Late Archaic period, c. 3800 BP (Ford, ed. 1985; Smith 1992; Fritz 1993; Yarnell 1993; Smith 2006; Smith and Yarnell 2009). These pre-maize crops are referred to as the Eastern Agricultural Complex (EAC). Several fell out of cultivation before Contact, leaving us with many questions about how they were cultivated. The core area where the EAC was cultivated encompasses parts of modern day Iowa, Missouri, Arkansas, Tennessee, Kentucky, Indiana, Illinois and Ohio (Fritz 1993; Figure 2.2). Within this area, and over time, reliance on particular crops within the EAC varied (e.g. Fritz 1986; Wymer 1993; Gremillion 1998; Simon and Parker 2006). It is likely that cultivation practices also varied, as kin groups and communities developed unique agricultural communities of practice over the course of many generations. The ecosystems that farmers engineered for their crops changed the selective environment, causing some of the crops to diverge from their relatives outside of cultivation. In addition to creating altered environments for their crops, farmers probably directly selected plants with desirable features, both consciously and unconsciously.

These diverse practices left their mark on the seeds or fruits of some EAC crops. Two EAC crops domesticated by ancient farmers are still cultivated today: sunflower (*Helianthus annuus* L.) and squash (*Cucurbita pepo* L. var. *ovifera* D.S. Decker). Morphological indicators of domestication have also been documented in “lost crops” of the EAC – plants that are only known as crops from the archaeological record: sumpweed (*Iva annua* L. var. *macrocarpa* Blake) (Yarnell 1978), goosefoot (*Chenopodium berlandieri* Moq. ssp. *jonesianum* Smith and Funk) (Fritz and Smith 1988; Gremillion 1993a, 1993b), and, more equivocally, little barley (*Hordeum pusillum* Nutt.) (Hunter 1992), which was also cultivated and domesticated in what is

now the Southwestern United States (Adams 2014). Recently, I have presented evidence that cultivation resulted in a morphologically distinct domesticated subspecies of erect knotweed (*Polygonum erectum* L. ssp. *watsoniae* N.G. Mueller) (Chapters 2-3). There is abundant evidence for the cultivation of one other seed crop within this complex, maygrass (*Phalaris caroliniana* Walter), although no domestication syndrome has been documented (Fritz 2014).



Figure 4.1: *Polygonum erectum* L. plants. Left: Summer fruits and flowers. Right: Senesced plant after period of simultaneous fruiting, late October- early November.

Erect knotweed is an annual, herbaceous plant that produces seeds from May to November. It is likely that ancient farmers collected its seeds during a period of simultaneous fruiting just before the plant senesces (Figure 4.1). Depending on the setting and the weather, this can occur between mid-October and late November. Erect knotweed produces dimorphic

achenes: two distinctly different types (morphs) of one seeded fruit with a hard pericarp (Figure 4.2). The production of these achenes is seasonally controlled. During the summer, plants produce only achenes with thick, tubercled pericarps (referred to hereafter as tubercled morphs). Beginning in mid-September, they begin to also produce achenes with smooth, thin pericarps (referred to hereafter as smooth morphs). Previous studies of closely related species suggested that these dimorphic achenes have different necessary conditions for germination. In the tubercled morphs of other species in *Polygonum*, thick layers of cuticle and wax, while preventing pathogens from attacking the seed, also prevent germination (Courtney 1968, Metzger 1992, Yurtseva 2001; Figure 4.2).

Cultivation wrought two changes in erect knotweed morphology: an increase in fruit size and a pronounced reduction in fruit dimorphism, resulting in assemblages made up only or primarily of large smooth morphs (Chapters 2-3; Figure 4.2). Although increases in seed size or dehiscence mechanism are usually the focus of domestication studies of annual seed crops, changes in the timing or reliability of germination are also very important from the perspective of the farmer (e.g. Abbo et al. 2011). In the case of erect knotweed, cultivated plants gradually stopped producing fruits that do not germinate reliably the year after they are produced (tubercled morphs). How could cultivation cause this change? This question was addressed by observing populations of erect knotweed in the field over the course of two growing seasons, by synthesizing previous observations of erect knotweed and closely related species, and by growing erect knotweed experimentally.

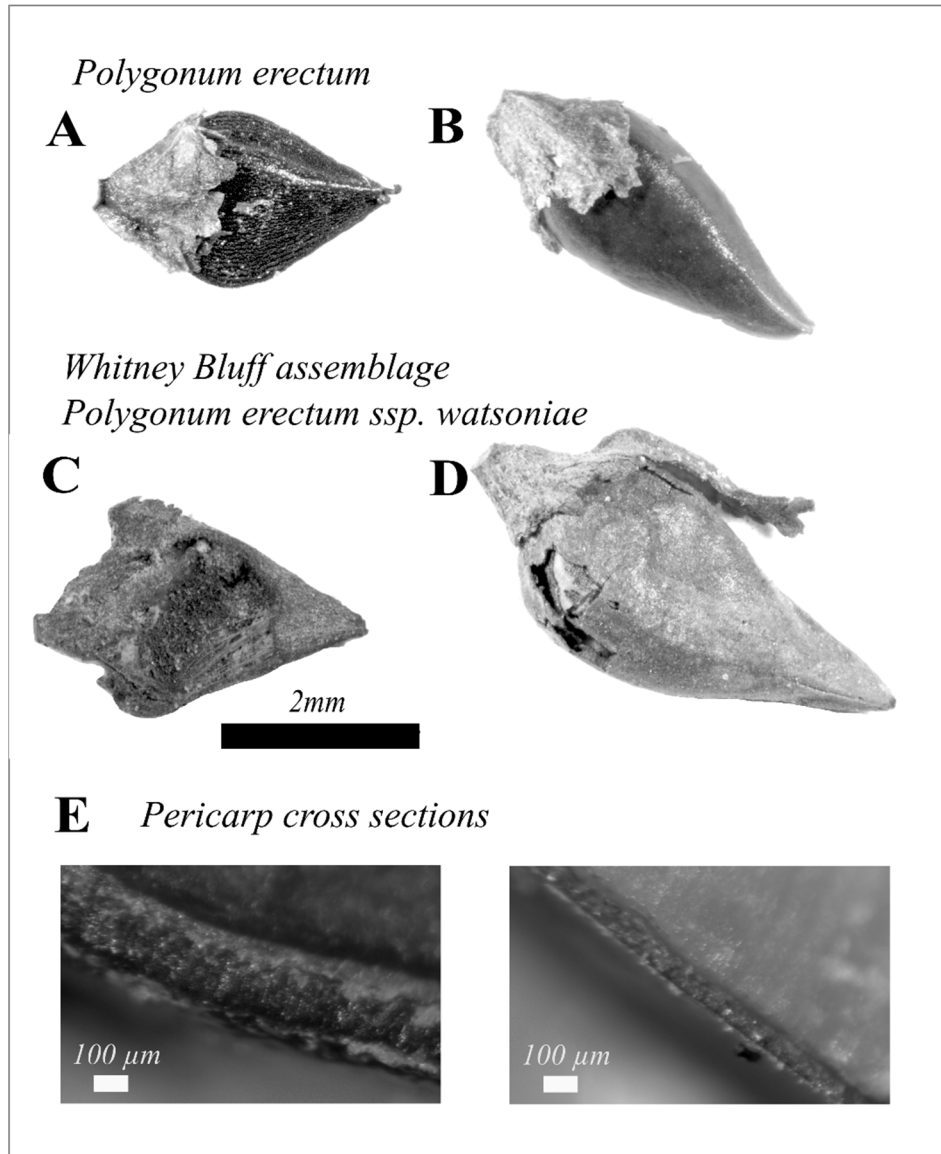


Figure 4.2: Erect knotweed dimorphic achenes, perianth removed or not preserved. A) Modern erect knotweed tuberled morph with diagnostic striate-tuberled surface texture; B) modern erect knotweed smooth morph; C) one of only two tuberled morphs from the Whitney Bluff site assemblage (n=1307), a domesticated assemblage dating to c. 850 BP. D) a typical smooth morph from Whitney Bluff, shown to scale with modern achenes; E: Cross sections of modern tuberled and smooth pericarps – tuberled pericarps are much thicker and include protective layers of cuticle and wax.

4.3 Reducing Germination Heteromorphism: Bet-Hedgers under Cultivation

“Dormancy [is a means of] avoiding unfavorable periods by escape in time...Dispersal is a means of avoiding unfavorable periods by escape in space and can be considered an alternative to dormancy”

-J.W. Silvertown 1984:9

Evolutionary bet-hedging refers to situations in which organisms sacrifice mean fitness for a reduction in fitness variance over time (Cohen 1966; Slatkin 1974; Childs et al. 2010). The quintessential and most well understood bet-hedging strategy is germination heteromorphism, which 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 erect knotweed and its relatives, produce one morph that is non-dormant, usually with a thin seed or fruit coat that is more permeable than that of the dormant morph. 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). Bet-hedging strategies are adaptive because fitness is a multiplicative process, making it sensitive to occasional low values. Even occasional instances 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. 2010:2).

Knotweeds (*Polygonum* L. subsect. *Polygonum*) produce trigonal achenes, which are one-seeded fruits consisting of seeds encased in a tough fruit coat, or pericarp (Figure 4.2). Most knotweeds exhibit seasonally controlled achene dimorphism: they produce two distinct fruit types in ratios that vary over the course of the growing season. Tubercled morphs have lower aspect ratios (*i.e.* their major and minor axes are closer to equal) and thicker pericarps with distinctive surface textures that are often diagnostic of particular species (Costea et al. 2005). During the summer and early fall, *Polygonum* plants produce only tubercled morphs. Smooth morphs have higher aspect ratio (*i.e.* a longer major axis compared to minor axis) and thinner pericarps that lack diagnostic surface textures, although their size and shape differs between

species (Chapter 2). Beginning in mid-September, plants begin to produce both morphs. The ratio of smooth to tubercled morphs by late October varies from species to species, and is possibly also influenced by yearly fluctuations in rainfall or temperature (Brenckle 1946). The population percentages of each morph on different species, at different times of year, and under different weather conditions, have not been well-studied.

Previous research on other species of *Polygonum* has shown that tubercled achenes have thicker walls and cuticle than smooth achenes. They also have layers of wax that prevent or slow the penetration of fungi and pathogens. These attributes both mechanically restrict germination and allow the tubercled fruits to remain healthy and viable in the soil over several years (Yurtseva 2001:524-5). Experiments have repeatedly shown that the pericarp directly controls the timing of germination in species closely related to erect knotweed (Courtney 1968; Metzger 1992; Sultan 1996). One of the goals of this study was to discover what percentage of erect knotweed tubercled and smooth morphs will germinate the spring after they are produced – in other words, to verify that erect knotweed also exhibits germination heteromorphism, and to determine the magnitude of the effect.

Erect knotweed seeds may be naturally dispersed by various means, including floods and possibly birds, but most seeds fall to the ground within a few centimeters of the parent plant. This means that erect knotweed cannot rely on its dispersal mechanism to allow its offspring to sample different environments. If evolutionary bet-hedging theory is correct, dormancy heteromorphism evolved in response to environmental instability coupled with minimal seed dispersal. By producing two different types of achenes, populations of erect knotweed can escape extinction *in time*, as some of the fruits produced each year will remain viable in the seed bank if the entire population is wiped out.

I argue that ancient farmers relaxed this source of natural selection on erect knotweed under cultivation by providing an escape *in space* – a new dispersal mechanism. Farmers usually 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 expand the habitat of cultivated plants to physiographic zones that they could not otherwise colonize. Under the protection of farmers, monomorphic harvests of fruits that germinate and grow quickly are less risky, from the perspective of the plant, and more reliable, from the perspective of the farmer. Neither party need be conscious of this benefit in order for it to result in the selection of plants that produce only smooth morphs: plants that produce such harvests are more likely to contribute to the next generation of plants under cultivation, but are quickly eliminated from the population outside of cultivation.

4.3 Materials and Methods

4.3.1 Herbarium and Field Survey. I began opportunistically searching for erect knotweed in 2012, by keeping an eye out for it in parks and wilderness areas, farms, archaeological sites, and roadsides throughout the eastern United States. I did not locate a single population until 2014: erect knotweed has become extremely rare and should perhaps be considered endangered. It does not occur in the frequently trafficked public places where it was once common, even those where it has previously been reported. The likely reason is that it has been out-competed by prostrate knotweed (*Polygonum aviculare* L. complex Costea & Tardif) (Costea and Tardif 2004). These cosmopolitan weeds are ubiquitous along trails, in the cracks of sidewalks and parking lots, in fairgrounds, pastures, and lawns where erect knotweed was reported in the 19th and early 20th century. Members of the prostrate knotweed complex are also usually found near surviving populations of erect knotweed, having colonized the patches that

are more frequently mowed or driven over. It seems likely that low-growing prostrate knotweed is more successful in 21st century towns, parks, and pastures than erect knotweed primarily because mowing is much more common than it once was. Preliminary observations indicate that prostrate knotweed also germinates earlier than erect knotweed and can survive longer into the winter. Murray and Sheehan (1984:289) observed populations of prostrate knotweed blooming in January. Their longer growing and reproductive season and greater tolerance of mowing probably contribute to the success of prostrate knotweeds at the expense of erect knotweed.

To get a sense of erect knotweed's historical habitat and distribution, I coded the habitat descriptions from 29 herbarium accessions from the National Herbarium and Missouri Botanical Garden Herbarium. While descriptions in common floras led me to believe that human disturbance and packed earth were the more salient features of erect knotweed habitat, in fact the most commonly mentioned attribute of erect knotweed habitat in herbarium specimen descriptions was proximity to water. Of the 29 accessions, 20 were growing in close proximity to water – on “banks,” “shores,” or “floodplains.” Eleven came from habitats that were definitely created and maintained by humans, including agricultural fields or pastures, roadsides, dumps, and parking lots. I also coded for mentions of sun or shade. Somewhat surprisingly for a weedy plant, there were nine mentions of shade or partial shade (“woods”, “thickets”), and only seven that implied full sun (“field,” “open ground”). Armed with this information, I renewed my search for erect knotweed in the summer of 2014 by visiting the exact locations where it had most recently been collected, and by focusing my searches along the bank of creeks, rivers, and lakes in areas of partial shade at the interface between woods and clearings. My previous seasons of searching had already convinced me that parking lots, roadsides, and other “waste place” populations had become uncommon, having been replaced with prostrate knotweeds.

Table 4.1: Survey populations

Population	Date	Life stage	Max height (cm)	Min height (cm)	Patch size (m ²)	Max plants/m ²	Number of achenes sampled for greenhouse experiments				
							Immature tubercled	Tubercled	Immature smooth	Smooth	
Peters Creek	9/2/2014	Flowering	5	1							
		/fruiting	0	0	2	15		20	20		
Crawford Creek	9/4/2014	Flowering	5	1							
		/fruiting	0	0	4	25		20	20		
Bellews Creek	9/17/2014	Flowering	5	1	1	>10					
	4	/fruiting	0	0	5	0		40	40		
Peters Creek	9/19/2014	Flowering	5	1							
	4	/fruiting	0	0	2	10		40	40		
Crawford Creek	10/4/2014	Flowering	5	3							
	4	/fruiting	0	0	4	10		20	40		20
Bellews Creek	10/14/2014	Flowering	5	1	1	>10					
	14	/fruiting	0	0	5	0		40			40
Crawford Creek	10/23/2014	Flowering	5	1							
	14	/fruiting	0	0	4	10		40	40	40	40
Bellews Creek	10/30/2014	Flowering	5	1	1	>10					
	14	Senesced	0	0	5	0		40	40		40
Bellews Creek	5/8/2015	Flowering	9	1	7	>10					
Crawford Creek	5/12/2015	Flowering	1			30					
	5	/fruiting	0	1	4	0					
Crawford Creek	9/22/2015	---	--	--	--	---					
	5	---	-	-	-	---					
Bellews Creek*	10/22/2015	Flowering	8			>10					
	15	/fruiting	1	5	4	0					
Bellews Creek*	11/12/2015	Flowering	8			>10					
	15	Senesced	1	5	4	0					

Table 4.1: Data on populations sampled for the greenhouse experiment from September 2014–November 2015. Greenhouse samples were taken only from the 2014 harvest. Only late season harvests contained smooth morphs (Table 4.2), so early season greenhouse batches contained only tubercled achenes. Populations at Bellews Creek and Crawford Creek were destroyed by late spring floods in 2015: * indicates that 2015 harvests came from a smaller patch, slightly above the floodplain of Bellews Creek.

Wherever I encountered erect knotweed, I took both herbarium and seed samples. The volume of seed that could be taken at any one time varied. I was careful to take only a small percentage (~ 10%) of all the seeds available in any one location, in order to protect the already vulnerable populations. I recorded the maximum plant density per square meter, total patch size, approximate ratio of flowers to fruits, and maximum and minimum plant height (Table 4.1). I also recorded qualitative observations about the habitat including nearby species, bodies of

water, roads, or paths. Whenever possible, I interviewed land owners or frequent visitors about recent conditions affecting the population, such as floods, mowing, and various types of traffic. During the summer of 2014 I was able to locate three populations within a day’s driving distance of St. Louis, which I visited several times until the first snow on October 31. I continued to monitor two of these populations during 2015.

All of the seed collected was sorted under a dissecting microscope into “Smooth” and “Tubercled” categories. These were further divided into “mature” and “immature” categories based on whether or not their pericarp could be indented with a metal tool (Table 4.2).

Table 4.2: Composition of harvests by morph						
Day/Month	Year	Total	Smooth	Tubercled	% Smooth	
9/2	2014	51	0	51	0.0	
9/4	2014	48	2	46	4.2	
9/17	2014	450	0	450	0.0	
9/19	2014	115	8	107	7.0	
10/4	2014	210	16	194	7.6	
10/14	2014	239	63	176	26.4	
10/22	2015	814	235	579	28.9	
10/23	2014	1253	901	352	*71.9	
10/30	2014	3011	1310	1701	43.5	
11/12	2015	2380	826	1554	34.7	

Table 4.2: Harvest composition, late September to early November. Harvests in bold were taken from completely senesced plants. * Indicates the highest proportion of smooth morphs observed, and may serve as a *preliminary* upper limit of natural variability in comparisons with archaeological assemblages. There is significant variability not explained by the timing of the harvest that requires further study. For example, harvests taken on 10/22 and 10/23, respectively, yielded almost perfectly inverse proportions of smooth morphs. The timing and intensity of smooth morph production may be population specific (heritable), plastic, or both. Bold entries came from fully senesced plant.

4.4 Growth Experiments

Subsamples of twenty seeds from each population and harvest date in 2014, for each morphological category (immature tubercled, immature smooth, smooth, tubercled), were taken for use in the growth experiment (Table 4.1). Exploratory tests revealed that no achenes of any type will germinate without cold stratification in moist soil, even under ideal greenhouse conditions. This is common for wild plants from temperate regions, but has interesting implications for ancient seed savers, as discussed below. In order to simulate winter and induce germination, each batch was embedded in 60 mL of moist potting mix in individual plastic bags, then stored at 4 °C for six weeks.

The first iteration was planted on March 24, 2015. A second iteration, using the same methods, was planted on July 28, 2015. Both iterations were planted as batches (n=20 achenes) in 0.06 m² plastic trays full of Metro 360 potting mix. Each batch in its wet soil matrix was removed from the freezer and spread evenly over the surface of the soil in each tray, then lightly covered with more soil, and watered in. Trays were placed on the mist bench for one month. On the mist bench, trays were misted for 15 seconds every 10 minutes from 6:00 AM–10:00 PM. The light regime was 16 hours of daylight and 8 hours of night, and plants were grown in full sun. The plants in these experiments experienced more consistent watering, warmer temperatures, less disturbance, and more light than their parent plants in the field. Their germination, growth, and reproduction rates are thus most likely at or above the upper boundary of normal variation.

On each greenhouse visit, for each batch, I recorded number of plants germinated, maximum and minimum height, maximum and minimum number of leaves and branches per plant, whether or not the plants were fruiting or flowering, and whether or not auxiliary branches

had developed. After four months the plants were put on a stress regime, wherein greenhouse managers allowed the soil to completely dry out before watering, to simulate late summer/autumn condition and induce senescence. Plants were harvested when all leaves were brown and no flowers remained. Upon harvesting, each individual plant's height was measured and its branches and auxiliary branches were counted. Achenes adhering to the plant were hand-stripped. Harvests were passed through a 2.8 mm sieve to remove twig and leaf fragments, then weighed. Subsamples of 1.5 mL were taken from each plant for observation under a dissecting microscope.

4.5 Results

4.5.1 Survey population descriptions. Quantitative observations regarding these populations are reported in Table 4.1; approximate locations are shown on Figure 2.2.

Population 1: Peters Creek. This population was growing along a dirt service road in Mark Twain National Forest about 100 m from Peters Creek, in Madison Co., Mo. The plants were distributed patchily in a ditch along the road and were also growing in muddy depressions in a four-wheeler trail nearby. The road is not a main public access point to the National Forest, and is not much used. It frequently floods where it crosses the small streams that feed into Peters Creek, and a flooded section divided the population of erect knotweed in two the first time I visited in early September 2014. The erect knotweed did not form a contiguous patch, but was interspersed with swamp smartweed (*Persicaria hyrdopiperoides* Michx.), dock (*Rumex sp.*L.) and Indian wood oats (*Chasmanthium latifolium* (Michx.) H.O. Yates). This was the least dense of the three populations and the shadiest location, occurring as it did on the border of mature forest. It also had the most delicate plants, which produced a much smaller amount of seed than plants in sunnier locations. Throughout the fall of 2014, this population was continuously

reduced every time I visited. The densest patches were in the middle of the ATV track, but they did not seem to be able to recover from being repeatedly run over. By late September, all of the plants in these patches were gone, and only the roadside plants remained. The following year, this location was inaccessible for most of the spring because of intermittent flooding. It was July by the time the road was passable, and I did not find any erect knotweed plants. The effects of early summer floods on erect knotweed plants are discussed in greater detail below.

Population 2: Crawford Creek. The second population was growing on a private wildlife reserve on the banks of Crawford Creek, in Calhoun Co., IL. This population formed a contiguous patch on steeply pitched alluvium, 5–10 m from the creek in early September, 2014. Above it, the ground leveled out into a grassy field margin, and below it was open sediment sparsely populated by sapling maple trees (*Acer* sp. L.) and swamp smartweed. A dirt road had created the cut bank where the erect knotweed was growing; prostrate knotweed dominated the packed dirt of this road. When I returned in early October, the bank had been scoured by a flood. Many of the plants on the creek bank were dead or completely covered in sediment, but several large erect knotweed plants had sprung back up from under a mat of vegetation and sediment. The smaller plants were all dead or buried. Compared to other populations I have observed, these had the largest and most robust stems, perhaps a plastic response to the frequent flooding of the creek bank. The surviving plants were still flowering and, surprisingly given the scouring they had received, were covered in mature brown achenes. This harvest yielded by far the highest proportion of smooth morphs (71.9%) of any harvest. One explanation is that more tubercled fruits, which accumulate on the plants over the course of the entire growing season, were washed away by the flood. The fruits that I harvested may constitute a sub-sample of all those produced

in 2014, consisting only of fruits that were still developing and thus tightly adhering to the mother plant in late October – mostly smooth morphs.

In early May 2015, this population seemed to be forming a patch of approximately the same size and density as the year before, but when I returned in September to start collecting seeds all of the plants were gone. Crawford Creek had been subject to severe flooding in June, as the entire region suffered through one the wettest early summers on record. June 2015 was the wettest in 100 years in Illinois, which received 8.71 inches of rain (about twice the average). The Illinois River, of which Crawford Creek is a tributary, was the most affected waterway in the state. The flood gauge below Crawford Creek, at Hardin, registered a crest of 36.50 feet on June 30, 4 inches over major flood stage, and this level was sustained for at least a day. According to the landowners, the population at Crawford Creek would have been completely submerged, not just scoured, for at least a matter of several hours. The timing and severity of these floods led to population extinction in 2015.

Population 3: Bellows Creek. Located in the yards and clearings of a farmhouse in Jefferson, Co. MO, this population was by far the largest and densest of the three. Plants grew in a dense patch over an area of 15 m², with smaller patches scattered around the barns and outbuildings 20–50 m from Bellows Creek. Scattered trees and buildings provided intermittent shade, but this was also the sunniest of the three locations. Prostrate knotweed and swamp smartweed were nearby, as usual, but various grasses (although not *Chasmanthium* in this case), chenopods, and mustards were also abundant in this farmyard setting. According to the landowner the patch of erect knotweed was rarely mowed, while the adjacent dirt road was frequently mowed and driven over. As at Crawford Creek, the road was inhabited by prostrate knotweed.

By October 31, 2014, the day before the first snow that year, all but four of the erect knotweed plants had senesced. The dead plants were completely covered in seed, “waiting for the harvester” (Figure 4.1). Although there were also some seeds scattered around on the ground, it was evident that there is a window of at least a few days when it is possible to harvest most of the achenes off of erect knotweed plants by hand stripping very efficiently. While it is easy to hand-strip dead plants, harvesting green plants is much more tedious: seeds have to be plucked or beaten from the plants (see also Murray and Sheehan 1984). The four plants that were still flowering revealed another interesting detail, which I would later observe in the greenhouse: just before senescing, plants produce large clusters of flowers in the axils of their branches. Whereas throughout most of the growing season 1-4 flowers per axil is normal and they are not blooming simultaneously, at the end of the season clusters of up to 20 flowers are produced. It would have behooved the ancient farmer in several ways to wait until her crop had completely senesced before harvesting, even if that meant losing a small amount of seed.

In early May 2015, this population was coming back up alongside dandelions (*Taraxacum officinale* F.H. Wigg), common plantain (*Plantago major* L.), violets (*Viola* sp.), and prostrate knotweed in an otherwise bare farmyard. But the June 2015 floods affected this population as well. Record rainfall was also recorded in the St. Louis area, with deadly flash floods occurring in tributaries of the Meramec and Big Rivers, including Bellows Creek. The densest patch of knotweed stood just a few meters above the creek, on its natural floodplain. According to the landowner, this part of his property had been completely submerged for 3–4 hours. Where thousands of plants had grown the year before, only two could be found in the fall of 2015. A few meters up the dirt road, above the flood line, the smaller patches I had observed the year before were thriving and had greatly expanded. These were the tallest erect knotweed

plants I had yet observed, and were scattered over an opening created by daily ATV traffic. In 2015, with a warmer fall, I tracked the plants through the middle of November. On November 12, all the plants were dead and a lot of seed had fallen (or been eaten by the local chickens), but sheltered plants in the middle of stands still retained most of their seeds.

4.5.2 Seasonal composition of harvests. Domesticated assemblages from archaeological sites exhibit reduced achene dimorphism in comparison to normal modern harvests from erect knotweed plants, regardless of the time of year when the harvest occurs, the details of habitat, or the growing season. The population proportion of smooth morphs (smooth/total harvested) is a useful metric for comparing domesticated assemblages to those that I observed. While the maximum population proportion of smooth morphs in an archaeological assemblage is 100% (Asch and Asch 1985b) the highest observed population proportion in modern erect knotweed was 71.9%.¹⁰ This single high population proportion was an outlier with respect to the other late season harvests, even those from completely senesced populations (Table 4.2). I consider it likely that this population proportion is an artifact of disproportionate tubercled morph loss caused by late season flooding in 2014, as described above.

Erect knotweed begins to produce smooth morphs in mid-September during some growing seasons, but in small numbers. Of 70 achenes taken from herbarium samples collected in September for a previous study, only four were smooth (Chapter 2). In my four September

¹⁰ When Asch and Asch (1985a:145) made the first report of domesticated erect knotweed in the Hill Creek site report, they also reported measurements of achenes from several harvests of erect knotweed made in Kansas and Illinois in 1977-1982. From one harvest – collected on November 9, 1977 – they measured 103 smooth morphs and only 2 tubercled morphs. However, it is unclear if this was the proportion of the sample, or if they disproportionately picked smooth morphs to increase the sample size for their morphometric analysis. The table includes an ambiguous footnote that reads: “Number of achenes measured for each type does not necessarily reflect the relative frequency of types in a collection.” All of the other sample proportions reported in their table are within the range of variation observed in this study, although many of the sample sizes are too small to be considered accurate reflections of population proportion.

harvests totaling 664 achenes, I collected only 10 smooth morphs, and all of these were immature. Beginning in October, plants start producing more smooth morphs. However, the ratio of smooth to tubercled morphs in any given harvest doesn't change systematically between mid-October and mid-November. Harvests taken from living plants and fully senesced plants in early November were also compared (Table 4.2). The highest proportion of smooth morphs came from a population that was still flowering, rather than one that was completely senesced, suggesting that the smooth morphs are not disproportionately produced in the last bout of simultaneous fruiting just before the plant dies.

4.5.3 Germination Heteromorphism and Early Growth. There is a clear germination heteromorphism between smooth and tubercled morphs: smooth morphs germinate more readily the year after they are produced than do tubercled morphs. The germination rate for smooth morphs varied between 7.5–100%, whereas the germination rate for tubercled morphs varied between 0–27.5 % (Table 4.3). Immature smooth morphs germinate at almost the same rate as mature smooth morphs, and at a much higher rate than mature tubercled morphs, whereas immature tubercled morphs rarely germinate. One batch of smooth morphs collected early in the season (October 14) germinated at an anomalously low rate, suggesting that these achenes may not have been completely developed despite their hardened pericarps. There is no clear correlation between tubercled morph germination rate and date of harvest (Table 4.3). This indicates that tubercled morphs mature throughout the growing season, unlike smooth morphs which mature simultaneously at the end of the season.

In the first month of growth, seedlings from smooth morphs grow faster than those from tubercled morphs. They also develop true leaves earlier and have more leaves after four weeks than plants grown from tubercled morphs (Figure 4.3). This is despite the fact that smooth

morphs germinated at higher rates, so there was more competition for light, water, and soil nutrients for the seedlings of smooth morphs (Table 4.3). I expected that the greater seedling densities in smooth morph batches would almost immediately swamp any benefit they received from greater parental provisioning, but this was not the case. Smooth morphs emerging in crowded environments grow faster than tubercled morphs emerging in open environments. The effects of seedling density begin to swamp the maternal effects of seed provisioning only around week five (Figure 4.3). Thereafter, during weeks 6 – 20, the largest plants were often in tubercled batches with low plant densities.

Table 4.3: Percent Germination for all Greenhouse Batches				
Harvest date (2014)	Smooth, immature	Tubercled, immature	Smooth	Tubercled
September 2 [*]		0		5.0
September 4 ^{**}		5.0		25.0
September 17 ^{***}		5.0		27.5
September 19 [*]		0		17.5
October 4 ^{**}		0	55.0	7.5
October 14 ^{***}			7.5	25.0
October 23 ^{**}	60.0		100.0	5.0
October 30 ^{***}	55.0		72.0	25.0
Mean	57.5	2.0	57.9	17.2

Table 4.3: Percent of all seeds planted that germinated per batch, averaged over two iterations. Germination heteromorphism by morph is evident. In addition, immature smooth morphs (those whose pericarp is still soft) germinate at about the same rate as mature ones, whereas immature tubercled morphs rarely germinate, indicating that smooth morphs are viable before their pericarp is fully developed.

*Peters Creek Population; **Crawford Creek Population; *** Bellows Creek Population

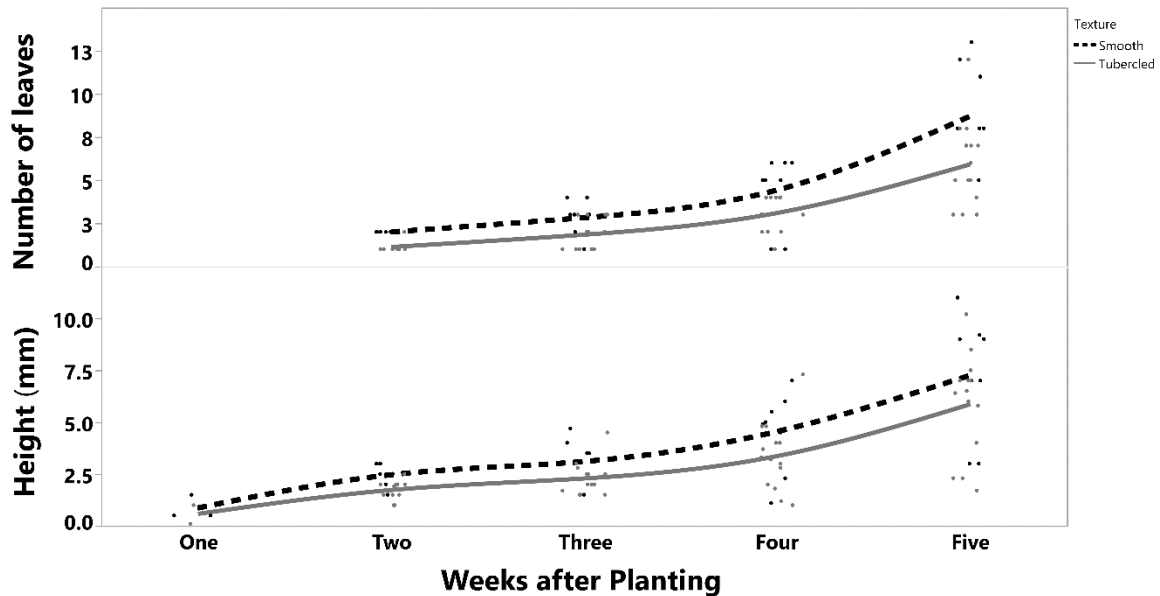


Figure 4.3: Early growth rates for smooth and tubercled morphs, in terms of maximum height per batch and maximum number of leaves per batch. Each dot represents the maximum plant height or leaf count per batch for that week, *i.e.* the biggest plant in the tray. In weeks 1 – 4, batches of plants grown from smooth morphs consistently have the tallest plants and are quicker to develop true leaves. The effects of greater seed provisioning and earlier germination in smooth morphs become less visible over time: by week 5, some of the biggest plants are in tubercled batches. Plant density begins to effect growth as individual plants get bigger and begin to crowd one another in some batches, but not others (see Figure 4.4 and Table 4.3).

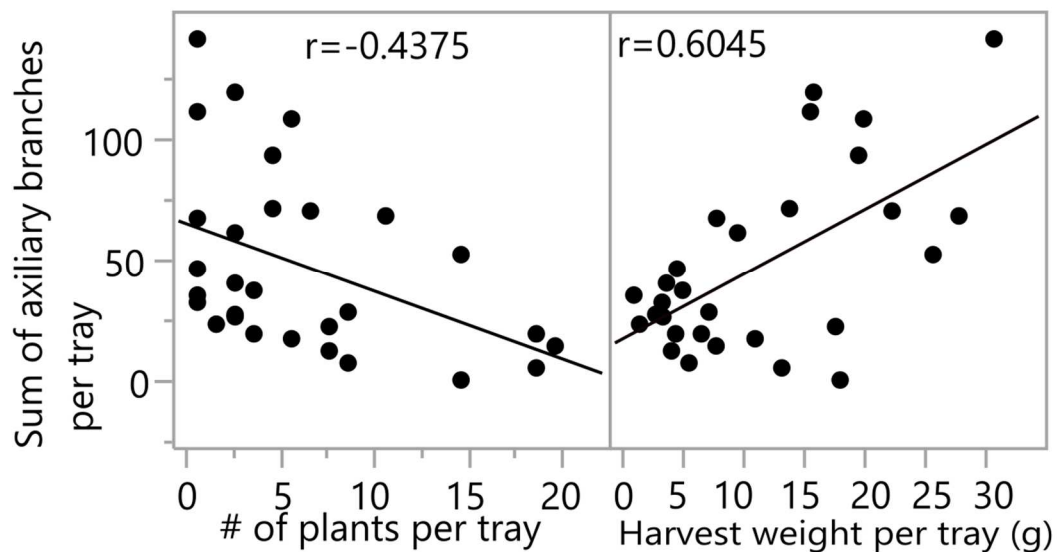


Figure 4.4: Covariation between the sum of auxiliary branches per tray, the # of plants per tray (plant density), and the weight of the harvest per tray. Plants growing at lower densities produced more auxiliary branches. Because

fruits are produced in the axils of branches, trays that had highly branched plants produced more abundant harvests. In other words, given a finite area, *less plants* usually produced *more seed*.

4.5.4 Plant spacing and yields. All batches were planted in the same size trays, but germination rates varied – a circumstance that allowed me to study how plant density affected reproductive output (Figure 4.4). Because erect knotweed plants each produce hundreds of seeds, natural stands tend to be quite dense (Table 4.1; Figure 6). Experimental results indicate that creating more space for each plant by thinning naturally occurring stands could have greatly increased yields for ancient harvesters. The highest yielding batch contained only one plant that yielded 31.31 g of seed, compared to the only batch with 100% germination (20 plants in a tray) which yielded only 8.35 g (Figure 6). In other words, thinning dense stands could more than triple yields. More so than plant density *per se*, yield is correlated with plant architecture. Erect knotweed produces fruits in the axils of its branches. This means that plants with more branches produce a lot more fruit (Figure 4.4). Plant density is correlated with the number of auxiliary branches per plant, and number of auxiliary branches is correlated with yield (Figure 4.4). For a farmer, the goal would be to maximize the number of *branches* per unit area, which would mean reducing the density of plants significantly from those observed in naturally occurring stands.

4.5.5 Harvest morphology. I took a 1.5 mL sub-sample of achenes from each plant after it had completely senesced, for morphometric analysis. I hoped to use these data to determine whether or not the production of smooth morphs was at all heritable. My plan was to select the plants that produced the most smooth morphs over several generations and measure the effect of my selection on the population proportion of smooth morphs over time. Unfortunately, this part of the experiment was a complete failure. Under greenhouse conditions (16 hours of light per day no matter the season) erect knotweed does not produce *any* smooth morphs. While this result stymied my initial attempt to begin the process of re-domestication, it also clearly demonstrated

that the production of smooth morphs is primarily triggered by decreasing day length, and is probably also encouraged by a shady environment, as discussed below. Variability in an individual plant's plastic response to day length and shadiness may be heritable, but answering this question will require several seasons of outdoor experiments.



Figure 4.5: Plant density in the field and in the greenhouse. A) Bellows Creek Population in October 2015 – typical plant density for a pure stand of erect knotweed that is infrequently disturbed; B) The only batch with 100% germination contained 20 plants that cumulatively produced only 8.35 g of seed; C) The highest yielding batch across two iterations contained only one plant – this highly branched individual produced 31.31 g of seed.

4.6 Implications: Reconstructing Agricultural Practice in the Eastern Woodlands

4.6.1 Adaptive transgenerational plasticity. Erect knotweed plants grown with plenty of room to branch out produce more seeds (Figure 4.4). Surely this fact was not lost on ancient farmers, and they would have responded by expanding or creating clearings and by thinning stands. But the production of smooth morphs is also controlled by sunlight: smooth morphs begin to appear as the days get shorter (Table 4.2). There is also evidence that a closely related species maintains seed provisioning in shady environments by sacrificing pericarp production. Experiments with *Persicaria maculosa* Gray, a smartweed, have shown that plants grown in shade will produce achenes that are the same weight, but have a pericarp that is 40% thinner than the offspring of their clones grown in full sun (Sultan 1996). The shade-grown plants are rationing their resources in a highly adaptive way: not only do they maintain seed provisioning under less than ideal conditions, they also prepare their offspring to germinate and grow quickly in the crowded environment they sense through lack of light (Herman and Sultan 2011). When Sultan (1996:1795) planted the offspring of this first generation, the progeny of the shade-grown plants, with their thinner pericarps, emerged an average of 1.6 days earlier than the progeny of the plants grown in full sun. Herman and Sultan (2011:1) have characterized this response as an example of *adaptive transgenerational plasticity*: situations in which parents alter the developmental traits of their progeny in response to environmental stress, and these alterations enhance offspring growth and reproductive success under the same stress. In this case, shade triggers the production of fruits with thin pericarps, and thin pericarps allow seeds to germinate and grow quickly in a crowded environment. Unlike erect knotweed and many other members of *Polygonum*, *Persicaria maculosa* does not exhibit achene dimorphism – instead, it has highly variable achenes with a range of shapes and pericarp thicknesses. But it is easy to imagine how

achene dimorphism could have arisen out of the transgenerational plasticity in pericarp thickness and seed provisioning demonstrated by Sultan's experiments.

My erect knotweed plants received 16 hours of light per day no matter the season and *did not produce a single smooth achene*. After spending fruitless hours searching for smooth morphs among 2.64 kg of greenhouse harvest, it occurred to me that something similar, although less extreme, might have happened during the early years of erect knotweed cultivation. As farmers created sunnier environments for their plants, the plants would have at first responded by producing more tubercled morphs, not less. Of the assemblages I analyzed from contexts dating to the Early and Middle Woodland period (c. 3000–1500 BP), only two were large enough samples to accurately estimate population proportion. Both conformed to my expectation: the Smiling Dan erect knotweed (n= 104) has a sample proportion of 26% smooth morphs, while the Meridian Hills assemblage (n=28) was only 7% smooth morphs (Chapter 6). Both of these sample proportions are low if we assume that these harvests were taken from senesced plants in late October or early November (Table 4.2).

