nature plants

PERSPECTIVE

PUBLISHED: 5 JULY 2017 | VOLUME: 3 | ARTICLE NUMBER: 17092

Growing the lost crops of eastern North America's original agricultural system

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Thousands of years before the maize-based agriculture practiced by many Native American societies in eastern North America at the time of contact with Europeans, there existed a unique crop system only known through archaeological evidence. There are no written or oral records of how these lost crops were cultivated, but several domesticated subspecies have been identified in the archaeological record. Growth experiments and observations of living progenitors of these crops can provide insights into the ancient agricultural system of eastern North America, the role of developmental plasticity in the process of domestication, and the creation and maintenance of diverse landraces under cultivation. In addition, experimental gardens are potent tools for public education, and can also be used to conserve remaining populations of lost crop progenitors and explore the possibility of re-domesticating these species.

When Native American agriculture is invoked, most people conjure up an image of the first Thanksgiving. The domesticated plant foods on the table between the pilgrims and their indigenous hosts are maize, beans, squash and pumpkin (*Cururbita pepo* L. ssp. *pepo*)—perhaps the most iconic of all Native American foods. These crops, while quintessentially Native American, are not native to eastern North America (ENA) and were not domesticated there. They originated in Mexico and reached ENA relatively recently (from an archaeological perspective). The histories of these crops are continually rewritten as new archaeological evidence comes to light, and old evidence is re-examined (Fig. 1). Maize appears between 300 BCE–1 CE in New York, Ohio and Ontario[1]. It evidently took several centuries to develop landraces adapted to ENA and to integrate maize into local cuisine: maize did not become a major crop in the midcontinent until *c*. 900 CE[2], although until recently archaeologists thought it was grown there much earlier[3]. Somewhat mysteriously, beans do not appear in the archaeological record until a century or two after this time[4], but agriculture was not a late pre-contact phenomenon.

By the time that maize, beans and Mexican squashes arrived, communities in parts of ENA had already been cultivating domesticated plants for ~2,000 years (Figs 1 and 2). These earlier crops include some familiar plants—the earliest domesticated sunflowers (*Helianthus annuus* var. *macrocarpus* (DC.) Ckll.) were found in Tennessee and are 4,000 years old[5–7]. Native squash varieties that were domesticated in ENA, such as acorn and crookneck squashes (*Cucurbita pepo* L. ssp. *ovifera* D.S. Decker), are ENA's earliest domesticates[8–10]. The other members of this pre-maize crop complex were lost to history, both oral and written, only to be rediscovered by archaeologists hundreds of years later. Archaeologists refer to these lost crops as the Eastern Agricultural Complex (EAC).

Beginning with the analysis of assemblages from dry rockshelters and caves by Melvin Gilmore[11], Volney Jones[12] and Richard Yarnell[13–15], and intensifying with the introduction of systematic recovery of plant remains by flotation[16,17], archaeologists realized that an entirely unknown agricultural system had taken shape in ENA, beginning some 5,000 years ago. Although the scattered and burned seeds and fruits of hundreds of different plant species have been recovered from archaeological sites in ENA, the evidence for at least five lost crops is overwhelming. The seeds of each of these species are found in dense, pure concentrations numbering in the tens of thousands or millions in storage pits[18–20]. They are also routinely recovered from the floors of ancient houses, trash pits and hearths. In dry rockshelters, their desiccated remains are found bundled or in baskets and bags[21]. They have even been recovered from human palaeofaeces[14]. In the order in which they entered the crop system, these are sumpweed (*Iva annua* L. and its domesticated subspecies, *Iva annua* var. *macrocarpa* S.F. Blake)[22,23], goosefoot (*Chenopodium berlandieri* Moq. and its domesticated subspecies, *Chenopodium berlandieri* ssp. *jonesianum* Smith and Funk)[24–26], maygrass (*Phalaris caroliniana* Walter)[27], erect knotweed (*Polygonum erectum* L. and its domesticated subspecies *Polygonum erectum* ssp. *watsoniae* N.G. Muell.)[28,29], and little barley (*Hordeum pusillum* Nutt.)[30] (Fig. 3).

In the early days of EAC research, botanists and palaeoethnobotanists commonly conducted studies of living plants. For example, Yarnell[23,31] synthesized studies of sumpweed both in the field and under cultivation, although these observations were actually made by botanists[32]. Heiser[33,34] studied wild, weedy and cultivated sunflowers for decades, Asch and Asch[18,35] made collections from the wild progenitors of all annual seed crops of the EAC and published their observations, and Munson and his students[36] did the same, in addition to conducting several enlightening processing experiments. Observations of wild populations of EAC plants, as well as the results of small-scale harvesting experiments, were synthesized by Smith[37]. Since then, observation or experimental cultivation of EAC crop progenitors has been rare, with a few palaeoethnobotanists conducting informal experiments[38,39], but with no new studies published. Most previous studies were of EAC crop progenitors in natural ecosystems. With the exception of Heiser's experiments with sumpweed and sunflower, nothing has been published on the behaviour of EAC crop progenitors under cultivation, despite the fact that

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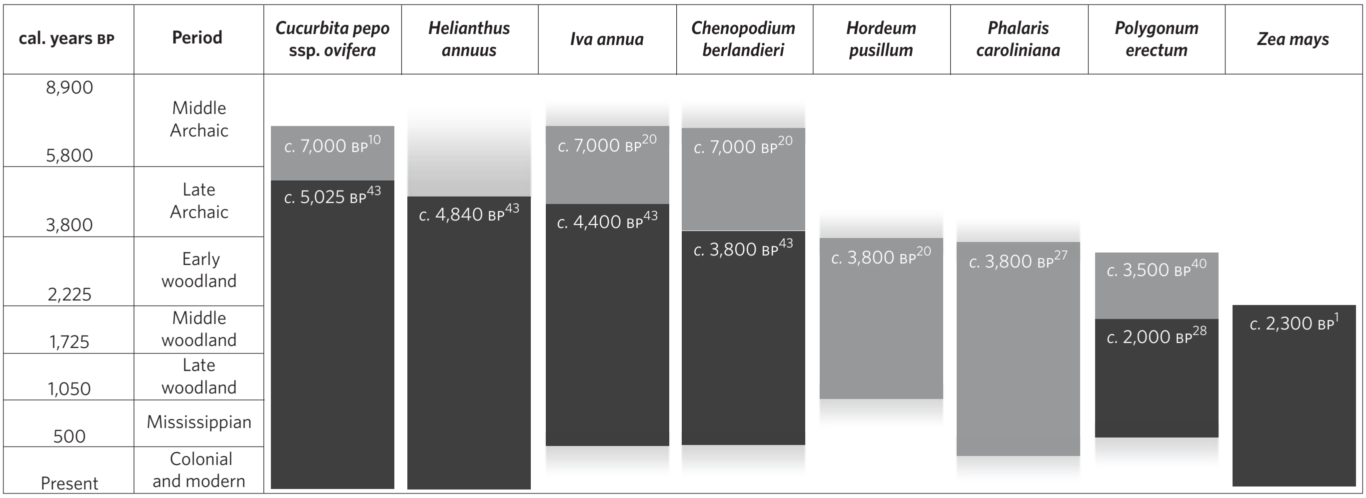

Figure 1 | Timeline of Eastern Agricultural Complex crop cultivation and domestication. Light grey boxes indicate probable period of cultivation prior to the earliest dated assemblage that exhibits morphological indicators of domestication. Dark grey boxes indicate the period of cultivation after the first domesticated assemblage. Shaded grey margins indicate that a direct radiocarbon date is not available for the earliest or latest reported assemblage.

these species sustained societies in ENA for thousands of years. We have initiated several research projects that involve growing the wild progenitors of these crops experimentally and in teaching gardens. These projects are nascent but show promise for expanding our understanding of the evolution and spread of food production as a knowledge system and the process of domestication[40]. In addition to these academic concerns, palaeoethnobotanists are also exploring the possibility of re-domesticating and commercializing ENA's original crops[41], and using gardens as tools for teaching and public outreach[42].