The experimental and archaeological data taken together, although preliminary, suggest that as farmers tried to increase yields, they may have inadvertently triggered a plastic response that led to less reliable germination (more tubercled morphs) in the next year's seed stock, at least in the short term (Table 4.4). If the effect of adaptive transgenerational plasticity under cultivation is to produce harvests of mostly tubercled morphs, the existence of domesticated archaeological assemblages are all the more remarkable. These assemblages, with their very high proportions of smooth morphs, *cannot be explained by plasticity* if erect knotweed's plastic response to cultivation produces the exact opposite effect. The effects of plasticity had to be

overcome by an altered selective environment that was maintained for many generations (Table 4.4).

Table 4.4: Plastic and Evolutionary Effects of Cultivation on Erect Knotweed			
Agricultural Practice	Rationale for agricultural practice	Plastic effects	Evolutionary effects
Seed saving	Farmers maintain seed security – they have seeds to plant if crops are wiped out before they reproduce. Landraces with desirable characteristics are shared.	None	Plants producing more smooth morphs are at no selective disadvantage: populations no longer need tubercled morphs to avoid extinction because 1) Farmers replace the bet-hedging function of tubercled morphs by acting as seed dispersers and by providing an alternative to storage in the seed bank. 2) Farmers plant a disturbance adapted crop in a predictable, protected environment for many generations.
Seed exchange			
Habitat expansion by land clearance	Erect knotweed crops can be destroyed by early summer floods. People move plants to more predictable environments on terraces and in uplands.	→Individual plants have more light	
		If smooth morph production is a plastic response to crowded (shady) conditions, then the sunnier conditions inhibit smooth morph production in cultivated stands.	
Thinning seedlings	Farmers notice that thinning stands produces plants with more branches, and more seeds. Farmers get a bigger harvest by growing fewer plants per area.	Harvests from early cultivated populations are mostly tubercled morphs	Farmers eliminate the smaller seedlings year after year, giving a selective advantage to plants producing fruits that germinate and grow quickly: large smooth morphs.

Table 4.4: Summary of hypothetical effects of cultivation on a bet-hedging crop like erect knotweed.

4.6.2 Domestication. By the Late Woodland period (c. 1500–1000 BP), archaeological assemblages of erect knotweed in some parts of the core area of EAC cultivation begin to show signs of domestication: larger seeds and/or higher sample proportions of smooth morphs. By the Mississippian period (c. 1000–600 BP), these morphologies are more pronounced at some sites, while at others people continued to cultivate wild-type erect knotweed (Chapter 6). While there is a trend towards the elimination of germination heteromorphism over time in some regions, there is no uniformity between roughly contemporaneous sites across the study area. This suggests that agricultural practice differed between communities, and that the flow of information and seeds was not uniform across the core area. It is also possible that food preferences varied between communities, causing some to invest more energy in certain crops. Among the communities that developed a domesticated variety of erect knotweed by Mississippian times, the data presented here allow us to come to several conclusions about their cultivation techniques.

The field and herbarium surveys reported here confirm that erect knotweed, like several other EAC crops, is primarily a floodplain species (Smith 1992). Globally, many wild progenitors of crops are disturbance-adapted. The related ideas that dump heaps (Anderson 1952; Sauer 1952) or floodplains (Struever and Vickery 1973) were the first gardens were proposed long ago. Flood plains and middens are frequently disturbed and highly enriched environments, natural clearings where gathering may have slowly graded into cultivation. These theories are global or at least regional in scope, and for simplicity's sake they equalize the many forms that disturbance can take, not to mention the timing of disturbance. Streuver and Vickery (1973), and

later Smith (1992), pointed out that spring flooding in ENA created openings for early farmers, and that many of the first crops were plants that naturally would have colonized these areas.

Thus these authors argued that farming evolved out of casual cultivation of floodplain annuals.

This theory assumes that any plant found growing in a floodplain makes a good floodplain crop, which is not true for erect knotweed. Early spring floods may create clearings and deposit soil nutrients, but flooding at other times of year would have been disastrous if farmers were relying primarily on floodplain clearings. The most robust plants on Crawford Creek weathered an autumn flood in 2014 and went on to produce some seeds, but most of that harvest was lost. All three floodplain populations that I monitored were wiped out by early summer floods in 2015, and went on to produce no seed at all that year. The *survival* of a species in an unpredictably disturbed environmental does not guarantee its ability to produce a reliable yearly harvest for humans. Germination heteromorphism is the trait that allows erect knotweed populations to survive in frequently flooded habitats, even though individual generations can't survive severe floods at certain times of year.

If a plant is unwanted or merely tolerated by people (a weed), then germination heteromorphism is also adaptive in human-disturbed habitats: such places, like flood plains, are unpredictable places for seedlings, which may be trampled on, crushed, or purposefully removed to make room for more desirable species. But if people are protecting populations, the production of tubercled achenes is not only unnecessary, it is maladaptive. A greater percentage of smooth morphs germinate, and they do so more quickly than tubercled morphs. The early growth of smooth morphs is also faster than that of tubercled morphs. The difference in early growth rates between the two morphs is so pronounced that it overwhelms the effects of seedling density during the first month of growth (Figure 4.3). In my greenhouse experiments seedlings were only

competing with their own relatives, but this is seldom, if ever, the case in natural settings. Erect knotweed seedlings have to compete with many other plants that germinate in open spaces in early spring. In a seed bed maintained by people, competition with other species would be reduced, but not eliminated. The higher germination rates and more robust early growth of smooth morphs give them a definite advantage over other species and over their sibling tubercled morphs.

Because seedlings sprung from smooth morphs grow faster, they are also more likely to survive thinning by cultivators. That thinning was a regular part of agricultural practice for ancient erect knotweed farmers is also supported by several other of the findings reported here. Erect knotweed tends to form very dense stands because every plant drops hundreds of seeds. Yet these experiments have shown that yields per area can be increased by giving individual erect knotweed plants room to branch out. The highest yielding plant in greenhouse experiments grew alone in an area of 0.06 m², a circumstance that would rarely occur without human intervention (Table 4.1; Figure 4.4). The archaeological record shows that the size of erect knotweed seeds under cultivation increased over time (Chapter 6). Although the effects of seed size on early growth were not tested here, it is generally assumed that large seeds will grow faster than small seeds, all other things being equal, because they contain more nutritive material for the seedling (Harlan et al. 1973) All of these pieces of evidence suggest that Woodland and Mississippian period farmers were thinning stands of young erect knotweed plants (Table 4.4).

Even though smooth morphs have advantages over tubercled morphs in the seedbed for both the plant and the farmer, cultivated varieties in some areas of the core area continued to exhibit normal germination heteromorphism even as domesticated varieties appeared elsewhere. Tubercled morphs could have persisted under cultivation wherever farmers were not adequately

insulating seedlings from risk. Twenty-first century farmers in ENA protect seedlings growing in floodplains by constructing massive levees, but there is no evidence that ancient farmers practiced flood control in any form. If a community chose to cultivate erect knotweed casually, by expanding and thinning out naturally occurring stands in the floodplain, the evolutionary advantage of producing tubercled morphs would be maintained: seedlings would still occasionally be wiped out by early summer floods and populations would regenerate from tubercled morphs stored in the seed bank.

Conversely, wherever domesticated varieties were developed, farmers must have been protecting populations. At least two forms of protection are suggested by the archaeological record: expanding erect knotweed habitat into upland or terrace clearings, and saving and exchanging seed stock. In eastern Kentucky, where some of the earliest caches of erect knotweed in the core area were recovered from rockshelters, Gremillion and colleagues (2008) have convincingly argued that Woodland period farmers were moving floodplain plants to clearings on colluvial slopes and upland benches. Pollen data show that forest clearance in uplands began in eastern Kentucky by 3000 BP, just as the first evidence for the cultivation of erect knotweed appears (Delcourt et al. 1998).¹¹ Evidence for the clearing of upland forests by fire was also found in eastern Tennessee around 2800 BP (Delcourt et al. 1986). Clearing fields above the floodplain is one way ancient farmers could have changed the selective forces acting on disturbance adapted crops like erect knotweed (Table 4.4).

Ancient farmers could also have acted as an alternative to the soil seed bank by saving seeds. On both the eastern and western peripheries of the core area, rockshelter sites are rich in

¹¹ It is important to note that by this time several other crops had already been cultivated in this area for almost a millennium, see Smith and Yarnell 2009.

the remains of EAC crops, strongly suggesting that some farmers were saving seeds by the Early Woodland period (Fritz 1986; Gremillion 1993c). At open sites, seeds may have been stored in perishable containers, ceramic vessels, or pits. This research has shown that wild erect knotweed must be subjected to winter-like conditions in moist soil in order to germinate. To achieve maximum germination, seed savers would have had to either 1) store their seed stock in moist subterranean pits or vessels full of moist soil; or 2) sow seed in early winter for the following spring. Whichever method they used, if farmers were careful with their seed stock, they would reserve some seeds each year as insurance against crop failure –in essence, taking over the role that the tubercled morphs play for wild erect knotweed (Table 4.4).

4.7 Conclusions

Germination heteromorphism is the classic example of a bet-hedging strategy (Cohen 1966). Rather than maximizing fitness per generation, erect knotweed plants reduce variation in fitness over many generations by diversifying their offspring – some germinate and grow quickly, others remain in the seedbank for multiple growing seasons. Germination heteromorphism and seed dispersal can be seen as two different strategies that allow the offspring of a single plant to sample a variety of different growth environments (Silvertown 1984). Germination heteromorphism provides escape from adverse conditions in time, whereas dispersal provides an escape in space.

When humans act as seed dispersers, they may provide a means of escape in both time and space for the seeds of their chosen plants, by saving and exchanging seed and opening up new habitats for their crops. Ancient farmers in ENA domesticated erect knotweed by expanding its habitat, protecting its seeds, and selecting seedlings that germinated reliably and grew quickly. Results also highlight the need for more longitudinal studies of crop progenitors in the

field. Germination heteromorphism allows *populations* of erect knotweed to survive in floodplains, but that doesn't guarantee that it could have reliably produced harvests in the floodplain, because individual plants can't survive summer flooding. The unpredictability of unprotected floodplains led farmers to invest energy in clearing terrace and upland fields, which changed the selective environment for their crops and resulted in domestication.

This case study illustrates how domestication trajectories and syndromes are each unique, shaped as they are by the pre-cultivation evolutionary history of each domesticate. Erect knotweed's plasticity was likely one factor that made it attractive to ancient farmers: cultivation (in this case, thinning naturally occurring stands) can immediately result in large increases in yield. But adaptive transgenerational plasticity may have slowed the domestication process because erect knotweed probably responds to sunnier, more spacious environments by producing seed stock that will not germinate reliably (more tubercled morphs). Perhaps this even caused some communities to eschew saving erect knotweed seeds, preferring to let the plants seed themselves, with each generation germinating naturally over the course of several years in its normal floodplain habitat. In these communities, domesticated erect knotweed was never developed.

Eventually, some communities created more predictable and safe environments for erect knotweed populations through seed saving and exchange and habitat expansion. The direct evidence for this is the presence of domesticated assemblages in the archaeological record (Chapters 2,3, and 6). When the evolutionary advantage of producing tubercled morphs disappeared, so did they. For erect knotweed outside of cultivation, a bet-hedging strategy (germination heteromorphism) is absolutely essential to avoid local extinction events in bad years. But germination heteromorphism is inherently a strategy that does not maximize fitness

per generation: tubercled morphs sprout into less competitive seedlings, and the fact that they remain in the seedbank for so long increases the chances that they will fall victim to pathogens or predators before they can reproduce themselves. The model underlying bet-hedging theory (Cohen 1966) suggests that where germination heteromorphism is not maintained by strong selective pressures it will tend to disappear.

Experimental cultivation and field observations have been invaluable tools in this domestication study, linking the morphologies I observe in ancient seeds to specific agricultural practices. As we come to a more nuanced understanding of the causes of morphological variation in crops and their wild progenitors, seeds and fruits from archaeological sites become more and more useful artifacts of ancient agricultural practice. An understanding of the day to day activities that structured and constrained early agricultural communities can provide insights into one of the most momentous shifts in human history – the advent of food producing economies.

4.8 References

Abbo, S., E. Rachamim, Y. Zehavi, I. Zezak, S. Lev-Yadun, and A. Gopher

2011 Experimental Growing of Wild Pea in Israel and its Bearing on Near Eastern Plant Domestication. *Annals of Botany* 107(8):1399-1404.

Adams, Karen R.

2014 Little Barley Grass (*Hordeum pusillum* Nutt.): A Prehispanic New World Domesticated Lost to History. In *New Lives for Ancient and Extinct Crops*. P.E. Minnis, ed. Pp. 139-179. Tuscon: The University of Arizona Press.

Anderson, Edgar

1952 *Plants, Man and Life*. St. Louis, MO: Missouri Botanical Garden.

Asch, David L., and Nancy B. Asch

1985a *Archaeobotany*. In *The Hill Creek Homestead and the Late Mississippian Settlement in the Lower Illinois River Valley*. M.D. Conner, ed. Pp. 115-170. Kampsville Archaeological Center, Vol. 1. Kampsville, IL: The Center for American Archaeology.

1985b *Prehistoric Plant Cultivation in West Central Illinois*. In *Prehistoric Food Production in North America*. R.I. Ford, ed. Pp. 149-203, Vol. 75. Ann Arbor, MI: Museum of Anthropology, University of Michigan.

Brenkle, Jacob F.

1946 *Notes on Avicularia II*. *Phytologia* 2(5):169-171.

Childs, Dylan Z., C.J.E. Metcalf, and Mark Rees

2010 *Evolutionary Bet-Hedging in the Real World: Empirical Evidence and Challenges Revealed by Plants*. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20100707:1-10.

Cohen, Dan

1966 *Optimizing Reproduction in a Randomly Varying Environment*. *Journal of Theoretical Biology* 12(1):119-129.

Costea, Mihai, and François J. Tardif

2004 *The Biology of Canadian Weeds: Polygonum aviculare L.* *Canadian Journal of Plant Science* 131:481-506.

Costea, Mihai, François J. Tardif, and Harold H. Hinds

2005 *Polygonum* L. In *Flor of North America North of Mexico*. F.o.N.A.E. Committee, ed, Vol. 5. New York and Oxford: eFloras.org.

Courtney, A.D.

1968 Seed Dormancy and Field Emergence in *Polygonum aviculare*. *Journal of Applied Ecology* 5(3):675-684.

Delcourt, Paul A, et al.

1986 Holocene Ethnobotanical and Paleoecological Record of Human Impact on Vegetation in the Little Tennessee River Valley, Tennessee. *Quaternary Research* 25(3):330-349.

Delcourt, Paul A, et al.

1998a Prehistoric human use of fire, the eastern agricultural complex, and Appalachian oak-chestnut forests: paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity*:263-278.

1998b Prehistoric Human Use of Fire, the Eastern Agricultural Complex, and Appalachian Oak-Chestnut Forests: Paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* 63(2):263-278.

Ford, Richard I., ed.

1985 *Prehistoric Food Production in North America*. Volume 75. Ann Arbor: Museum of Anthropology, University of Michigan.

Fritz, Gayle J.

1986 Prehistoric Ozark Agriculture: The University of Arkansas Rockshelter Collections.

Dissertation, University of North Carolina.

1993 Early and Middle Woodland Period Paleoethnobotany. *In* Foraging and Farming in the Eastern Woodlands. C.M. Scarry, ed. Pp. 39-56. Gainesville: University Press of Florida.

2014 Maygrass: Its Role and Significance in Native Eastern North America *In* New Lives for Ancient and Extinct Crops. P.E. Minnis, ed. Pp. 12-43. Tucson, AZ: University of Arizona Press.

Fritz, Gayle J., and Bruce D. Smith

1988 Old Collections and New Technology: Documenting the Domestication of *Chenopodium* in Eastern North America. *Midcontinental Journal of Archaeology* 13(1):3-27.

Gremillion, Kristen J.

1993a Crop and Weed in Prehistoric Eastern North America: The *Chenopodium* Example. *American Antiquity* 58(3):496-509.

1993b The Evolution of Seed Morphology in Domesticated *Chenopodium*: An Archaeological Case Study. *Journal of Ethnobiology* 13:149-169.

1993c Plant Husbandry at the Archaic/Woodland Transition: Evidence from the Cold Oak Shelter, Kentucky. *Midcontinental Journal of Archaeology* 18:161-189.

1998 Changing Roles of Wild and Cultivated Plant Resources Among Early Farmers of Eastern Kentucky. *Southeastern Archaeology* 17(2):140-157.

Gremillion, Kristen J., Jason Windingstad, and Sarah C. Sherwood

2008 Forest Opening, Habitat Use and Food Production on the Cumberland Plateau, Kentucky: Adaptive Flexibility in Marginal Settings. *American Antiquity* 73(3):387-411.

Harlan, Jack R., J.M.J. De Wet, and E. Glen Price

1973 Comparative Evolution of Cereals. *Evolution* 27(2):311-325.

Herman, Jacob J., and Sonia E. Sultan

2011 Adaptive Transgenerational Plasticity in Plants: Case Studies, Mechanisms, and Implications for Natural Populations. *Frontiers in Plant Science* 2:1-10.

Hunter, Andrea A.

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, Eric

2002 Ecological Consequences and Ontogeny of Seed Heteromorphism. *Perspectives in Plant Ecology, Evolution and Systematics* 5(1):13-36.

Metzger, James D.

1992 Physiological Basis of Achene Dormancy in *Polygonum convovulus* (Polygonaceae). *American Journal of Botany* 79(8):882-886.

Murray, Priscilla M., and Mark C. Sheehan

1984 Prehistoric Polygonum Use in the Midwestern United States. *In Experiments and Observations on Aboriginal Wild Plant Food Utilization in Eastern North America*. P.J. Munson, ed. Prehistory Research Series, Vol. VI. Indianapolis: Indian Historical Society.

Sauer, Carl O.

1952 *Seeds, Spades, Hearths, and Herds: The Domestication of Animals and Foodstuffs.*
Cambridge: MIT Press.

Silvertown, Jonathan W.

1984 Phenotypic Variety in Seed Germination Behavior: The Ontogeny and Evolution of
Somatic Polymorphism in Seeds. *American Naturalist* 124(1):1-16.

Simon, Mary L., and Kathryn E. Parker

2006 Prehistoric Plant Use in the American Bottom: New Thoughts and Interpretations.
Southeastern Archaeology 25(2):212-57.

Slatkin, Montgomery

1974 Hedging One's Evolutionary Bets. *Nature* 250:704-705.

Smith, Bruce D.

1992 The Floodplain Weed Theory of Plant Domestication in Eastern North America. *In*
Rivers of Change: Essays on Early Agriculture in North America. B.D. Smith, ed.
Washington, DC: Smithsonian Institution Press.

2006 Eastern North America as an Independent Center of Plant Domestication. *Proceedings of*
the National Academy of Sciences 103(33):12223-12228.

Smith, Bruce D., and Richard A. Yarnell

2009 Initial Formation of an Indigenous Crop Complex in Eastern North America at 3800 B.P.
Proceedings of the National Academy of Sciences 106(16):6561-6566.

Struever, Stuart, and Kent D. Vickery

1973 *The Beginnings of Cultivation in the Midwest-Riverine Area of the United States.*
American Anthropologist 75(5):1197-1220.

Sultan, Sonia E.

1996 Phenotypic Plasticity for Offspring Traits in *Polygonum persicaria*. *Ecology* 77(6):1791-1807.

Venable, D. Lawrence

1985 The Evolutionary Ecology of Seed Heteromorphism. *American Naturalist* 126(5):577-595.

Wymer, Dee Anne

1993 Cultural Change and Subsistence: The Middle Woodland and Late Woodland Transition in the Mid-Ohio Valley. *In* Foraging and Farming in the Eastern Woodlands. C.M. Scarry, ed. Pp. 138-156. Gainesville: University Press of Florida.

Yarnell, Richard A.

1978 Domestication of Sunflower and Sumpweed in Eastern North America. *In* The Nature and Status of Ethnobotany. R.A. Ford, ed. Pp. 289-299. Anthropological Papers No. 67. Ann Arbor, MI: Museum of Anthropology, University of Michigan.

1993 The Importance of Native Crops During the Late Archaic and Woodland Periods. *In* Foraging and Farming in the Eastern Woodlands. C.M. Scarry, ed. Pp. 13-26. Gainesville: University Press of Florida.

Yurtseva, O.V.

2001 Ultrasculpture of Achene Surface in *Polygonum* section *Polygonum* (Polygonaceae) in Russia. *Nordic Journal of Botany* 21(4):513-528.

5. Carbonization, Differential Preservation, and Sampling Biases in Domestication Studies: An Erect Knotweed (*Polygonum erectum* L.) Case Study¹²

5.1 Abstract

Population morphometrics can be employed to explore the process of domestication, but only after accounting for biases introduced by taphonomic processes and sampling. For every cultivated plant, the challenges associated with carbonization, differential preservation, and sampling bias are different, as are the morphological characteristics of interest in domestication studies. This case study establishes correction factors and sampling parameters for assessing morphological indicators of domestication in erect knotweed (*Polygonum erectum* L.), an annual plant that was cultivated by Indigenous people in Eastern North America for about 2500 years. Documenting the unique domestication syndrome of erect knotweed creates three different sets of taphonomic and sampling problems that need to be addressed through experimentation and modeling: 1) Assess the morphometric effects of carbonization; 2) assess the effects of differential preservation; and 3) assess the effects of sampling error. The results of this study can be used by other analysts to identify domesticated assemblages of erect knotweed. These analyses also have implications for studies of plant domestication from the morphology of archaeological assemblages in general, especially when nominal variables are used to differentiate wild from domesticated populations (for example, the presence/absence of an abscission scar in cereals or the seed coat texture of chenopods).

¹² 2017, Journal of Archaeological Science: Reports 13:303-311.

5.2 Introduction

The analyses reported here were undertaken in the course of a study on erect knotweed (*Polygonum erectum* L.), an annual seed crop that was cultivated by ancient farmers in Eastern North America (ENA) from c. 3000–600 BP. Elsewhere, I have argued on the basis of population morphometrics that some assemblages of erect knotweed exhibit a unique domestication syndrome as a result of hundreds of generations of selection in agroecosystems (Chapters 2-3). It is only possible to make such arguments, which are built on morphological comparisons of crop plants and their wild progenitors, after first exploring the many possible ways that archaeological assemblages may be altered and biased. For every cultivated plant, the challenges associated with carbonization, differential preservation, and sampling bias are different, as are the morphological characteristics of interest in domestication studies (Boardman and Jones 1990; Smith 2014; Wright 2003; 2008; Yarnell 1978). The purposes of this paper are 1) to provide guidelines for the identification of domesticated erect knotweed from its carbonized fruits; and 2) to address sampling and preservation issues common to all domestication studies that rely on the morphology of carbonized remains.

In ENA, an indigenous agricultural system began to develop c. 4000 BP. These early crops include some familiar plants: sunflowers (*Helianthus annuus* var. *macrocarpus* (DC.) Cockerell) and native squash varieties, such as acorn and crookneck squashes (*Cucurbita pepo* L. ssp. *ovifera* D.S. Decker), are among ENA's earliest domesticates (Crites 1993; Kay 1980). Sumpweed (*Iva annua* L. and its domesticated subspecies, *Iva annua* ssp. *macrocarpa* S.F. Blake) and goosefoot (*Chenopodium berlandieri* Moq. and its domesticated subspecies, *Chenopodium berlandieri* ssp. *jonesianum* Smith and Funk) were also domesticated by c. 3800 BP (Smith and Funk 1985; Smith and Yarnell 2009; Yarnell 1972; 1978). By the Early

Woodland period, c. 3,000 BP, three new crops had entered the crop complex. These were maygrass (*Phalaris caroliniana* Walter), erect knotweed (*Polygonum erectum* L. and its domesticated subspecies *Polygonum erectum* ssp. *watsoniae* N.G. Muell.), and little barley (*Hordeum pusillum* Nutt.) (Asch and Asch 1978; 1985; Fritz 1986; 1993; Chapters 2-3; Simon and Parker 2006). By the time of European colonization, several of these locally domesticated crops had apparently fallen out of use and were thus lost to history (Smith 1992; 2006).

Collectively, the native seed crops of ENA are referred to as the Eastern Agricultural Complex (EAC). EAC crops are commonly recovered from storage pits, hearths, and middens at archaeological sites spanning parts of modern day Arkansas, Illinois, Indiana, Iowa, Kentucky, Missouri, Ohio, and Tennessee (the “core area,” Fritz 1993; Figure 1.2). Erect knotweed has been recovered from sites spanning the core area. It seems to have entered the crop complex in western Appalachia c. 3,000 BP and was cultivated at least until c. 600 BP. Domesticated assemblages have been recovered from the Middle Woodland Walker Noe site, Kentucky (c. 2000 BP), and from Mississippian sites in Illinois, Missouri, and Arkansas (1000-600 BP) (Chapter 6).

Erect knotweed produces *achenes*: one-seeded fruits with hard pericarps (fruit coats). Each plant produces two distinctly different types of achenes, a phenomenon known as fruit dimorphism (Figure 5.1). Throughout the growing season, erect knotweed produces tubercled achenes, which have thicker pericarps and do not germinate readily (Chapter 4). Beginning in mid-September, it begins to produce smooth achenes, which have thinner pericarps and almost always germinate the spring after they are produced. This phenomenon is called germination heteromorphism, and is a form of evolutionary bet-hedging (Slatkin 1974; Silvertown 1984; Childs et al. 2010). The tubercled morphs persist in the seed bank, allowing populations to

survive adverse growing seasons (Chapter 4). Domesticated erect knotweed (*Polygonum erectum* ssp. *watsoniae* N.G. Muell.) differs from its wild progenitor in that 1) its achenes are larger and differently shaped and; 2) harvests from domesticated plants contain very few or no tubercled morphs (Chapters 2-3). Documenting this unique domestication syndrome creates three different sets of taphonomic and sampling problems that need to be addressed through experimentation and modeling.

- 1) *Assess the morphometric effects of carbonization.* Carbonization preserves plant parts which would otherwise be subject to decay by converting starch, protein, lignin and other constituents of plant tissues into inert compounds when plant parts are exposed to heat in an anoxic or near anoxic environment (Braadbart et al. 2004). Unfortunately, the process also distorts the original shape and size of the seed. In order to compare carbonized assemblages to modern reference collections and desiccated archaeological assemblages, correction factors must be applied. For erect knotweed, only preliminary correction factors for achene length and width existed prior to this study (Asch and Asch 1985:144). Changes in shape had never been investigated.
- 2) *Assess the effects of differential preservation.* An important part of the domestication syndrome in erect knotweed is the elimination of germination heteromorphism: domesticated erect knotweed produced almost no tubercled achenes, instead producing smooth achenes that germinate more reliably and contain less inedible material (Chapter 4). Can the sample proportions (% smooth achenes) of carbonized assemblages be taken at face value, or is one morph more likely to be preserved via carbonization than the other?

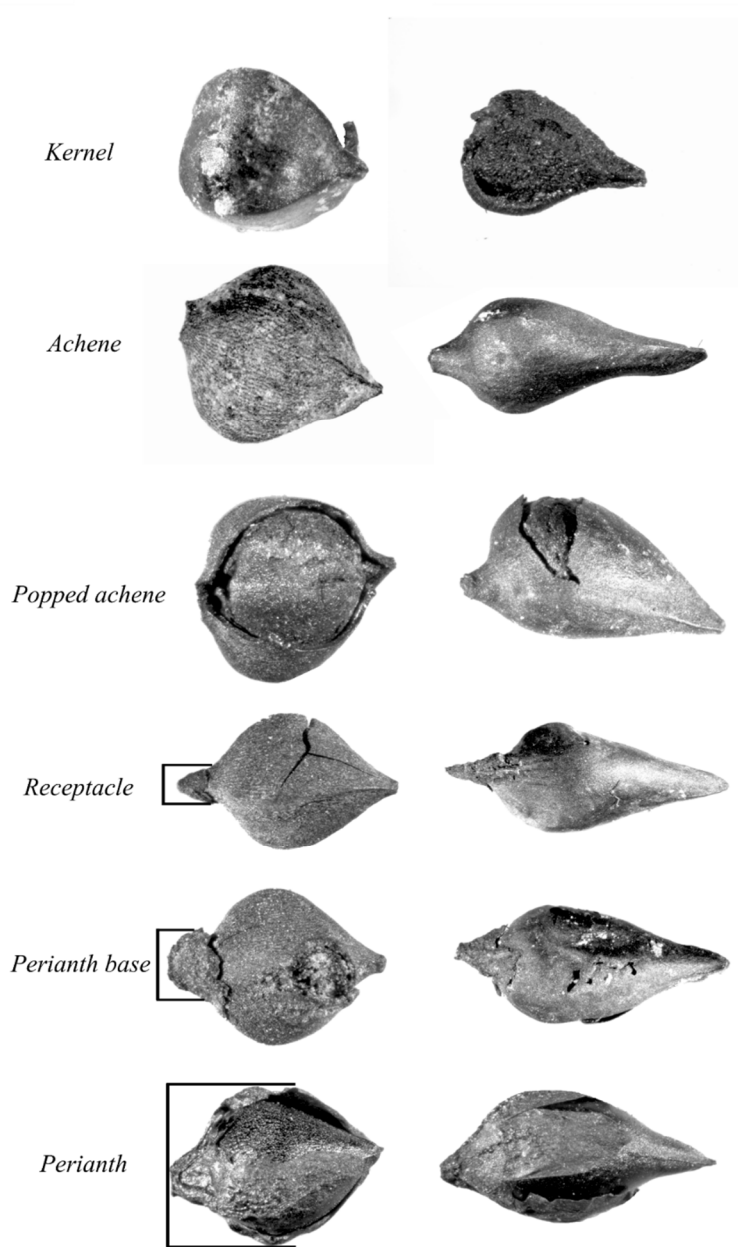


Figure 5.1: Shows different preservation states for carbonized erect knotweed and achene dimorphism. Kernels are usually identified as erect knotweed by association – without associated achenes they are not diagnostic to species. They are of no known value for domestication studies. Well preserved achenes are the subject of morphometric analyses, but are less useful when they popped because their shape is then distorted to varying degrees. Achenes with receptacles (thickened portion of the stem to which the fruit adheres) and perianth base are another well-preserved form that can be analyzed in domestication studies. Corrections for comparing specimens with and without preserved receptacles are given in Table 5.2. The perianth is the flower, which adheres to mature erect knotweed achenes but is almost always absent on carbonized achenes. The examples with most of their perianth preserved shown here are from my carbonization experiments; the rest of the pictured achenes are from archaeological assemblages.

3) *Assess the effects of sampling error.* Small sample size is a problem in and of itself for the study of variability in a population. It is rare for entire erect knotweed achenes to be preserved; most assemblages are made up of many kernels and fragments of pericarp (Figure 5.1). Even if every effort is made to sample well-preserved contexts, it is rare to find a sample of >50 well-preserved achenes from a single well-defined context (Chapter 6). Estimates of population proportion derived from small samples have large margins of error, so clear guidelines are needed to recognize which assemblages are likely to be outside the natural range of variation after taking into consideration the uncertainty introduced by sampling error. This is a problem shared by any researcher who is attempting to differentiate between wild and domesticated populations on the basis of nominal variables (for example, the presence/absence of an abscission scar in cereals or the seed coat texture of chenopods).

The first two problems were addressed in a series of carbonization experiments. The effects of sampling error were explored probabilistically.

5.3 Carbonization Background

Two variables are fundamental to any carbonization experiment: temperature and duration of exposure to heat. Different seeds and fruits will carbonize with more or less exposure to heat, depending on their physical and chemical characteristics. Märkle and Rösch (2008) tested the seeds or fruits of seven different taxa to determine minimum conditions for inducing carbonization and maximum conditions under which diagnostic attributes of the seed or fruit would be retained. Some taxa had very small temperature ranges in which they could be carbonized without disintegrating. Oil seed crops in particular had very specific necessary

conditions for preservation (2008:S260). For example, Wright (2008:145) suggests that sunflower achenes are unlikely to be preserved unless they are carbonized at temperatures somewhere between 300–440°C. Below 300° they still contain enough uncarbonized material to be susceptible to decay, and above 440° they become more friable and less likely to survive. Several different varieties of wheat (*Triticum* spp.) and barley (*Hordeum vulgare* L.) have larger ranges of conditions that will lead to preservation by carbonization, both in terms of temperature and duration of exposure (Boardman and Jones 1990:5). Their comparably large survival window may contribute to their abundance at archaeological sites. A seed or fruit may be preserved by carbonization, but the characteristics of interest may be destroyed or distorted. Braadbaart and Bergen (2005) found that emmer wheat (*Triticum dicoccum* Schrank), bread wheat (*Triticum aestivum* L.), and durum wheat (*Triticum durum* Desf.) can be distinguished from one another on the basis of aspect ratio (called slenderness in their study). But the characteristic shapes of each type of wheat disappear when they are heated at 290°C, making their identification to species impossible. For this study, I had to take into particular consideration the preservation of the pericarp, the characteristics of which are fundamental to the study of erect knotweed domestication. Temperature and duration of exposure needed to be set at levels that would consistently preserve the pericarp.

When plant tissues are carbonized, they generally shrink as water and oils evaporate and other tissue constituents change chemical structure. To account for this shrinkage, the use of carbonization correction factors is common, especially in domestication studies where seed and fruit size is often the object of study. For the EAC domesticates sumpweed and sunflower, correction factors were derived from average shrinkage in carbonization experiments and applied as multipliers to the length and width of carbonized assemblages (Asch and Asch 1978; Powell

2000; Tarighat et al. 2011; Yarnell 1972; 1978; Smith 2014; Wright 2008). This method is employed to approximate size change, even though experiments have shown that multiple factors, especially temperature and duration of heat exposure, affect post-carbonization size (Braadbart and Wright 2007). Temperature and duration of heat exposure lead to differential deformation, but few methods are available to reconstruct carbonizing conditions in order to take this variation into account (but see Braadbart et al. 2004; Braadbart et. al. 2007; Braadbart and Wright 2007). For erect knotweed, there is relatively small temperature window in which whole achenes will be preserved, but the carbonization corrections derived by these experiments should still be seen as preliminary estimates to be refined by future studies.

The chemical composition of seeds and fruits can also determine how they are affected by carbonization. For example, Braadbart and Wright (2007) used an heirloom variety of sunflower seeds for their study because modern commercial varieties have been bred to increase oil content. This is problematic if the goal is to compare them to ancient varieties with lower oil content because lipids evaporate rather than carbonize. Fat content of the seed or fruit will thus affect how much it shrinks when carbonized (Braadbart et al. 2007). Studying a closely related species of knotweed, Yurtseva (2001) has shown that the pericarp of the tubercled achenes is thicker than that of the smooth achenes partly because it is fortified with layers of wax, which are absent in smooth achenes. Wax (a lipid) is not at all likely to be preserved by carbonization, so tubercled achenes can be expected to shrink more than smooth ones. On the other hand, smooth morphs (since they are not protected by layers of moisture-retardant wax) are likely to have a higher water content. Since water evaporates during carbonization, this might offset the difference. Asch and Asch (1985:144), in what are only described as “preliminary experiments,”

found that the length of both morphs decreased by 20% when carbonized, but that the width of smooth morphs was not affected, whereas the width of tubercled morphs also decreased by 20%.

5.4 Materials and Methods

Phase I

From observing archaeological collections, it is clear that many carbonized erect knotweed achenes become puffed or popped as they are subjected to heat (Figure 5.1). Parts of their perisperm bubble through the pericarp, obscuring their shape and size. When this occurs, the pericarp usually splits into pieces and falls away from the kernel (Figure 5.1). Pericarp fragments and kernels are commonplace in archaeological assemblages, but these fruit parts are not very useful for the purposes of identifying domestication syndrome in erect knotweed. The goal of Phase 1 was to determine the temperature threshold at which pericarps begin to fracture and disintegrate.

I carbonized batches of erect knotweed achenes to determine what temperature resulted in assemblages of undistorted achenes. I pulled four groups of five achenes each from herbarium specimens and removed their perianths (adhering flower parts, see Figure 5.1) before photographing them. I then embedded them in quartz sand in aluminum containers, covering each achene with sand grains to provide near-anoxic conditions. I fired them at 250, 275, 300, and 325°C for 30 minutes. All the achenes fired above 300°C were puffed or popped, whereas none of the achenes fired at or below 300°C were, so I set the temperature for the larger experiment at 300°C. Phase I suggests that the window of sufficient conditions for achene preservation is quite narrow: any fruits subjected to temperatures above 300°C are likely to be represented by kernels and pericarp fragments in archaeological samples.

Phase II

The goal of Phase II was to determine how carbonization affected the size and shape of erect knotweed achenes in general, and if there were differential effects depending on 1) pericarp texture; 2) achene size; or 3) achene maturity. I selected 50 tubercled and 50 smooth morphs from a batch harvested at the Bellows Creek Farm, Jefferson County, MO, on October 30, 2015 (Chapter 4). At the time of the experiment, these achenes had been in cold storage for about 9 months. Of these, 25 of each were mature and 25 were immature. Mature and immature in the context of this experiment refer to whether or not the pericarp could be deformed by pressing it with a metal tool, not to their viability. Greenhouse experiments have shown that “immature” achenes are often viable. Maturity still seems to be a reasonable adjective to describe this attribute, though, since the softness of the pericarp is developmental and the proportion of mature (hard pericarp) achenes increases as the season progresses (Chapter 4). Each achene was given a unique number and stored in a separate, labeled capsule throughout the experiment.

I photographed each achene with its perianth intact (Figure 5.1) because I also wanted to see what effect carbonization would have on perianth preservation. In archaeological assemblages of carbonized seeds, it is very uncommon for any part of the perianth to be preserved, yet it seemed likely that many erect knotweed achenes retained their perianth up until the time that they were carbonized for two reasons. First, in the only large, uncarbonized assemblage of archeological erect knotweed available, the Whitney Bluff site assemblage, 75% retain some or all of their perianth. Second, it seems time consuming and pointless to remove the perianth from erect knotweed achenes without also fracturing or removing the pericarp. The tough pericarp presents more of a barrier to digestion than the open, papery perianth. If ancient farmers were successful in removing the pericarp, the perianth would also be eliminated as a matter of course, so there would be little reason to remove the perianth but not the pericarp. The

most parsimonious explanation for the lack of perianths on carbonized archaeological specimens seemed to be that they are easily destroyed during carbonization.

After they were photographed, achenes were transferred to ceramic crucibles, covered in quartz sand, and fired for 30 minutes in a muffle furnace pre-heated to 300°C. Each achene was then photographed again. Both pre- and post-carbonization images were subjected to the morphometric analysis to ascertain changes in both shape and size. Morphometric measures were taken using ImageJ open source image analysis software; formulas are given in Table 5.1.

Table 5.1: Morphometric Measurements		
Measurements	Description	Procedure/Formula
Area	# of pixels within the margins of object	Select image of achene, area measured in mm ²
Length	#of pixels along major axis of selected object	Draw line to measure length in mm
Width	Number of pixels along minor axis of selected object	Draw line to measure length in mm
Shape Factors		
Aspect Ratio	Degree of elongation; major axis divided by (mean of) minor axis (axes). Axes derived from an ellipse fitted around the selected object.	[Major axis]/[Minor axis]
Roundness	Roughly inverse of aspect ratio, a measure of elongation of the major axis with respect to the object's area. Axis derived from an ellipse fitted around the selected object.	$4 \times ([Area]/(\pi \times [Major\ axis]))$
Circularity	Relationship between perimeter and area; degree of departure from a circle. 1.0 is a perfect circle, 0.0 is a straight line.	$4\pi \times [Area]/[Perimeter]^2$

Table 5.1: Gives the formulas used to generate the morphometric measures. All image analysis was completed using ImageJ open source image analysis software.

Phase III

Given the major differences in the chemical composition and structure of the pericarps of smooth and tubercled morphs, I wanted to know if one was more likely to preserve via carbonization than the other. I carbonized 100 achenes of each morph, 50 each at 300° C and 350°C (n=200). I then counted how many of each type retained an intact pericarp, how many were popped, and how many pericarps had completely fractured leaving only a kernel.

Receptacle, and Perianth base.