Landraces and agricultural knowledge

Morphological variation within and among archaeobotanical assemblages reveals the presence of diverse cultivated varieties or ancient landraces. For example, there are two domesticated types of ancient *C. berlandieri*, probably best understood as landraces or crop breeds, which have been identified from contexts as early as cal. 3,800 BP[43]. These types are distinguished from wild *C. berlandieri* on the basis of seed morphology: the domesticated subspecies *C. berlandieri* ssp. *jonesianum* typically possesses a smooth testa with a thickness of less than 20 μm and a truncated seed margin. A second 'pale variety' of *C. berlandieri* is distinguished by a greatly reduced outer epidermis seed coat layer, giving uncarbonized specimens a pale golden colour, and an especially truncated seed margin[44]. Fortuitous contexts where specimens were preserved in an uncarbonized state, such as the Riverton Site in Illinois and dry rockshelters in Kentucky and across the Arkansas and Missouri Ozarks, have yielded both morphological types[26,43,44]. Similar variation in cultivated chenopods is also recognized in South America, where palaeoethnobotanists have coded for a combination of quantitative and qualitative attributes to distinguish not only between wild, weedy and domesticated *Chenopodium*, but also to recognize at least two different species of cultigen Andean chenopods: quinoa (*Chenopodium quinoa*) and kañawa (*Chenopodium pallidicaule*), as well as distinct-looking types of early populations of quinoa[45,46]. In ENA, the coexistence of wild, weedy and domesticated types in archaeological collections has been used to explore differences in garden ecology[47].

Figure 2 | Map of the core area where Eastern Agricultural Complex crops were cultivated (light grey area), as indicated by the archaeological record.

Morphometric analyses have the potential to track the development and spread of landraces across ENA. Mueller's assessment of variation in erect knotweed morphology from 20 sites spanning ~2,500 years revealed that erect knotweed was probably domesticated at least twice, once in eastern Kentucky and once in the American Bottom region at the confluence of the Missouri and Mississippi rivers[40]. Within domesticated assemblages, there are significant differences in seed shape and size, indicating that, as with modern small-scale farmers, ancient farmers were maintaining distinct landraces through on-farm seed selection and the creation of unique local agroecosystems[48]. Ethnographic studies of historic and contemporary farmers suggest that landraces may be particularly good artifacts of shared communities of practice[49,50]. Complex knowledge systems are deployed when farmers select and prepare fields, sow seeds and tend and harvest crops, all of which can exert community-specific selective pressures on crops. Seed selection in particular is a highly specialized and skilled task. The ethnographic record of descendent communities provides some interesting examples of the kinds of institutions that may have been involved. For example, Bowers[51] describes how women's age grade societies were responsible for selecting, keeping and distributing seed among the Mandan and Hidatsa. Like any artifact, seeds may be casually exchanged between communities. But as with pottery, stone tools or works of art, if knowledge is not also exchanged, then the landrace cannot be recreated in the new community. Reconstructing the social institutions involved in the creation and transmission of agricultural knowledge can reveal how food-producing economies, and innovations in general, are developed and spread between communities.

By observing wild plants and conducting growth experiments, we can also use morphometric analyses of ancient seeds and fruits to reconstruct the evolutionary processes that resulted in domestication. For example, germination experiments by Patton and Williams[41] have indicated the necessity for wild goosefoot to undergo stratification before germinating, that is, winter must be simulated by storing seeds in moist, cold soil for a period of several weeks. As expected, domesticated varieties of goosefoot from Mexico (*Chenopodium berlandieri* ssp. *nutalliae*) germinate almost immediately after they are placed in a moist substrate; however, exposure to prolonged cold temperatures leads to near 100% mortality in young sprouts, confirming the dependence of domesticated thin-testa varieties on humans for propagation in prehistory. If domesticated varieties are allowed to reseed themselves, their seeds will germinate immediately in the fall and then die when temperatures drop. Human seed-savers are necessary to collect seeds and keep them high and dry until spring. Mueller's experiments with erect knotweed have demonstrated a similar relationship[52]. Erect knotweed naturally produces two different fruit types, one of which has far stronger germination inhibitors and can remain viable in a seed bank for more than a year. These thick pericarp fruit morphs gradually disappear from the archaeological record of cultivated populations over the course of several hundred years, resulting in a domesticated subspecies with monomorphic fruits that would have germinated more readily[40].