Two different types of well-preserved achenes occur. Type 1 consists of only the achene proper, and Type 2 consists of the achene and an adhering receptacle covered in remnants of the perianth – referred to here as the perianth base (Figure 5.1). A receptacle is a thickened portion of a stem to which the fruit adheres. In the case of erect knotweed, it is usually covered by pieces of perianth (outer flower parts, commonly referred to as petals) that adhere to the mature fruit. Achenes lacking perianth bases will be, on average, shorter and smaller than those with preserved perianth bases, as well as differently shaped. I developed a set of correction factors for achenes missing their perianth base so that I could include both types in the morphometric analysis that were part of a larger study (Chapter 6). The application of these correction factors increased the number of measurable archaeological achenes in the assemblages I analyzed from 747 to 1,267, and can be employed in future morphological studies of this crop species in order to maximize sample size. To develop the corrections, I photographed and measured twenty achenes of both morphs from modern populations before and after removing their perianth base.

5.5 Carbonization experiments: Results

Morphology

Size. The effects of carbonization on the size of achenes are pronounced. By any measure, both morphs shrink significantly ($p > 0.0001$ for change in area, length, width, and

LXW for both morphs). But this effect is not uniform between the two morphs. Tubercled morphs shrink more, averaging only 70% of their previous area, whereas smooth morphs average 76%. This difference is not a result of size differences between the two morphs: there is a very low correlation between original area and percentage remaining ($r^2=0.106$). It is likely that differential shrinkage rate between the two morphs is caused by the composition of the pericarp itself. This conclusion is further supported by the fact that there are differences between how mature and immature achenes are effected by carbonization. In both morphs, soft, immature achenes whose pericarps haven't finished developing shrink less than fully developed achenes. The recommended correction factors reported in Table 5.2 are derived from the pooled effects on mature and immature achenes. They are thus probably conservative since ancient harvests taken in late October or early November, when the seeds are most abundant and easy to remove, are unlikely to have contained many immature achenes.

Shape. Carbonization also affects achene shape. Differential effects between the two morphs are present but subtle. The aspect ratio of smooth morphs is not significantly different before and after carbonization ($p=0.8634$), whereas the aspect ratio of tubercled morphs decreases an average of 0.10, and this difference is significant ($p=0.0001$). This makes sense because the minor axis is differentially effected by carbonization between the two morphs (Table 5.3). The same is true of achene roundness: tubercled morphs roundness increases significantly, on average 0.50 (Table 5.4; $p=0.0001$), and smooth morphs do not change significantly one way or the other (Table 5.4; $p=0.2741$). But carbonization correction factors should not be used for aspect ratio or roundness because for both of these measures one standard deviation from the mean difference before and after carbonization includes both positive and negative values – *i.e.*

shape, as measured by these descriptors, does not change in a predictable manor due to carbonization (Table 5.4).

Table 5.2: Recommended correction factors for archaeological assemblages of erect knotweed				
Corrections for changes due to carbonization				
	Smooth		Tuberclcd	
<i>Size</i>	<i>w/ perianth</i>	<i>No perianth</i>	<i>w/perianth</i>	<i>No perianth</i>
Area	$A_2 * 1.24 = A_1$	$A_2 * 1.18 = A_1$	$A_2 * 1.30 = A_1$	$A_2 * 1.22 = A_1$
Length X Width	$LXW_2 * 1.20 = LXW_1$	$LXW_2 * 1.17 = LXW_1$	$LXW_2 * 1.29 = LXW_1$	$LXW_2 * 1.23 = LXW_1$
<i>Shape</i>				
Circularity	$C_1 = [(C_2 - 0.503) / -0.486] + C_2$			
Corrections for changes due to missing perianth base and receptacle				
	Smooth		Tuberclcd	
Area	$A_{no\ receptacle} * 1.10 = A_1$		$A_{no\ receptacle} * 1.13 = A_1$	
Length	$L_{no\ receptacle} * 1.12 = L_1$		$L_{no\ receptacle} * 1.17 = L_1$	
Aspect ratio	$AR_{no\ receptacle} + 0.14 = AR_1$		$AR_{no\ receptacle} + 0.19 = AR_1$	
Roundness	$R_{no\ receptacle} - 0.03 = R_1$		$R_{no\ receptacle} - 0.10 = R_1$	

Table 5.2: Recommended correction factors. Correction factors are only suggested for aspects of shape and size that change significantly *and* predictably (i.e. change is always in the same direction). See *Results* for more detailed discussion.

Table 5.3: Effects of Carbonization on Size			
N=100		Smooth	Tuberclcd
Area	Mean ± Std. Dev.	3.12 ± 0.467	3.41 ± 0.489
	Std. Err. of Mean	0.0674	0.0692
Area carbonized	Mean ± Std. Dev.	2.37 ± 0.396	2.37 ± 0.367
	Std Err of Mean	0.0571	0.0518
% remaining	Mean ± Std. Dev.	0.76 ± 0.089	0.70 ± 0.080
	Std Err of Mean	0.0128	0.0113
Length			
Length	Mean ± Std. Dev.	3.12 ± 0.254	2.83 ± 0.183
	Std Err of Mean	0.0366	0.0259
Length carbonized	Mean ± Std. Dev.	2.81 ± 0.237	2.47 ± 0.193
	Std Err of Mean	0.0342	0.0273

% remaining	Mean \pm Std. Dev.	0.90 \pm 0.036	0.87 \pm 0.042
	Std Err of Mean	0.0052	0.0060
Width	Mean \pm Std. Dev.	1.6 \pm 0.189	1.90 \pm 0.226
	Std Err of Mean	0.0272	0.0319
Width carbonized	Mean \pm Std. Dev.	1.43 \pm 0.212	1.53 \pm 0.171
	Std Err of Mean	0.0306	0.0241
% remaining	Mean \pm Std. Dev.	0.89 \pm 0.088	0.81 \pm 0.080
	Std Err of Mean	0.0127	0.0114
L X W	Mean \pm Std. Dev.	5.01 \pm 0.807	5.37 \pm 0.809
	Std Err of Mean	0.1164	0.1144
L X W carbonized	Mean \pm Std. Dev.	4.02 \pm .0730	3.79 \pm 0.589
	Std Err of Mean	0.1054	0.0834
% remaining	Mean \pm Std. Dev.	0.80 \pm 0.089	0.71 \pm 0.089
	Std Err of Mean	0.0129	0.0125

Table 5.4: Effects of carbonization on achene shape

N=100		Smooth	Tubercled
Aspect ratio (AR ₁)	Mean \pm Std. Dev.	1.94 \pm 0.254	1.46 \pm 0.169
	Std. Err. of Mean	0.0366	0.0239
Aspect ratio carbonized(AR ₂)	Mean \pm Std. Dev.	1.93 \pm 0.368	1.57 \pm 0.194
	Std Err of Mean	0.0531	0.0275
AR ₁ - AR ₂	Mean \pm Std. Dev.	0.01 \pm 0.250	-0.10 \pm 0.138
	Std. Err. of Mean	0.0361	0.0195
Roundness (R ₁)	Mean \pm Std. Dev.	0.52 \pm 0.063	0.69 \pm 0.076
	Std. Err. of Mean	0.0091	0.0107
Roundness carbonized (R ₂)	Mean \pm Std. Dev.	0.54 \pm 0.092	0.64 \pm 0.082
	Std. Err. of Mean	0.0133	0.0116

R ₁ – R ₂	Mean ± Std. Dev.	0.00 ± 0.070	0.05 ± 0.062
	Std. Err. of Mean	0.0102	0.0088
Circularity (C ₁)	Mean ± Std. Dev.	0.46 ± 0.086	0.41 ± 0.073
	Std. Err. of Mean	0.0124	0.0103
Circularity carbonized (C ₂)	Mean ± Std. Dev.	0.52 ± 0.060	0.61 ± 0.055
	Std. Err. of Mean	0.0087	0.0078
C ₁ – C ₂	Mean ± Std. Dev.	-0.10 ± 0.113	-0.20 ± 0.071
	Std. Err. of Mean	0.0164	0.0100

The most sensitive measure of shape deployed here is circularity, because it measures the relationship between area and perimeter, rather than relying on single point-to-point distances across the shape. Probably due to its greater sensitivity, circularity is the most effective shape descriptor for quantifying the slight differences in shape that result from carbonization. The circularity of both morphs increases significantly ($p=0.0007$ for smooth morphs, $p=0.0004$ for tubercled morphs; Table 5.4). Change in circularity is correlated with original circularity (Figure 5.2): the most circular achenes change shape less, whereas the least circular achenes gained the most circularity with carbonization. The effect is that the same assemblage of achenes is more homogenous with a smaller range of circularity values after carbonization than it was before carbonization. A simple additive correction factor using the average change in circularity overcorrects and yields a reconstructed mean that is too low (Table 5.5). A more accurate correction factor was derived from the equation of the least-squares regression line fit to a plot of post-carbonization circularity versus change in circularity ($C_1 - C_2$) (Table 5.2). I solved the equation of the least squares regression line for change in circularity (the unknown variable for archaeological assemblages):

$$C_2 = 0.503 - 0.486 * (C_1 - C_2) \rightarrow C_1 - C_2 = (C_2 - 0.503) / -0.486$$

The expected change in carbonization for a particular achene can be calculated and applied to its post-carbonization circularity to reconstruct its original circularity using the following formula:

$$C_1 = [(C_2 - 0.503) / -0.486] + C_2$$

I checked this correction factor using the known values for the pre-carbonization assemblage. It calculated the mean circularity of the assemblage to within .01 of the real value (Table 5.5).

Table 5.5: Tests of circularity correction factor			
Actual metrics		Reconstructed metrics	
		$C_1 = [(C_2 - 0.503) / -0.486] + C_2$	Smooth $C_1 = C_2 - 0.10$ Tubercled $C_1 = C_2 - 0.20$
Mean	0.435	0.437	0.414
Min	0.62	0.68	0.52
Max	0.23	0.29	0.24
Range	0.39	0.38	0.28

Table 5.5: Reports the results of tests on two different types of correction factors for changes in achene circularity due to carbonization: a linear function correction, and an additive correction factor. The linear function correction is able to more accurately predict the real values for the assemblage before carbonization from the post carbonization measurements.

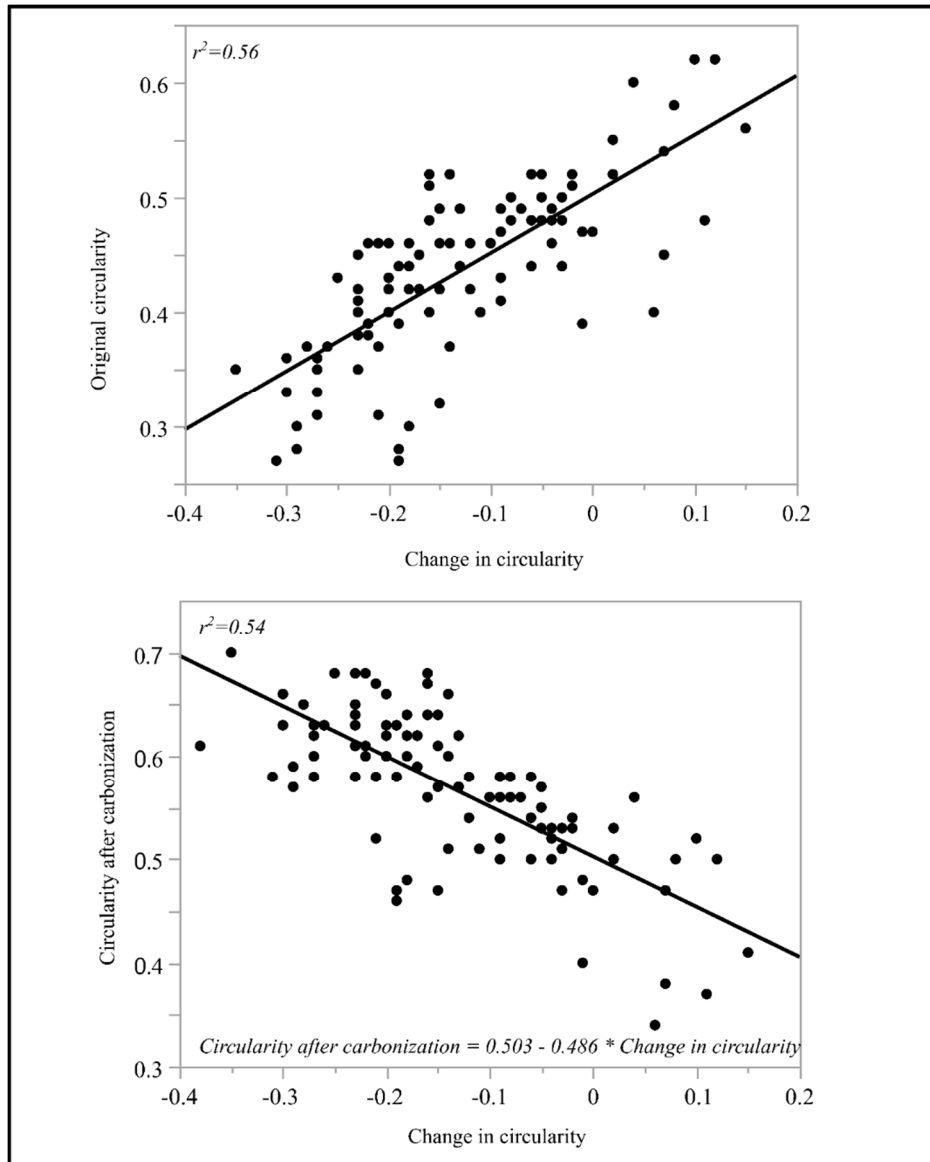


Figure 5.2: Shows the strong correlations between achene circularity and change in circularity. The equation of the line fit to the correlation between post-carbonization circularity and change in circularity was used to derive the correction factor recommended for achene shape (Table 5.2; Table 5.5).

Receptacle, and Perianth base. There was a significant difference between the size of the perianth bases between the two morphs: the smooth morph perianth base accounts for a smaller percentage of total achene area than does the perianth base of the tubercled morph, and is smaller in absolute terms (Table 5.6). Not surprisingly, removing the perianth base also changes the

shape of the achene (Table 5.6). Here, aspect ratio and roundness show more clear differences than does circularity because the shape of the achene mostly changes in that its major axis is reduced when the perianth base is removed. Recommended correction factors are given in Table 5.2.

Table 5.6: Effects of perianth base and receptacle size and shape			
N=20		Smooth	Tubercled
Area (A_1)	Mean \pm Std. Dev.	2.42 \pm 0.264	2.93 \pm 0.298
	Std Err of Mean	0.0836	0.0942
$A_{\text{no perianth base}}$	Mean \pm Std. Dev.	2.19 \pm 0.252	2.53 \pm 0.219
	Std Err of Mean	0.0797	0.0693
% remaining	Mean \pm Std. Dev.	0.90 \pm 0.029	0.87 \pm 0.031
	Std Err of Mean	0.009	0.0099
$A_1 - A_{\text{no perianth base}}$	Mean \pm Std. Dev.	0.23 \pm 0.071	0.40 \pm 0.116
	Std Err of Mean	0.0226	0.0368
<hr/>			
Length (L_1)	Mean \pm Std. Dev.	2.94 \pm 0.201	2.68 \pm 0.098
	Std Err of Mean	0.0635	0.031
$L_{\text{no perianth base}}$	Mean \pm Std. Dev.	2.58 \pm 0.152	2.23 \pm 0.132
	Std Err of Mean	0.048	0.0417
% remaining	Mean \pm Std. Dev.	0.88 \pm 0.024	0.83 \pm 0.044
	Std Err of Mean	0.0077	0.0139
$L_1 - L_{\text{no perianth base}}$	Mean \pm Std. Dev.	0.36 \pm 0.085	0.45 \pm 0.124
	Std Err of Mean	0.0268	0.0393
<hr/>			
Aspect ratio (AR_1)	Mean \pm Std. Dev.	2.12 \pm 0.270	1.46 \pm 0.118
	Std Err of Mean	0.0853	0.0373
$AR_{\text{no perianth base}}$	Mean \pm Std. Dev.	1.99 \pm 0.194	1.27 \pm 0.090
	Std Err of Mean	0.0612	0.0285
$AR_1 - AR_{\text{no perianth base}}$	Mean \pm Std. Dev.	0.14 \pm 0.137	0.19 \pm 0.104

	Std Err of Mean	0.0434	0.0328
Roundness (R_1)	Mean± Std. Dev.	0.48±0.055	0.69±0.056
	Std Err of Mean	0.0175	0.0178
$R_{\text{no perianth base}}$	Mean± Std. Dev.	0.51±0.048	0.79±0.058
	Std Err of Mean	0.0153	0.0184
$R_1 - R_{\text{no perianth base}}$	Mean± Std. Dev.	-0.03±0.028	-0.10±0.057
	Std Err of Mean	0.0088	0.0179
Circularity (C_1)	Mean± Std. Dev.	0.49±0.055	0.46±0.051
	Std Err of Mean	0.0175	0.0161
Circularity $_{\text{no perianth base}}$	Mean± Std. Dev.	0.57±0.061	0.57±0.091
	Std Err of Mean	0.0193	0.0287
$C_1 - C_{\text{no perianth base}}$	Mean± Std. Dev.	-0.08±0.080	-0.11±0.092
	Std Err of Mean	0.0252	0.0290

Preservation

The perianth is almost never preserved on archaeological carbonized specimens. At the outset of this experiment I considered it likely that the perianth was destroyed by carbonization. Results suggest that, to the contrary, the perianth is not at all likely to be destroyed by carbonization, at least under the conditions used in this study. Of 100 achenes carbonized in Phase III, 36 retained their entire perianth after carbonization, and 60 retained parts of it. Only 4 completely lacked a perianth as a result of carbonization. It is possible that a different firing temperature or duration would destroy the perianth, or that taphonomic processes after carbonization removed the perianths from carbonized archaeological specimens. Still, the fact that perianth fragments are extremely rare on carbonized archaeological specimens and are almost universally retained on experimentally carbonized achenes suggests that perianth removal may have been a processing task prior to and separate from pericarp fracturing or removal.

Differential preservation of smooth and tubercled pericarps. At 300°C, smooth morphs were slightly more likely to fracture (Figure 5.3). At 350°C, the difference in preservation between the two morphs increased greatly: only 4/50 smooth achenes remained intact, compared to 27/50 tubercled achenes (Figure 5.3). We can thus expect tubercled morphs to be preserved in carbonized assemblages in greater numbers than smooth morphs. Until methods for reconstructing the carbonizing conditions that effected particular assemblages improve, it will be impossible to correct for this differential preservation quantitatively. Qualitatively, this result makes the existence of carbonized assemblages composed primarily of smooth morphs all the more compelling evidence of domestication: it is highly unlikely that such assemblages are the result of a preservation bias. On the contrary, this indicator of domestication is evident *in spite of* a preservation bias that would tend to obscure it.

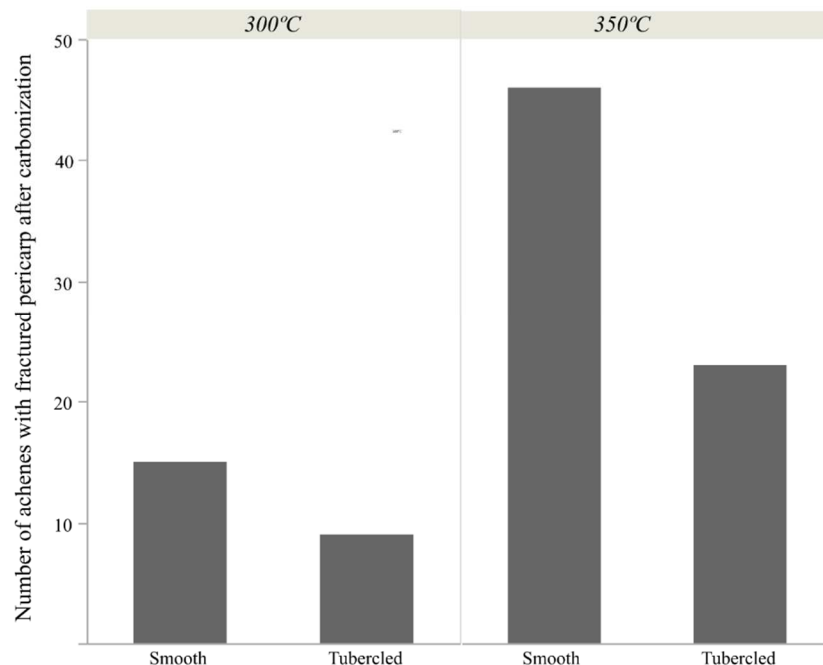


Figure 5.3: Shows the differential preservation of smooth and tubercled morphs after 30 minutes at 300°C and 350°C, respectively.

5.6 Sampling Bias

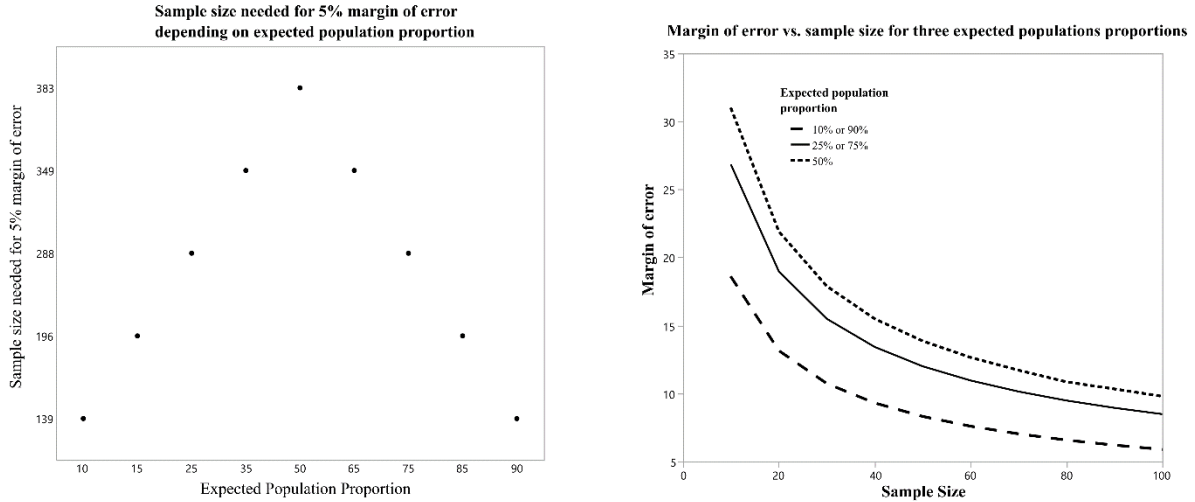


Figure 5.4. These two charts are visualizations of the probabilistic relationship between population proportion and sample size. For both graphs, confidence is set at 95%. Left: It is more difficult to estimate population proportion accurately from a sample the closer the population proportion is to 50/50. If the true population proportion is skewed towards one or the other type (90% or 10% in this chart), it is relatively easy to estimate. Right: Since the ideal sampling conditions cannot always be met, the graph on the right shows the margins of error for different sample sizes given different true population proportions (which are unknown for archaeological assemblages). The maximum population proportion of smooth morphs observed in modern wild populations is 72%. Example: With a sample of 30, the margin of error for a population proportion of 75% is 15.49. In other words, we cannot be confident that a sample ($n=30$) with a proportion of 90% smooth morphs is outside of the range of natural variation. At $n=40$, these two hypothetical populations (75% and 90%) still have slightly overlapping expected sample proportion ranges: 61 – 89% and 81 – 99%, respectively. However, if we have a sample of 40 with a proportion >89% smooth morphs, we can be confident that it is outside the natural range of variation. There is some overlap in expected ranges even with large samples of >100, which makes it hard to draw definite conclusions about the domestication syndrome of archaeological samples, even large ones, with sample proportions in the high 70s or low 80s, like the Westpark assemblage (see text).

Accurately Estimating Population Proportion.

Population proportion is the percentage of a given population that has a particular nominal (non-continuous) characteristic. Sample proportion is the percentage of a given sample that has that characteristic. In the case of erect knotweed domestication, the characteristic of interest is the percentage of a given harvest made up of smooth morphs. I sampled populations of erect knotweed between mid-October and mid-November over two growing seasons in order to estimate the range of normal population proportions of smooth morphs for erect knotweed (see

Chapter 4). There was a large range of sample proportions in modern erect knotweed, from 29 – 72% smooth morphs at sample sizes varying from 814–3011 achenes. Figure 5.4 shows the sample size necessary to estimate population proportion with a 5% margin of error at 95% confidence for different population proportions. It is more difficult to accurately predict population proportions close to 50/50 than it is to estimate highly skewed population proportions, but the sample sizes necessary for estimates at this level of accuracy even for skewed populations are larger than most of the archaeological samples of erect knotweed available.

Archaeologists cannot dictate sample size but must instead account for the error and uncertainty inherent to our small samples. I calculated the margin of error for different sample sizes at 95% confidence for three hypothetical populations of erect knotweed: 1) an assemblage made up of 90% smooth morphs, which is outside of the natural range of variation and constitutes evidence for domestication; 2) an assemblage made up 75% smooth morphs, which is just over the highest observed wild population proportion; and 3) an assemblage that is 50% smooth morphs and 50% tubercled morphs, normal for wild erect knotweed (Figure 5.4). Given the large margins of error, we can expect samples of ten from all three hypothetical populations to overlap. That is, even if all ten in the sample are smooth morphs, the sample could very easily come from a normal wild population (Figure 5.4). Because of the dynamic relationship between observed sample proportion, sample size, and margin of error, I decline to set a sample proportion above which an assemblage is domesticated and below which it is wild. The sample proportion should be assessed along with assemblage size for each individual case, as, for example, in the following case study (see also Chapter 6).

Case Study: The Westpark Assemblage.

The largest archaeological assemblage that I analyzed came from Feature 300 of the Westpark site, IL. Westpark is a multi-component site that was occupied from at least c. cal. 650 -- 1100 CE) (Lopinot et al. 1991; Powell 2000; Chapter 6). A direct date on the analyzed knotweed yielded a date of cal. 1037-1183 CE (uncal. 910 BP +/- 20). Feature 300 was an irregular oval shaped pit. The bottom 2-5 cm of the pit contained a homogenous mass of erect knotweed kernels and achenes. For my initial morphometric analysis, I randomly sub-sampled 100 achenes from the tens of thousands that were recovered from this context. These achenes are significantly larger, on average, than my modern comparative sample (Chapters 2-3). The proportion of smooth morphs in this first sub-sample was 81%, somewhat outside of the natural range of variation, but within the 95% confidence estimate for a population proportion of 75% with a sample of 100 (Figure 5.4). I took advantage of this unusually large assemblage to independently confirm the confidence and accuracy estimates generated mathematically. An additional 20 random samples of 10 yielded sample proportions ranging widely from 30–100% smooth morphs – exactly as predicted if the true population proportion was ~75% smooth morphs. Ten random samples of 20 yielded sample proportions of 70–90%, again as predicted by the laws of probability.

For the entire sample of 500 that this process yielded, the Westpark assemblage sample proportion was 78% smooth morphs. Since a sample of 500 is more than is required for a 5% confidence margin no matter what the true population proportion (Figure 5.4), this means that the Westpark assemblage has *at least* a slightly higher proportion of smooth morphs than has been observed in a wild population: somewhere between 73–83% smooth morphs. Considering that smooth morphs are likely to be systematically underrepresented in carbonized assemblages due to differential preservation (Figure 5.3), this sample proportion constitutes equivocal evidence

for the effects of human selection at the Westpark site. Taken together with the fact that the Westpark achenes are significantly larger than is normal for erect knotweed, and come from a context that clearly indicates large scale cultivation (Powell 2000), a strong case can be made for domestication at this site.

5.7 Conclusions

The analyses reported here were conducted primarily to facilitate the study of a particular crop: erect knotweed. But the issues raised pertain to other studies of plant domestication using archaeological assemblages in several ways. Previous studies have shown that carbonization can affect the shape and size of seeds differently depending on the composition of the seed, duration of exposure to heat, and fire temperature. Carbonization can also lead to differential preservation, biasing the archaeological record and sometimes eliminating the very characters necessary for recognizing a species or domesticated subspecies. Both of these effects present problems for the study of domestication through morphology. But in this case, the narrow window of conditions under which the pericarp is preserved helps narrow down the possible effects of carbonization on erect knotweed achenes. Experiments showed that the pericarp of erect knotweed achenes, especially on smooth morphs, is unlikely to survive intact at temperatures above 300°C. This means that carbonization corrections derived from low-temperature fires (300°C in this study) are likely to be accurate for *all* well-preserved archaeological assemblages, because specimens burned in hotter fires are probably only preserved in the form of kernels. Such triangulation may be possible for other crop species as well.

Variation in the effects of carbonization has led some researchers to call for the use of nominal (present/absent) characteristics to argue for domestication (Wright 2003). The state of

the art in cereal domestication studies is to use the presence or absence of non-shattering inflorescences as an indicator of domestication, either along with seed size or independently of it (i.e. Fuller et al. 2009; Tanno and Wilcox 2012). For chenopods, seed coat texture and margin configuration are crucial nominal characteristics for identifying taxa and for distinguishing between wild and domesticated assemblages (Bruno 2006; Fritz and Smith 1988), and some researchers have used the sample proportions of wild and domesticated types to argue for divergent management practices (and thus crop evolution) between communities (Gremillion 1993). For erect knotweed, the nominal characteristic of interest is the proportion of smooth morphs in a population. Because wild erect knotweed also produces smooth morphs, *their presence alone does not suggest domestication*. While this may seem like a problem unique to erect knotweed, it is not. The characteristics associated with domestication (testa characteristics and margin configuration for chenopods, tough rachises in cereals) are also present at low frequencies in wild populations, and become more common over time as selective pressures associated with cultivation begin to leave their mark.

For each domesticate, it is necessary to determine what sample proportion (at what sample size) is necessary to recognize an assemblage that is outside the range of variation for wild plants. In some cases, this will probably involve first establishing what that range of natural variation is. The characterization of erect knotweed variability presented here and elsewhere should be considered preliminary. Harvest proportions of smooth morphs varied from 29%-72% across two growing seasons and two populations – such variance requires explanation. The same problem applies to another EAC crop, goosefoot (*C. berliandieri*) in ENA. The syndrome of domestication includes, among other characters, a reduction in testa thickness. Specimens exhibiting this characteristic are similar to “red morphs” – a thin-testa seed type present in small

proportions on wild plants (Fritz and Smith 1988). Very few studies have attempted to quantify the frequency of red morphs in wild populations. Asch and Asch (1985:179-180) state that “most wild plants have at least a few” of this type, but they also encountered a population in which the red morph predominated. Their subsequent harvests convinced them that this condition was rare and probably resulted from unusual growing conditions. Smith (1985:122) made a collection of 5,736 fruits from four different populations. Red morphs constituted 1-3% of these samples. As for erect knotweed smooth morphs, a much larger sampling effort could be made to determine what genetic or environmental factors govern the production of red morphs.

For wheat and barley, even if we assume that wild populations originally had negligible proportions of domesticated types on the theoretical grounds that such a trait would be maladaptive (Hillman and Davies 1990:167), changes over time in the population proportion of brittle to tough rachises are used to track the process of domestication (i.e. Asouti and Fuller 2012; 2013). The same is true for rice; for example, a shift from 27.3% domesticated type to 38.8% domesticated type over ~300 years at one site has been reported as evidence of the process of domestication (Fuller et. al. 2009). Such subtle shifts in population proportion are only detectable with very large samples (>100) that are at least arguably drawn from the same living population. Aggregating many small samples from across an entire site to estimate population proportion may lead to large sampling errors. The more evenly mixed an assemblage is between domesticated and wild types, the greater the margin of error (Figure 5.4) and potential for mistaking sampling error for a real trend, and the larger the sample needed to recognize subtle changes in proportion confidently.

The correction factors and sampling models presented here should be of use to paleoethnobotanists who wish to assess where their assemblages of erect knotweed fall on the

continuum between wild and domesticated. I expect that both experimental corrections and assessments of variability in wild populations will be refined and amended by future studies, but the analyses presented here should allow researchers to track the process of erect knotweed domestication in the archaeological record, thus adding to our knowledge of agricultural practice across ancient ENA.

5.8 References

Asch, David L. and Nancy B. Asch

1985 Prehistoric Plant Cultivation in West Central Illinois. In *Prehistoric Food Production in North America*, edited by Richard I. Ford, pp. 149-203. Anthropological Papers. vol. 75. Museum of Anthropology, University of Michigan, Ann Arbor, MI.

Asch, Nancy B. and David L. Asch

1978 The Economic Potential of *Iva annua* and its Prehistoric Importance in the Lower Illinois Valley. In *The Nature and Status of Ethnobotany*, edited by Richard A. Ford, pp. 301-343. Anthropological Papers. vol. 67. Museum of Anthropology, University of Michigan, Ann Arbor, MI.

Asouti, Eleni and Dorian Q. Fuller

2012 From Foraging to Farming in the Southern Levant: The Development of Epipalaeolithic and Pre-Pottery Neolithic Plant Management Strategies. *Vegetation History and Archaeobotany* 21(2):149-162.

2013 A Contextual Approach to the Emergence of Agriculture in Southwest Asia. *Current Anthropology* 54(3):299-345.

Boardman, Sheila and Glynis Jones

1990 Experiments on the effects of charring on cereal plant components. *Journal of Archaeological Science* 17(1):1-11.

Braadbaart, Freek, Jaap J Boon, H Veld, P David and Pim F van Bergen

2004 Laboratory simulations of the transformation of peas as a result of heat treatment: changes of the physical and chemical properties. *Journal of Archaeological Science* 31(6):821-833.

Braadbaart, Freek and Pim F van Bergen

- 2005 Digital imaging analysis of size and shape of wheat and pea upon heating under anoxic conditions as a function of the temperature. *Vegetation History and Archaeobotany* 14(1):67-75.

Braadbaart, Freek and Patti J. Wright

- 2007 Changes in Mass and Dimensions of Sunflower (*Helianthus annuus* L.) Achenes and Seeds Due to Carbonization. *Economic Botany* 61(2):137-153.

Bruno, Maria C.

- 2006 A Morphological Approach to Documenting the Domestication of *Chenopodium* in the Andes. In *Documenting Domestication: New Genetic and Archaeological Paradigms*, edited by Melinda A Zeder, Daniel G. Bradley, Eve Emshwiller and Bruce D Smith, pp. 32-45. University of California Press, Berkeley.

Childs, Dylan Z., C.J.E. Metcalf and Mark Rees

- 2010 Evolutionary Bet-Hedging in the Real World: Empirical Evidence and Challenges Revealed by Plants. *Proceedings of the Royal Society of London B: Biological Sciences* rspb20100707:1-10.

Crites, Gary D.

- 1993 Domesticated Sunflower in the Fifth Millennium B.P. Temporal Context: New Evidence from Middle Tennessee. *American Antiquity* 58(1):146-148.

Fritz, Gayle J.

- 1986 Prehistoric Ozark Agriculture: The University of Arkansas Rockshelter Collections. Dissertation, Anthropology, University of North Carolina, Chapel Hill.

- 1993 Early and Middle Woodland Period Paleoethnobotany. In *Foraging and Farming in the Eastern Woodlands*, edited by C. Margaret Scarry, pp. 39-56. University Press of Florida, Gainesville.

Fritz, Gayle J. and Bruce D. Smith

- 1988 Old Collections and New Technology: Documenting the Domestication of *Chenopodium* in Eastern North America. *Midcontinental Journal of Archaeology* 13(1):3-27.

Fuller, Dorian Q., Ling Qin, Yunfei Zheng, Zhijun Zhao, Xugao Chen, Leo Aoi Hosoya and Sun. Guo-Ping

2009 The Domestication Process and Domestication Rate in Rice: Spikelet Bases from the Lower Yangtze. *Science* 323:1607-1610.

Gremillion, Kristen J.

1993 The Evolution of Seed Morphology in Domesticated Chenopodium: An Archaeological Case Study. *Journal of Ethnobiology* 13:149-169.

Kay, Marvin, Francis B. King and Christine K. Robinson

1980 Cucurbits from Phillips Spring: New Evidence and Interpretations. *American Antiquity* 45(4):806-822.

Lopinot, Neal H., Gayle J. Fritz and John E. Kelly

1991 The Archaeological Context and Significance of *Polygonum erectum* Achene Masses from the American Bottom Region. *Proceedings of the 14th Annual Society for Ethnobiology Conference*. St. Louis.

Märkle, Tanja and Manfred Rösch

2008 Experiments on the effects of carbonization on some cultivated plant seeds. *Vegetation history and archaeobotany* 17(1):257-263.

Powell, Gina

2000 Charred, Non-Maize Seed Concentrations in the American Bottom Area: Examples from the Westpark Site (11-MO-96), Monroe County, Illinois. *Midcontinental Journal of Archaeology* 25(1):27-48.

Silvertown, Jonathan W

1984 Phenotypic Variety in Seed Germination Behavior: The Ontogeny and Evolution of Somatic Polymorphism in Seeds. *American Naturalist* 124(1):1-16.

Simon, Mary L. and Kathryn E. Parker

2006 Prehistoric Plant Use in the American Bottom: New Thoughts and Interpretations. *Southeastern Archaeology* 25(2):212-257.

Slatkin, Montgomery

1974 Hedging One's Evolutionary Bets. *Nature* 250:704-705.

Smith, Bruce D.

1985 *Chenopodium berlandieri* ssp. *jonesianum*: evidence for a Hopewellian domesticate from Ash Cave, Ohio. *Southeastern Archaeology* 4(2):107-133.

1992 *Rivers of Change: Essays on Early Agriculture in Eastern North America*. Smithsonian Institution Press, Washington.

2006 Eastern North America as an Independent Center of Plant Domestication. *Proceedings of the National Academy of Sciences* 103(33):12223-12228.

2014 The Domestication of *Helianthus annuus* L. (Sunflower). *Vegetation History and Archaeobotany* 23(1):57-74.

Smith, Bruce D. and Vicki A. Funk

1985 A Newly Described Subfossil Cultivar of *Chenopodium* (Chenopodiaceae). *Phytologia* 57(7):445-448.

Smith, Bruce D. and Richard A. Yarnell

2009 Initial Formation of an Indigenous Crop Complex in Eastern North America at 3800 B.P. *Proceedings of the National Academy of Sciences* 106(16):6561-6566.

Tanno, Ken-ichi and George Willcox

2012 Distinguishing Wild and Domestic Wheat and Barley Spikelets from Early Holocene Sites in the Near East. *Vegetation History and Archaeobotany* 21(2):107-115.

Tarighat, Somayeh S., David L. Lentz, Stephen F. Matter and Robert Bye

2011 Morphometric Analysis of Sunflower (*Helianthus annuus* L.) Achenes from Mexico and Eastern North America. *Economic Botany* 65(3):260-270.

Volney, Jones H.

1936 The Vegetal Remains of Newt Kash Hollow Shelter. In *Rock Shelters of Menifee County, Kentucky*, edited by W.S. Webb and W.D. Funkhouser, pp. 147-165. vol. 3. University of Kentucky Reports in Archaeology and Anthropology, Lexington.

Wright, Patti J.

2003 Preservation or destruction of plant remains by carbonization? *Journal of Archaeological Science* 30(5):577-583.

2008 Understanding the Carbonization and Preservation of Sunflower and Sumpweed Remains. *Midcontinental Journal of Archaeology* 33(2):139-153.

Yarnell, Richard A.

1972 *Iva annua* var. *macrocarpa*: Extinct American Cultigen? *American Anthropologist* 74:335-341.

1978 Domestication of Sunflower and Sumpweed in Eastern North America. In *The Nature and Status of Ethnobotany*, edited by Richard A. Ford, pp. 289-299. Anthropological Papers No. 67. Museum of Anthropology, University of Michigan, Ann Arbor, MI.

Yurtseva, O.V.

2001 Ultrasculpture of Achene Surface in *Polygonum* section *Polygonum* (Polygonaceae) in Russia. *Nordic Journal of Botany* 21(4):513-528.

6. Seeds as Artifacts: The Domestication of Erect Knotweed in Eastern North America

6.1 Domestication and Landraces: Artifacts of Ancient Agricultural Practice

“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, *The Origin of Species*

The origins of food production are often explained either with macroevolutionary theories or with morphological analysis of domesticated plants and animals. The former try to explain *why* human societies began to produce food in the context of large scale processes such as climate change, human population growth, increasing socio-economic complexity, or competition among elites (reviewed in Price and Bar-Yosef 2011). The latter examine *what* happened to plants and animals as a result of human selection and ecosystem engineering. These studies document morphological or genetic changes in domesticated plants and animals (e.g. Yarnell 1972; Fritz and Smith 1988; D’Andrea et al. 2001; Wilcox 2004; Fuller 2009 et al.; Langlie et al. 2011). There is an explanatory gap between these two approaches that needs to be filled. Agricultural practices are niche-constructing or ecosystem engineering behaviors that modify the selective pressures on plants and animals living near people (Jones et al. 1994; Odling-Smee et al. 2003; Rindos 1984). Niche construction has been proposed as a mechanism to bridge the gap between *what* and *why* approaches, allowing researchers to explain *how* specific cultural practices resulted in domestication (Crites 1987; Smith 2007; Fuller et al. 2010; Rowley-Conwy and Layton 2011; Wollstonecroft 2011).

The morphologies of cultivated plants are artifacts of agricultural practices and of the agroecosystems they maintained. I define domestication as a process of co-evolution whereby

human practice changes the bodies and behaviors of plants and animals. By this definition, domesticates are artifacts, shaped as they are by human knowledge and skill. The habitual actions that result in domestication also have the potential to transform aspects of human society, including the scheduling and organization of labor, norms governing the accumulation and distribution of surplus, the consumption and exchange of food, and the role of gender and other identities in structuring all of these processes. Agricultural practice structures change both in domesticate biology and in the organization of human society. Via this explanatory link, the seemingly esoteric study of seed morphology is ideally suited to shed light on a key transformation in human history: the development of systems of food production out of systems of food procurement.

Humans do not cease their shaping of domesticated plants and animals at the moment that they can be distinguished from their wild progenitors. They continue to exert selective pressure on their 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. Since the discovery of hybrid vigor prompted the breeding of genetically homogenous crop varieties, the trend within industrialized agriculture has been towards greater homogeneity in crop morphology and genetics. This trend has only increased with the addition of patentable genes to elite hybrid varieties. In this context, it is easy to lose sight of the simple fact pointed out by Darwin in the opening lines of *The Origin of Species*: domestication usually creates a remarkable degree of variation in comparison to natural selection. Happily, we need only look around the local dog park or community garden to be reminded. Within each domesticated species, hundreds or thousands of locally adapted varieties have been developed by individuals or communities (Brush, ed. 2000).

The development and exchange of ancient landraces has increasingly been the subject of study within archaeology, using both ancient DNA and morphometrics (e.g. Freitas 2003; Lema et al. 2008; da Fonseca et al 2014; Toulemonde et al. 2015; Liu et al. 2016). Meanwhile, a great deal of effort has been expended in the past decade elucidating how contemporary farmers maintain morphologically and functionally distinct landraces. This body of research demonstrates that landrace morphologies are artifacts of communities of practice, and of the diffusion (or lack thereof) of knowledge and material between them (e.g. Louette and Smale 2000; Perales et al. 2005; Badtsue et al. 2006; Kiptot et al. 2006; Moreno et al. 2006; McGuire 2008; Misiko 2010; Stromberg et al. 2010; Calvet-Mir et al. 2012; Mathieu et al. 2012; Pautasso et al. 2012;). Making the connection between crop morphology in the archaeological record and the myriad social dynamics they embody requires 1) a high resolution morphological dataset; and 2) experimental studies designed to test the effects of specific practices on the morphologies that are observable in archaeological specimens.

6.2 The Erect Knotweed Domestication Project

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 Eastern North America (ENA). This is a particularly interesting region in which to use seeds as artifacts, because it was home to a pre-maize indigenous agricultural system 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 for thousands of years before the introduction of maize and other tropical crops from Mexico (Ford, ed. 1985; Smith

2006). Erect knotweed is one of these native annual seed crops, commonly recovered from storage pits, hearths, and middens at archaeological sites in ENA dating between c. cal. 1000 BCE – CE 1400.

Erect knotweed was cultivated for its edible seeds. It produces seeds that are encased in an inedible pericarp, or fruit coat. This type of fruit is called an achene. Both achenes (fruits) and kernels (seeds) are commonly recovered from archaeological sites, although the latter are usually more abundant in carbonized assemblages. Erect knotweed exhibits seasonally controlled achene dimorphism, which means that individual plants produce two distinct fruit types in ratios that vary over the course of the growing season (Costea et al. 2005; Chapter 2). The two morphs are called *smooth* and *tubercled* with reference to the surface texture of their pericarp. During the summer and early fall, plants produce only tubercled morphs. Beginning in mid-September, plants begin to produce both tubercled and smooth morphs. 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 (Brenckle 1946; Chapter 4). The two different types are sometimes referred to as *late season morphs* and *early season morphs*, but I will use *smooth* and *tubercled* here: the former terms are misleading since both morphs are produced late in the season Chapter 4). The functional difference between them is that smooth morphs will germinate immediately the spring after they are produced, whereas tubercled morphs can probably survive in the seedbank for at least 18 months (Yurtseva 2001; Chapter 4). As an annual seed crop, a useful starting hypothesis is that domesticated erect knotweed will exhibit the *domestication syndrome* characteristic of many such crops (Harlan et al 1973). In this context, a syndrome is a suite of characteristics shared by unrelated taxa that have to contend with similar environmental constraints (ex. similar floral morphology among plants that share the

same class of pollinators). Aspects of the domesticate syndrome in annual seed crops that are observable from seeds and fruits includes an increase in seed/fruit size, a loss of natural dehiscence mechanisms, and a reduction in germination inhibitors.

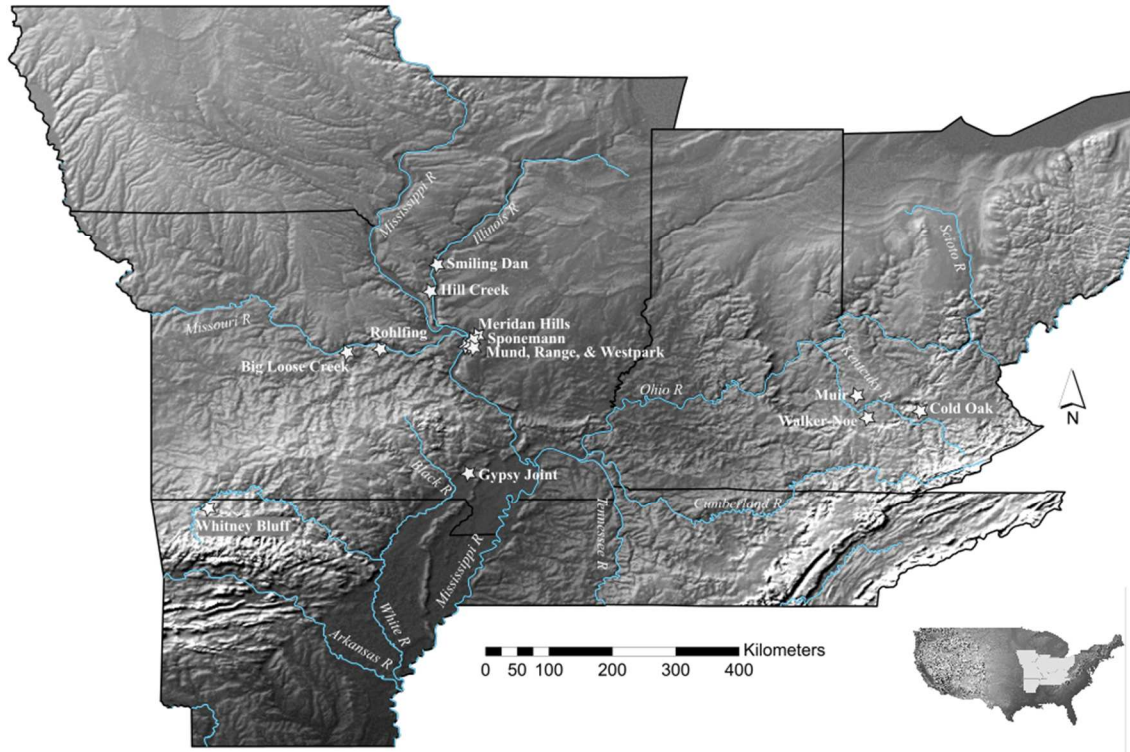
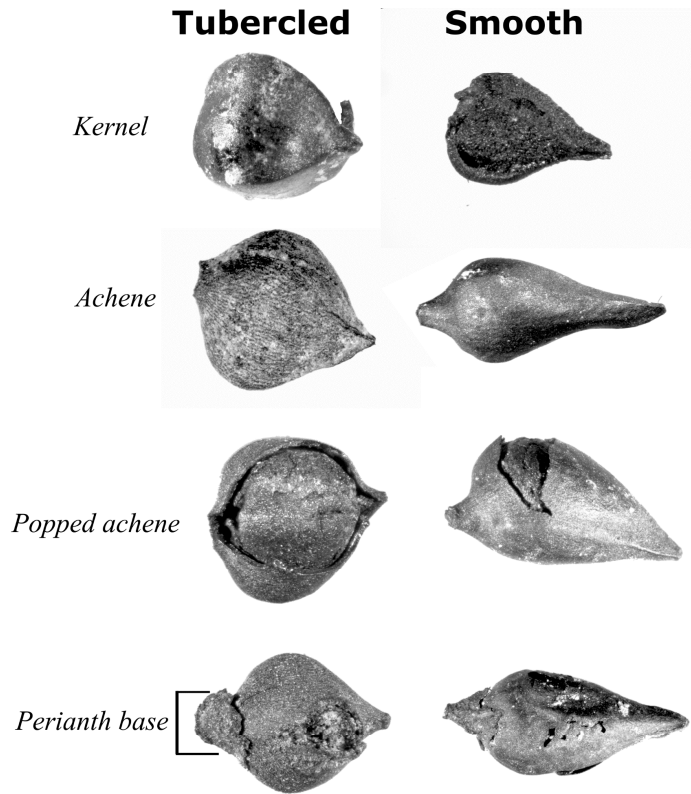


Figure 6.1. Map of study area including rivers mentioned in text and sites with analyzed assemblages

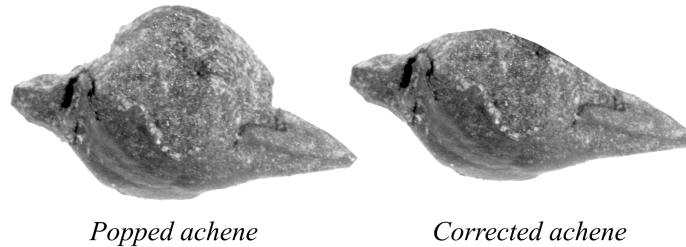
Beginning in the 1980s, paleoethnobotanists recognized that one species of knotweed had been cultivated by ancient Native Americans in what Fritz (1993:41) has called the “core area” of pre-maize agriculture: from western Iowa, Missouri, and Arkansas to eastern Ohio, Illinois, Indiana, Kentucky, and Tennessee (Figure 6.1). They identified the cultivated species as erect knotweed based on the striate-tubercled surface texture and shape of archaeological tubercled morphs (Asch and Asch 1985c; Figure 6.2). The morphology of smooth achenes has not been the subject of much study by either botanists or archaeologists prior to this study, and they 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 erect knotweed plants. This bit of taxonomic esoterica complicates the identification of assemblages that lack tubercled morphs (Chapter 2; Chapter 3).

**Experimentally carbonized
modern erect knotweed**



Domesticated erect knotweed, Gypsy Joint



 **2mm**

Figure 6.2. Examples of photographs used in morphometric analysis. The images of experimentally carbonized modern erect knotweed show the different states of preservation commonly found in the archaeological record. Kernels are the seed of the erect knotweed plant, lacking its pericarp. They are common in the archaeological record, but were not included in the morphometric analyses for this study. Examples of complete achenes of both tubercled and smooth morphs are shown, as well as popped achenes with part of their perisperm protruding. Many complete achenes retain their perianth (flower) base. Morphometric corrections have been developed to correct for missing perianth bases so that all complete achenes can be directly compared (Appendix 3.2). A typical domesticated smooth morph from Gypsy Joint is shown, both for a visual size comparison with modern achenes, and to demonstrate how images of popped achenes were sometimes corrected so that they could be included in the morphometric analysis. The side by side images are the same achene before and after correction.

Speculation about a domesticated subspecies of erect knotweed began when two curious assemblages were reported in the mid-1980s. First, Asch and Asch (1985b; 1985c) reported a carbonized assemblage from the Late Mississippian Hill Creek site, IL that was composed exclusively of abnormally large smooth morphs. Fritz (1986) reported a similar nearly monomorphic assemblage of large smooth morphs from the Mississippian Whitney Bluff site, AR. The latter has been the subject of a comparative analysis that resulted in the naming of a new sub-species, domesticated erect knotweed (*Polygonum erectum* ssp. *watsoniae*). Domesticated erect knotweed differs from its wild progenitor morphologically in two ways: its achenes are larger, and achene dimorphism is reduced or eliminated in favor of smooth morphs (Chapter 3; Chapter 3). The selective pressures that may have led to these changes under cultivation, informed by two years of observations of wild populations and cultivation under controlled conditions, are explored in greater depth elsewhere (Chapter 4).

6.3 Archaeological background

ENA is one of the independent centers of plant domestication, where hunters and gatherers domesticated plants (in this case not animals) and developed food producing economies in the absence of any obvious influence from pre-existing agricultural societies. Domestication of annual plants began c. 3000 BCE, during the Late Archaic period. The earliest domesticates were squash (*Cucurbita pepo* ssp. *ovifera*) sumpweed (also referred to as marshelder; *Iva annua*), sunflower (*Helianthus annuus*), and goosefoot (*Chenopodium berlandieri*). 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; Yarnell 1972; Smith 2014). 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 1984; Smith and Funk 1985; Fritz and Smith 1988; Gremillion 1993a). For squash, domestication is recognized by an increase in seed size and an increase in rind thickness (Kay et al. 1980; Cowan and Smith 1993; Fritz 1999). 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 and Shapiro 2011; Kistler et al. 2015). Bottle gourds (*Lagenaria siceraria*) were also cultivated during the Archaic (Kay et al. 1980; Doran et al. 1990). 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, *contra* Erickson et al. 2005).

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 cal. 3000 BCE (Smith and Yarnell 2009). 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 (Fritz 1999). 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 BCE, 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 developed or obtained domesticated sumpweed by c. cal. 2,200 BCE: 44 abnormally large sumpweed achenes come from the Late Archaic strata of this site. Unlike the 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 Eastern Agricultural Complex (EAC), including squash, goosefoot, and sunflower. In addition to these, the inhabitants of Napoleon Hollow were also evidently experimenting with giant ragweed (*Ambrosia trifida* L.), which never became an important crop (Asch and Asch 1986). By c. cal. 1,800 BCE, 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 populations 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. This is also evident at the shell-mound Archaic sites of the Green River in Kentucky, where 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, these populations of hunter-gatherers developed and maintained

domesticated landraces of at least four different plants, which means that they subjected these species to some form of consistent selective pressure. During this 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, a few knotweed seeds, species unknown, were recovered from Carlston Annis and Peter Cave (Crawford 1982). Given the weedy nature of these species, a few seeds may simply represent the local vegetation (Simon 2009). 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.

The Early Woodland period is marked by either an interruption of settlement or movement 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). Not surprisingly, the most abundant evidence for Early Woodland food production comes from the upland rockshelters, especially in eastern Kentucky and Tennessee. This is likely only partially caused by preservation or sampling bias: there is strong evidence that cultivation also moved out of the floodplain and onto upland terraces in this region at this time (Gremillion 2004; Gremillion et al. 2008). Significant clearance of upland forest, most likely by anthropogenic fire, was coincident with the movement of people out of the major floodplains on the eastern periphery of the core area (Delcourt et al. 1986; Delcourt et al. 1998). 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). Small amounts of erect knotweed

are also sometimes recovered from rockshelters and caves dating to the Early Woodland, including the assemblage from Cold Oak, reported below, and the assemblages from the Salts and Mammoth cave system (Gremillion 1993b; Yarnell 1974b).

On the western margin of the core area, EAC assemblages have been recovered from the dry rockshelters of the Ozark escarpment in northwestern Arkansas (Fritz 1986). Marble Bluff is one such Early Woodland assemblage, which includes a remarkable 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*)”. Four direct dates on four different species from this rockshelter (Fritz 1986; Mueller unpublished data) confirm that this assemblage dates to the Terminal Late Archaic – Early Woodland transition, cal. 1200 – 900 BCE. The knotweed from Marble Bluff was analyzed as a part of the larger study and is not erect knotweed, as Fritz suspected. In fact, according to the latest taxonomies, it is not a member of the same genus: it is a species of smartweed (*Persicaria* sp.). This fascinating assemblage is further evidence of experimentation with species that eventually fell out of cultivation (smartweed, ragweed, mint) and also provides tentative evidence for the selection and separation of superior seed stock for planting (the bags of domesticated goosefoot).

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 also consumed. 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. cal. 200 BCE (Faulker 1991) and “knotweed or smartweed” was recovered from several of the Salts and Mammoth cave paleofeces (Yarnell 1969).

At the end of the Early Woodland period, the appearance of Adena 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. At an Adena hamlet on a tributary of the Hocking River, the Archaic crops are supplemented by maygrass and erect knotweed, two of the three crops (the third being little barley) that became increasingly important throughout the Woodland period (Wymer and Abrams 2003). By Middle Woodland times, the full suite of EAC crops was being grown in the Ohio valley (Wymer 1996, 2009), the Illinois valley (Asch and Asch 1985c, 1985b), the American Bottom (Simon and Parker 2006), central Tennessee (Crites 1987), northwestern Arkansas (Fritz 1986), and in the central Mississippian valley as far northwestern Arkansas (Fritz 1993, 2000). Localized evidence for land clearance and erosion is present for at least one large Middle Woodland earthwork (the Fort Ancient site, see McLauchlan 2003). I have suggested elsewhere that exchange at Middle Woodland mound centers and earthworks may have included the seeds of superior landraces of cultivated plants (Mueller 2014). 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 very diverse food system that relied on a patchy landscape of cultivated fields, open woodlands, and marshes. Three Middle Woodland assemblages of erect knotweed were analyzed for this analysis: Walker-Noe (Kentucky River), Smiling Dan (Lower Illinois River), and Meridian Hills (American Bottom).

The timing and social dynamics of the introduction of maize into Woodland economies remain topics of active research. Middle Woodland maize is scanty and scattered, with direct dates on macrobotanical remains from Holding in the American Bottom (Riley et al. 1994), Icehouse Bottom in eastern Tennessee (Chapman and Crites 1987), and Edwin Harness in southern Ohio (Crawford et al. 1997). Mysteriously, despite the fact that maize probably came to ENA from the Southwest via the Great Plains, the earliest dates on maize phytoliths and starch come from the Northeast (Thompson et al. 2004; Hart et al. 2007; Hart and Lovis 2013). 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 (Simon 2017).

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 central Mississippi and Arkansas River valleys, the EAC supported the Late Woodland mound-building Plum Bayou culture (Nassaney 1994; Fritz 2000). In the American Bottom, populations were gradually coalescing into the more nucleated and complex

predecessors of Mississippian towns (Kelly 1990; 2002) and leaving behind increasingly abundant evidence of EAC cultivation (Simon and Parker 2006). Recent direct dating of maize remains has revealed that much of the Late Woodland maize in the American Bottom and western Illinois is intrusive from later occupations (Simon 2014; 2017). However, evidence from stable isotopes indicates that some early Late Woodland (c. cal CE 400) individuals in western Illinois were consuming significant amounts of maize (Rose 2008). Meanwhile, along the Missouri River, EAC cultivation continued and maize cultivation was picked up patchily and relatively late, with evidence of small-scale maize cultivation by c. cal 900 CE (Wright and Shaffer 2014; Lopinot and Powell 2015). It is clear that by the Terminal Late Woodland, 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 river valley were analyzed for this analysis in order to document spatially and temporally related populations. I focused on obtaining several diachronic samples from a single sub-region rather than assemblages from several different sub-regions because previous research indicated that the Late Woodland was the period of interest for the domestication of erect knotweed. Asch and Asch (1985) 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. I wanted to see if I could document changes in morphology over time, from

an Early or Middle Woodland wild-type baseline to a domesticated sub-species by Mississippian times.

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” by Lopinot (1997), and again by 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 2016), but overall, the change in agricultural practice coincident with the rise of Cahokia has been given a remarkable amount of both credit and blame, considering that the evidence for any such change is minimal. One Stirling Phase (early Mississippian) assemblage from the American Bottom is included in the analysis. It can testify to whether or not erect knotweed domesticated landraces were maintained across the hypothetical agricultural boundary between Late Woodland and Mississippian agricultural practice in the American Bottom.

Two Mississippian assemblages (Whitney Bluff, AR; Hill Creek, IL) and their associated food production systems needed to be considered with special care in this analysis because they were recognized as potentially domesticated by previous researchers (Asch and Asch 1985b; Fritz 1986). These two assemblages provide windows into the state of the EAC in two different regions, northwestern Arkansas and the Lower Illinois valley, in the centuries after the integration of maize into local economies. During the 12th century, when the Whitney Bluff assemblage was most likely deposited, the bluff shelters of northwestern Arkansas were on the periphery of the Caddo region. Mississippian towns and mounds 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 (Trubowitz 1983; Fritz 1984; Sabo 1986). Although maize was present in all but one of the 18 bluff shelter collections analyzed by Fritz (1986), this is because the rock shelters represent palimpsests of agricultural practice spanning thousands of years. Direct dates on maize indicate that it 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. cal CE 900 – 1000. Fritz also observed changes in the maize landraces cultivated in this region from the small, thin Late Woodland cobs recovered from Edens Bluff to the larger Mississippian cobs from Putnam shelter (Fritz 1986:185-8). Meanwhile, as at Cahokia, the older EAC crops were still being cultivated, and, in the case of erect knotweed, improved.

The Hill Creek assemblage is later, dating to the mid-1300s. 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 in this analysis: 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 (Goldstein 1980; Conner 1985; Farnsworth et al. 1991; Delaney-Rivera 2004). The crux of the mystery is the paucity of Lohman and Stirling phase (early Mississippian) sites in the Lower Illinois Valley, despite the obvious influence of Cahokia further north, in the Central Illinois Valley (Bardolph 2014). One large cemetery (Schild) and a moderately sized village (Audrey) have been excavated, but most Mississippian sites are small homesteads like Hill Creek, and very few have been excavated. Goldstein (1980) and Conner (1985b) argued that the Lower Illinois Valley was a resource procurement area for Cahokia – populated by immigrant homesteaders who provided surplus agricultural products to town-dwellers to the north and south. Delaney-Rivera (2004) and Farnsworth and colleagues (1991) have argued that Late Woodland populations remained essentially in place and gradually integrated Mississippian material culture and institutions into their way of life. Either way, it is possible that the remarkable 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 represent a landrace developed in the Lower Illinois valley, where erect knotweed was one of the most important EAC crops throughout the Middle and Late Woodland periods.

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). 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 – a kind of reverse

domestication. In this scenario, a decrease in the quality of seed stock should be apparent before the crop disappears from the record all together. The latest assemblages would be more similar to modern wild plants or archaeological assemblages from the Early and Middle Woodland period. These scenarios were investigated with two additional Mississippian assemblages.

While a variety of crops continued to be important to the livelihoods of farmers in the Middle Mississippian and Caddo regions until c. 1400 CE, Fort Ancient Mississippian agriculture in the Ohio valley developed along different lines (Wagner 1987). The older EAC crops are seldom recovered from Fort Ancient sites, and maize was a clear staple crop even at the earliest sites (Wagner 1987; Rossen 1988). Stable isotopes also indicate a rapid adoption of maize (Price and Cook 2015). 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 (Rossen 1988). This assemblage is included in the analysis as an outlier: what was happening to EAC crops under cultivation by farmers who were upon a path towards maize-focused agriculture? The final Mississippian assemblage comes from a Powers Phase hamlet in the central Mississippi valley. With a date at least in the mid- 1300s, it is the latest large concentration of erect knotweed that I was able to obtain. Like the Hill Creek and Whitney Bluff assemblages, it may be either a distinct local landrace or a relative of the assemblages from the American Bottom. Resolving this issue will require diachronic studies in both of these sub-regions.

6.4 Materials and Methods

The sites and contexts sampled for this study are listed in Appendix 2, along with 14 new radiocarbon dates and their calibrated ranges (OxCal13, unmodeled, 95.4%; Reimer et al. 2013). Two of the sampled contexts had been previously directly dated, and those dates are also

reported in Appendix 2. I sought out well-defined contexts that contained >20 measureable erect knotweed achenes. This sampling strategy was adopted so that each sample would represent, as nearly as possible for an archaeological assemblage, what had once constituted a living population – not a palimpsest of many different harvest locations and years. It is impossible to be sure that seed concentrations from well-defined contexts were deposited at the same time without a much larger radiocarbon dating program. But homogenous masses of seed in well-defined contexts are more likely to represent living populations than many small samples taken from middens and other contexts throughout the site. With one exception, a sub-mound burial feature at the Walker-Noe site, the sampled contexts were pits. I analyzed samples smaller than 20 from some of the older sites (Cold Oak, Walker-Noe, and five out of six Smiling Dan contexts; Table 6) because large concentrations of erect knotweed are much more rare before the Late Woodland. It may seem strange that it is so difficult to find samples of >20 well-preserved achenes when frequencies of erect knotweed are routinely reported in the hundreds or thousands. The discrepancy comes from various taphonomic processes that distort and fragment achenes so that they are still recognizable as erect knotweed, but not suitable for morphometric analysis. These processes are outlined below and discussed in detail elsewhere (Chapter 5).

The assemblages included in this analysis had been pre-sorted to the most specific possible taxon by other paleoethnobotanists using a variety of subtly different lab methodologies. Generally speaking, paleoethnobotanists working in ENA will group all identifiable *Polygonum* together, whether kernels, pericarp fragments, or complete achenes, although they may report separate totals for achenes and kernels. Upon procuring a new sample, I selected a photosample using the following procedure. I first recorded the initial weight of all identifiable *Polygonum*

(kernels, achenes, and pericarp fragments) from a given context. Next, I sorted the entire sample, counting all achenes that had sufficient observable pericarp to classify them as either smooth or tubercled. I did not count fragments of pericarp smaller than 50% of a complete pericarp to avoid double counting. Of these, I separated achenes that had well-preserved pericarps and had not grossly changed shaped during carbonization. Many achenes were popped: they had perisperm extruding from cracks in the pericarp (Figure 6.2). Others were obviously puffed: one face was distorted with respect to the other face. These were excluded from the analysis unless they could be easily corrected by manually removing the extruding tissue from the photography. An example of a corrected popped achene is shown in Figure 6.2. Achenes both with and without adhering receptacles and/or perianth bases were included. Examples of these types are also shown in Figure 6.2. Correction factors for missing perianth bases were developed experimentally (Chapter 5) and applied to achenes lacking perianth bases. I then sampled one achene per 0.01 grams in order not to bias the photosample against poorly preserved (usually older) assemblages – or if there were fewer measureable achenes than one per 0.01 g, then I sampled all of them. The exception to this sampling strategy was the Westpark assemblage, which contained tens of thousands of achenes and kernels: I took an arbitrary sample of 100 well-preserved achenes for the initial photosample. The morphometric analysis reported here is based on this photosample.

I also collected modern comparative samples of erect knotweed and closely related species. First, I obtained achenes from the loose materials packets of herbarium specimens. A complete list of sampled specimens can be found in Chapter 2, Appendix 1. I then supplemented the erect knotweed sample with additional achenes from my surveys of wild populations

(Chapter 4). Table 6.1 summarizes the composition and provenience of the modern comparative sample.

Table 6.1: Modern comparative collection of erect knotweed summary		
Source	Smooth	Tubercled
Bellews Creek	48	120
Crawford Creek	35	110
Peters Creek	0	40
Herbarium sample	17	109
Sum	100	379

Table 6.1. Summary of the source and sample size of the comparative sample used in this analysis. For more details on the three survey populations see Mueller, in press, and for information on the herbarium sample and on the sample composition for the other species reported in Appendix 6, see Chapter 2.

I took grayscale photographs of each achene in the same orientation with the widest of their three sides down using a Zeiss SV11 microscope fitted with a manual stage, z-stepping motor, and an AxioCam MRC5 digital camera. I recorded the texture of each pericarp as “Smooth” or “Tubercled.” Using ImageJ open source software, I measured several shape factors and area, length, and width. In order to take area and shape measurements, the object to be measured must be thresholded (differentiated from the background on the basis of color or shade). With solid objects such as 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 color to the background. The shape factors collected for each achene are aspect ratio, roundness, and circularity (Table 2.2). Length and width are the two longest perpendicular straight line distances across the image of the achene. All morphometric measurements were taken using ImageJ. Correction factors for both size and some aspects of shape were applied to the measurements. These correction factors were developed experimentally (Chapter 5), and are reported in Appendix 3.2.

Domesticated erect knotweed differs from its wild progenitor in two ways: an increase in fruit size and a decrease in fruit dimorphism. To facilitate comparison of fruit size between assemblages, every assemblage is graphically compared to both the modern comparative sample and the Whitney Bluff assemblage, which has been described in detail as the type specimen for domesticated *P. erectum* ssp. *watsoniae* (Chapter 2; Chapter 3). The size of tubercled and smooth morphs are considered separately in terms of *area*, as determined from microphotographs. This procedure has some advantages to measuring size by length and width. Seed volume is the property that we would ideally measure in domestication studies, but volume is not easily measured for objects as small as seeds. Instead, it is customary in studies of EAC crops to report length and width, and sometimes to calculate length X width as a size index (e.g..Yarnell 1978). Length and width are easy and quick to measure, but fail to capture all size increases due to changes in shape. By becoming more circular, an object can have a greater area (as viewed from above) and volume without the maximum perpendicular distances from edge to edge changing at all. Length and width are also reported (Appendix 3) to facilitate comparison with other studies. Where sample sizes are large enough and variances are not significantly different, the means of each sample are compared to the two reference populations (modern and Whitney Bluff) using Tukey's Honestly Significant Differences test. Where variances differ significantly, pairwise Welch's t-tests was used instead. For significant differences, p-values are stated in the text. Non-significant difference refers to p-values greater than >0.05 .

The second aspect of erect knotweed's domestication syndrome, decreasing achene dimorphism in favor of smooth achenes, is more difficult to measure in carbonized assemblages because of preservation and sampling bias (Chapter 4). Observed population proportions in modern populations range between ~25 – 75% smooth morphs by time the plant is ready to

harvest in late October or early November. Based on these observations, the proportion of smooth morphs must exceed 75% in order to constitute evidence of domestication syndrome. There are two complicating factors. First, smooth morphs are more easily destroyed by carbonization and are thus systematically underrepresented in the archaeological record (Chapter 4). Second, estimating population proportion accurately enough to recognize such a shift requires an adequately large sample, which cannot always be obtained from archaeological collections. There is an established probabilistic relationship between the true population proportion and the difficulty of estimating it accurately from a sub-sample: the closer the true population proportion is to 50-50, the larger the sample required to accurately estimate it (Figure 5.4). In archaeology, we cannot always dictate sample size, and must instead be explicit about the error inherent in our estimates given sample size (Figure 5.4). For example, if the true proportion of smooth morphs in an ancient population was 90%, a random sample of 10 from that population can be expected to contain 7, 8, 9, or 10 smooth achenes (Figure 5.4). The situation deteriorates further if the true population proportion was 75% -- now our sub-sample of 10 can now be expected to contain 5, 6, 7, 8, 9, or 10 smooth achenes. In other words, we cannot confidently distinguish between these two population proportion (75% and 90%) with such a small sample. The relationship between these factors at 95% confidence is modeled in Figure 5.4 for reference to particular cases in the results and discussion. Appendix 4 reports sample size by context, and sample proportion of smooth morphs.

6.5 Results

6.5.1 Terminal Late Archaic – Early Woodland

The only Terminal Late Archaic – Early Woodland assemblage analyzed came from a rockshelter on the eastern extremity of the study area – the Cumberland Escarpment of Eastern

Kentucky. Cold Oak is a large sandstone overhang located in a tributary hollow of Big Sinking Creek. Excavations in 1984 by the Forest Service and in 1994-5 by Gremillion (1993, 1998) revealed well-stratified Early Woodland and Terminal Archaic strata. The sampled contexts came from Zone II, a compact sandy loam layer that contained numerous storage pits, burned areas, and shallow basins. The context that provided the most measureable achenes (Feature 8) was an Early Woodland pit that was excavated in antiquity into Terminal Late Woodland Zone III. A wood fragment from Feature 8 returned a date of 2470 +/- 90 BP (Gremillion 1998:143), while the direct date on the erect knotweed yielded a date of 3200 +/-100 BP – a 730 radiocarbon year spread from within a single feature. The erect knotweed is evidently intrusive from the Terminal Late Archaic stratum into which the pit was dug. Another measureable achene came from Feature 51, which Gremillion (1998) dated to the Early Woodland – Middle Woodland transition (Appendix 2). These dates indicate that erect knotweed was harvested by inhabitants for approximately 2,000 years. Although erect knotweed counts are not high at Cold Oak compared to later sites, is very unlikely that erect knotweed would naturally grow in such a setting, as it is generally found in frequently flooded, low-lying habitats (Chapter 4).

The seven Terminal Archaic achenes recovered from Feature 8 provide a small glimpse of what may be some of the earliest cultivated knotweed, and provide a morphological baseline for later populations. All seven appear to be perfectly normal tubercled morphs, fitting right into a distribution of measurements taken from modern populations (Figure 6.3; Appendix 3). Although it is impossible to know for certain how old the other two achenes are, the date from Feature 51 indicates that they may be over 1000 years later. As noted by Gremillion (1998:147), one of the two smooth morphs is unusually large, but still within the range of variation for modern erect knotweed (Figure 6.3; Appendix 3). While this large smooth morph is tantalizing,

without a larger sample it is impossible to determine if late Early Woodland erect knotweed at Cold Oak was beginning to exhibit domestication syndrome.

6.5.2 Middle Woodland

Walker-Noe. The earliest of the three Middle Woodland sites analyzed is Walker-Noe, and it is also the only assemblage from a ritual context analyzed. This small mound is part of a large, multi-component site that was intermittently occupied from the Paleoindian period until the Fort Ancient period. Sprawling over 49.4 ha, this site is mostly characterized by a high density debitage scatter. It was probably used for lithic production: both Boyle and Crab Orchard chert outcrop on-site (Pollack et al. 2005). The analyzed assemblages come from a small mound located on a low-ridge beside Walker Branch, a tributary of Paint Lick Creek. Unlike most Adena mounds in the Kentucky Bluegrass region, Walker-Noe is not accretionary and lacks a log crypt or any extended burials. Instead, this mound caps at least 17 human cremations, including infants, adolescents, and adults (Pollack et al. 2005). Also unusual, the burials were accompanied by abundant plant food remains, including several members of the EAC, of which erect knotweed was the best represented, the seeds of wild fruits, and nutshell fragments (Pollack et al. 2005:71-72; Appendix).

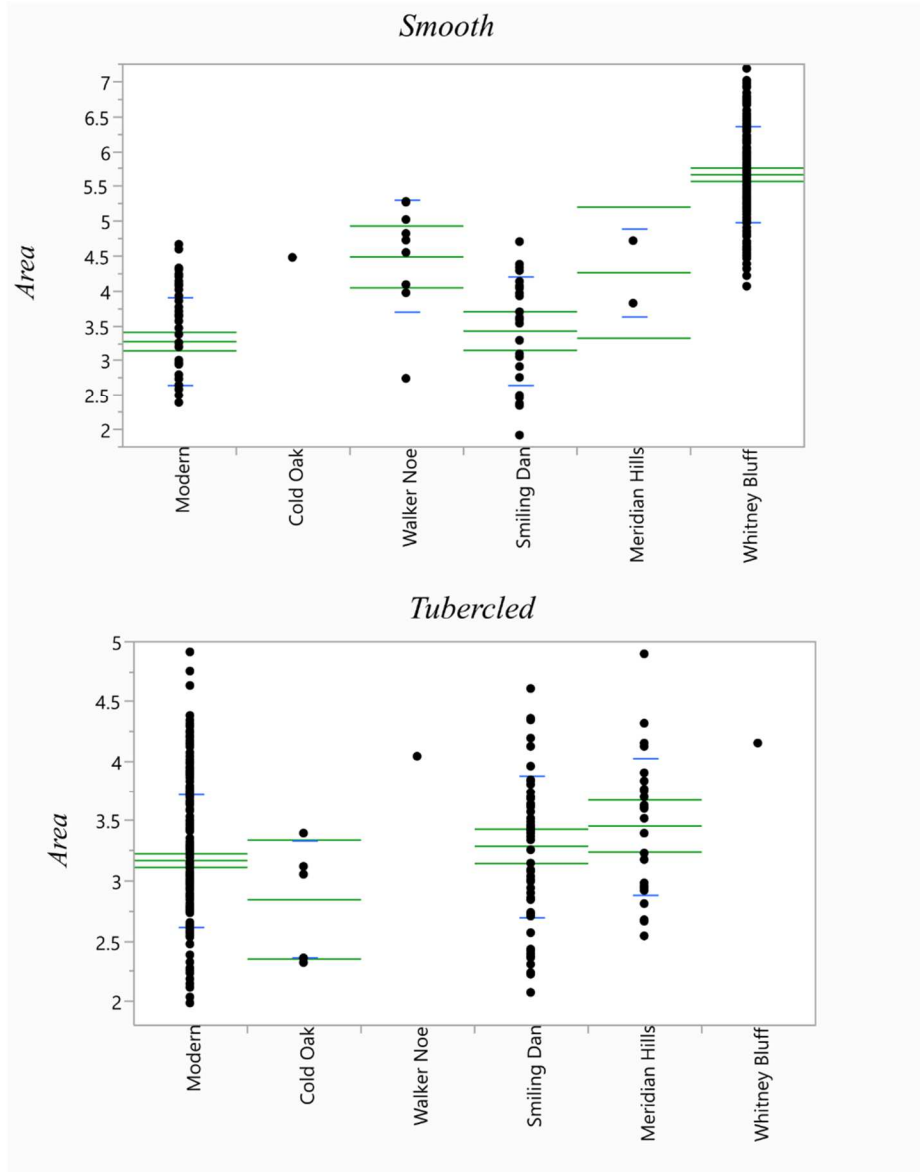


Figure 6.3. Distribution of values for achene size, in terms of area, for the Early and Middle Woodland sites, in comparison to the modern comparative sample and the domesticated Mississippian assemblage from Whitney Bluff. Long horizontal lines are mean and confidence interval of the mean, short horizontal lines are standard deviation. The single smooth morph from Cold Oak is from Feature 51 and is quite large, but still within the range of modern variation. The tubercled morphs from Cold Oak comes from different contexts (Features 8 and 49) and are normal for a wild population. The Walker-Noe assemblage is has significantly larger fruits than the modern comparative collection and is composed almost exclusively of smooth morphs – it is the earliest domesticated assemblage. The lone tubercled morph from this site is also abnormally large. The Smiling Dan assemblage has a normal size distribution if considered as a single population (see also Figure 6.4 for fruit size by context). The Meridian Hill assemblage is significantly larger than the modern comparative collection, but is composed mostly of tubercled morphs.

Smiling Dan Intrasite Comparison

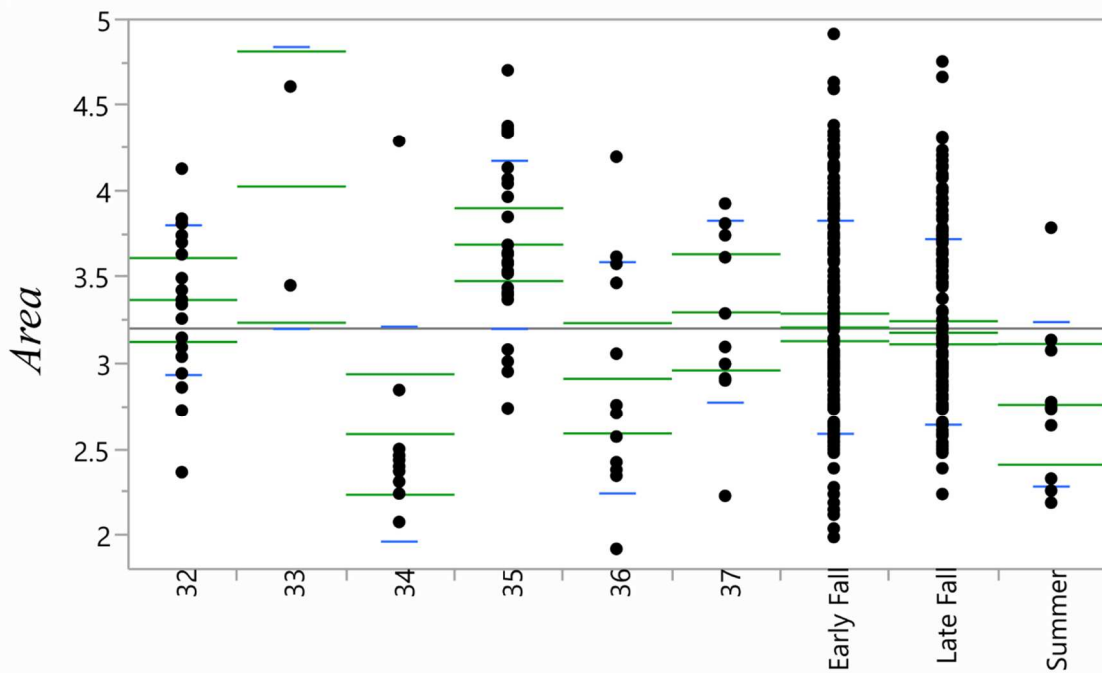


Figure 6.4. Distribution of values for achene size, in terms of area, by context at Smiling Dan, in comparison to the modern comparative sample broken down by season of harvest. Long horizontal lines are mean and confidence interval of the mean, short horizontal lines are standard deviation. The smallest assemblage from Context 34 (see Appendix 4) may represent a harvest of immature fruits. The largest, from Context 35, is significantly larger than the modern comparative population as a whole.