Plasticity and domestication

Phenotypic plasticity is the ability of a single genotype to produce different phenotypes when exposed to different environmental conditions. Genetic assimilation is the mechanism by which adaptive plasticity may become genetically fixed in a population[53]. Plasticity may become genetically assimilated when a plastic organism is subject to a new environmental condition in which one of its phenotypic responses confers a selective advantage. If the new environmental condition persists over many generations, the organism may lose its ability to express other phenotypes. This phenomenon is hard to document in natural populations because it is difficult to determine which traits were originally environmentally dependent (plastic) after they become genetically assimilated (constitutive)[54,55]. This conundrum makes domesticated species particularly useful for the study of genetic assimilation, because the plastic versus constitutive variation of extant ancestral wild populations can be studied in comparison to domesticated descendants[56].

Within anthropology, interest in the role of plasticity in the process of domestication has been growing. For example, Piperno and colleagues[57] wondered why early foragers in southern Mexico were drawn to the seemingly unappealing seeds of teosinte, the wild progenitor of maize. According to optimal foraging models, these ancient foragers do not seem particularly rational: teosinte seeds are difficult to harvest and process considering their low caloric return. Piperno and colleagues wondered if ancient teosinte exhibited a different, more attractive phenotype than it does under modern environmental conditions. They undertook a study of teosinte's plastic response to temperature and CO_2 levels and 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.

We would further argue that even if the climate was identical, the morphology and productivity of crop progenitors in natural ecosystems are 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. For example, Horton's cultivation experiments have yielded preliminary data indicating an increase in seed size in the second generation of sumpweed grown in the artificially enriched garden soil. While both the wild parent population and the first year of cultivated sumpweed produced the normal range of seed size, with maximum sizes of approximately 4 mm along the major axis, the second generation of cultivated sumpweed produced seeds that measure as 5–5.5 mm along the major axis[42]. While data

Figure 3 | The lost crops of the Eastern Agricultural Complex. a, Goosefoot (*Chenopodium berlandieri*). **b**, Sumpweed/marshelder (*Iva annua*). **c**, Little barley (*Hordeum pusillum*). **d**, Erect knotweed (*Polygonum erectum*). **e**, Maygrass (*Phalaris caroliniana*). Image in **a** courtesy of S.C.; images in **b**–**e** courtesy of N.G.M.

collection of seed measurements is ongoing, the presence of larger seed was notable during periodic harvests from September into November of 2016.

Mueller's experiments with erect knotweed provide an example of how plasticity may have played a pivotal role in forager choice. Erect knotweed's natural habitat is a frequently and unpredictably disturbed creek or river bank, where it grows in a highly competitive microenvironment with other annual weedy plants. In this habitat, it is a small herb (30–50 cm) with an erect growth habit and minimal branching. When it is grown in a garden its architecture is completely different. It transforms from a herb to a small shrub with far more auxiliary branches, a physiological response to light availability that is the inverse of the shade avoidance syndrome documented in many plants[58,59]. Knotweed plants produce fruits in the axils of their branches, so plants that produce auxiliary branches also produce a lot more seed. Growth experiments have shown that erect knotweed is much more productive when it has fewer neighbours[52]. Less plants can produce more seed in the same area if competing species are removed and erect knotweed plants are thinned early in the season by human cultivators. By making small adjustments to growth environment, ancient foragers-cum-farmers would have seen 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 plants as plastic as erect knotweed and sumpweed, would have been obvious.

Education, conservation and re-domestication

Today, sunflower and squash are the only EAC species that are grown as crops. The domesticated varieties of the other EAC species only exist in archaeological contexts, but the re-establishment of these crops may prove advantageous in the battle against food insecurity and the loss of agrobiodiversity. As we consider renewing cultivation of these plants, we have encountered several impediments: (1) at least three of these species are now rare plants, due to competition from their invasive cousins, shrinking field margins and increased herbicide use; (2) we lack data on yields and market potential; and (3) researchers have difficulty accessing seed stock. Ongoing research into these challenges is currently being undertaken by the authors as part of the Survey for Lost Crops, Lost Crops Garden Network, and Native Cultigen Project initiatives.