A photosample of 11 was drawn from two different sub-mound samples (Appendix 4).

Both were associated with cremation burials. The three radiocarbon dates from the site (two from the sampled contexts, reported in Appendix 2, and one other from the sub-mound burned area; Pollack et. al. 2005) all cluster around cal. 1 CE. These dates support the excavators' impression that the cremations and mound-building occurred over a short period – perhaps only one year (Pollack et al. 2005:74-75). Because the contexts of the two samples are continuous and both have been directly dated to the same period, I treat them as a single morphometric sample here.

The morphology of the Walker-Noe erect knotweed is as extraordinary as its context. Figure 6.3 illustrates that while the Walker-Noe smooth morphs are not quite as large on average as those from Whitney Bluff, they are larger on average than modern erect knotweed. This assemblage falls squarely in between the two reference populations, and the differences are highly significant (Tukey HSD $p < 0.0001$ for all three comparisons). The Walker-Noe assemblage also displays the second aspect of domestication syndrome: reduction in achene dimorphism. A total of 41 achenes had enough pericarp preserved to observe texture. Of these, 95% were smooth morphs (this total includes the photosample, of which all but one were smooth morphs; Appendix 4). Assuming that all of the sub-mound achenes come from the same population, this population proportion is statistically distinguishable from observed modern erect knotweed harvest proportions (Figure 5.4). The Walker-Noe assemblage clearly exhibits the domestication syndrome that characterizes later Mississippian assemblages.

Smiling Dan. Smiling Dan presents a unique opportunity to examine the development (or lack thereof) of one household's cultivated erect knotweed over a period of a few hundred years. Smiling Dan is located on the floodplain of Campbell Creek, a small stream that drains the uplands east of the Illinois River. The site is bisected by what was during the Middle Woodland an even smaller intermittent stream, and sprawls onto the floodplain of Campbell Creek and the adjacent bluff slopes (Sant and Stafford 1985:87). Middle Woodland deposits range in thickness from a 30 – 60 cm layer over most of the site, to a 2 m deep midden within the old stream channel. Six dates were obtained by the excavators of the site from well-defined Middle Woodland contexts. These range from uncal. 1830 +/- 50 – 1700 +/- 70 BP, suggesting a Middle Woodland occupation ~200 years, from cal. CE 125 – 400 (Hajic 1985:49). I obtained dates for the two analyzed assemblages that were most clearly associated with structures. The calibrated

95% confidence spreads from the two structures overlap very slightly, supporting the excavators' impression that they represent sequentially occupied houses (Appendix 2; Stafford 1985:449). But strangely, the new dates reverse the sequence based on relative frequencies of ceramics: the excavators believed that Structure C was earlier than Structure B, but my dates indicate the opposite. Smiling Dan was probably abandoned sometime around CE 300, then reoccupied about 400 years later. Twelve later Late Woodland features occupy the northwest part of the site and some late Woodland material was recovered from middens. None of the analyzed assemblages come from features associated with this later occupation.

The Middle Woodland Smiling Dan homestead consists of three small houses and their associated pits and middens. It was subject to a very thorough botanical analysis for such a small site, with 1,200 liters of sediment floated and analyzed (Asch and Asch 1985a:344; Appendix 5). This sampling effort yielded a richly detailed portrait of Middle Woodland agriculture in the Lower Illinois Valley. Nuts continued to be very important food resource. As at other Middle Woodland sites, hazelnut shell (*Corylus americana* Marshall) is especially abundant. This Middle Woodland preference has been linked to increasing forest margin habitats and perhaps clearance of land for cultivation by fire, which encourages the growth of hazelnuts (Asch and Asch 1985a: 351-353). All of the members of the EAC were present in abundance. By count and percentage of the seed assemblage, erect knotweed was second after maygrass, followed by little barley and goosefoot. Sumpweed and sunflower were also present in small numbers, as were dozens of other species that are known to be edible, medicinal, or both. Such thorough sampling even yielded the elusive remains of wild root crops such as groundnut (*Apios americana* Medik.) and possibly prairie spud (also known as spring beauty, *Claytonia virginiana* L.; Asch and Asch 1985a:354-8).

Not surprisingly given the richness of the assemblage, Smiling Dan also provides the largest assemblage of Middle Woodland erect knotweed in this analysis by far, with a total of 103 achenes in the photosample. These come from six distinct contexts, three of which are clearly associated with one or the other house (Appendix 4). Considered as a single sample or as individual samples, the Smiling Dan erect knotweed is very similar to the modern comparative sample (Figure 6.3; Figure 6.4). While Smiling Dan smooth and tubercled morphs are on average slightly larger than those of modern populations, they are statistically indistinguishable, and none of the individual samples has a percentage of smooth morphs higher than 50% (Appendix 4).

Smiling Dan is the only site in this study for which I have analyzed more than two large concentrations of erect knotweed for analysis, and provides an opportunity for intra-site comparison. Feature 194 was an interior pit of Structure B, a square house with interior walls 7.5 m long. This context yielded a tiny photo sample of 2 and the earlier of the two dates (Appendix 2; Appendix 4). Structure B is the more substantially constructed (having interior post molds) of two similarly sized houses on the west side of the small stream that bisects the site. Feature 110 is an exterior pit associated with Structure C, another house of indeterminate dimensions located directly east of Structure B on the other side of the stream channel. The other four analyzed features are all pits located on the western side of the stream. There are slight differences in terms of fruit size between the individual photosamples from Smiling Dan. Pooling both morphs to increase the sample size for the analysis, the F164 achenes are larger on average than those from all of the other Smiling Dan contexts, while the achenes from F110 (Structure C) are smaller (Figure 6.4). To reiterate, the assemblage as a whole is statistically indistinguishable in terms of achene size from the modern comparative population.

One explanation for the variation in size between contexts, other than human mediated selection, is that some of these assemblages represent late fall harvests and others are immature seeds harvested from plants in the summer or early fall. By separating the modern comparative populations into three categories (Summer=July- August; Early Fall=September; Late Fall = October- November), I tested this possibility. The sizes of early and late fall fruits are not significantly different. The summer harvested modern seeds are significantly smaller than the early and late fall seeds, and not significantly different from the archaeological sample from F110 (Figure 6.4). Before erect knotweed plants senesce in late October or early November, their fruits adhere more firmly. It is much less efficient to harvest fruits from living plants, as they must be individually plucked or beaten off of the plants (Chapter 4; Murray and Sheehan 1984). However, it is possible that under some circumstances erect knotweed was harvested early, and assemblages like that from F110, and possibly the assemblages from Mund and /or Muir, discussed below, may represent this practice.

Features 242, 205, and 92 are not significantly different from the early and late fall modern samples, and Feature 134's sample size is too small for comparison, but the sample from F164 is significantly larger than any subset of the modern population. With no direct date it is impossible to say if this assemblage is later than the others, but it may represent the first small effects of human mediated selection on erect knotweed in the Lower Illinois Valley. Further morphometric analysis and more extensive dating will be necessary to test this hypothesis.

Meridian Hills. Meridian Hills was a Middle Woodland site 1.3 km east of the bluff edge of the northern American Bottom at the headwaters of an intermittent stream running west into Cahokia Creek. It was destroyed by development in 1984. A salvage excavation was carried out by a local amateur archaeologist, Robert A. Williams, who documented 72 features – mostly pits,

with remnants of midden and three post holes. It is likely that many more features, including the remains of any Middle Woodland structures, were destroyed by grading before excavations began (Williams et al. 1993). Feature 55 yielded the analyzed erect knotweed assemblage: it was an 80 cm diameter pit that was 40 cm deep when excavated (Williams et. al. 1988). The site was dated using diagnostic ceramics to the American Bottom Holding Phase, named for the nearby floodplain Middle Woodland village of the same name. This is consistent with the date on the erect knotweed (Appendix 2). A calibrated range of CE 130-237 indicates that the occupation of Meridian Hills was contemporaneous with at least the earlier part of the occupation of Smiling Dan, some 100 km to the north.

The botanical remains recovered from the Meridian Hills site were typical of Middle Woodland farming communities in the region in terms of their diversity and abundance. Although the sample is much smaller, the assemblage is strikingly similar to that of Smiling Dan and other Middle Woodland sites in the nearby Illinois River valley. A large cache of domesticated chenopods was recovered, along with smaller amounts of domesticated sunflower and sumpweed, maygrass, little barley, several different kinds of nuts, and various seeds of fleshy fruits (Williams et al. 1988; Williams 1993). Like Smiling Dan, Meridian Hills is a good representation of the heyday of Middle Woodland food production, characterized as it was by a diversity of wild and domesticated plants that must have relied on an equally varied set of management practices.

The erect knotweed assemblage from Meridian Hills is small – only 28 achenes were well-preserved enough for the photosample. Of those, 26 were tubercled morphs and these are significantly larger than the modern sample (Figure 6.3: Welch's t-test, $p < 0.0001$). The two measurable smooth morphs do not contradict the impression that Meridian Hills erect knotweed

had larger achenes on average larger than is typical for modern populations (Figure 6.3). No increase in the prevalence of smooth morphs is noted. On the contrary, the proportion of smooth morphs (6%) in Feature 55 is lower than normal. However, given the small sample size and the fact that carbonization biases against the preservation of smooth morphs with respect to tubercled morphs, this population proportion can plausibly be attributed to sampling error and preservation bias.

6.5.3 The American Bottom sequence: Late Woodland -- Mississippian

Mund. Mund is located in the southern American Bottom, occupying 10.7 ha on a broad alluvial fan extending out from a small bluff opening called Cement Hollow. It is a complex multi-component site with occupations from the Archaic through Mississippian periods. It is the type site for the Mund phase, an early Late Woodland phase from which the analyzed assemblage was drawn. In the American Bottom, the Late Woodland is a period of gradual change, during which the stage was set for the “Big Bang” of construction and population aggregation at Cahokia by a series of *in situ* cultural developments (Kelly 1990; McElrath and Fortier 2000). The integration of maize into the agricultural system was once thought to have been gradual, beginning at a very low level during the Middle Woodland, becoming more visible during the early Late Woodland Mund phase, and intensifying during the concurrent late Late Woodland Patrick and Sponemann phases (c. cal CE 650-900; reviewed in Simon 2014). It now seems more likely that maize was not regularly cultivated in the American Bottom until the Terminal Late Woodland/Emergent Mississippian, c. CE 900. Mund phase plant remains represent the “pre-maize” Late Woodland (Fortier et al. 2006): a continuation and intensification of Middle Woodland agricultural practices, with a shift in site locations from primarily floodplain locations during the Late Middle Woodland, to primarily bluff base and upland creek

locations in the early Late Woodland. The Mund phase is thought to represent a reoccupation of the American Bottom after a short hiatus – probably with populations returning from the Illinois Valley (McElrath and Fortier 2000). The date obtained on the erect knotweed from Mund indicates that it was deposited between cal. CE 672 – 770 – very late for a Mund phase context, which normally date to cal. CE 300 – 650 (McElrath and Fortier 2000:99).

The Mund phase of the Mund site consisted of 165 features, 99% of which were pits. Two small structures, one of which was associated with a limestone hearth and a dog burial, were the only other types of features encountered (Fortier et al. 1983:111). The sampled feature was a pit in Cluster C, which did not contain either of the two structures. Feature 90 was a 1.3 m diameter, 1 m deep flat-bottomed pit that the excavators characterized as an earth oven. Like ethnographically recorded earth ovens, Feature 90 was flat bottomed with a layer of burnt limestone at the bottom, overlain by a layer of greasy grass matting, presumably used to steam fish. Over and among the thatch, abundant seeds and fish bones were recovered, including the erect knotweed assemblage analyzed for this study (photosample n=45; Appendix 4; Figure 6.5).

The morphology of the Mund knotweed 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 (Figure 5.4; especially when we also consider the fact that smooth morphs are likely to be underrepresented in carbonized assemblages; Chapter 4). 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 monomorphic assemblages of smooth morphs (see discussion of Whitney Bluff and Hill Creek assemblages, below). The possibility that some other species of knotweed is represented at Mund must be considered.

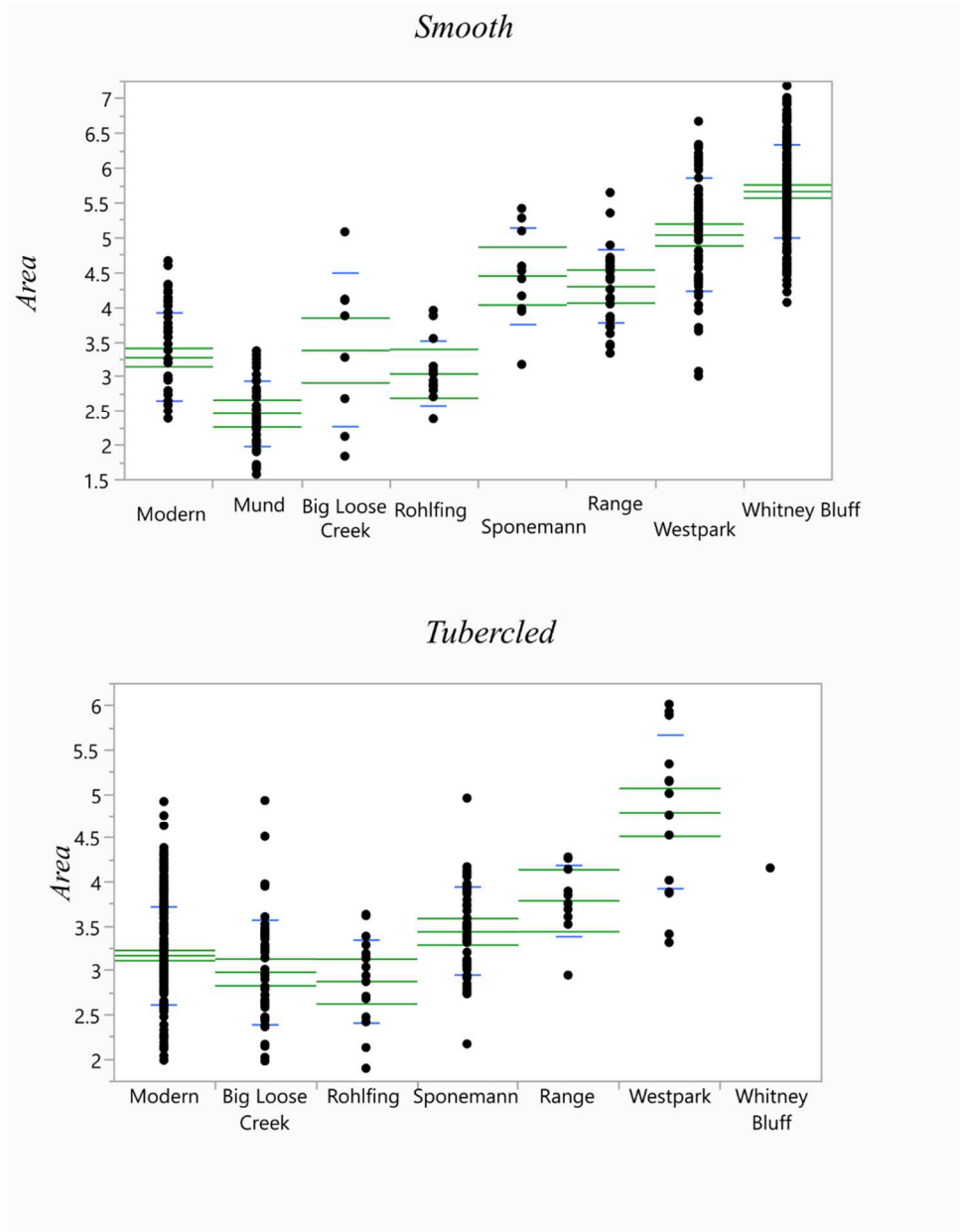


Figure 6.5. Distribution of values for achene size, in terms of area, for Late Woodland and Early Mississippian sites in the American Bottom and lower Missouri valley, in comparison to the modern comparative sample and the domesticated Mississippian assemblage from Whitney Bluff. Long horizontal lines are mean and confidence interval of the mean, short horizontal lines are standard deviation. The early Late Woodland Mund site is both monomorphic and abnormally small-fruited. The two late Late Woodland/Emergent Mississippian sites from the lower Missouri valley (Big Loose Creek and Rohlfig) are both indistinguishable from modern erect knotweed in terms of fruit size. The other three sites, all from the American Bottom, show a clear increase in fruit size and sample proportion of smooth morphs, from c. CE 900 – 1100.

There are four species of knotweed native to the study area with similarly shaped achenes and fruit dimorphism: erect knotweed, *P. achoreum*, *P. aviculare* ssp. *buxiforme*, and *P. ramosissimum* (see Chapter 2 for the taxonomic background)¹³. Shape descriptors are not particularly helpful for distinguishing between the smooth morphs of these four species, but size is. Two of the four species have significantly different sized smooth morph achenes, so size can be used as a diagnostic criteria: *P. aviculare* ssp. *buxiforme* has the smallest smooth achenes, *P. ramosissimum* has the largest. *P. erectum* and *P. achoreum* have smooth morphs of approximately the same size: they cannot be differentiated from one another reliably on the basis of size, but can be differentiated from the other two species (Chapter 2; Chapter 3). Erect knotweed's smooth morphs are more circular than the other three species, although the difference is not statistically significant (Welch's t-test for unequal variances).

I also compiled morphometric data on immature erect knotweed achenes in the course of a taphonomic study. I included these measurements in this comparative analysis in order to consider the possibility that the Mund assemblage represents immature erect knotweed smooth morphs. It would be impossible to procure such a harvest from modern plants without the aid of a microscope and the benefit of many hours to sort mature from immature fruits. Not only is it difficult to harvest plants before they have senesced, when immature achenes are present, but immature smooth morphs are always mixed with mature achenes of both morphs on living plants of extant populations (Chapter 4; Murray and Sheehan 1984). But it is possible that the Mund erect knotweed was domesticated – fruit dimorphism had been eliminated through human

¹³ The summary statistics for *P. achoreum*, *P. aviculare* ssp. *buxiforme*, and *P. ramosissimum* (Table 8) are identical to those presented in Chapters 1 and 2. Details about how these samples were collected are reported in Chapter 2. The summary statistics are slightly different for *P. erectum*, because the sample also includes 360 additional modern achenes from surveys of contemporary populations (Table 2; Chapter 4). Overall, the mean measurements for erect knotweed achenes of both morphs changed very little with the addition of these specimens, suggesting that the original sampling effort was adequate.

mediated selection – *and* that these domesticated erect knotweed plants were harvested before most they senesced, when most of the achenes were still immature, in order to minimize seed loss. Hypothetically, this combination of circumstances would yield an assemblage of immature smooth morphs.

The results of the comparative analysis are reported in Appendix 6a. In terms of area, the Mund achenes are smaller than all extant species except *P. aviculare* ssp. *buxiforme*. They are somewhat smaller than even the immature achenes of erect knotweed. They have exactly the same average aspect ratio, roundness, and circularity as immature erect knotweed smooth morphs. However, they are equally similar in terms of shape to the smooth morphs of *P. ramosissimum*. *P. ramosissimum* is known to occasionally produce monomorphic harvests of smooth morphs as a plastic response to as-yet unknown environmental circumstances (Chapter 2; Chapter 3). The mature smooth morphs of *P. ramosissimum* are much larger than those of the Mund assemblage, but I do not have morphometric data describing their immature achenes.

The Mund achenes have a unique morphology. Although the Mund achenes do not exactly match any extant group in terms of shape and size, the morphometric analysis provides an equal amount of support for either of two hypotheses: 1) the Mund achenes are a particularly diminutive sample of erect knotweed smooth morphs or; 2) the Mund achenes are a sample of *P. ramosissimum* immature smooth morphs – although their morphology is currently unknown. If the Mund achenes *are* a landrace of domesticated erect knotweed, they exhibit a unique morphology that either evolved under cultivation or resulted from different cultivation techniques: ancient farmers at Mund may have harvested erect knotweed in mid-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. 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). Alternatively, the Mund knotweed may be a domesticated erect knotweed with a different domestication syndrome than that documented at Whitney Bluff. Not all annual plants exhibit increases in seed size when domesticated. For example, t'ef (*Eragrostis tef* Trotter) is very prone to lodging, and this factor may have prevented the evolution of large grains under cultivation, resulting in the smallest seeded of all annual domesticates (D'Andrea 2008). Based on my limited experience cultivating erect knotweed, no particular mechanism for the selection of a small-seeded landrace occurs to me, but further experiments may present an explanation.

Sponemann. Located in the northern American Bottom, about 20 km north of Mund, Sponemann is a large multi-component site situated at the confluence of several different productive zones and was repeatedly reoccupied from the Archaic through Mississippian periods. The analyzed assemblage dates to the Sponemann phase, cal. 800 – 900. The Sponemann phase is geographically distinct from the material culture tradition that replaces the Mund phase in the southern American Bottom (the Patrick phase, discussed in relation to the Range site, below). During the Sponemann phase, the site would have been situated on a low ridge with easy access to fresh water from the Schoolhouse Branch creek and aquatic resources from an enormous marsh occupying an old meander scar of the Mississippi River. It is also likely that backwater lakes formed nearby due to flooding of both the Mississippi and its nearby small tributaries. The bluff line is less than 2 km away, providing access to upland resources (Fortier et al. 1991).

The Sponemann phase at Sponemann consists of 901 excavated features, including 38 structures, but this is only a small portion of the estimated extent of the site. The densest part of the Sponemann phase occupation likely lies outside the excavated area to the west. The analyzed

assemblage came from Feature 592, a flat-bottomed, irregularly round pit about 1.4 m in diameter and 0.64 m deep. This pit was located in Cluster 2 and not associated with any particular structure. It lies near the westward extent of the excavation, so the house that it was associated with may remain unexcavated. Cluster 2 provided the most complete community plan of the six clusters defined by the excavators. Eleven structures form a rough oval around what may have been a courtyard. Several pits occupy the courtyard, and more are concentrated north of the cluster of houses. These two areas may represent community cooking and storage areas, respectively. Several of the features in this cluster have been interpreted as ceramic production areas: buildings for the storage of raw clay and finished pots, and a hearth area associated with burned clay. Feature 592 lies outside of the pottery production area and the major concentrations of pits – it is a deep earth oven, similar to the context of the analyzed assemblage from Mund in both size and shape (Fortier et al. 1991). The calibrated date range for the erect knotweed assemblage is CE 776 – 950, placing it most probably in the Sponemann phase.

Feature 592 contained over 15,000 erect knotweed seeds and fruits – the highest concentration of erect knotweed of any Sponemann phase feature. Domesticated goosefoot and erect knotweed dominate the archaeobotanical assemblage for the Sponemann phase, with 34,446 and 36,841 identifiable seeds respectively out of a total of 77,259 identifiable seeds from all Sponemann phase features (Parker 1991:403). Fruits with domesticated morphology constituted 95.3% of a 100 seed sub-sample of goosefoot from Feature 869 (Ibid:411). For many years the Sponemann phase of the Sponemann site was thought to provide the earliest clear evidence for maize cultivation in the American Bottom. Parker (1991) reported fragments of maize from ~1/3 of all analyzed contexts for this phase. The increasing ubiquity of maize during the Sponemann phase was compatible with a model of agricultural development in which maize

gradually became a more important crop throughout the Late Woodland in the American Bottom and Western Illinois. More recent analyses of single component Sponemann phase sites recovered no maize, leading researchers to wonder if the maize at Sponemann was intrusive from later Mississippian occupations. A series of four direct dates on seemingly Sponemann phase maize fragments returned Mississippian dates (Simon 2014). Based on this reanalysis, it seems unlikely that the analyzed erect knotweed assemblage from Sponemann was contemporaneous with the beginnings of maize farming; at most, it may have been harvested at the same time as very first maize crops, after 900 CE.

Both smooth and tubercled morphs from Feature 592 are significantly larger on average than the modern comparative samples, but the smooth morphs are also significantly smaller than those from Whitney Bluff (Tukey HSD $p < 0.0001$ for all three comparisons). They represent an intermediate stage in the process of domestication with respect to increasing fruit size. This population provides no evidence for a reduction in fruit dimorphism. A relatively low percentage of the achenes with observable pericarps were smooth morphs (24%). With a sample size of 124, this is probably a fairly accurate estimate of the true population proportion, with the caveat, as usual, that smooth morphs are more likely to be destroyed by carbonization.

Range. Range is also a large, multi-component site in the American Bottom that was reoccupied several times between the Archaic and Oneota periods. The Emergent Mississippian phases of the Range site have been described as part of a large scale nucleation and ritualization of settlements in the central and southern American Bottom directly preceding the “Big Bang” at Cahokia. Sites participating in this phenomenon are referred to as the Pulcher tradition (Kelly 2002). Range is a key site for the modeling of Pulcher tradition social dynamics, because the extensive excavations there revealed several superimposed iterations of the same community

spanning the transition from Late Woodland to Mississippian community organization (Kelly 2002; Kelly et al. 2007; Kelly et al. 1990). The analyzed assemblage comes from the Emergent Mississippian Lindeman Phase, the very last Late Woodland phase in American Bottom chronologies, CE 1000 – 1050. I did not obtain a direct date on the erect knotweed because an earlier AMS date comes from the same feature (cal. CE 880-1213; Appendix 2; Kelly 2007:470). In this case, the phase chronology is considerably more refined than the radiocarbon determination. If the erect knotweed is accurately dated by association, which seems likely given the secure context, then it represents the form of erect knotweed landraces in the American Bottom just before the “Big Bang.”

The Lindeman phase at Range consisted of 686 features, of which 147 were structures. These were organized around a series of courtyards. The analyzed assemblage came from F501, a large pit that also contained concentrations of maize and wild-type goosefoot (Parker 2007). By the Lindeman phase, maize had become ubiquitous at the Range site, appearing in 94.4% of sampled features. EAC crops were still just as widespread as ever, with 97.1% of sampled features containing one or more of the starchy EAC crops: erect knotweed, goosefoot, maygrass, or little barley. There may have been a slight trend towards homogenization of the crop complex, with little barley seemingly falling out of cultivation during this period (Parker 2007:463).

The Range achenes are very similar in size to those from Sponemann: the assemblages are not significantly different. Range achenes of both morphs are also significantly larger than those from the modern comparative sample, and Range smooth morphs are significantly smaller than those from Whitney Bluff ($p < 0.0001$ for all three comparisons), just as for the Sponemann assemblage. But at Range, the other half of the domestication syndrome is also present: of 110

achenes with observable pericarps, 80% were smooth morphs. This is a higher percentage than has been observed in modern populations, with a sample size large enough to be confident that it is not the result of sampling error (Figure 5.4). The Range assemblage represents an earlier and less extreme form of the domestication syndrome exhibited by the Whitney Bluff assemblage. Nor is it an isolated example: the assemblage from the Westpark site, less than 8 km away to the south and roughly contemporaneous, exhibits much the same morphology.

Westpark. The largest single concentration of erect knotweed that I analyzed came from Feature 300 of the Westpark site, IL. Westpark is a multi-component site that was occupied from at least the Late Woodland Patrick phase (cal. 650-900 CE) until the Mississippian Lohman phase (cal. 1050-1100 CE), and perhaps into the Stirling phase (cal. 1100-1200 CE) (Lopinot et al. 1991; Powell 2000; Appendix 2). The site was excavated by John Kelly and a team of volunteers ahead of a residential development. Over 200 features including 28 structures were mapped and excavated, but the site probably is much more extensive (Lopinot et al. 1991), and includes an unexcavated Mississippian component to the north of the excavations (John Kelly, pers. comm. 2016). Feature 300 was an irregular oval shaped pit measuring 1.1.6 X 1.02 m. Only the bottom 8 cm of the pit remained when it was salvaged after machine scraping. The bottom 2-5 cm of the pit contained a homogenous mass of erect knotweed kernels and achenes (Powell 2000). The pit was located ~20 m west of the Emergent Mississippian Dohack phase community on the bluffs overlooking the southern American Bottom (Powell 2000:32). Feature 300 was one of four pits believed to date to the Dohack phase (CE 900-950) that each contained thousands of erect knotweed kernels and achenes. Lopinot et al. (1991) estimated that Feature 300 alone contained 63 liters of erect knotweed achenes and kernels. A direct date on the analyzed knotweed yielded a date somewhat later than expected: uncal. 910 +/- 20 (cal. 1037-1183 CE).

This places the Westpark erect knotweed from Feature 300 in the early Mississippian era, although the age of the other three knotweed masses from the site remains uncertain. It seems likely that Feature 300, isolated as it was from the Emergent Mississippian community, was associated with the Mississippian component of the site, some of which may have been destroyed by machine scraping before the excavations began.

For my initial morphometric analysis, I randomly sub-sampled 100 achenes from the tens of thousands that were recovered from this context. The smooth achenes are significantly larger than those of the modern comparative sample and significantly smaller than the those from the Whitney Bluff assemblage, while the tubercled morphs are also significantly larger than the modern comparative sample (similar to the Sponemann and Range assemblages, but slightly larger; Figure 6.5). I observed the pericarp texture on a larger sample of 500 in order to more accurately estimate the population proportion of smooth morphs (78%; Appendix 4). The Westpark assemblage has *at least* a slightly higher proportion of smooth morphs than has been observed in a wild population: somewhere between 73–83% smooth morphs (Figure 5.4). Considering that smooth morphs are likely to be systematically underrepresented in carbonized assemblages due to differential preservation, this sample proportion constitutes equivocal evidence for decreased fruit dimorphism at the Westpark site. Taken together with the fact that the Westpark achenes are significantly larger than modern erect knotweed achenes, come from a context that clearly indicates large scale cultivation (Powell 2000), and are part of a sequence of increasing expression of domestication syndrome in the American Bottom, a strong case can be made for this assemblage as a domesticated form of erect knotweed.

6.5.4 Lower Missouri River Late Woodland Assemblages

The regional analysis of the American Bottom assemblages demonstrates that the Late Woodland was a period of interest with respect to erect knotweed domestication, but erect knotweed was an important crop during this period well beyond the American Bottom. While it was not possible to analyze multiple assemblages from every region where erect knotweed was an important crop, two Late Woodland assemblages from the Lower Missouri River were also analyzed for comparison with the American Bottom assemblages.

Big Loose Creek. A large Late Woodland or Emergent Mississippian village on the banks of the creek of the same name, Big Loose Creek occupies an advantageous location, with access to the fertile bottomlands of the Missouri River, but protected from its floods by a high bluff (Grantham 2010; Wright and Shaffer 2014). The extent of the site is unknown, but it covers at least 8.1 hectares of a high alluvial terrace. Two houses and associated pits and features were excavated. The three radiocarbon dates obtained by the excavators range from cal. CE 790 – 1040; the excavators classify the assemblages as Emergent Mississippian (Grantham et al. 2010:22). A date on the erect knotweed from Feature 19 yielded a 95% calibrated range of 774-943 CE, which does not contradict this interpretation, although the assemblages may also date to the late Late Woodland.

Big Loose Creek was subject to a comprehensive archaeobotanical analysis and yielded abundant plants remains (Lopinot and Powell 2015). EAC crops are abundant, especially domesticated goosefoot and maygrass. An unusually large concentration of tobacco seeds was also recovered, along with the usual Woodland diversity of fleshy fruits and nut crops. This assemblage bears on the question of when maize was introduced to central Missouri, and when it was integrated into local economies (Lopinot and Powell 2015; Wright and Shaffer 2014). Maize

was present, but ubiquity was low – maize fragments occurred in only five of the analyzed features (about 10%; Lopinot and Powell 2015). Given the recent revelation that much of the maize in Late Woodland contexts in the American Bottom is contamination from later occupations, and the relative abundance of other seed crops at Big Loose Creek, this meager evidence indicates that maize was at most a minor crop at this site during the late Late Woodland – Emergent Mississippian.

Two contexts provided photosamples. Feature 32 was a deep storage pit about 1.3 m in diameter and 0.85 m deep. It may have been a receptacle for refuse associated with craft production: it contained fragments of turtle shell rattles and bone beads. It also contained a concentration of burned grass thatch, perhaps an old lining or discarded roof, or perhaps another earth oven context like those at Mund and Sponemann (Grantham 2010:167). A small photosample of ten achenes was analyzed from this context. Feature 19 was a ~0.80 m diameter by 0.36 m deep pit. This pit did not contain many artifacts, but the preservation of charred plant materials must have been good because fragile sunflower and squash achene fragments were recovered, along with a dense layer of nutshell and hundreds of erect knotweed achenes and kernels. Neither of these features was closely associated with a particular house.

The two photosamples are significantly different from one another. While the sample size from Feature 32 of smooth morphs ($n=2$) is not large enough for statistical comparison, the tubercled morphs from Feature 32 are significantly larger than those from Feature 19 when compared to each other and the modern sample using Tukey HSD ($p=0.0012$). However, the Feature 32 tubercled morphs are not so large as to be significantly different from the modern sample. The Feature 32 sample also has a high proportion of smooth morphs (82%), although with a sample size of only 11 with observable pericarps, this population proportion estimate is

very likely to be inaccurate (Figure 5.4). Treated as a separate population, the Feature 32 assemblage is somewhat unusual for wild erect knotweed, but the sample size is not large enough to say for certain if it exhibits the beginnings of domestication syndrome. The Feature 19 assemblage (or both assemblages treated as a single population) is indistinguishable from modern erect knotweed, both in size and population proportion of smooth morphs.

Rohlfing. In many ways, Rohlfing is similar to Big Loose Creek. It is also situated close to the Missouri River (2 km upstream) on a minor tributary, Big Berger Creek. It is a single component Late Woodland site with two house clusters and associated features excavated. Located on a ridge spur above the creek, it is also protected from seasonal flooding (Herndon 2006). Two calibrated dates obtained by the excavators range from CE 680-960, while a date on the analyzed erect knotweed from Feature 7 returned a calibrated range of CE 774-943. The median calibrated ages of the Big Loose Creek and Rohlfing sites are only 18 years apart, and both were probably also deposited around the same time as the Sponemann assemblage, whose median calibrated date falls in between the two (Appendix 2).

According to a spatial analysis carried out by Wright and Shaffer (2014), the Rohlfing site is surrounded by more rugged topography with less access to fertile bottomlands than the Big Loose Creek site. They argue that this may partially explain why Late Woodland farmers at Big Loose Creek experimented with maize, while those at Rohlfing evidently did not. Aside from the absence of maize, the botanical assemblage from Rohlfing is also similar to that from Big Loose Creek, although less rich and diverse. The EAC crops sunflower, sumpweed, and little barley are entirely absent. This may simply be due to sampling error, as less than half as many liters of sediment were analyzed at Rohlfing, and these three absent crops were the least well-represented at Big Loose Creek (Lopinot and Powell 2015; Erikson 2006; Appendix 5). There is

a well-established relationship between the size of the overall sample and the visibility of rare species, both in ecology and in archaeology (Lyman and Ames 2007). The smaller sample size at Rohlfling also provides an alternative explanation to that proposed by Wright and Shaffer (2014) for the absence of maize, which was also vanishingly rare at Big Loose Creek.

Feature 7, which yielded the photosample, was probably a bell-shaped storage pit, although it had partially collapsed. It was nearly circular with a 1.39 m diameter and a depth of 0.96 m. The analyzed assemblage came from Zone IV of the pit, interpreted as the remains associated with the original bell-shaped pit. This fill zone contained a high density of plant remains and artifacts, including a small reconstructed vessel from the immediate vicinity of the analyzed assemblage. The vessel was a small cup or bowl (Vessel No. 28; 12 cm diameter, max height 8.7 cm). It is plausible that the analyzed erect knotweed from Zone IV of Feature 7 represents the remains of an actual meal – a rare circumstance for non-paleofecal botanical remains at archaeological sites. Erickson (2006:197) writes: “The association of a high density of seeds within a one liter sample from beneath an over-turned clay vessel in Zone IV of Feature 7 may connect two interrelated events: the over cooking of the seeds and the damage to the pot, all of which was subsequently discarded.”

While the context of the Rohlfling erect knotweed is somewhat extraordinary, their morphology is not. Both smooth and tubercled morphs are slightly smaller on average than the modern sample, though not significantly different. The sample marked “contents of vessel” (presumably the one referenced in the quote from Erickson, above) did contain mostly smooth morphs (82%) – but again the sample size (n=11) is too small to be confident that this is not a sampling error. The larger sample from nearby the vessel had a normal sample proportion of 57% smooth morphs. Erickson also noted the presence of erect knotweed sprouts in this

assemblage, although there are no unequivocal examples in my photosample (Erickson 2006:194).

6.5.5 Mississippian Sites

The final four sites in the analysis all date to the Mississippian era, and come from four different sub-regions: the Lower Illinois Valley, Northwestern Arkansas, the Central Mississippi Valley, and the Ohio River Valley. They represent a survey of the state of cultivated erect knotweed just before it apparently fell out of cultivation, sometime around CE 1400.

Whitney Bluff. During the 1920s and 1930s a team from the University of Arkansas Museum excavated the Whitney Bluff site, along with 80 other Ozark rockshelters. The crop plant remains from 19 rockshelters, including Whitney Bluff, were analyzed 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 1986:20).

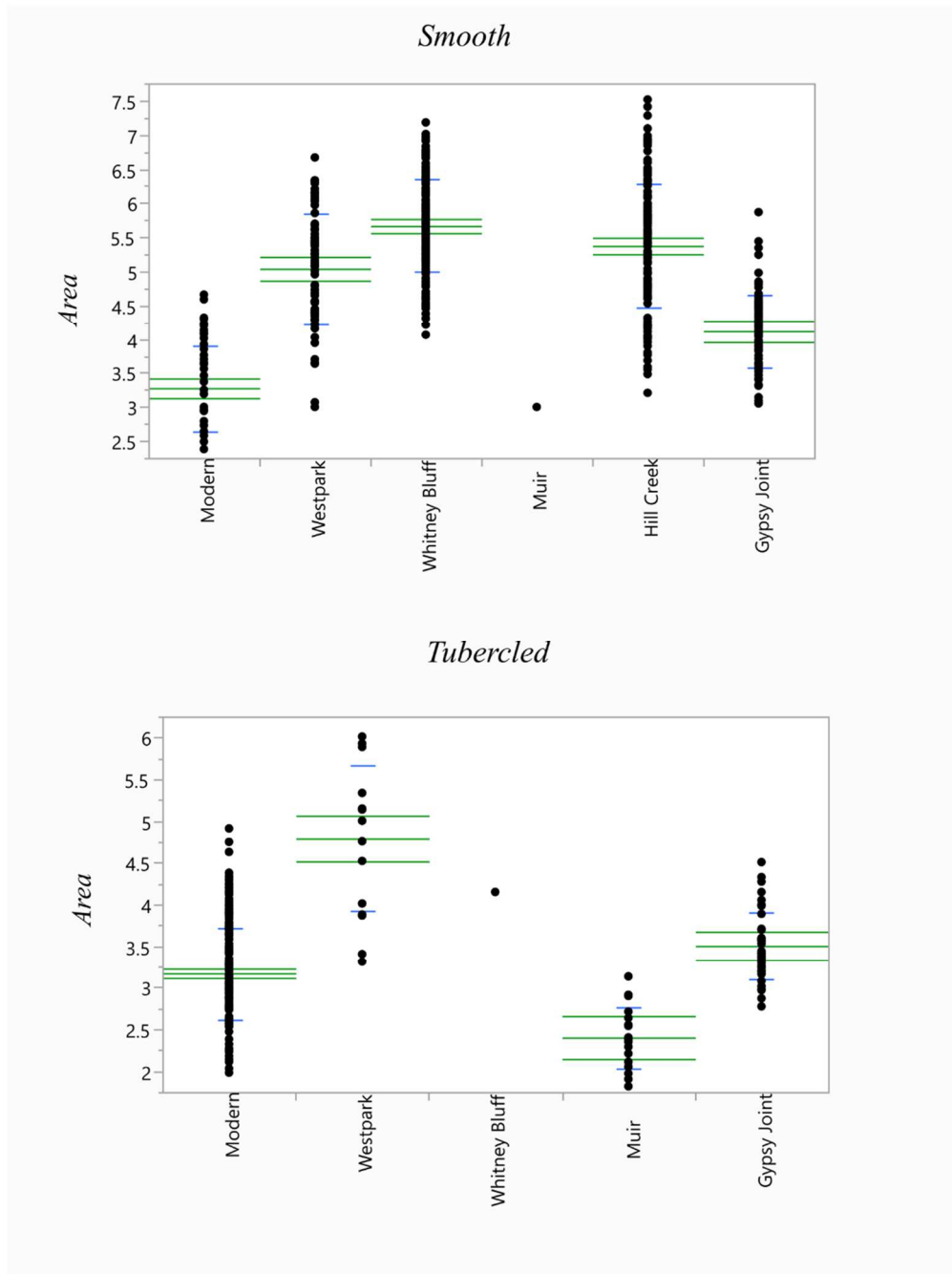


Figure 6.6. Distribution of values for achene size, in terms of area, for Mississippian sites. Long horizontal lines are mean and confidence interval of the mean, short horizontal lines are standard deviation. Westpark, which is also shown in Figure 6.5, is included again for easier comparison with the later assemblages. Three out of the four analyzed assemblages have significantly larger fruits than the modern comparative assemblage. Whitney Bluff and Hill Creek have the most pronounced reduction in fruit dimorphism, but Westpark and Gypsy Joint also have high sample proportions of smooth morphs. Muir, from the Fort Ancient area, is the exception. Not only is it almost entirely composed of tubercled morphs, these are abnormally small. They way represent a summer or early fall harvest of wild plants.

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 (Fritz 1986:107; 1986:92). Domesticated *Chenopodium berlandieri* subsp. *jonesianum* was also recovered from this context (Fritz 1986: 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 1986:107-8). They are treated as a single sample in this analysis. A fragment of the gourd from this context was dated by Fritz to cal. CE 1040-1386. The new direct date from one of the knotweed achenes returned a date of cal. CE 1046-1217.

Unlike all of the other assemblages in this analysis, the Whitney Bluff assemblage was preserved via desiccation, rather than carbonization. The measurements presented here are thus uncorrected and were taken directly from the photographed achenes. The assemblage was so well preserved that I was able 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. Per sampling protocol for the larger study, I randomly sampled 1 achene per 0.01 g for the photosample. Many of the Whitney Bluff achenes retain some or all of their perianth parts, as discussed below. The presence of the perianth or parts of the perianth may somewhat inflate size measurements compared to the modern assemblage, which was photographed with no perianth, but perianths of the Whitney Bluff achenes are generally tightly conforming to the shape of the underlying fruit. Of the 1307 achenes I examined, all but two were smooth morphs. Measurements of length and width reported here are very similar to those reported by Fritz on two different sub-samples of 100 achenes (Fritz 1986:108). The size and shape of the Whitney Bluff achenes have been described in great detail elsewhere, where I compared the morphology of this assemblage to various closely related species, and concluded that the most parsimonious

explanation for this assemblage is that it represents a domesticated sub-species of erect knotweed (Chapter 2; Chapter 3). The achenes are much larger than the modern sample, and the assemblage is composed of 99% smooth morphs. This assemblage provides strong evidence of domestication syndrome in terms of both fruit size and reduction in fruit dimorphism.

Muir. The Muir site was included as a Mississippian period outlier, in the sense that it is part of a tradition (Fort Ancient) that did not make much use of EAC crops. Muir is an early Fort Ancient village site dating between CE 950-1200. The analyzed erect knotweed assemblage was evidently deposited towards the end of this occupation: it dates to cal. 1180 – 1260, and is the third latest date of seven from the site as a whole. The site is located in the Inner Bluegrass region, in an upland setting ~ 1 km southeast of Jessamine Creek, and ~10 km north of the Kentucky River. It is likely that the site's inhabitants used one of the many nearby springs for drinking water (Turnbow and Sharp 1988).

Four structures, pit houses similar to those from the Emergent Mississippian American Bottom, and their associated pits and features were excavated. Feature 22 was an oval shaped pit with a 0.98 X 0.77 m orifice, 17 cm deep, classified as a small basin shaped pit. It was located 2.5 m west of Structure 2, and was itself dug into the floor of what was probably an older pit house or other type of basin-floored structure (several post molds appeared in its irregular floor) (Turnbow and Sharp 1988:76). Feature 22 contained the highest concentration of identified seeds at the site, including maize and domesticated beans (*Phaseolus vulgaris* L.) (Rossen 1988). These beans have not been directly dated, but if they can be dated by association with the erect knotweed assemblage from the same context, then they are among the oldest beans in Eastern North America, and certainly the oldest known from the Lower Ohio River Valley (Rossen 1988; Hart et al. 2002; Monaghan et al. 2014). Overall, Muir was typical of Fort Ancient sites in that

the plant assemblage was dominated by maize and beans – except for the presence of a large concentration (n=547) of erect knotweed in Feature 22.

The Muir erect knotweed is actually significantly smaller than the modern comparative sample (only the tubercled morphs could be statistically compared, as there was only 1 smooth morph; $p < 0.0001$). Compared to the other three Mississippian assemblages, which are all much larger than modern erect knotweed, it appears even more anomalous. As for the Mund assemblage, it is necessary to demonstrate that this assemblage actually represents erect knotweed, and not some other species. Instead of comparing smooth morphs, this time a comparison of tubercled morph was undertaken and these have more distinctive shapes than smooth morphs, and also diagnostic surface textures (Chapter 2; Appendix 6b). In terms of size, the Muir assemblages most similar to the small achenes of *P. aviculare* ssp. *buxiforme*. In terms of circularity, *P. achoreum* and *P. aviculare* ssp. *buxiforme* form one group, and *P. erectum* and *P. ramosissimum* form another. The Muir assemblage is less circular than either group, and most similar to immature erect knotweed (Appendix 6b). *P. ramosissimum* is the only species with a significantly different aspect ratio and roundness; Muir groups with the other three species. Of the 19 tubercled morphs, 11 are visibly striate-tubercled, a surface texture that is most often associated with *P. erectum*, although it also sometimes appears in other species (Chapter 2; Chapter 3). It seems likely that the Muir site represents an immature harvest of *P. erectum* achenes, perhaps one collected in late September or early October when smooth morphs are just beginning to appear. It may also be a summer harvest of *P. achoreum* or *P. aviculare* ssp. *buxiforme*, species which I do not have immature achene metrics for. It may be that ancient farmers' folk taxonomies did not differentiate between these species, or that farmers in the Fort Ancient area did not share a knowledge of, or preference for, erect knotweed.

Hill Creek. Hill Creek is located on the floodplain of a small creek of the same name, 3 km west of its opening into the Illinois River valley floodplain. It is a Mississippian homestead consisting of two houses and their associated pits and features. All five of the dates from the site and an additional direct date on the erect knotweed from Feature 1 are consistent with a short occupation sometime between CE 1100 – 1300 (Appendix 2; Conner 1985:13). Feature 1, which yielded the two latest dates from the site, is associated with Structure 1, which yielded the earliest date, and the ceramic assemblages and other artifacts do not show any temporal patterning between the two structures (Conner 1985b). Though they were different in terms of size and construction, both houses were probably occupied simultaneously by a nuclear or small extended family for a single generation (there is no evidence of rebuilding). As at Gypsy Joint (see below; Smith 1978), the most parsimonious explanation is that the two structures were the warm and cold weather houses of a single family (Conner 1985).

The analyzed erect knotweed came from Feature 1, a large bell-shaped pit with a rounded bottom. Although Feature 1 was highly structured with several individually discernable episodes of burning, it was evidently filled quickly. The erect knotweed assemblage at the bottom of the pit and a date from the final deposit of charcoal at the top of the pit were essentially identical (680 \pm 15 and 690 \pm 70, respectively; Appendix 2; Conner 1985:13). The pit contained abundant thatch and fish bones and evidence of multiple episodes of in situ burning: like the analyzed contexts at Mund, Sponemann, and Big Loose Creek, Feature 1 may have been an earth oven (Conner 1985:210). Of the 1263 identifiable erect knotweed seeds and fruits recovered from Hill Creek, all but one came from the lowest burning event in Feature 1 (Asch and Asch 1985c).

This assemblage bears the distinction of having sparked the initial speculation about a domesticated subspecies of erect knotweed in the mid-1980s. Asch and Asch (1985a; 1985b)

described a large carbonized assemblage composed exclusively of smooth morphs that were also larger than the erect knotweed smooth morphs in their reference collections. To ascertain whether or not erect knotweed 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 1985c). Their survey suggested that erect knotweed 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. Asch and Asch (1985b:144-5) 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*...” In particular, Asch and Asch (1985b:146) suggested that if the Hill Creek assemblage was not erect knotweed, it might instead belong to a closely related species, *P. ramosissimum*, which is known to produce many smooth achenes under certain (unspecified) conditions (Mertens and Raven 1965).

Although a domesticated assemblage of erect knotweed has now been described, and a new sub-species formally named (Chapter 2; Chapter 3), it is still possible that the second hypothesis of Asch and Aschs is a better explanation for the Hill Creek assemblage. Lacking any diagnostic tubercled morphs and being larger than any other assemblage of erect knotweed achenes but Whitney Bluff, it is necessary to compare the Hill Creek assemblage to the relatively large smooth morphs of *P. ramosissimum*, as Asch and Asch suggested over 30 years ago. The summary statistics presented in Appendix 6a are drawn from a subset of the total photosample

(n=95) that were not sprouted. The sprouts are obviously longer and differently shaped and would skew the morphometric analysis.

The Hill Creek erect knotweed is similar to modern erect knotweed smooth morphs in terms of both aspect ratio and roundness, although these shape descriptors are not different enough between species to be used for positive identification. The Hill Creek achenes are also significantly larger than the modern smooth morphs of any species, meaning that if this is a harvest of *P. ramosissimum*, it is a domesticated one. This is an unlikely explanation because there is no history of *P. ramosissimum* cultivation, and Hill Creek is located in a region that has been the subject of extensive archaeological investigations. The other two criteria used to identify the Whitney Bluff assemblage as erect knotweed, achene deflation and perianth morphology, are not preserved in the Hill Creek assemblage (Chapter 2; Chapter 3). The Whitney Bluff assemblage was also found to have a distinct shape, being significantly more round and having a significantly lower aspect ratio than all extant species. This is not true of the Hill Creek assemblage (Appendix 6a).

There are three different explanations for the fact that the Hill Creek assemblage does not share the distinctive shape of the Whitney Bluff assemblage: 1) Hill Creek is a domesticated form of some other species (*P. ramosissimum* is only the most likely in that we know it sometimes produces monomorphic harvests); 2) the Hill Creek assemblage is domesticated erect knotweed, and the differences in shape between it and the Whitney Bluff assemblage represent the development of distinct landraces under cultivation, or; 3) carbonization accounts for the difference. Given the weight of the archaeological evidence for the cultivation and gradual improvement of erect knotweed over a period of thousands of years, the second and third explanations seem far more likely. The presence of unique landraces is also to be expected for

domesticated annual plants. An additional unique feature of the Hill Creek assemblage is that more than one third of the photosample (51/146) is composed of sprouts (Figure 6.7). The significance of this fact with respect to the syndrome of domestication and agricultural practice is discussed below.

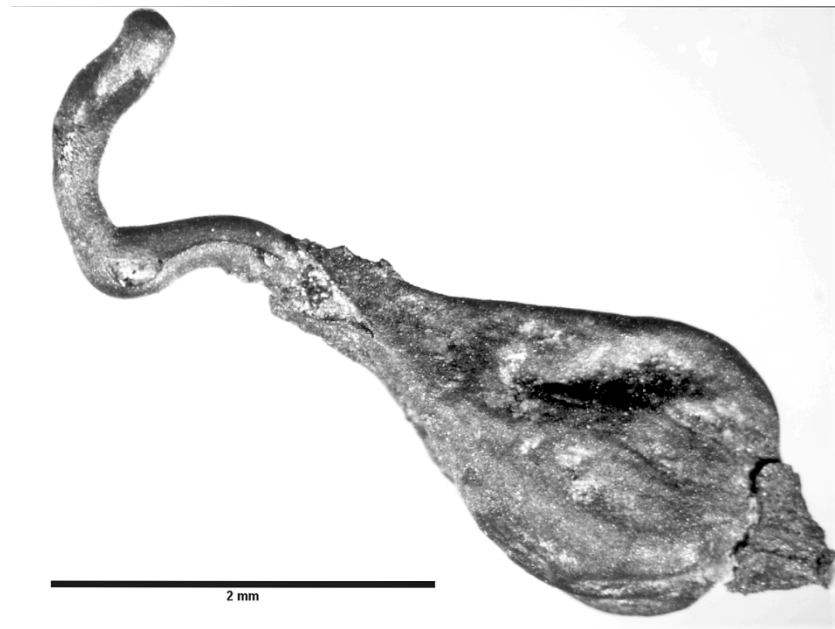


Figure 6.7. Typical example of a sprouted achene from the Hill Creek assemblage.

Gypsy Joint. Gypsy Joint is a Mississippian homestead consisting of two houses and associated features. It is located on a low sand ridge among the ridge and swale topography of the Western Lowlands of southern Missouri and northern Arkansas. This region is located at the western edge of the Mississippi Valley, where it meets the Ozark Escarpment, and is characterized by linear marshes or small streams interdigitated with more well drained ridges. It is about 25 km south of Powers Fort, a contemporaneous fortified village (Smith 1978). The Powers Phase sites are mostly located at the interface between the floodplain and the Ozark uplands on a terrace consisting of low sand ridges no more than 4.6 m above the surrounding

swampland. Most have been dated to the 14th century (Morse and Morse 1983). A direct date on the erect knotweed from Feature 5b at Gypsy Joint yielded a date of cal. 1310–1415 – the latest date associated with erect knotweed in this study, or elsewhere.

The inhabitants of Gypsy Joint were definitely growing maize: a maize cache and abundant scattered kernel and cob fragments were recovered. Both domesticated sumpweed and a single ambiguous sunflower seed are also present. Abundant goosefoot was also recovered, much of it from the same context as the analyzed erect knotweed, but was not evaluated for domestication syndrome because the existence of domesticated goosefoot was still largely unknown at the time. Like Hill Creek, Gypsy Joint has been interpreted as the farmstead of a single nuclear family, with a winter and summer house, that was probably occupied for only a short period of time – perhaps as briefly as 2 – 3 years (Smith 1978).

Feature 5 was actually two pits – Feature 5a and Feature 5b, adjacent to one another within a space that was almost certainly a plant food processing area. Feature 5 was 6 m northeast of Structure 1, the proposed summer house. The analyzed erect knotweed actually came from both of the small pits, and from the surface of the work space surrounding them (Appendix 4). Both pits contained rich and varied plant remains, particularly hickory nut shell, goosefoot, and erect knotweed. The erect knotweed from Feature 5, although still significantly larger than the modern comparative collection, is smaller than the earlier Mississippian assemblages from Westpark, Whitney Bluff, and Hill Creek (Figure 6.6). All but one of the sampled contexts had abnormally high proportions of smooth morphs ranging from 86 – 90%. The one exception (Pit 5a, n=48) also had the smallest sample size and thus the greatest associated error (Figure 5.4). In terms of both size and population proportion of smooth morphs, this latest of erect knotweed assemblage exhibits domestication syndrome. It differs from the

earlier domesticated landraces in that the achenes are smaller. This may be evidence for a decrease in the quality of the seed stock prior to the abandonment of erect knotweed as a crop, or simply another regional landrace.

6.6 Discussion

Erect knotweed cultivation may have begun in the Late Archaic, although the small numbers of seeds recovered from sites in the American Bottom and west-central Kentucky may also represent the vegetation at the site being incidentally burned. There is a much stronger case for cultivation in the Early Woodland era, especially in the upland region of eastern Kentucky and Tennessee. Assemblages like the one from Cold Oak are unlikely to be the result of accidental burning of a weedy camp followers, because erect knotweed does not naturally occur in such high and dry locations (Murray and Sheehan 1984; Asch and Asch 1985c; Chapter 4). It is also clear from paleofecal specimens that Early Woodland people on the eastern margin of the core area were consuming erect knotweed (Faulkner 1991). On the highland western margin of the core area, the Ozark Escarpment, people were evidently experimenting with one or more members of genus *Periscaria*, the smartweeds, based on the directly dated assemblage from Marble Bluff, AR, but there is no evidence that they were also harvesting erect knotweed at this time.

If casual gathering of erect knotweed began in the major river valleys of the core area during the Terminal Archaic, and continued in the eastern highlands when populations abandoned the major floodplains during the Early Woodland, this may have been a significant moment in the evolution of domesticated erect knotweed. The fruit dimorphism exhibited by wild erect knotweed is a form of evolutionary bet-hedging (reviewed in Chapter 3 and 3).

Organisms that are evolutionary bet-hedgers exhibit strategies that do not maximize fitness per generation, but which tend to reduce variation in fitness over many generations. In the case of erect knotweed, most of its tubercled morphs do not germinate the spring after they are produced, which means that they are subject to an entire year of potential predation and pathogen risks before they germinate. Once they do germinate, they also grow more slowly than seedlings sprung from smooth morphs, meaning that they are less competitive in the dog-eat-dog world of a seasonally scoured river bank, where dozens of different weedy species compete for light and space. Smooth morph germination rates are much higher, sometimes 100%. In short, a mother plant that uses resources producing tubercled morphs that could otherwise be used to produce smooth morphs is not maximizing its fitness for the next generation – so why has the production of tubercled morphs evolved, and how is it maintained?

The specific source of strong selective pressure suggested by my observations is the unpredictability of flooding from year to year. When floods occur in the early spring, they are probably beneficial because they clear the riverbanks for plants like erect knotweed and deposit soil nutrients. Robust erect knotweed plants can also survive fall floods. But floods that occur in the early summer can eliminate an entire generation of erect knotweed plants (Chapter 4). When this occurs, the near-100% germination rate of smooth morphs is a liability that could lead to localized extinctions. Tubercled morphs allow the population to regenerate the following year, because they are able to weather bad years in the seedbank. In order for fruit dimorphism to be eliminated under cultivation, I have hypothesized that humans were protecting populations of erect knotweed from the effects of unpredictable flooding, both by creating clearings for erect knotweed seedlings in micro-topographic zones that rarely or never flood and by storing seed stock, which provided an alternative to the soil seed bank.

A combination of lines of evidence suggests that this co-evolutionary process began during the Early Woodland period. First, human populations evidently abandoned the floodplains in several regions of ENA to escape the effects of unpredictable and/or severe floods (Kidder 2006). It is clear that they took their floodplain adapted Archaic crops, including erect knotweed, with them, because we find the cached seeds of these plants in upland rockshelters both in the Ozarks and western Appalachia (Fritz 1986; Gremillion 1993b). There are floodplains in the uplands, albeit narrower ones, and people may have used a variety of micro-topographic zones to grow their crops. There are also “uplands” near the major river valleys: zones that are protected from flooding by relatively small differences in altitude. But during the Early Woodland, there is evidence for the clearance of upland forests (Delcourt et al. 1998), and upland terraces offer low slopes and fertile soils that could have been turned into productive gardens (Gremillion et al. 2008). Perhaps these Early Woodland refugees of severe flooding in the major river valleys were the first EAC farmers to recognize the importance of altitudinal diversity in field placement. It was probably more work to clear terrace forests for cultivation than to it was to grow crops along the annually scoured riverbanks (Smith 1992), but it may also have been critical for maintaining food security during a period of climate change. By cultivating erect knotweed in gardens where flooding never occurred, as well as by saving seeds in rockshelters like Cold Oak, Early Woodland farmers would have relaxed the selective pressures that maintain fruit dimorphism in wild erect knotweed.

Direct evidence in support of this scenario also comes from Walker-Noe, the earliest Middle Woodland assemblage analyzed, and the closest to western Appalachia. Here we have an assemblage exhibiting the full domestication syndrome of erect knotweed – increase in fruit size and decrease in fruit dimorphism – hundreds of years before such a landrace was developed in

the American Bottom. A morphometric analysis of other Middle Woodland assemblages from the Ohio valley is obviously warranted to determine how widespread this early domesticated landrace was. The Walker-Noe assemblage also provides preliminary evidence for a scenario in which Middle Woodland interregional trade facilitated the exchange of superior seed stock and agricultural knowledge between communities (Mueller 2014). Unlike later Middle Woodland assemblages from domestic contexts, this sub-mound assemblage, deposited in association with burials, is domesticated. Perhaps it is time to consider the possibility that high quality seed stock was a prestige good on par with exotic materials or iconographically rich pottery and pipes. Such an investigation might also make more space for us to imagine the role of women in Adena and Hopewell ceremonialism and exchange, since it is likely that women were the keepers of seeds (Watson and Kennedy 1991; Mueller and Fritz 2016).

Further to the west, in the Illinois valley and American Bottom, the contemporaneous Middle Woodland homesteads Smiling Dan and Meridian Hills evidently had not obtained or developed a similar domesticated landrace of erect knotweed by c.150 years later, although the Meridian Hills erect knotweed *is* significantly larger than the modern comparative sample. The Meridian Hills assemblage is the first in a diachronic series of assemblages from the American Bottom which demonstrate a consistent trajectory of domestication, culminating with the early Mississippian Westpark assemblage. The only possible exception is the Mund assemblage, which may be a precocious domesticated assemblage that was harvested early in the season when many of the achenes were still immature.

By the Terminal Late Woodland in the American Bottom, domesticated landraces of erect knotweed seem to have been slowly developed *in situ*. Nearby, in the lower Missouri valley, the seeds of cultivated erect knotweed still looked the same as those of modern erect

knotweed. Agricultural communities of practice in the lower Missouri valley also differed from those in the American Bottom in another important way – they were relatively slow to adopt maize as a crop. Perhaps communities in these two nearby regions were not regularly exchanging either seeds or agricultural knowledge. It is also interesting that the communities at Range and Westpark, who had fully integrated maize into their economy, were also continuing to improve erect knotweed, whereas the more agriculturally conservative farmers of the lower Missouri valley were not. This circumstance contradicts the prevailing wisdom that the adoption of maize spelled doom for the cultivation of older EAC crops.

During the Mississippian period, each of the sites with domesticated assemblages of erect knotweed (Whitney Bluff, Hill Creek, and Gypsy Joint) looks slightly different. Whitney Bluff and Hill Creek achenes have distinct shapes, whereas Gypsy Joint knotweed has slightly smaller fruits. These morphologies may be plastic or inherited, but either way they represent the subtle effects of different local communities of practice. The Hill Creek assemblage also has another curious feature: many of the achenes are sprouted. Two different explanations present themselves, and both potentially illuminate aspects of lost agricultural practice. First, the sprouts may be accidental. When cultivating modern erect knotweed, even the smooth morphs need to be *stratified* before they will germinate. This means that they need to be subjected to a simulated version of conditions in the soil seed bank, six weeks in moist soil at 4°C in my experiments (Chapter 4). Ancient farmers could have dealt with this by planting in the fall, as modern farmers do with a crop of winter wheat, or they could have stored seed stock in moist subterranean pits to prepare them for spring. The latter strategy has the advantage of protecting the seeds from predation over the winter. But the seeds at Hill Creek had sprouted – perhaps this was an emergent quality of domesticated erect knotweed that took the Hill Creek farmers by

surprise. Most of our domesticated plants do need to have their seeds pre-treated to ensure germination: this is one of the many ways that they differ from their wild ancestors. Perhaps the sprouts at Hill Creek are evidence for the evolution of this additional piece of the domestication syndrome in erect knotweed. Another explanation is that sprouts were the preferred form in which to consume erect knotweed. The hard pericarp of erect knotweed is indigestible and difficult to remove (Murray and Sheehan 1984). Allowing achenes to sprout before consuming them would not only fracture the pericarp without expending any human effort, but also increase the nutritive value of each seed. Sprouts are often more nutritious than seeds because the chemical transformations that allow the young plant to consume the seed's stored resources also render these resources more abundant or easily digestible by humans. Buckwheat (*Fagopyrum esculentum* Moench) is the closest crop relative of erect knotweed, and may serve as an illustrative example. The nutritional content of buckwheat sprouts and seeds have been compared by Kim and colleagues (2004), who found that the sprouts of buckwheat have a greater concentration of monosaccharides (glucose and fructose) and four times the free amino acid content of buckwheat seeds. Sprouting is one possible processing technique that may have been used by ancient farmers to render erect knotweed more edible and palatable.

In the case of the latest dated assemblage from Gypsy Joint, where both indicators of domestication are less pronounced than at Hill Creek and Whitney Bluff, fruit morphology may reflect a more casual form of cultivation. If seedlings were offered less protection, introgression with wild populations could quickly become evolutionarily advantageous, as diversity of offspring once again became necessary for the survival of populations. Knotweeds are thought to be mostly self-fertilizing, but it is clear that their flowers sometimes outcross with nearby plants because sub-species within the *P. aviculare* complex are known to hybridize when growing in

close proximity (Costea and Tardiff 2004). At the Muir site, we have another possible example of possible feralization, although in this case the problem may be loss of knowledge rather than deterioration of seed stock. The most likely explanation for the morphology of the Muir knotweed is that 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. If they were harvesting for food, they got a lot less of it and exerted more effort than they would have 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 in my experiments had by far the lowest germination rates (mean 2%; Chapter 4).

6.7 Conclusions

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 archaeobotanical record also provides evidence for the development of erect knotweed landraces: morphologically distinct varieties of domesticated plants developed by individual communities to meet local needs or satisfy local preferences.

Domesticated plants and animals are not *faits accomplis*. They cannot be maintained in a consistent form without an equally consistent management regime or selective breeding. For example, dingoes (*Canis lupus* ssp. *dingo*) diverged from their domesticated dog progenitors when they were brought to Australia some 4,000 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 (or wild), with only the occasional puppy becoming a tame camp dingo (reviewed in 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 (Smith and Litchfield 2010). 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. In this paper, I have tried to highlight some of the possible practices that may have led to unique morphologies such as diminutive fruits and sprouts. I have also briefly reviewed the practices that may have led to increasing seed size and decreasing fruit dimorphism (see also Chapter 3; Chapter 4).

Landraces can spread from their point of origin through exchange, but in order for a plant variety to be maintained in its new community it must be accompanied by agricultural knowledge. Predictable and frequent exchange between communities is important for maintaining seed security, and for obtaining knowledge about new cultivation, processing, and cooking techniques. Institutionalized exchange like that reflected in the Hopewell Phenomenon is one way that seed stock and associated knowledge might spread (Mueller 2014). The movement of women through marriage or adoption is another. Hart (2001) argued that matrilocality contributed to the improvement of maize landraces, because multiple generations of women were able to continuously grow the same populations of maize under the same local conditions. But the movement of women, through patrilocality or institutions of adopting

members of other communities, might result in an infusion of seeds and knowledge into a new community. Sodalities, which cross-cut kin groups, that bring together members of different communities, may have played a role in spreading seed and knowledge. Where landraces are similar or follow the same trajectory, as in the American Bottom, there is evidence for institutionalized exchange and/or the movement of women between communities. Where agricultural communities of practice diverge, as for Fort Ancient Mississippian and Middle Mississippian communities, or between the Late Woodland American Bottom and lower Missouri river communities, the opposite conclusion is supported.

All of the conclusions reached by this analysis are preliminary. This is the first study of erect knotweed domestication syndrome or landraces, so I have attempted to cover a huge temporal and spatial range at the expense of detailed coverage of any region or time period. This analysis suggests several avenues for future research. The Walker-Noe assemblage, with its precocious domestication syndrome, needs to be put into context with the morphometric analysis of other Adena and Hopewell assemblages from across ENA. What happened to this landrace? Did domesticated erect knotweed die out at the end of the Middle Woodland, only to be re-domesticated during the later Late Woodland, or was it maintained in some communities but not others?

The diachronic study of American Bottom landraces presents another interesting question. It is clear from this analysis that domesticated erect knotweed was developed in situ by American Bottom farmers, with continuous improvement between c. CE 200 – 1200. These farmers are perhaps best considered to be part of the same community of practice as those in the Illinois valley, since it is thought that the American Bottom populations retreated to that region between the Middle and Late Woodland periods (Fortier and McElrath 2000), and the two

regions were also involved via either colonization or exchange during the Mississippian period (Goldstein 1980; Conner 1985; Farnsworth et al. 1991; Delaney-Rivera 2004; Bardolph 2014). If so, the Hill Creek assemblage can also be considered part of this trajectory. Was domesticated erect knotweed one of the many innovations exported by Cahokia to the rest of the Mississippian world, or was erect knotweed domesticated several times in different sub-regions? The most obvious way to investigate this possibility is to gather more morphometric data from erect knotweed assemblages in Arkansas and southern Missouri. Farmers in western Arkansas deposited a domesticated landrace of erect knotweed at Whitney Bluff that looks quite different from the slightly later assemblage at Hill Creek. Was the Whitney Bluff landrace developed by late Woodland Baytown or Plum Bayou farmers in the Mississippi or Arkansas valleys – or by the Late Woodland inhabitants of the Ozark highlands? That latter possibility doesn't seem particularly likely, since there are no Late Woodland assemblages of erect knotweed in the rockshelters collections (Fritz 1986),¹⁴ but this absence may be accidental and it is possible that a renewed investigation would turn up western Arkansas precedents for the Whitney Bluff assemblage

Other open questions pertain to strength of the inferences that can be made from fruit morphology, and these can only be answered with further study of living plants. Erect knotweed and its relatives are incredibly plastic organisms, and it is possible that the morphologies of some archaeological assemblages can be explained with reference to plastic responses to particular

¹⁴ Besides the Whitney Bluff and Marble Bluff assemblages discussed above, one other assemblage of knotweed, from Green Bluff, was reported by Fritz (1986). Fritz noted that these achenes looked similar to those from Marble Bluff, and indeed they are also likely a species of smartweed (recently moved to genus *Persicaria*). A direct date on these achenes yielded a calibrated range of CE 713 – 885. It seems that from the Early to Late Woodland, smartweed may have been collected or cultivated in the Ozarks, although both assemblages are quite small to build a case upon.

environmental conditions. Since the environmental conditions experienced by cultivated plants are shaped by humans, a more nuanced understanding of plasticity in erect knotweed could lead to better and more detailed inferences about agricultural practices. Such an understanding would also allow us to more confidently differentiate between the multigenerational hereditary effects of cultivation and the immediate plastic effects of cultivation (see also Chapter 7)

Finally, it is my hope that this analysis, preliminary though it may be, illustrates the utility of 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, but usually limited by a lack of experimental data linking specific morphologies to their causes. We can increase the usefulness of seeds as artifacts both by observing how contemporary farmers maintain or subtly change their cultivated landraces, and by growing crops and wild progenitors experimentally.

6.8 References

Asch, David L. and Nancy B. Asch

1985a Archaeobotany. In *Smiling Dan: Structure and Function at a Middle Woodland Settlement in the Lower Illinois River Valley*, edited by Barbara D. Stafford and Mark B. Sant, pp. 327-400. Center for American Archaeology, Kampsville, IL.

1985b Archaeobotany. In *The Hill Creek Homestead and the Late Mississippian Settlement in the Lower Illinois River Valley*, edited by Michael D. Conner, pp. 115-170. Kampsville Archaeological Center. vol. 1. The Center for American Archaeology, Kampsville, IL.

1985c Prehistoric Plant Cultivation in West Central Illinois. In *Prehistoric Food Production in North America*, edited by Richard I. Ford, pp. 149-203. vol. 75. Museum of Anthropology, University of Michigan, Ann Arbor, MI.

Asch, Nancy B. and David L. Asch

1986 Woodland Period Archaeobotany of the Napoleon Hollow Site. In *Woodland Period Occupations of the Napoleon Hollow Site in the Lower Illinois River Valley*, edited by Michael D. Wiant and Charles R. McGimsey, pp. 427-512. Center for American Archeology, Kampsville, IL.

Badstue, Lone B., Mauricio R. Bellon, Julien Berthaud, Xóchitl Juárez, Irma Manuel Rosas, Ana María Solano and Alejandro Ramírez

2006 Examining the Role of Collective Action in an Informal Seed System: A Case Study from the Central Valleys of Oaxaca, Mexico. *Human Ecology* 34(2):249-273.

Bardolph, Dana

2014 Evaluating Cahokian Contact and Mississippian Identity Politics in the Late Prehistoric Central Illinois River Valley. *American Antiquity* 79(1):69-89.

Benson, Larry V., Timothy R. Pauketat and Edward R. Cook

2009 Cahokia's Boom and Bust in the Context of Climate Change. *American Antiquity* 74(3):467-483.

Blake, Sidney Fay

1939 A New Variety of *Iva ciliata* from Indian Rock Shelters in the South-Central United States. *Rhodora* 41(483):81-86.

Brenkle, Jacob F.

- 1946 Notes on Avicularia II. *Phytologia* 2(5):169-171.
- Brush, Stephen B.
- 2000 *Genes in the Field: On-Farm Conservation of Crop Diversity*. International Plant Genetic Resources Institute, Rome, Italy.
- Calvet-Mir, Laura, Maria Calvet-Mir, J Luis Molina and V Reves-Garcia
- 2012 Seed exchange as an agrobiodiversity conservation mechanism. A case study in Vail Fosca, Catalan Pyrenees, Iberian Peninsula. *Ecology and Society* 17(1):29.
- Chapman, Jefferson and Gary D Crites
- 1987 Evidence for early maize (*Zea mays*) from the Icehouse Bottom site, Tennessee. *American Antiquity* 52(2):352-354.
- Conner, Michael D. (editor)
- 1985 *The Hill Creek Homestead and the Late Mississippian Settlement in the Lower Illinois Valley*. 1. Center for American Archaeology, Kampsville, IL.
- Cook, Robert A. and T. Douglas Price
- 2015 Maize, mounds, and the movement of people: Isotope analysis of a Mississippian/Fort Ancient region. *Journal of Archaeological Science* 61:112-128.
- Costea, Mihai and François J. Tardif
- 2004 The Biology of Canadian Weeds: *Polygonum aviculare* L. *Canadian Journal of Plant Science* 131:481-506.
- Costea, Mihai, François J. Tardif and Harold H. Hinds
- 2005 *Polygonum* L. In *Flora of North America North of Mexico*, edited by Flora of North America Editorial Committee. vol. 5. eFloras.org, New York and Oxford.

Cowan, C. Wesley and Bruce D. Smith

- 1993 New Perspectives on a Wild Gourd in Eastern North America. *Journal of Ethnobiology* 13:17-54.

Crawford, Gary W.

- 1982 Late Archaic Plant Remains from West-central Kentucky: A Summary. *Midcontinental Journal of Archaeology* 7(2):205-224.

Crawford, Gary W., David G. Smith and Vandy E. Bowyer

- 1997 Dating the Entry of Corn (*Zea mays*) into the Lower Great Lakes region. *American Antiquity* 62(1):112-119.

Crites, Gary D.

- 1987 Human-Plant Mutualism and Niche Expression in the Paleoethnobotanical Record: A Middle Woodland Example. *American Antiquity* 52(4):725-740.
- 1993 Domesticated Sunflower in the Fifth Millennium B.P. Temporal Context: New Evidence from Middle Tennessee. *American Antiquity* 58(1):146-148.

D'Andrea, A. Catherine, M. Klee and J. Casey

- 2001 Archaeobotanical Evidence for Pearl Millet (*Pennisetum glaucum*) in Sub-Saharan West Africa. *Antiquity* 75:341-348.

D'Andrea, A. Catherine

- 2008 T'ef (*Eragrostis tef*) in Ancient Agricultural Systems of Highland Ethiopia. *Economic Botany* 62(4):547-566.

Da Fonseca, Rute R, Bruce D Smith, Nathan Wales, Enrico Cappellini, Pontus Skoglund, Matteo Fumagalli, José Alfredo Samaniego, Christian Carøe, María C Ávila-Arcos and David E Hufnagel

2015 The origin and evolution of maize in the Southwestern United States. *Nature Plants* 1.

Delaney-Rivera, Colleen

2004 From Edge to Frontier: Early Mississippian Occupation of the Lower Illinois River Valley. *Southeastern Archaeology* 23(1):41-56.

Delcourt, Paul A., Hazel R. Delcourt, Patricia A. Cridlebaugh and Jefferson Chapman

1986 Holocene Ethnobotanical and Paleoecological Record of Human Impact on Vegetation in the Little Tennessee River Valley, Tennessee. *Quaternary Research* 25(3):330-349.

Delcourt, Paul A., Hazel R. Delcourt, Cecil R. Ison, William E. Sharp and Kristen J. Gremillion

1998 Prehistoric human use of fire, the Eastern Agricultural Complex, and Appalachian oak-chestnut forests: Paleoecology of Cliff Palace Pond, Kentucky. *American Antiquity* 63(2):263-278.

Doran, Glen H., David N. Dickel and Lee A. Newsom

1990 A 7,290-Year-Old Bottle Gourd from the Windover Site, Florida. *American Antiquity* 55(2):354-360.

Emerson, Thomas E. and Kristin M. Hedman

2014 The Dangers of Diversity: The Consolidation and Dissolution of Cahokia, Native America's First Urban Polity. In *Beyond Collapse: Archaeological Perspectives on Resilience, Revitalization, and Transformation in Complex Societies.*, edited by Ronald K. Faulseit, pp. 147-175. Occasional Paper. Center For Archaeological Investigations, Southern Illinois University Press, Carbondale.

Erickson, Annette G.

- 2006 *Ethnobotanical Analysis, in Phase III Investigations at the Rohlfing (23Fr525) and Schove (23Fr526) sites in Frankling County, Missouri.* Cultural Resource Analysts, Inc.

Erickson, David L., Bruce D. Smith, C. Clarke Andrew, Daniel H. Sandweiss and Noreen Tuross

- 2005 An Asian Origin for a 10,000-Year-Old Domesticated Plant in the Americas. *Proceedings of the National Academy of Sciences of the United States of America* 102(51):18315-18320.

Farnsworth, Kenneth B., Thomas E. Emerson and Rebecca M. Glenn

- 1991 Patterns of Late Woodland/Mississippian Interaction in the Lower Illinois Valley: A View from Starr Village. In *Cahokia and the Hinterlands: Middle Mississippian Cultures of the Midwest*, edited by T.E. Emerson and R.B. Lewis, pp. 83-118. University of Illinois Press, Champaign-Urbana.

Faulkner, Charles T.

- 1991 Prehistoric diet and parasitic infection in Tennessee: Evidence from the analysis of desiccated human paleofeces. *American Antiquity* 56(4):687-700.

Ford, Richard I. (editor)

- 1985 *Prehistoric Food Production in North America.* 75. Museum of Anthropology, University of Michigan, Ann Arbor.

Fortier, Andrew C., Thomas E. Emerson and Dale L. McElrath

- 2006 Calibrating and Reassessing American Bottom Culture History. *Southeastern Archaeology* 25(2):170-211.

Fortier, Andrew C. and Fred A. Finney

- 1983 Mund Phase Features. In *The Mund Site, FAI-270 Site Reports*, edited by Andrew C. Fortier, Fred A. Finney and Richard B. Lacampagne, pp. 111-154. University of Illinois, Champaign-Urbana.

Fortier, Andrew C. and Douglas K. Jackson

- 2000 The formation of a Late Woodland heartland in the American Bottom, Illinois ca. AD 650–900. In *Late Woodland Societies: Tradition and Transformation across the Midcontinent*, edited by Thomas E. Emerson, Dale L. McElrath and Andrew C. Fortier, pp. 123-147. University of Nebraska Press, Lincoln, NE.

Fortier, Andrew C., Thomas O. Maher and Joyce A. Williams

- 1991 *The Sponemann Site: The Formative Emergent Mississippian Sponemann Phase Occupation, FAI-270 Site Reports*. University of Illinois, Champaign-Urbana.

Freitas, Fabio Oliveira, Gerhard Bendel, Robin G. Allaby and Terence A. Brown

- 2003 DNA from primitive maize landraces and archaeological remains: Implications for the domestication of maize and its expansion into South America. *Journal of Archaeological Science* 30(7):901-908.

Fritz, Gayle J.

- 1984 Identification of Cultigen Amaranth and Chenopod from Rockshelter Sites in Northwest Arkansas. *American Antiquity* 49(3):558-572.
- 1986 Prehistoric Ozark Agriculture: The University of Arkansas Rockshelter Collections. Dissertation, Anthropology, University of North Carolina, Chapel Hill.

- 1993 Early and Middle Woodland Period Paleoethnobotany. In *Foraging and Farming in the Eastern Woodlands*, edited by C. Margaret Scarry, pp. 39-56. University Press of Florida, Gainesville.
- 1994 Precolumbian *Cucurbita argyrosperma* ssp. *argyrosperma* (Cucurbitaceae) in the Eastern Woodlands of North America. *Economic Botany* 48(3):280-292.
- 1997 A Three-Thousand-Year-Old Cache of Crop Seeds from Marble Bluff, Arkansas. In *People, Plants and Landscapes: Studies in Paleoethnobotany*, edited by Kristen J. Gremillion, pp. 42-62. University of Alabama Press, Tuscaloosa.
- 1999 Gender and the Early Cultivation of Gourds in Eastern North America. *American Antiquity* 64(3):417-429.
- 2000 Native Farming Systems and Ecosystems in the Mississippi River Valley. In *Imperfect Balance: Landscape Transformations in the Precolumbian Americas*, edited by David L. Lentz, pp. 224-249. Columbia University Press, New York.
- 2014 Maygrass: Its Role and Significance in Native Eastern North American In *New Lives for Ancient and Extinct Crop*, edited by Paul E. Minnis, pp. 12-43. University of Arizona Press, Tucson, AZ.