Just as archaeological data indicate EAC species were cultivated as crops across the mid-continent, herbaria specimens show that in some cases, their wild relatives were more widespread historically than they are today. Erect knotweed has been largely replaced where it was collected in the nineteenth and early twentieth centuries by its Eurasian cousins (*Polygonum aviculare* complex Costea and Tardif)[52]. Maygrass is under threat from the expansion of herbicide-tolerant crops and the elimination of field margins. Surveys in the spring of 2016 revealed that many previously recorded populations of maygrass along field margins in parts of Mississippi, Arkansas and Missouri have disappeared. While this species is still common on conserved prairie remnants, it is disappearing from increasingly homogenous and intensively cultivated agricultural landscapes where it was once common. The disappearance of stands of maygrass on field margins is symptomatic of a global loss of biodiversity in and around agroecosystems related to intensification and herbicide use[60–62]. Similarly, the use of herbicides to target goosefoot in agricultural fields and the spread of herbicide-resistant Eurasian (*Chenopodium album*) species[63] threatens native goosefoot (*C. berlandieri*). Conservation of these ancient crops is necessary if we are to establish their economic and dietary potential.

One way in which conservation efforts are being achieved is through the collection of wild seeds that are then propagated in educational and research gardens. The Survey for Lost Crops uses herbarium records and state survey data to revisit previously recorded populations in order to document their presence or absence and collect seeds for the development of gardens and seed banks. For example, the establishment of the Plum Bayou Garden at Toltec Mounds Archeological State Park has provided an EAC seed source that serves palaeoethnobotanical laboratories and educational and research gardens. Similarly, research gardens at Ohio University and Washington University in St. Louis, as part of the Lost Crops Garden Network, and the Native Cultigen Project at the University of the South have undertaken EAC seed propagation as well as experimental research to establish best practices for growing EAC species.

Few studies to date have explored the productivity of EAC species in a field cultivation setting. However, the precedent for goosefoot cultivation, as demonstrated by the archaeological record, suggests that this native plant could prove a viable alternative to meet the existing and growing demand for quinoa. Previous studies suggested goosefoot could produce comparable harvests to major agricultural crops (that is, wheat, corn, quinoa)[64]. Preliminary studies by Patton and Williams[41] indicate that an acre of native goosefoot could offer approximate yields of 1,152 lbs per acre of edible seed, compared to 450–1,070 lbs per acre of quinoa using similar methods[65]. Similar studies by Carmody suggest approximate yields of 1,597 lbs per acre of goosefoot seed or about 1,117 lbs per acre after processing. Re-establishment of ancient crop characteristics (that is, thinner seed coat, larger size, denser inflorescence, and so on) through selective breeding or genetic modification might improve upon on these yields.

Concluding thoughts

Although we have been aware of the EAC for over 50 years, we still know very little about how most of these plants were cultivated and their specific evolutionary pathways to domestication. We cannot draw on detailed historic or ethnographic descriptions to understand how they were cultivated because none exist, and so we have to rely on our own observations of living plants and experimental cultivation for insights into these methods and processes. We have described several challenges and new initiatives in reviving the experimental study of EAC crops as parts of complex, human-mediated agroecosystems. We are hopeful that in the next few years, these projects will bear considerable fruit, allowing us to better understand the historical ecology of this region and apply insights from the past to the contemporary problems of food and economic insecurity in rural America.

Received 3 January 2017; accepted 16 May 2017;
published 5 July 2017

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Acknowledgements
Funding and support for these projects was provided by the Arkansas Humanities Council, the National Endowment for the Humanities, Arkansas Archeological Survey, Arkansas State Parks, US National Science Foundation Doctoral Dissertation Improvement Grant #58292, the Wenner-Gren Foundation, the Lynne Cooper Harvey Fellowship in American Culture Studies at Washington University, the Sugar Bush Foundation, Voinovich School of Leadership and Public Affairs at Ohio University, and the College of Arts and Sciences at Ohio University. We would also like to thank D. Piperno for her thoughtful comments, and G. Stone for his suggestion that we write this Perspective.

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All authors contributed to writing this article.

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How to cite this article: Mueller, N. G., Fritz, G. J., Patton, P., Carmody, S. & Horton, E. T. Growing the lost crops of eastern North America's original agricultural system. *Nat. Plants* **3,** 17092 (2017).

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The authors declare no competing financial interests.