Fritz, Gayle J. and Tristram R. Kidder

- 1993 Recent investigations into prehistoric agriculture in the Lower Mississippi Valley. *Southeastern Archaeology* 12(1):1-14.

Fritz, Gayle J. and Neal H. Lopinot

- 2007 Native Crops at Early Cahokia: Comparing Domestic and Ceremonial Contexts. *Illinois Archaeology* 15 & 16:90-111.

Fritz, Gayle J. and Bruce D. Smith

1988 Old Collections and New Technology: Documenting the Domestication of *Chenopodium* in Eastern North America. *Midcontinental Journal of Archaeology* 13(1):3-27.

Fuller, Dorian Q.

2007 Contrasting patterns in crop domestication and domestication rates: Recent archaeobotanical insights from the Old World. *Annals of Botany* 100(5):903-924.

Fuller, Dorian Q., Robin G. Allaby and Chris Stevens

2010 Domestication as innovation: the entanglement of techniques, technology, and chance in the domestication of cereal crops. *World Archaeology* 42(1):13-28.

Fuller, Dorian Q., Ling Qin, Yunfei Zheng, Zhijun Zhao, Xugao Chen, Leo Aoi Hosoya and Sun. Guo-Ping

2009 The Domestication Process and Domestication Rate in Rice: Spikelet Bases from the Lower Yangtze. *Science* 323:1607-1610.

Goldstein, Lynne

1980 *Mississippian Mortuary Practices: A Case Study of Two Cemeteries in the Lower Illinois Valley*. Scientific Papers 4. Northwestern University Archaeological Program, Evanston, IL.

Grantham, Larry

2010 *Archaeological Investigations at the Big Loose Creek Site, Osage County, Missouri: Mitigation of Adverse Effects from Road Construction on Route C*. Missouri Department of Transportation.

Gremillion, Kristen J.

- 1993a The Evolution of Seed Morphology in Domesticated Chenopodium: An Archaeological Case Study. *Journal of Ethnobiology* 13:149-169.
- 1993b Plant Husbandry at the Archaic/Woodland Transition: Evidence from the Cold Oak Shelter, Kentucky. *Midcontinental Journal of Archaeology* 18:161-189.
- 1998 Changing Roles of Wild and Cultivated Plant Resources Among Early Farmers of Eastern Kentucky. *Southeastern Archaeology* 17(2):140-157.
- 2004 Seed Processing and the Origins of Food Production in Eastern North America. *American Antiquity* 69(2):215-233.

Gremillion, Kristen J., Jason Windingstad and Sarah C. Sherwood

- 2008 Forest Opening, Habitat Use and Food Production on the Cumberland Plateau, Kentucky: Adaptive Flexibility in Marginal Settings. *American Antiquity* 73(3):387-411.

Hajic, Edwin R.

- 1985 Geomorphological and Stratigraphic Investigations. In *Smiling Dan: Structure and Function at a Middle Woodlands Settlement in the Lower Illinois River Valley*, edited by Barbara D. Stafford and Mark B. Sant, pp. 41-82. Center for American Archaeology, Kampsville, IL.

Harlan, Jack R., J.M.J. De Wet and E. Glen Price

- 1973 Comparative Evolution of Cereals. *Evolution* 27(2):311-325.

Hart, John P., David L Asch, C Margaret Scarry and Gary W Crawford

- 2002 The age of the common bean (*Phaseolus vulgaris* L.) in the northern Eastern Woodlands of North America. *Antiquity* 76(292):377-383.

Hart, John P.

2001 Maize, Matrilocality, Migration and Northern Iroquoian Evolution. *Journal of Archaeological Method and Theory* 8(2):151-182.

2008 Evolving the three sisters: The changing histories of maize, bean, and squash in New York and the greater Northeast. In *Current Northeast Paleoethnobotany II*, edited by John P. Hart, pp. 87-99. vol. Bulletin 512. New York State Museum, Albany.

Hart, John P., Hetty Jo Brumbach and Robert Lusteck

2007 Extending the Phytolith Evidence for Early Maize (*Zea mays* ssp. *mays*) and Squash (*Cucurbita* sp.) in Central New York. *American Antiquity* 72(3):563-583.

Hart, John P. and William A. Lovis

2013 Reevaluating What We Know About the Histories of Maize in Northeastern North America: A Review of Current Evidence. *Journal of Archaeological Research* 21(2):175-216.

Heiser, Charles B.

1954 Variation and Subspeciation in the Common Sunflower, *Helianthus annuus*. *American Midland Naturalist* 51(1):287-305.

Herdon, Richard L.

2006 *Phase III Investigations at the Rohlving (23Fr525) and Schove (23Fr526) sites in Frankling County, Missouri*. Cultural Resource Analysts, Inc.

Johannessen, Sissel

1983 Plant Remains from the Mund Phase. In *The Mund Site, FAI-270 Site Reports*, edited by Andrew C. Fortier, Fred A. Finney and Richard B. Lacampagne, pp. 299-317. University of Illinois Press, Urbana.

Jones, Clive G., John H. Lawton and Moshe Shachak

1994 Organisms as Ecosystem Engineers. *Oikos* 69(3):372-386.

Kay, Marvin, Francis B. King and Christine K. Robinson

1980 Cucurbits from Phillips Spring: New Evidence and Interpretations. *American Antiquity* 45(4):806-822.

Kelly, John E.

1990 The Emergence of Mississippian Culture in the American Bottom Region. In *The Mississippian Emergence*, edited by Bruce D. Smith, pp. 113-152. Smithsonian Institution Press, Washington.

2002 The Pulcher tradition and the ritualization of Cahokia: A perspective from Cahokia's southern neighbor. *Southeastern Archaeology* 21(2):136-148.

2007 An Interpretation of the Lindeman Phase Occupation of the Range Site. In *The Range Site 4: Emergent Mississippian George Reeves and Lindeman Phase Occupations*, edited by John E. Kelly, Steven J. Ozuk and Joyce A. Williams, pp. 469-490. University of Illinois and Illinois Transportation Archaeological Research Program, Champaign-Urbana, IL.

Kelly, John E., Steven J. Ozuk and Joyce A. Williams

2007 *The Range Site 4: Emergent Mississippian George Reeves and Lindeman Phase Occupations*. University of Illinois and Illinois Transportation Archaeological Research Program, Champaign-Urbana, IL.

Kidder, Tristram R.

- 2006 Climate change and the Archaic to Woodland transition (3000-2500 cal BP) in the Mississippi River Basin. *American Antiquity* 71(2):195-231.
- Kim, Sun-Lim, Sung-Kook Kim and Cheol-Ho Park
- 2004 Introduction and nutritional evaluation of buckwheat sprouts as a new vegetable. *Food Research International* 37(4):319-327.
- Kiptot, Evelyne, Steven Franzel, Paul Hebinck and Paul Richards
- 2006 Sharing seed and knowledge: Farmer to farmer dissemination of agroforestry technologies in western Kenya. *Agroforestry systems* 68(3):167-179.
- Kistler, Logan, Álvaro Montenegro, Bruce D. Smith, John A. Gifford, Richard E. Green, Lee A. Newsom and Beth Shapiro
- 2014 Transoceanic drift and the domestication of African bottle gourds in the Americas. *Proceedings of the National Academy of Sciences* 111(8):2937-2941.
- Kistler, Logan, Lee A. Newsom, Timothy M. Ryan, Andrew C. Clarke, Bruce D. Smith and George H. Perry
- 2015 Gourds and squashes (*Cucurbita* spp.) adapted to megafaunal extinction and ecological anachronism through domestication. *Proceedings of the National Academy of Sciences* 112(49):15107-15112.
- Kistler, Logan and Beth Shapiro
- 2011 Ancient DNA Confirms a Local Origin of Domesticated Chenopod in Eastern North America. *Journal of Archaeological Science* 38(3549-3554).
- Kruska, Dieter C.T.
- 2005 On the evolutionary significance of encephalization in some eutherian mammals: Effects of adaptive radiation, domestication, and feralization. *Brain, Behavior and Evolution* 65(2):73-108.

Langlie, BrieAnna S., Christine A. Hastorf, Mario C. Bruno, Marc Bermann, Bonzano. Renée M. and William C. Condarco

- 2011 Diversity In Andean Chenopodium Domestication: Describing A New Morphological Type From La Barca, Bolivia 1300-1250 B.C. *Journal of Ethnobiology* 31(1):72-88.

Lema, Verónica, Aylen Capparelli and María Lelia Pochettino

- 2008 Taxonomic identification of dry and carbonized archaeobotanical remains of Cucurbita species through seed coat micromorphology. *Vegetation history and archaeobotany* 17(1):277-286.

Liu, Xinyi, Diane L. Lister, Zhijun Zhao, Richard A. Staff, Penelope J. Jones, Liping Zhou, Anil K. Pokharia, Cameron A. Petrie, Anubha Pathak, Hongliang Lu, Giedre Motuzaite

Matuzeviciute, Jennifer Bates, Thomas K. Pilgram and Martin K. Jones

- 2016 The virtues of small grain size: Potential pathways to a distinguishing feature of Asian wheats. *Quaternary International*.

Lopinot, Neal H.

- 1997 Cahokian Food Production Reconsidered. In *CahokiaL Domination and Ideology in the Mississippian World*, edited by Timothy R. Pauketat and Thomas E. Emerson, pp. 52-68. University of Nebraska Press, Lincoln.

Lopinot, Neal H., Gayle J. Fritz and John E. Kelly

- 1991 The Archaeological Context and Significance of *Polygonum erectum* Achene Masses from the American Bottom Region. *Proceedings of the 14th Annual Society for Ethnobiology Conference*. St. Louis.

Lopinot, Neal H. and Gina Powell

- 2015 Archaeobotanical Remains from Big Loose Creek. *The Missouri Archaeologist* 76:88-115.

Louette, D. and M. Smale

- 2000 Farmers' seed selection practices and traditional maize varieties in Cuzalapa, Mexico. *Euphytica* 113(1):25-41.

Lyman, R. Lee and Kenneth M. Ames

- 2007 On the use of species-area curves to detect the effects of sample size. *Journal of Archaeological Science* 34(12):1985-1990.

Marquardt, William H. and Patty Jo Watson

- 2005 *Archaeology of the Middle Green River Region, Kentucky*. Institute of Archaeology and Paleoenvironmental Studies, University of Florida, Gainesville.

McElrath, Dale L. and Andrew C. Fortier

- 2000 The Early Late Woodland Occupation of the American Bottom. In *Late Woodland societies: Tradition and Transformation Across the Midcontinent*, edited by Thomas E Emerson, Dale L McElrath and Andrew C Fortier, pp. 97-122. University of Nebraska Press, Lincoln, NE.

McGuire, Shawn J.

- 2008 Securing Access to Seed: Social Relations and Sorghum Seed Exchange in Eastern Ethiopia. *Human Ecology* 36(2):217-229.

McLauchlan, Kendra

- 2003 Plant cultivation and forest clearance by prehistoric North Americans: pollen evidence from Fort Ancient, Ohio, USA. *The Holocene* 13(4):557-566.

Mertens, Thomas R. and Peter H. Raven

- 1965 Taxonomy of *Polygonum*, section *Polygonum* (Avicularia) in North America. *Madrono* 18(3):85-92.

Misiko, Michael

- 2010 Indigenous Seed Institutions in Fragile Communities. Paper presented at the Innovations and Partnerships to Realize Africa's Rice Potential, Bamako, Mali.

Monaghan, G. William, Timothy M. Schilling and Kathryn E. Parker

- 2014 The Age and Distribution of Domesticated Beans (*Phaseolus vulgaris*) in Eastern North America: Implications for Agricultural Practices and Group Interaction. *Occasional Papers of the Midwest Archaeological Conference* 1:33-52.

Moreno, Luis Latournerie, John Tuxill, Elaine Yupit Moo, Luis Arias Reyes, Jairo Cristobal Alejo and Devra I Jarvis

- 2006 Traditional maize storage methods of Mayan farmers in Yucatan, Mexico: implications for seed selection and crop diversity. *Biodiversity & Conservation* 15(5):1771-1795.

Morse, Dan F. and Phyllis A. Morse

- 1983 *Archaeology of the Central Mississippi Valley*. Academic Press, New York.

Mueller, Natalie G. and Gayle J. Fritz

- 2016 Women as Symbols and Actors in the Mississippi Valley: Evidence from Female Flint-Clay Statues and Effigy Vessels. In *Gendered Perceptions of Native American Landscapes*, edited by Cheryl Claassen. University of Tennessee Press, Knoxville, TN.

Munoz, Samuel E., Sissel Schroeder, David A. Fike and John W. Williams

- 2014 A record of sustained prehistoric and historic land use from the Cahokia region, Illinois, USA. *Geology* 42(6):499-502.

Murray, Priscilla M. and Mark C. Sheehan

- 1984 Prehistoric Polygonum Use in the Midwestern United States. In *Experiments and Observations on Aboriginal Wild Plant Food Utilization in Eastern North America*, edited by Patrick J. Munson. Prehistory Research Series. vol. VI. Indiana Historical Society, Indianapolis.

Nassaney, Michael S

- 1994 The historical and archaeological context of Plum Bayou culture in central Arkansas. *Southeastern Archaeology* 13(1):36-55.

Newsome, Thomas M., Guy-Anthony Ballard, Mathew S. Crowther, Peter J.S. Fleming and Christopher R. Dickman

- 2014 Dietary niche overlap of free-roaming dingoes and domestic dogs: The role of human-provided food. *Journal of Mammalogy* 95(2):392-403.

Odling-Smee, John F., Kevin N. Laland and Marcus W. Feldman

- 2003 *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.

Parker, Kathryn E.

- 1991 Sponemann Phase Archaeobotany. In *The Sponemann Site: The Formative Emergent Mississippian Sponemann Phase Occupation, FAI-270 Site Reports*, edited by Andrew C. Fortier, Thomas O. Maher and Joyce A. Williams, pp. 377-420. University of Illinois, Champaign-Urbana.
- 2007 Lindeman Phase Plant Remains. In *The Range Site 4: Emergent Mississippian George Reeves and Lindeman Phase Occupations*, edited by John E. Kelly, Steven J. Ozuk and Joyce A. Williams, pp. 457-468. University of Illinois and

Illinois Transportation Archaeological Research Program, Champaign-Urbana,
IL.

Pautasso, Marco, Guntra Aistara, Adeline Barnaud, Sophie Caillon, Pascal Clouvel, Oliver T
Coomes, Marc Delêtre, Elise Demeulenaere, Paola De Santis and Thomas Döring

2013 Seed exchange networks for agrobiodiversity conservation. A review. *Agronomy
for Sustainable Development* 33(1):151-175.

Perales, Hugo R., Bruce F. Benz and Stephen B. Brush

2005 Maize diversity and ethnolinguistic diversity in Chiapas, Mexico. *Proceedings of
the National Academy of Sciences of the United States of America* 102(3):949-
954.

Pollack, David, Eric J. Sclarb, William E Sharp and Teresa W. Tune

2005 Walker-Noe: An Early Middle Woodland Adena Mound in Central Kentucky. In
Woodland Period Systematics in the Middle Ohio Valley, edited by Darlene
Applegate and Robert C. Mainfort Jr., pp. 64-75. The University of Alabama
Press, Tuscaloosa.

Powell, Gina

2000 Charred, Non-Maize Seed Concentrations in the American Bottom Area:
Examples from the Westpark Site (11-MO-96), Monroe County, Illinois.
Midcontinental Journal of Archaeology 25(1):27-48.

Price, T. Douglas and Ofer Bar-Yosef

2011 The Origins of Agriculture: New Data, New Ideas: An Introduction to
Supplement 4. *Current Anthropology* 52(S4):S163-S174.

Reimer, Paula J, Edouard Bard, Alex Bayliss, J Warren Beck, Paul G Blackwell, Christopher Bronk Ramsey, Caitlin E Buck, Hai Cheng, R Lawrence Edwards and Michael Friedrich

2013 IntCal13 and Marine13 radiocarbon age calibration curves 0-50,000 years cal BP. *Radiocarbon* 55(4):1869-1887.

Riley, Thomas J., Gregory R. Walz, Charles J. Bareis, Andrew C. Fortier and Kathryn E. Parker

1994 Accelerator Mass Spectrometry (AMS) Dates Confirm Early *Zea mays* in the Mississippi River Valley. *American Antiquity* 59(3):490-498.

Rindos, David

1984 *The Origins of Agriculture: An Evolutionary Perspective*. Academic Press, Orlando.

Robbins, Louise M.

1974 Prehistoric People of the Mammoth Cave Area. In *Archaeology of the Mammoth Cave Area*, edited by Patty Jo Watson, pp. 137-162. Academic Press, New York.

Rose, Fionnuala

2008 Intra-community variation in diet during the adoption of a new staple crop in the Eastern Woodlands. *American Antiquity* 73(3):413-439.

Rossen, Jack

1988 Botanical Remains. In *Muir: An Early Fort Ancient Site in the Inner Bluegrass*, edited by Christopher Turnbow and William E Sharp, pp. 243-264. Program for Cultural Resources Assessment, Department of Anthropology, University of Kentucky.

Rowley-Conwy, Peter and Robert Layton

- 2011 Foraging and Farming as Niche Construction: Stable and Unstable Adaptations.
Philosophical Transactions of the Royal Society 366:849-862.

Sabo, George

- 1986 *Contributions to Ozark Prehistory*. Arkansas Archeological Survey, Little Rock.

Sant, Mark B. and Barbara D. Stafford

- 1985 Cultural Components. In *Smiling Dan: Structure and Function at a Middle Woodlands Settlement in the Lower Illinois River Valley*, edited by Barbara D. Stafford and Mark B. Sant, pp. 83-94. Center for American Archaeology, Kampsville, IL.

Simon, Mary L.

- 2009 A Regional and Chronological Synthesis of Archaic Period Plant Use in the Midcontinent. In *Archaic Societies: Diversity and Complexity Across the Midcontinent*, edited by Dale L. McElrath Thomas E. Emerson, and Andrew C. Fortier, pp. 81-112. SUNY Press, Albany.
- 2014 Reevaluating the introduction of maize into the American Bottom and western Illinois. *Occasional Papers of the Midwest Archaeological Conference* 1(1):97-134.
- 2017 Reevaluating the Evidence for Middle Woodland Maize from the Holding Site. *American Antiquity* 82(1):140-150.

Simon, Mary L. and Kathryn E. Parker

- 2006 Prehistoric Plant Use in the American Bottom: New Thoughts and Interpretations. *Southeastern Archaeology* 25(2):212-257.

Smith, Bradley P. and Carla A. Litchfield

- 2009 A review of the relationship between indigenous Australians, dingoes (*Canis dingo*) and domestic dogs (*Canis familiaris*). *Anthrozoös* 22(2):111-128.
- 2010 Dingoes (*Canis dingo*) can use human social cues to locate hidden food. *Animal Cognition* 13(2):367-376.

Smith, Bruce D.

- 1978 *Prehistoric Patterns of Human Behavior: A Case Study in the Mississippi Valley*. Academic Press, New York.
- 1984 Chenopodium as a Prehistoric Domesticated in Eastern North America: Evidence from Russell Cave, Alabama. *Science* 226(4671):165-167.
- 1992 *Rivers of Change: Essays on Early Agriculture in Eastern North America*. Smithsonian Institution Press, Washington.
- 1997 The Initial Domestication of *Cucurbita pepo* in the Americas 10,000 Years Ago. *Science* 276(5314):932-934.
- 2001 Low-Level Food Production. *Journal of Archaeological Research* 9(1):1-42.
- 2006 Eastern North America as an Independent Center of Plant Domestication. *Proceedings of the National Academy of Sciences* 103(33):12223-12228.
- 2007 Niche Construction and the Behavioral Context of Plant and Animal Domestication. *Evolutionary Anthropology* 16:188-199.
- 2011 The Cultural Context of Plant Domestication in Eastern North America. *American Antiquity* 52(S4):S471-S484.
- 2014 The domestication of *Helianthus annuus* L. (sunflower). *Vegetation History and Archaeobotany* 23(1):57-74.

Smith, Bruce D. and Wesley C. Cowan

- 1987 Domesticated *Chenopodium* in Prehistoric Eastern North America: New Accelerator Dates from Eastern Kentucky. *American Antiquity* 52(2):355-357.
- Smith, Bruce D. and Vicki A. Funk
- 1985 A Newly Described Subfossil Cultivar of *Chenopodium* (Chenopodiaceae). *Phytologia* 57(7):445-448.
- Smith, Bruce D. and Richard A. Yarnell
- 2009 Initial Formation of an Indigenous Crop Complex in Eastern North America at 3800 B.P. *Proceedings of the National Academy of Sciences* 106(16):6561-6566.
- Stromberg, Per M., Unai Pascual and Mauricio R. Bellon
- 2010 Seed Systems and Farmers' seed Choices: The Case of Maize in the Peruvian Amazon. *Human Ecology* 38:539-553.
- Thomas, Mathieu, Elise Demeulenaere, Julie C. Dawson, Abdul Rehman Khan, Nathalie Galic, Sophie Jouanne-Pin, Carine Remoué, Christophe Bonneuil and Isabelle Goldringer
- 2012 On-farm dynamic management of genetic diversity: the impact of seed diffusions and seed saving practices on a population-variety of bread wheat. *Evolutionary applications* 5(8):779-795.
- Thompson, Robert G., John P. Hart, Hetty Jo Brumbach and Robert Lusteck
- 2004 Phytolith Evidence for Twentieth Century B.P. Maize in Northern Iroquoia. *Northeast Anthropology* 68:25-40.
- Toulemonde, Françoise, Frédérique Durand, Laura Berrio, Emmanuelle Bonnaire, Geneviève Daoulas and Julian Wiethold
- 2015 Records of “new” glume wheat in France: A review. *Vegetation History and Archaeobotany* 24(1):197-206.

Trubowitz, Neal L.

- 1983 Caddoan Settlements in the Arkansas Ozarks: The Upper Lee Creek Valley. *Midcontinental Journal of Archaeology* 8(2):197-210.

Wagner, Gail E.

- 1987 Uses of Plants by the Fort Ancient Indians. Dissertation, Department of Anthropology, Washington University, St. Louis.

Watson, Patty Jo and Mary C. Kennedy

- 1991 The Development of Horticulture in the Eastern Woodlands of North America: Women's Role. In *Engendering Archaeology*, edited by Joan Gero and Margaret W. Conkey, pp. 255-275. Blackwell Publishing, Oxford.

Watson, Patty Jo and Richard A. Yarnell

- 1966 Archaeological and Paleoethnobotanical Investigations in Salts Cave, Mammoth Cave National Park, Kentucky. *American Antiquity* 31(6):842-849.

Willcox, George

- 2004 Measuring grain size and identifying Near Eastern cereal domestication: Evidence from the Euphrates valley. *Journal of Archaeological Science* 31(2):145-150.

Williams, Joyce A.

- 1993 Meridian Hills: An Upland Holding Phase Middle Woodland Habitation Site. *Illinois Archaeology* 5(1 and 2):193-199.

Williams, Joyce A., T.O. Maher and Katherine E. Parker

- 1988 The Meridian Hills Site (11-Ms01258). *Illinois Antiquity* 2:8-12.

Wollstonecroft, Michèle M.

- 2011 Investigating the Role of Food Processing in Human Evolution: A Niche Construction Approach. *Archeological and Anthropological Science* 3:141-150.
- Wright, Patti J. and Christopher A. Shaffer
- 2014 Crop Selection: Perspectives from the Lower Missouri River Basin. *Occasional Papers of the Midwest Archaeological Conference* 1:73-96.
- Wymer, DeeAnne
- 1996 The Ohio Hopewell Econiche: Human-Land Interaction in the Core Area. In *A View from the Core: A Synthesis of Ohio Hopewell Archaeology*, edited by Paul J. Pacheco, pp. 36-53. The Ohio Archaeological Council, Inc., Columbus, OH.
- 2009 The Paleoethnobotanical Assemblage from the 1971–1977 Excavations at the Seip Earthworks. *Midcontinental Journal of Archaeology* 34(1):123-142.
- Wymer, DeeAnne and Elliot Abrams
- 2003 Early Woodland Plant Use and Gardening: Evidence from an Adena Hamlet in Southeastern Ohio. *Midcontinental Journal of Archaeology* 28(2):175-194.
- Yarnell, Richard A.
- 1969 Contents of human paleofeces. In *The Prehistory of Salts Cave, Kentucky*, edited by Patty Jo Watson, pp. 41-54. Reports of Investigations. vol. 16. Illinois State Museum, Springfield, IL.
- 1972 *Iva annua* var. *macrocarpa*: Extinct American Cultigen? *American Anthropologist* 74:335-341.
- 1974a Intestinal Contents of the Salts Cave Mummy and Analysis of the Initial Salts Cave Flotation Series. In *The Archaeology of the Mammoth Cave Area*, edited by Patty Jo Watson, pp. 109-112. Academic Press, New York.

- 1974b Plant food and cultivation of the Salts Cavers. In *The Archaeology of the Mammoth Cave Area*, edited by Patty Jo Watson, pp. 113-122. Academic Press, New York.
- 1978 Domestication of Sunflower and Sumpweed in Eastern North America. In *The Nature and Status of Ethnobotany*, edited by Richard A. Ford, pp. 289-299. Anthropological Papers No. 67. Museum of Anthropology, University of Michigan, Ann Arbor, MI.
- 1993 The Importance of Native Crops During the Late Archaic and Woodland Periods. In *Foraging and Farming in the Eastern Woodlands*, edited by C. Margaret Scarry, pp. 13-26. University Press of Florida, Gainesville.

Yurtseva, O.V.

- 2001 Ultrasculpture of Achene Surface in *Polygonum* section *Polygonum* (Polygonaceae) in Russia. *Nordic Journal of Botany* 21(4):513-528.

7. Concluding Thoughts

7.1 Introduction

I define domestication as a process of co-evolution whereby the bodies and behaviors of plants and animals change as a result of human selection or environmental modification. For the purposes of this discussion, food production is what people do to enhance the productivity of their environment: burning, clearing, tilling, sowing, thinning, weeding, pruning, seed saving – just to mention a few possibilities with respect to plants. A food producing economy is one that is primarily based on such deliberately enhanced resources, as opposed to a system of food procurement in which resources are taken and consumed as they are encountered. According to these definitions, the process of domestication and the origins of food producing economies are not as intimately linked as anthropologists once believed. It has been clear for over a decade that in some regions, domestication precedes recognizable agriculture or pastoralism by millennia and is the result of what Smith (2001) has called low-level food production. In eastern North American (ENA) the first domesticated plants appear in low concentrations at what appear to be the seasonal camps of hunter gatherers (Smith and Yarnell 2009). In some cases, researchers have actually argued that plants were domesticated *before they were ever cultivated* (Abbo et al. 2011; Ladizinsky 1987). For other crops, the opposite is true. Pre-domestication cultivation, leaving signatures that look a lot like those of an agricultural society but without morphologically domesticated plants, evidently took place for several thousand years (Fuller 2007; Gross and Zhao 2014). Bottle gourds (Langlie et al. 2014) and dogs (Ovodov 2011) were domesticated thousands of years before the earliest evidence for food producing economies. Humans repeatedly trundled a mix of ostensibly wild and domesticated animals onto boats and brought them to Cyprus during the Pre-Pottery Neolithic C, subsequently hunting some of these

animals and tending others (Vigne et al. 2011). This is only a small sampling of domestication proceeding strangely. Domestication is an historical process with many possible outcomes, which depend both on what people do and on the biological and behavioral potentials of each domesticate.

Contrary to classic models of cultural evolution (Service 1962), the appearance of the first domesticated plants and animals is not always associated with social or economic change, nor were domesticated plants and animals necessary to the development of stratified, sedentary societies. As Arnold and colleagues (2016) eloquently and succinctly put it, if we are interested in the origins of food production and its attendant social changes, “Rather than diet, it is the ways that people integrate and use labor that demands our attention.” The ethnographic record, and even more so the archaeological record, make it clear that there are many ways for societies to organize production in the absence of domesticates in order to support the kinds of complex political and social institutions that were associated with the origins of agriculture in classic social evolutionary schemes (Arnold et al. 2016; Sassaman 2004). To borrow a phrase from popular culture, domestication and the origins of food production need to be consciously uncoupled. In this conclusion, I will consider the implications of my approach and results first within the context of domestication theory, and then for the study of the origins of food production.

If we remove the tantalizing promise of explaining structural inequality, urbanism, and the other trappings of the Neolithic Revolution from domestication studies, what remains for anthropologists? Domestication provides a simplified system through which to better understand evolution in general, and domesticated plants and animals underwrite almost all contemporary economic systems. The process of domestication is one common outcome of environmental

engineering or niche construction, and these activities *are* connected to the development of food producing economies. We can read the histories of human mediated ecosystems from the bodies and behaviors of domesticated plants and animals. The relationships between people and domesticates are co-evolutionary, meaning that people and societies are shaped by the process of domestication just as much so as plants and animals.

7.2 Domestication

A debate has been intensifying within domestication studies for the past several years between the proponents of Human Behavioral Ecology (HBE) (Gremillion et al. 2014) and the proponents of Niche Construction Theory (NCT) (Zeder 2015; Smith 2016). I will briefly discuss my results with respect to each of these perspectives, and argue that they are not really competing frameworks because they explain different aspects of the process of domestication. HBE is concerned with resource selection, and NCT explains resource enhancement (Smith 2006).

HBE is a framework adapted from evolutionary ecology that borrows heavily from microeconomic theory. Many practitioners of HBE create optimal foraging models, which assume that humans are rational actors who strategize to maximize energy intake, while minimizing energy expenditure. Resources are ranked based on the net energy they yield (their caloric value, minus the energy expended to find, capture, and process them) (Kennett and Winterhalder 2006). HBE and optimal foraging models are widely applied by archaeologists, but with respect to domestication, they are often linked to an influential theory called the Broad Spectrum Revolution (Flannery 1969). In this model of initial domestication in the Near East, population growth caused humans to move into less productive areas where highly ranked resources were scarce. As a result of resource depression, these hunter gatherers had to focus on

lower ranked resources, broadening the spectrum of their foraging. The lowest ranked of all resources in optimal foraging models are the small seeds of annual plants – the progenitors of many of our most important domesticates. Thus within HBE, resource depression must be invoked to explain the focus of hunter gatherers on small seeds preceding their domestication (Winterhalder and Smith 2000; Zeder 2015).

It is possible to criticize HBE on many levels. Some detractors have focused on the “seductive lure of simply accepting, a priori, the universal applicability of foraging theory principles...in lieu of any requirement for empirical data-based testing and confirmation,” which leads to assumptions masquerading as conclusions (Smith 2006:297). The assumption that humans behave rationally in the economic sense of the word, without respect to the cultural and political context in which their decisions are made, is far from an unassailable fact (Sahlins 1976). Some of the many persistent critiques of rational choice theory are: 1) rational decisions are based on knowledge, and knowledge flows unevenly and imperfectly between social actors (Henrich 2001; Rogers 2003); 2) path dependency can lead to persistent inefficiencies (David 1985); and 3) social emulation is often as important as empirical assessment in decision making (Stone et. al. 2014) There is also a logical disconnect in the adaptationist framework of optimal foraging models. It is assumed, but never demonstrated, that maximizing foraging efficiency is equivalent to maximizing evolutionary fitness: the number and survivorship of offspring. In other words, economic success and biological success are conflated. A recent defense of HBE provides an apt example: “[optimal foraging] models should explain the behavior of an organism *foraging optimally to maximize reproductive success*” (Gremillion et al. 2014:6174, emphasis added). But the connection between economic success (having more resources) and evolutionary fitness (having more offspring) is not direct nor unproblematic in human societies

(Bamforth 2002; Boyd and Richerson 1988). Neither the ethnographic nor the archaeological record supports a conception of ancient hunter gatherers whose children were in constant danger of starvation if they failed to forage with the utmost efficiency. Even among modern hunter gatherers, most of whom had been pushed into the most marginal environments and subjected to the worst of colonial policies, getting enough food to eat required less time actively foraging than the 40-hour per week put in by the average post-industrial worker to make a living (Sahlins 1972). The idea that economic success reflects evolutionary fitness in human societies is linked to Social Darwinism and neo-Malthusianism, schools of thought that, in Marxist terms, reify poverty (Ross 1998).

In the interest of starting with a more manageable critique, and one more closely related to the data at hand, I will assume for the moment that humans do behave rationally and ignore the issue of whether or not there is a universal connection between the economic efficiency of a social group and its evolutionary fitness. Meaningful optimal foraging models still require comprehensive knowledge of the yield potentials and nutritional values of various resources, and of the methods used to procure and process them. Such a comprehensive model can only be constructed through participant observation of a foraging group, coupled with extensive physiological, nutritional, and ecological analyses. When modeling ancient foragers, we have to reconstruct both the ecosystem and the methods and tools applied to hunting and foraging from imperfect proxies. There are also important seasonal and social aspects to both the costs and benefits of procuring certain resources. Gremillion (2004) applied an optimal foraging model to subsistence data from Early Woodland Kentucky and discovered a profound lack of fit. While optimal foraging theory suggests that humans only intensify exploitation of small seeds when faced with resource depression or when technological advances enable more efficient processing,

she found that during the Early Woodland evidence for reliance on small seeds increased without there being any indication of either of these causes. She reasoned that the optimal foraging model did not take into account the reduced opportunity cost of processing seeds during the winter, when other foraging opportunities were scarce. Gendered division of labor also complicates cost-benefit analyses, because time consuming processing tasks could be carried out by inherently less mobile members of society, such as pregnant and nursing women, young children, and the elderly. Moving resources closer to a home base, for example by creating clearings and planting the seeds of annual plants, also increases the potential productivity of less mobile members of society and reduces transportation costs associated with small children (Lee 1980). The value of predictability also needs to be accounted for. Early manipulation of wild plants and animals may have been primarily geared towards ensuring predictable access, rather than increasing overall abundance (Marshall and Hildebrand 2002). Since annual plants can easily be sown close to a home base, produce roughly the same amount of food every year, and produce food that is easy to store for months or even years, they are highly predictable. All of these factors suggest that small seeded annual plants may be consistently ranked too low with respect to other resources in HBE models, just as Gremillion's (2004) analysis indicated. If this is the case, then we need not invoke resource depression to explain why so many societies around the world came to rely on the small seeds of annual plants.

The data gathered for this dissertation contributes to a more accurate estimation of both yields and costs for one EAC crop, and also suggests that developmental plasticity may be another factor that changed the math in favor of small seeded annual plants in the cost-benefit analysis of ancient foragers. In the greenhouse, plants growing at something similar to the density of a natural stand, where humans have neither thinned erect knotweed plants nor

removed competing species, produced 8.35 g of seed per 0.06 m², while a single plant growing alone in the same area produced 31.31 g. Although the absolute yields generated in a greenhouse should not be extrapolated to a field situation, the difference between these two treatments implies that simple cultivation techniques like weeding and thinning could have more than tripled yields. This is one example of how plasticity in an annual seed crop progenitor may have made it attractive to ancient people. By making small adjustments to the environment they would see immediate increases in yield over the course of a single growing season. Early cultivators probably could not have predicted the long-term evolutionary effects of their practices (domestication), but the immediate effects of cultivation, at least for a plant as plastic as erect knotweed, would have been obvious.

Gremillion and Piperno (2009) have suggested that developmental plasticity is an underappreciated factor in the process of domestication. Continuing this line of inquiry, Piperno and colleagues (2014) undertook a study of teosinte's plastic response to temperature and CO₂ levels. They found that under simulated Late Pleistocene conditions, teosinte exhibits some of the key phenotypic characteristics of domesticated maize. They concluded that we cannot assume that observations of crop progenitors in modern climates accurately reflect the phenotypes encountered by early foragers. I would further argue that even if the climate was identical, the morphology and productivity of crop progenitors in natural ecosystems is almost certainly not representative of their phenotypes and yield potential under cultivation, even before any selection towards domesticated varieties has occurred. This is especially true of disturbance adapted annuals. Anyone who has been moved by curiosity or pity to spare a weedy plant in their garden can attest to the unexpected phenotypes that arise when weeds are freed from the relentless competition they have evolved to tolerate. Experimental studies of crop progenitors

should be widely undertaken, especially by those who seek to build accurate optimal foraging models for ancient societies.

Erect knotweed, contrary to previous reports (Murray and Sheehan 1984), is remarkably easy to harvest after it has senesced. Also attractive from the point of view of a forager, the mature seeds do not fall off of the plant for several weeks, leaving a long window when she could expect to visit a stand and find her harvest waiting for her. All of these experimental results suggest that gathering large harvests from stands of erect knotweed, even before it was domesticated, would have required very little work and uncomplicated scheduling. Gremillion (2004) observes that most of the energetic cost of consuming small seeds lies in post-harvest processing tasks such as winnowing, parching, and grinding, but estimating this cost also requires solid experimental data. One of my short term goals is to use the seeds harvested from more extensive experimental plots grown during 2016 to explore different methods of processing erect knotweed. Murray and Sheehan (1984), authors of the study that was used to construct processing costs in Gremillion's (2004) ENA optimal foraging model, had considerable difficulty fracturing the pericarp mechanically, but their study was on a very small scale. Sprouting is a method suggested by the archaeological record that would require no additional labor and would likely increase the nutritive value of each seed (Chapter 5). The ethnographic and historic record of ENA suggests that porridge food cultures were dominant. Hominy and its derivatives have been staples since at least the 11th century CE (Briggs 2015; 2016). If EAC crops were also consumed as porridge, then processing costs would have been less than if seeds were ground into flour. The carbonization experiments presented in Chapter 5 suggest that erect knotweed achenes are easily popped at low temperatures. Popping achenes over low heat, rather than grinding or pounding them, is another relatively easy way in which erect knotweed achenes

may have been rendered digestible. Perhaps erect knotweed seeds were consumed as whole grain porridge, as buckwheat is consumed as kasha by contemporary Central Asian peoples. The larger point is that “small seeded annuals” is not an adequate category for modeling the energetic costs and benefits associated with EAC crops, which are taxonomically diverse and for which we have limited experimental data (Smith 2006). We do not know nearly enough about how productive these crops are under cultivation or how much labor goes into rendering them palatable to model the cost-benefit analysis of a knowledgeable ancient forager.

HBE, if its assumptions are granted and its models are carefully constructed, is most useful for understanding why foragers chose to focus on particular species or types of resources. HBE and NCT are not really at odds as explanatory models for domestication because they explain different aspects of the process. HBE does not explain how humans modified ecosystems or manipulated particular species – the processes that led to domestication. This is where NCT becomes useful. NCT 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 cultures and 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. Niche construction is very similar to the concept of ecosystem engineering (Jones et al. 1994) which describes how organisms modify energy flows within their ecosystem by changing physical elements of it. Engineered ecosystems are inherited, and they change the selective pressures on subsequent generations, both the engineers’ own descendants, and other organisms in their ecosystem (Odling-Smee et al. 2003). This path dependency element of niche construction

theory complements and reinforces the tenets of historical ecology, a paradigm developed largely by anthropologists and archaeologists, which rejects the idea of a pristine environment and contends that all contemporary ecosystems have resulted in part from historical processes (Balée 2006; Crumley 1994).

The domestication syndrome of erect knotweed is an artifact of the niche construction of ancient people as they transitioned from something that we would recognize as foraging to something we would describe as farming. For them, this distinction may well have been meaningless as they continued to manipulate plants and the environment using traditional ecological knowledge throughout this transition. The hunter gatherers of the Pacific Northwest, for example, manage hundreds of plant species (where communal land rights still permit them to do so). Historically, they mostly relied on perennial plants, which are much more difficult to domesticate because of their long life cycles. They enhanced the production of these plants in various ways. They also owned gardens and patches of particular plants, as families and as individuals (Deur 2002). In addition to plants, Northwest coast people cultivated animals. They expanded the habitats for certain shellfish, creating clam gardens. They used engineered landscapes, including gardens, to attract prey, and some groups bred special wool dogs. These they kept isolated from other canids on islands, and sheered like sheep to create clothing and blankets (Crockford and Pye 1997). While none of these actions were recognized as food production by European explorers, or indeed by an entire generation of ethnographers, they are all examples of ecosystem engineering (Deur and Turner, eds. 2005). Pacific Coast hunter gatherers lived in a super abundant landscape partly of their own making, just as a good farmer does. Niche construction theory is useful because it does away with the false distinction between

hunter gatherers and farmers based on their possession or lack of domesticated plants and animals, and instead forces us to focus on what humans were doing to make a living.

To briefly reiterate the conclusions of Chapters 2 and 3, the archaeological and experimental data presented here suggest both small and large scale niche constructing activities. It is likely that cultivation of erect knotweed included weeding and thinning from the very beginning. The natural habitat of erect knotweed is a dog-eat-dog world of intense competition with other annual plants. If foragers recognized the potential of erect knotweed to produce abundant, easily harvestable seeds, it would not have taken them long to notice that plants with more space and sun produced more seeds than crowded plants (Chapter 4). There is also direct evidence for thinning in the domestication syndrome itself. The evolution of larger seeds and a higher proportion of fruits with thin pericarps would be favored by removing small, slow growing seedlings from each generation (Chapter 3). Erect knotweed was first cultivated probably during the Late Archaic and certainly during the Early Woodland. During the latter period, there is evidence for forest clearance in the uplands of eastern Kentucky and Tennessee, the regions with the strongest evidence for early cultivation (Chapter 5). If erect knotweed experienced a sunnier environment because of human forest clearance, weeding, and thinning, its plastic response was likely to produce more tubercled morphs, since the production of smooth morphs is triggered by low-light conditions (Chapter 3; Chapter 4). It is therefore all the more remarkable that by c. 1 CE at the Walker-Noe site, a domesticated variety with a high proportion of abnormally large smooth morphs had been developed.

To understand how this domestication syndrome evolved, I turn to the theory of evolutionary bet-hedging. Annual plants producing seeds with germination heteromorphism, like erect knotweed, are the classic example of a bet-hedging organism. Bet-hedging is an

evolutionary solution to the problem of unpredictability. There may be a phenotype or behavior that leads to greater fitness under normal conditions, but is disastrously unfit under different, unpredictable conditions. A different phenotype or behavior is necessary for the population to survive these unpredictable events. In this case, natural selection will result in a bet-hedging species that has two or more distinct types. Its hedging individuals are less fit under normal conditions, but enable it to survive unpredictable events (Cohen 1966). In the case of erect knotweed, tubercled morphs are likely to be significantly less fit on average than smooth morphs under normal conditions. Many of them do not germinate the year after they are produced, which means they are at risk from predation or pathogens for more than a year before they have a chance to reproduce themselves. Even when they do germinate, their seedlings grow more slowly than those of smooth morphs, an attribute which disadvantages them in their crowded habitat (Chapter 4). Yet the production of tubercled morphs has evolved and persists because tubercled morphs allow the population to survive when an entire generation of plants is wiped out by an unpredictable event. The unpredictable event that I witnessed in my surveys was an early summer flood, which struck after the seedlings had emerged but before they were tall and strong enough to survive a few hours immersion.

This flood event would have resulted in at least two local extinctions if the erect knotweed plants had been producing only smooth morphs. Smooth morphs germinate immediately the spring after they are produced, so if that year is a bad year there are none left to reproduce the population the following spring. Thus it is adaptive for erect knotweed plants to allocate precious resources to producing both smooth and tubercled morphs every year, just in case. Consider the evolutionary effects of reducing unpredictability for this species. Imagine that ancient foragers witness the disastrous effects of an early summer flood on a patch of erect

knotweed they were planning to harvest. Wanting to prevent this loss from recurring in future years, they clear a patch of ground in a less frequently disturbed area, which would ordinarily be occupied by intermediate or climax species and inaccessible to a species like erect knotweed. Even if they never select or sow seed, but merely help the population persist in this new environment by preventing ecological succession, the result is likely to be the evolution of a variety of erect knotweed that only produces smooth morphs because any individual plant that produces more smooth morphs will enjoy greater fitness. Its offspring will germinate and grow more quickly, which is especially important if our hypothetical foragers-cum-farmers were thinning the stand to give the most robust seedlings more room. It will also lose less of its offspring to predation and pathogens, because fewer of its seeds will remain dormant in the seed bank.

Of course, farmers are not able to completely eliminate unpredictability for their crops, which is why maintaining seed security is crucially important to subsistence farmers. Seed security is the ability of a farmer to obtain enough seed for next year's planting, even if her entire crop is wiped out. Modern farmers maintain seed security both on-farm, by always keeping some seed in reserve, and through exchange networks (reviewed in Mueller 2013). We know that by the end of the Late Archaic, people were storing seeds in rockshelters in the western Appalachian Mountains (Chapter 5). Although they are not always successful, humans go to great lengths to protect their stored seeds from predation and pathogens, providing a less-risky alternative to storage in the seed bank. Again, the practice of saving seeds does not select *for* individual plants that produce a high proportion of smooth morphs, but rather eliminates a source of selection that maintains germination heteromorphism. Because tubercled morphs are not fitness maximizing

phenotypes to begin with, according to theory of evolutionary bet-hedging, they will tend to disappear as soon as they are no longer necessary for survival.

Every domesticated plant or animal has its own unique history, just as each has its own unique biology. To take this particularistic point of view is not a retreat from theory, least of all evolutionary theory, as some detractors have claimed (Gremillion et al. 2014). To understand these histories of co-evolution, of course we must draw on evolutionary theory. For example, it would be impossible to understand the domestication syndrome of erect knotweed without reference to evolutionary bet-hedging models. The particularistic view of domestication also relies on NCT, historical ecology, and the concept of traditional ecological knowledge (TEK) – all of which focus attention on the ways that humans transform environments using their unique capacity for maintaining knowledge and practice through culture.

7.3 Food Production

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 procurement and food production as TEK systems. A TEK system is composed of information, organizing principles or beliefs, expertise, and institutions that structure practice and the transmission of knowledge (Turner et al. 2000). 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 TEK systems, domestication results 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 TEK to maintain it, they could not reproduce themselves. It seems likely that this did sometimes occur, since at least one community in the Ohio River valley had a domesticated variety of erect knotweed hundreds of years before it was independently developed in the American Bottom (Chapter 5). 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. 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. 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). Matrilocality and patrilocality 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 TEK among communities. When the morphologies of various landraces of EAC crops 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.

I conceive of food procuring and food producing systems as synonymous with Woodburn's (1982) immediate and delayed return systems. These are not dichotomous terms, but rather opposite ends on a spectrum of possible economies. In delayed return systems, people (or groups) hold rights over valued assets. These assets are tools, infrastructure, lands, or organisms that have been improved by the application of labor over time. An immediate return/food procurement system might dictate that someone visit a naturally occurring stand of erect knotweed in early November and harvest its seeds. Because this wild stand would only occur in an unpredictable and frequently disturbed environment, it might not always yield a good harvest, but that loss could be absorbed because no time or effort had been invested. In a food producing/delayed return system, people engage more frequently in niche construction or ecosystem engineering. The TEK embedded in such a system might dictate the maintenance of clearings in the early spring, the weeding and thinning of patches throughout the summer, and the creation of pits or vessels for the secure storage of seed stock over the winter. The evolution of domesticated erect knotweed is the outcome of the development of a food producing economy, not its cause. I invoke Woodburn's scheme because it provides a link between intensifying ecosystem engineering and the social changes associated with the Neolithic Revolution in classic cultural evolutionary schemes, such as ownership of land, inheritance, ascribed status, and large sedentary populations. These aspects of society are predicated on food

producing/delayed return systems, not on the presence of domesticates *per se* (Arnold et al. 2016).

In the core area of EAC cultivation, the so-called Big Bang at Cahokia, c. 1050 CE, marks the beginning of many fascinating late prehistoric trends, including nascent urbanism, structural inequality, regional political confederacies, and shifting religious beliefs reflected in the development of widespread iconographic systems. Many researchers assume that this all has something to do with maize (see discussions in Fritz and Lopinot 2007; Lopinot 1997; Simon 2014). We now know that maize did indeed become an important part of the agricultural system of the American Bottom just prior to the Big Bang (Simon 2014). However, we also know that the subsistence system that supported Cahokia was largely composed of the same plants and animals that had supported earlier societies going back to highly mobile and seemingly egalitarian hunter gatherers of the Archaic period. Although the species were the same, the way that they were managed was not. Maize was integrated into what was already a fully formed agricultural food production system, capable of supporting aggregated sedentary populations, specialists, and aggrandizers. The fact that early Mississippian farmers continued to practice and transmit a TEK system focused on EAC cultivation is evidenced by the continuing improvement of erect knotweed during this era, culminating in the exceptionally domesticated assemblages from Hill Creek and Whitney Bluff.

7.4 Directions for Future Research

My work as a paleoethnobotanist began with the analysis of 1,800 year old plant remains associated with a series of Middle Woodland burial mounds from western Illinois. This time period is distinguished by two major trends: the intensification of food production, and the establishment of an interregional religious system and trade network called Hopewell. My

analysis suggested that these two developments were intimately linked: institutionalized exchange of religious and prestige goods facilitated the exchange of seed stock and agricultural knowledge (Mueller 2013). The Walker Noe assemblage, a sub-mound assemblage with a precocious domestication syndrome, lends further credence to this idea. However, the Middle Woodland communities in western Illinois that gave rise to my original hypothesis *did not* cultivate a domesticated variety of erect knotweed, despite their participation in the Hopewell phenomenon (Chapter 5). Further morphological analysis of plant remains from different regions during the Middle Woodland period has the potential to reveal the intensity or nature of exchange between communities, and reveal the range of the domesticated landrace from Walker-Noe.

Now that the range and causes of variability in erect knotweed morphology are better understood, the seeds of this plant can be used as artifacts to understand the evolution of agricultural communities of practice. My analysis shows that erect knotweed was domesticated at least twice, once in Early or Middle Woodland Kentucky, and again in Late Woodland Illinois. Later, domesticated assemblages appear in southern Missouri and the Ozark Mountains. Did these landraces arrive through trade, and if so, how was the TEK necessary to maintain them transmitted? Or were they also developed locally over hundreds of years? These questions can be answered with targeted excavations in these regions, and with re-analysis of museum collections. Discovering the genetic basis for domestication syndrome in erect knotweed is also a priority. The assembly of a reference genome for modern erect knotweed is already underway. By comparing the DNA of experimentally grown plants exhibiting different phenotypes, we can better understand the genetic basis for plasticity. After conducting these studies of modern plants, we may also be able to use aDNA to understand the genetic basis of the domestication

syndrome exhibited by the Whitney Bluff assemblage, and recover the phylogeographic relationships between ancient landraces – and, by proxy, relationships between their keepers.

Domestication studies are usually focused on differentiating wild from domestic types, but I would like to instead focus on variation under cultivation. As Darwin pointed out in the opening passage of *The Origin of Species*, human selection usually leads to greater variation than natural selection, often yielding hundreds of distinct breeds or landraces of each domesticated animal or plant species. Contemporary small-scale farmers carefully select seed for next year's sowing from plants that best express the characteristics of their elite landraces and maintain agroecosystems that produce the desired plastic responses from their crops. The better we understand how a crop progenitor responds to different environmental stimuli, the more useful seeds become as artifacts of communities of practice. This will necessarily entail the study of living plants, both in the wild and under cultivation. The wild progenitors of some of ENA's lost crops have become rare. They are all disturbance adapted plants that inhabit the margins of an agricultural landscape now dominated by herbicide tolerant genetically modified crops – margins that are shrinking in both size and species diversity. I have initiated a survey using herbarium records to revisit the locations of previously recorded populations of EAC lost crop progenitors. This survey is ongoing, and will be a first step in advocating for and contributing to the conservation of these plants, which have immense cultural and historical importance.

Because I study “lost crops,” I am frequently asked why people eventually stopped cultivating the EAC. The gradual loss of TEK related to the EAC is suggested by the assemblages from Gypsy Joint and Muir (Chapter 5). At these sites, we see domestication in reverse: the biological effects of lost knowledge and altered practice on a crop as it returns to its wild state. There may be useful theoretical perspectives for exploring this process in the

literature on contemporary loss of TEK in an era of globalization and climate change. Understanding how the EAC was lost has the potential to add historical depth to our understanding of the environmental and social effects of TEK loss.

7.5 References

Abbo, S., E. Rachamim, Y. Zehavi, I. Zezak, S. Lev-Yadun and A. Gopher

2011 Experimental Growing of Wild Pea in Israel and its Bearing on Near Eastern Plant Domestication. *Annals of Botany* 107(8):1399-1404.

Arnold, Jeanne E., Scott Sunell, Benjamin T. Nigra, Katelyn J. Bishop, Terrah Jones and Jacob Bongers

2016 Entrenched disbelief: complex hunter-gatherers and the case for inclusive cultural evolutionary thinking. *Journal of Archaeological Method and Theory* 23(2):448-499.

Asouti, Eleni and Dorian Q. Fuller

2012 From Foraging to Farming in the Southern Levant: The Development of Epipalaeolithic and Pre-Pottery Neolithic Plant Management Strategies. *Vegetation History and Archaeobotany* 21(2):149-162.

2013 A Contextual Approach to the Emergence of Agriculture in Southwest Asia. *Current Anthropology* 54(3):299-345.

Balée, William

2006 The Research Program of Historical Ecology. *Annual Review of Anthropology*
35:75-98.

Bamforth, Douglas B.

2002 Evidence and Metaphor in Evolutionary Archaeology. *American Antiquity*
67(3):435-452.

Boyd, Robert and Peter J. Richerson

1988 *Culture and the Evolutionary Process*. University of Chicago Press, Chicago.

Briggs, Rachel V.

2015 The Hominy Foodway of the Historic Native Eastern Woodlands. *Native South*
9:112-146.

2016 The Civil Cooking Pot: Hominy and the Mississippian Standard Jar in the Black
Warrior Valley, Alabama. *American Antiquity* 81(2):316-332.

Cohen, Dan

1966 Optimizing Reproduction in a Randomly Varying Environment. *Journal of*
Theoretical Biology 12(1):119-129.

Crockford, Susan J. and Cameron J. Pye

1997 Forensic Reconstruction of Prehistoric Dogs from the Northwest Coast. *Canadian*
Journal of Archaeology 21(2):149-153.

Crumley, Carole L.

- 1994 Historical Ecology: A Multidimensional Ecological Orientation. In *Historical Ecology: Culture, Knowledge and Changing Landscapes*, edited by Carole L. Crumley, pp. 1-16. School of American Research Press, Sante Fe, NM.

Darwin, Charles

- 1902 [1859] *On the Origin of Species by Means of Natural Selection, or the Preservation of Favored Races in the Struggle for Life*. P.F. Cormier and Son, New York.

David, Paul A.

- 1985 Clio and the Economics of QWERTY. *The American Economic Review* 75(2):332-337.

Deur, Douglas

- 2002 Rethinking Precolonial Plant Cultivation on the Northwest Coast of North America. *Professional Geographer* 54(2):140-157.

Deur, Douglas and Nancy J. Turner (editors)

- 2005 *Keeping It Living: Traditions of Plant Use and Cultivation on the Northwest Coast of North America*. University of Washington Press, Seattle.

Flannery, Kent V.

- 1969 Origins and ecological effects of early domestication in Iran and the Near East. In *The Domestication and Exploitation of Plants and Animals.*, edited by Peter J. Ucko and G.W. Dimbleby, pp. 73-100. Duckworth, London.

Fuller, Dorian Q., George Willcox and Robin G. Allaby

- 2011 Cultivation and Domestication had Multiple Origins: Arguments Against the Core Area Hypothesis for the Origins of Agriculture in the Near East. *World Archaeology* 43(4):628-652.

Gremillion, Kristen J.

- 2004 Seed Processing and the Origins of Food Production in Eastern North America. *American Antiquity* 69(2):215-233.

Gremillion, Kristen J., Loukas Barton and Dolores R. Piperno

- 2014 Particularism and the retreat from theory in the archaeology of agricultural origins. *Proceedings of the National Academy of Sciences* 111(17):6171-6177.

Gremillion, Kristen J. and Dolores R. Piperno

- 2009 Human Behavioral Ecology, Phenotypic (Developmental) Plasticity, and Agricultural Origins. *Current anthropology* 50(5):615-619.

Gross, Briana L. and Zhijun Zhao

- 2014 Archaeological and genetic insights into the origins of domesticated rice. *Proceedings of the National Academy of Sciences* 111(17):6190-6197.

Hart, John P.

- 2001 Maize, Matrilocality, Migration and Northern Iroquoian Evolution. *Journal of Archaeological Method and Theory* 8(2):151-182.

Henrich, Joseph

- 2001 Cultural Transmission and the Diffusion of Innovations: Adoption Dynamics Indicate That Biased Cultural Transmission Is the Predominate Force in Behavioral Change. *American Anthropologist* 103(4):992-1013.

Jones, Clive G., John H. Lawton and Moshe Shachak

- 1994 Organisms as Ecosystem Engineers. *Oikos* 69(3):372-386.

Kennett, Douglas J. and Bruce Winterhalder

- 2006 *Behavioral Ecology and the Transition to Agriculture*. University of California Press, Berkeley.

Ladizinsky, G.

- 1987 Pulse domestication before cultivation. *Economic Botany* 41(1):60-65.

Langlie, BrieAnna S., Natalie G. Mueller, Robert N. Spengler and Gayle J. Fritz

- 2014 Agricultural Origins from the Ground Up: Archaeological Approaches to Plant Domestication. *American Journal of Botany* 101(10):1601-1617.

Lavé, Jean and Etienne Wenger

- 1991 *Situated learning: Legitimate peripheral participation*. Cambridge University Press, Cambridge.

Lee, Richard B.

- 1980 Lactation ovulation infanticide and womens work: A study of hunter-gatherer population regulation. In *Biosocial Mechanisms of Population Regulation*, edited by M.N. Cohen, R.S. Malpass and H.G. Klein, pp. 321-348. Yale University Press, New Haven.

Lopinot, Neal H.

- 1997 Cahokian Food Production Reconsidered. In *CahokiaL Domination and Ideology in the Mississippian World*, edited by Timothy R. Pauketat and Thomas E. Emerson, pp. 52-68. University of Nebraska Press, Lincoln.

Marshall, Fiona and Elisabeth Hildebrand

- 2002 Cattle before crops: the beginnings of food production in Africa. *Journal of World Prehistory* 16(2):99-143.

Mueller, Natalie G.

- 2013 *Mound Centers and Seed Security: A Comparative Analysis of Botanical Assemblages from Middle Woodland Sites in the Lower Illinois Valley*. Springer Briefs in Plant Science. Springer, New York.

Mueller, Natalie G. and Gayle J. Fritz

- 2016 Women as Symbols and Actors in the Mississippi Valley: Evidence from Female Flint-Clay Statues and Effigy Vessels. In *Gendered Perceptions of Native American Landscapes*, edited by Cheryl Claassen. University of Tennessee Press, Knoxville, TN.

Murray, Priscilla M. and Mark C. Sheehan

- 1984 Pehistoric Polygonum Use in the Midwestern United States. In *Experiments and Observations on Aboriginal Wild Plant Food Utilization in Eastern North America*, edited by Patrick J. Munson. Prehistory Research Series. vol. VI. Indiana Historical Society, Indianapolis.

Odling-Smee, John F., Kevin N. Laland and Marcus W. Feldman

- 2003 *Niche Construction: The Neglected Process in Evolution*. Princeton University Press, Princeton.

Ovodov, Nikolai D., Susan J. Crockford, Yaroslav V. Kuzmin, Thomas F.G. Higham, Gregory W.L. Hodgins and Johannes van der Plicht

- 2011 A 33,000-year-old incipient dog from the Altai Mountains of Siberia: evidence of the earliest domestication disrupted by the Last Glacial Maximum. *PLoS One* 6(7):e22821.

Piperno, Dolores R., Irene Holst, Klaus Winter and Owen McMillan

- 2015 Teosinte Before Domestication: Experimental Study of Growth and Phenotypic Variability in Late Pleistocene and Early Holocene Environments. *Quaternary International* 363:65-77.

Rogers, Everett

- 2003 *Diffusion of Innovation*. Free Press, New York.

Ross, Eric B.

1998 *The Malthus factor: Poverty, politics and population in capitalist development*.
Zed Books, London.

Sahlins, Marshall D.

1972 *Stone age economics*. Aldine-Atherton, Chicago.

1976 *Culture and practical reason*. University of Chicago Press, Chicago.

Sassaman, Kenneth E.

2004 Complex hunter–gatherers in evolution and history: A North American
perspective. *Journal of Archaeological Research* 12(3):227-280.

Service, Elman

1962 *Primitive Social Organization: An Evolutionary Perspective*. Random House,
New York.

Simon, Mary L.

2014 Reevaluating the Introduction of Maize into the American Bottom and Western
Illinois. *Occasional Papers of the Midwest Archaeological Conference* 1(1):97-
134.

Smith, Bruce D.

2001 Low-Level Food Production. *Journal of Archaeological Research* 9(1):1-42.

2006 Human Behavioral Ecology and the Transition to Food Production. In *Behavioral Ecology and the Transition to Agriculture*, edited by Douglas J Kennett and Bruce Winterhalder, pp. 289-303. University of California Press, Berkeley.

2016 Neo-Darwinism, niche construction theory, and the initial domestication of plants and animals. *Evolutionary Ecology* 30(2):307-324.

Smith, Bruce D. and Richard A. Yarnell

2009 Initial Formation of an Indigenous Crop Complex in Eastern North America at 3800 B.P. *Proceedings of the National Academy of Sciences* 106(16):6561-6566.

Stone, Glenn Davis, Andrew Flachs and Christine Diepenbrock

2014 Rhythms of the herd: Long term dynamics in seed choice by Indian farmers. *Technology in Society* 36:26-38.

Turner, Nancy J. , Marianne Boelscher Ignace and Ronald Ignace

2000 Traditional Ecological Knowledge and Wisdom of Aboriginal Peoples in British Columbia. *Ecological Applications* 10(5):1275-1287.

Vigne, Jean-Denis, Isabelle Carrère, François Briois and Jean Guilaine

2011 The Early Process of Mammal Domestication in the Near East: New Evidence from the Pre-Neolithic and Pre-Pottery Neolithic in Cyprus. *Current Anthropology* 52(S4):S255-S271.

Watson, Patty Jo and Mary C. Kennedy

- 1991 The Development of Horticulture in the Eastern Woodlands of North America: Women's Role. In *Engendering Archaeology*, edited by Joan Gero and Margaret W. Conkey, pp. 255-275. Blackwell Publishing, Oxford.

Winterhalder, Bruce and Eric Alden Smith

- 2000 Analyzing adaptive strategies: Human behavioral ecology at twenty-five. *Evolutionary Anthropology Issues News and Reviews* 9(2):51-72.

Woodburn, James

- 1982 Egalitarian Societies. *Man, New Series* 17(3):431-451.

Zeder, Melinda A.

- 2015 Core questions in domestication research. *Proceedings of the National Academy of Sciences* 112(11):3191-3198.

Appendices

Appendix 1: Herbarium specimens examined for this study

Polygonum achoreum S.F. Blake						
HS ID	Herbarium	Number	Determined by	State	Collection Month	Photosample
11	National	1826799	Costea	MN	June	2
51	Missouri	2224128	Katz	NE	June	2
10	National	2876171	Costea	MT	July	5
50	Missouri	3667043	Rhode	ND	July	5
8	National	2329091	Costea	QC	Aug	4
9	National	1826754	Costea	SD	Aug	5
7	National	2004170	Costea	ND	Sep	5
49	Missouri	4957772	Cusick	OH	Sep	9
53	Missouri	5839142	Yurtseva	MO	Sep	10
52	Missouri	5288218	Yurtseva	MO	Oct	13
Subtotal						60
Polygonum aviculare L. ssp. buxiforme (Small) Costea & Tardif						
HS ID	Herbarium	Number	Determined by	State	Collection Month	Photosample
1	National	1465810	Costea	KY	June	3
2	National	1465809	Costea	KY	June	1
6	National	1436192	Costea	AK	June	5
4	National	2235643	Costea	IA	July	3
55	Missouri	2588081	Hinds	IL	July	
3	National	1113306	Costea	ME	Aug	5
58	Missouri	4074038	Brant	MO	Aug	13

5	National	1925995	Costea	RI	Sep	5
54	Missouri	4641381	Brant	MO	Sep	
56	Missouri	3671302	Hinds	AL	Sep	8
57	Missouri	4005057	Hinds	TX	Sep	20
70	Missouri	2158865	Brant	MO	Oct	22
72	Missouri	5093323	Hudson	MO	Oct	
71	Missouri	5093336	Hudson	MO	Oct	7
Subtotal						92

Polygonum erectum L.

HS ID	Herbarium	Number	Determined by	State	Collection Month	Photosample
16	National	2727807	F.R. Fosberg	VA	June	5
38	Missouri	5393684	Reed	KY	June	
39	Missouri	5393682	Reed	KY	June	
48	Missouri	5400840	Moe	IL	June	
17	National	2667449	Costea	OH	Aug	2
34	Missouri	4292384	Brant	MO	Aug	3
42	Missouri	3450151	Thomas	TN	Aug	6
44	Missouri	4292383	Brant	MO	Aug	
12	National	1925748	Costea	PA	Sep	5
13	National	298208	Costea	PA	Sep	4
15	National	3495558	L.B. Smith	PA	Sep	3
18	National	228405	Costea	IN	Sep	3
20	National	309488	Costea	IN	Sep	4
21	National	797318	Costea	WV	Sep	3
29	National	2746624	Kral	AL	Sep	
30	National	2605290	Costea	NY	Sep	
33	Missouri	4292359	Brant	MO	Sep	

35	Missouri	5814504	Smith	PA	Sep	11
36	Missouri	4074041	Brant	IL	Sep	5
37	Missouri	6152618	Reid and Gentry	AR	Sep	5
40	Missouri	5393680	Pretz	PA	Sep	10
41	Missouri	3680707	Hill	MD	Sep	
43	Missouri	3476886	Raven	MO	Sep	
45	Missouri	3913996	Christ	MO	Sep	
46	Missouri	3226768	Brant	MO	Sep	17
47	Missouri	3493891	Brant	MO	Sep	
65	Missouri	5151138	Brant	MO	Sep	
14	National	298794	Costea	PA	Oct	5
19	National	2664048	Costea	KY	Oct	4
31	Missouri	1135807	Brant	MO	Oct	10
32	Missouri	2158858	Brant	MO	Oct	10
69	Missouri	5159294	Mueller	MO	Oct	18
22	Washu Pbot	65	Blake	MO	Oct	20
Subtotal						153

Polygonum ramosissimum Michaux

HS ID	Herbarium	Number	Determined by	State	Collection Month	Photosample
23	National	2067911	Webster and Wilbur	TX	June	4
60	Missouri	5970916	Brant	MO	June	10
59	Missouri	4236452	Brant	MO	Aug	10
64	Missouri	2005129	Katz	ND	Aug	10
24	National	1125	Costea	TX	Sep	
25	National	1888718	Costea	KY	Sep	
73	Missouri	4J657068	Summers	MO	Sep	14
28	National	2802647	Costea	KY	Sep	

26	National	1885904	Costea	TX	Oct	
27	National	329	Costea	MO	Oct	
61	Missouri	6013115	Brant	MO	Oct	10
62	Missouri	1757520	Brant	MO	Oct	4
63	Missouri	5387653	Skykora	OK	Oct	4
66	Missouri	4610390	Henderson	MO	Oct	12
67	Missouri	4074031	Brant	MO	Oct	12
68	Missouri	5074499	Jacobs	MO	Oct	10
Subtotal						100
Total achenes analyzed						405

Appendix 2: Sites, contexts, and dates for analyzed assemblages of erect knotweed

Site name & number	State, County	Museum	Contexts sampled	Age	Error	NOSAMS # or source	Calibrated age range (94.5%)	Median
Cold Oak 15Le50	KY, Lee	Gremillion Lab	Feature 8	3200	100	136216	1733 – 1224 BCE	1476
				2470	90	Gremillion 1998:143	793 – 404 BCE	BCE 602 BCE
			Feature 51 FS49	2060	60	Gremillion 1998:143	346 BCE – CE 68	82 BCE
Walker-Noe 15GD56	KY, Garrard	Webb	Unit 9, Z2 L2	2000	60	Pollack et al. 2006:67-8	167 BCE – CE 125	8 BCE
			Feature 2	1950	25	134355	21BCE – CE 125	CE 52
Smiling Dan 11ST123	IL, Scott	ISM	F242					
			F194 Structure B	1840	20	134362	CE 125 – 238	CE 176
			F110 Structure C	1750	20	134363	CE 236 – 347	CE293
			F164					
			F205 F92 Structure C					
Meridian Hills 11MS1258	IL, Madison	ISAS	F55	1830	20	134359	CE 130 – 237	CE 182
Mund 11S435	IL, St. Clair	ISAS	Feature 90	1280	20	134357	CE 672 – 770	CE 717
Big Loose Creek 23OS1208	MO, Osage	MODOT	F32					
			F19	1,170	20	136215	CE 774 – 943	CE 845
Sponemann 11MS517	IL, Madison	ISAS	F592	1160	15	134358	CE 776 – 950	CE 878
Rohlfing 23FR525	MO, Franklin	MODOT	F7, Z4					
			F7, contents of vessel	1,140	20	134365	CE 777 – 977	CE 924
Range 11S47	IL, St. St. Clair	ISAS	F501	1010	75	Kelly 2007:470	CE 880 – 1213	CE 1029

Westpark 11MO86	IL, Monroe	Fritz Lab	Feature 300	910	20	134356		CE 1037 – 1183	CE 1094
Whitney Bluff 3BE20	AR, Benton	UARK	32-57-5 32-57-3	885	20	134366		CE 1046 – 1217	CE 1163
Muir 15JS86	KY, Jessamine	Webb	F22	825	15	134361		CE 1180 – 1260	CE 1223
Hill Creek 11PK525	IL, Pike	ISAS	Feature 1	680	15	136214		CE 1277 – 1383	CE 1291
Gypsy Joint 23RI101a	MO, Ripley	NMNH	Pit 5b	575	20		134351	CE 1310-1415	CE 1345

Appendix 3: Mean achene size in terms of area, length, width, and length X width for all assemblages

Table 5: Mean achene size for all sites and modern comparative sample										
Site	N		Area		Length		Width		LXW	
	Smooth	Tubercled	Smooth	Tubercled	Smooth	Tubercled	Smooth	Tubercled	Smooth	Tubercled
Modern	100	379	3.28	3.17	3.10	2.76	1.76	1.80	5.49	5.00
Cold Oak	1	5	4.47	2.85	3.76	2.86	1.95	1.83	7.04	4.80
Walker Noe	9	1	4.49	4.04	3.68	3.2	2.02	2.21	7.15	6.48
Smiling Dan	23	60	3.43	3.29	3.40	3.18	1.75	2.16	5.80	6.44
Meridian Hills	2	26	4.26	3.46	3.40	2.93	2.10	2.07	6.85	5.58
Mund	44	0	2.46	---	2.92	---	1.40	---	3.96	---
Big Loose Creek	8	53	3.38	2.98	3.24	2.73	1.72	1.88	5.40	4.73
Rohlfing	14	19	3.04	2.88	3.07	2.68	1.65	1.87	4.84	4.61
Sponemann	10	54	4.45	3.44	3.70	2.87	2.16	2.11	7.68	5.55
Range	32	10	4.30	3.79	3.73	3.04	2.02	2.23	7.22	6.21
Westpark	70	16	5.04	4.79	4.03	3.96	2.19	2.31	8.45	8.38
Whitney Bluff	195	1	5.67	4.15	4.17	3.40	2.30	2.23	9.58	7.58
Muir	1	18	3.00	2.40	2.83	2.39	1.68	1.64	4.55	3.64
Hill Creek	146	0	5.37	---	4.27	---	2.21	---	9.05	---

Gypsy Joint	83	40	4.12	3.50	3.76	3.01	1.91	2.08	6.90	5.73
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Appendix 4: Photosample size, total sample size, and sample proportion of smooth morphs

Site	ID	Context	Photo Sample	Weight	Total achene	Smooth	Tubercled	% Smooth
Cold Oak 15Le50	45	Feature 8	7	0.4	10	0	10	0
	46	Feature 51	1	0.01	1	1	0	N/A
	47	Feature 49	1	0.01	1	1	0	N/A
Walker-Noe 15GD56	16	Unit 9, Z2 L2	3	0.22	24	24	0	100
	17	Feature 2	8	0.17	16	15	1	94
Smiling Dan 11ST123	32	F242	22	1.62	43	10	33	23
	33	F194 Structure B	2	0.19	14	0	14	0
	34	F110 Structure C	14	0.14	40	11	29	28
	35	F164	34	0.86	79	29	50	37
	36	F205	15	0.22	35	12	23	34
	37	F92 Structure C	13	0.15	30	13	17	43
Meridian Hills 11MS1258	28	55	28	2.37	31	2	29	6
Mund 11S435	21	Feature 90	45	1.08	124	124	0	100
Big Loose Creek 23OS1208	40	F32	10	0.06	11	9	2	82
	41	F19	56	0.85	97	21	76	22
Sponemann 11MS517	25	F592	79	18.54	123	30	93	24
Rohlfing 23FR525	43	F7, Z4	46	1.99	54	31	23	57
	44	F7, contents of vessel	3	0.05	11	9	2	82
Range 11S47	26	F501	70	0.5	137	110	27	80
Westpark 11MO86	19	Feature 300	100	500	500*	390	110	78
Whitney Bluff 3BE20	12	32-57-5	81	0.88	706	704	2	100
	13	32-57-3	120	1.2	601	601	0	100

Muir 15JS86	31	F22		19	0.2	65	9	56	14
Hill Creek 11PK525	22	Feature 1		146	2.38	400	400	0	100
Gypsy Joint 23RI101a	01	Pit 5 520 N 595 E		69	9.13	387	338	49	87
	02	Pit 5 525 N 600 E		19	2.52	184	163	21	89
	03	Pit 5B		20	2.9	195	175	20	90
	04	Pit 5A		12	1.34	48	33	15	69
	05	Pit 5 Skim		20	2.53	229	198	31	86

Appendix 4: The photosample was selected using the following procedure: 1) record the initial weight of all identifiable *Polygonum* (kernels, achenes, and pericarp fragments) from a given context; 2) Sort the entire sample, counting all achenes that had sufficient observable pericarp to classify them as either smooth or tubercled. I did not count fragments of pericarp smaller than 50% of a complete pericarp to avoid double counting; 3) Separate achenes that had well-preserved pericarps and had not grossly changed shaped during carbonization (Figure 6.2); 4) Sample one achene per 0.01 g, or if there were fewer measurable achenes than one per 0.01 g, sample all of them. The exception to this sampling strategy was the Westpark assemblage, which contained tens of thousands of achenes and kernels: I took an arbitrary sample of 100 well-preserved achenes for the initial photosample. The morphometric analysis is based on this photosample. The total smooth and tubercled and population proportions include the photosample and other achenes that were not well-preserved enough to be measured.

Appendix 5: Summary of composition of botanical assemblages

Site name & number	Analyst	Liters (L)	Samples analyzed	Sumpweed	Sunflower	Erect knotweed	Goosefoot	Maygrass	Little barley	Maize (all parts, g or N)	Source
Cold Oak 15Le50	Gremillion	??	58	<100	<100	>100	>100	>100	---	---	Gremillion 1998
Walker-Noe 15GD56	??	139	25	? 15	? 3	225	? 161	84	---	---	Pollack 2005
Smiling Dan 11ST123	Asch & Asch	1,200	746	39	35	4374	1176	5155	2040	---	Asch and Asch 1985
Meridian Hills 11MS1258	Parker	??	59	Yes	Yes	> 31	>600	Yes	Yes	---	Williams 1993
Mund 11S435	Johannessen	1496	46	32	20	*2166	? 2100	1838	---	N=3	Johannessen 1983
Big Loose Creek 23OS1208	Lopinot & Powell	515	52	1	5	745	1,725	5,279	83	0.03 g	Lopinot and Powell 2015
Sponemann	Parker	6400	436	8	9	36,841	34,446	2734	75	N=675	

11MS517											
Rohlfing 23FR525	Erickson	191	20	---	---	2672	396	156	---	---	Erickson 2006
Range 11S47	Parker	364	35	---	---	634	245	2578	3	N=4835	Parker 2007
Westpark 11MO86	Powell	??	??	??	Hundreds	Tens of thousands	Tens of thousands	Hundreds	---	Yes	Powell 2000
Whitney Bluff 3BE20	Fritz	N/A	??	>10	Yes	1200	<1000	---	---	N=26	Fritz 1986
Muir 15JS86	Rossen	1468	73	---	8	560	---	---	---	N=5882	Rossen 1988
Hill Creek 11PK525	Asch & Asch	364	34	105	9	1263	71	---	2	N=>200	
Gypsy Joint 23RI101a	Smith & Cutler	?	36	189	1	12,000	? 8,000	---	---	40.0 g	Smith 1978

Appendix 5: Summary of botanical assemblages that contained the analyzed erect knotweed assemblages. For multicomponent sites, statistics reflect the analysis only for the component that the erect knotweed sample was drawn from. Counts were chosen as the metric for comparison because they were available for almost all of the assemblages. Maize is reported in terms of either weight or count because lab procedures vary with respect to this taxon. If there were only a few fragments and weight was not reported, maize is described as “trace.” This column is a sum of all maize parts (kernel, cob, and glume). Count of domesticated assemblages are in bold. For sumpweed and sunflower, this is based on achene size indices (Yarnell 1972; 1978; 1981; Smith 2014); for goosefoot, if the assemblage >50% domesticated type goosefoot (Smith and Funk 1988); for erect knotweed it is defined as an assemblage that is significantly larger than the modern comparative collections, with a higher proportion of smooth morphs than has been observed in modern populations (see Figure 5.4 for estimating population proportion with small samples). ? indicates that the assemblage was not evaluated for domestication syndrome. * indicates an erect knotweed assemblage that is outside of the range of modern variation, but does not fit the description of domesticated erect knotweed in Chapter 2.

Appendix 6: Multispecies comparisons

Appendix 6a: Multispecies morphometric comparison, smooth morphs								
	<i>achoreum</i>	<i>buxiforme</i>	<i>erectum</i>	<i>erectum, immature</i>	<i>ramosissimum</i>	<i>Mund</i>	<i>Hill Creek</i>	<i>Whitney Bluff</i>
Area	3.38 +/- 0.257	2.28 +/- 0.349	3.28 +/- 0.514	3.04 +/- 0.499	4.21 +/- 1.338	2.46 +/- 0.480	5.38 +/- 0.908	5.66 +/- 0.683

Length	3.20 +/-0.222	2.69+/-0.270	3.30+/-0.330	3.12 +/- 0.287	3.64+/-0.609	2.92 +/- 0.291	4.26+/-0.353	4.16+/-0.243
Width	1.70+/-0.095	1.35+/-0.163	1.76+/-0.157	1.53 +/- 0.202	1.78+/-0.366	1.40 +/- 0.205	2.21+/-0.279	2.30+/-0.257
Circularity	0.54+/-0.137	0.52+/-0.154	0.44+/-0.113	0.49 +/- 0.071	0.49+/-0.091	0.49 +/-0.072	0.53+/-0.078	0.46+/-0.073
Aspect Ratio	1.89 +/- 0.126	2.00+/-0.434	1.91+/-0.265	2.04 +/-0.281	2.03 +/-0.283	2.04 +/- 0.269	1.95+/-0.288	1.76+/-0.227
Roundness	0.53+/-0.034	0.52+/-0.108	0.53+/-0.070	0.50+/-0.065	0.50+/-0.07	0.50 +/- 0.060	0.52+/-0.077	0.58+/-0.069

Appendix 6b: Multispecies morphometric comparison, tubercled morphs						
	<i>achoreum</i>	<i>buxiforme</i>	<i>erectum</i>	<i>erectum, immature</i>	<i>ramosissimum</i>	<i>Muir</i>
Area	3.43 +/-0.651	2.37 +/-0.354	3.28+/-0.528	3.32+/-0.516	2.99+/-0.761	2.40+/-0.364
Length	2.85+/-0.309	2.40+/-0.197	2.76+/-0.202	2.81+/-0.284	2.79+/-0.433	2.39+/-0.244
Width	1.88+/-0.222	1.55+/-0.171	1.88+/-0.208	1.85+/-0.265	1.63+/-0.181	1.64+/-0.189
Circularity	0.64+/-0.199	0.65+/-0.515	0.54+/-0.104	0.42+/-0.082	0.56+/-0.086	0.42+/-0.080
Aspect Ratio	1.47+/-0.125	1.52+/-0.156	1.50+/-0.147	1.50+/-0.354	1.65+/-0.192	1.47+/-0.158
Roundness	0.69+/-0.058	0.66+/-0.063	0.67+/-0.065	0.68+/-115	0.61+/-0.067	0.70+/-0.082
Striate-tubercled/total	10/51	14/62	131/131	50/50	7/59	11/19

Appendix 6: The summary statistics for *P. achoreum*, *P. aviculare* ssp. *buxiforme*, and *P. ramosissimum* are identical to those presented in Mueller Chapters 1 and 2. Details about how these samples were collected are reported in Chapter 2. The summary statistics are slightly different for *P. erectum*, because the sample also includes 360 additional modern achenes from surveys of contemporary populations (Table 6.1; Chapter 4). Overall, the mean measurements for erect knotweed achenes of both morphs changed very little with the addition of these specimens, suggesting that the original sampling effort was adequate. The measurements for the immature erect knotweed come from the carbonization experiment reported in Chapter 5. The criteria for sorting mature from immature achenes was whether or not the pericarp could be depressed with a metal implement

