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Authors: Mueller, Natalie G., White, Andrea, and Szilagyi, Peter

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Experimental Cultivation of Eastern North America's Lost Crops: Insights into Agricultural Practice and Yield Potential

Natalie G. Mueller^{1*}, Andrea White², and Peter Szilagyi²

Abstract. Since the 1930s, archaeologists have been accumulating data on the lost crops of eastern North America. These are a group of annual plants (*Chenopodium berlandieri*, *Hordeum pusillum*, *Iva annua*, *Phalaris caroliniana*, and *Polygonum erectum*) that were cultivated by Indigenous societies for thousands of years. No published written or oral histories attest to the methods used in their cultivation, and their domesticated forms are thought to be extinct. The potentials and constraints of this agricultural system can only be reconstructed experimentally. We report two experiments designed to investigate germinability, phenology, and yield, which resulted in yield estimates for two of the lost crops, goosefoot (*Chenopodium* sp.) and erect knotweed (*Polygonum erectum*). A polyculture of these two crops is more productive than either grown as a monoculture, higher yielding than global averages for closely related domesticated crops, and comparable to yields for traditionally grown maize (*Zea mays*). We also report several novel insights into germination requirements and phenology for all five lost crops that contribute to a more accurate reconstruction of this crop complex. However, we failed to answer several of our research questions, and instead came away with many new questions. Obtaining seed is merely a necessary pre-condition for raising a crop. Without guidance from experienced cultivators, best practices must be developed over the course of many growing seasons. Experimentation with crop progenitors is necessary to fully understand the dynamics of ancient agroecosystems and their interaction with ecological knowledge systems.

Keywords: Eastern Agricultural Complex, domestication, polyculture, agroecology, traditional ecological knowledge

Introduction

In the 1930s, ethnobiologists Melvin Gilmore and Volney Jones pioneered the field of paleoethnobotany in North America. After analyzing collections of ancient plants recovered from rockshelters in Kentucky and Arkansas, they were the first to suggest the existence of lost crops in eastern North America—species that were once cultivated, of which no published historical or ethnohistorical record remains (Gilmore 1931; Jones 1936). Beginning in the 1960s, archaeologists in North America began to systematically recover plant remains by using water separation of soil samples from hearths, middens, and storage pits to capture tiny organic remains from the heavier soil matrix, a method

called flotation (Struever 1968). Within two decades of this methodological revolution, it became clear that a previously unknown crop complex had supported societies in eastern North America for millennia before maize (*Zea mays*) was adopted as a staple crop (Asch and Asch 1977, 1985a; Fritz and Smith 1988; Smith and Yarnell 2009; Yarnell 1972, 1978). Ongoing research in caves and rockshelters continues to make important contributions to this research, particularly by: 1) yielding exceptionally well-preserved specimens that can be examined for signs of domestication (Gremillion 1993; Mueller 2017a; Smith 1984, 1985; Yarnell 1972); 2) providing examples of unambiguous seed storage contexts, such as baskets and bags full

¹Washington University, Department of Anthropology, 1 Brookings Drive, Campus Box 1114, St. Louis, MO 63130.

²Cornell University, College of Arts and Sciences, Ithaca, NY.

*Corresponding author (ngmueller@wustl.edu)

of seeds (Fritz 1984, 1986, 1997); and 3) generating direct evidence of human consumption of the lost crops in the form of human paleofeces and intestinal contents (Gremillion 1996; Gremillion and Sobolik 1996; Robbins 1971; Yarnell 1969).

By the early 1990s, it was widely accepted by archaeologists that a diverse group of annual seed crops, now lost, had been cultivated and, in some cases, domesticated in eastern North America (Scarry 1993; Smith 1992). These crops are referred to as the Eastern Agricultural Complex (EAC) and include native squashes (*Cucurbita pepo* ssp. *ovifera* D.S. Decker); two spring-maturing grasses, maygrass (*Phalaris caroliniana* Walt.) and little barley (*Hordeum pusillum* Nutt.); two members of the Asteraceae, sumpweed (*Iva annua* L.) and sunflower (*Helianthus annuus* L.); goosefoot (*Chenopodium berlandieri* Moq.); and erect knotweed (*Polygonum erectum* L.) (hereafter referred to by their common names). Of these, only squashes and sunflowers are still cultivated. The other five crops fell out of cultivation at or just before the beginning of European colonization of eastern North America (Asch and Asch 1977). Researchers have documented the domestication of some of these lost crops by showing how the morphology of ancient seeds from archaeological sites differs from that of modern populations (Blake 1939; Hunter 1992; Mueller 2017a; Smith and Funk 1985).

Enormous progress has been made since the lost crops were discovered, but many unanswered questions remain. Because we do not have historical records, published oral histories, or living farmers to refer to, the only way to learn more about how these crops may have been encountered on the landscape and cultivated by ancient people is by observing and experimenting with their free-living¹ progenitors. When research on the lost crops began to expand in the 1970s, it was common for paleoethnobotanists to locate populations of these plants and make observations and collections from them.

Richard Yarnell (1978) made a particular study of sumpweed, studying harvests from free-living populations and even quantifying its responses to cultivation, the only such published study from that era to do so. Wesley Cowan (1978) used herbarium records to analyze the distribution of maygrass. Patrick Munson (1984) and his students published a volume documenting their surveys and experiments in Indiana, though some of the species they studied have since been ruled out as crop progenitors. David and Nancy Asch (Sidell) (1978, 1985a, 1985b) harvested maygrass, erect knotweed, and sumpweed, and studied the morphology of the seeds they collected. Bruce Smith (1992) harvested stands of goosefoot and sumpweed to estimate yield for both.

Since the publication of Smith's (1992) *Rivers of Change* nearly three decades ago, which synthesized much of this research on live plants and populations, very little has been written about the ecology or variation of the living lost crop progenitors. Moreover, with the exception of Yarnell's (1978) experiments with sumpweed, no one had published the results of their attempts to cultivate the free-living progenitors of the lost crops until recent experimental studies on erect knotweed (Mueller 2017b) and goosefoot (Halwas 2017). While harvests of free-living stands give us some idea of how productive the lost crops could have been, we have no practical knowledge of how cultivating these plants would have structured, constrained, or enabled the development of ancient human ecologies and economies. We can infer from the presence of extinct domesticates that ancient people did not limit themselves to harvesting from free-living stands that occurred naturally near their homes. The domestication syndromes (Harlan et al. 1973) of their crops attest to the fact that at some point they began saving and planting seeds. Additionally, at least one of the lost crops (maygrass) was cultivated far north of its native range (Fritz 2014). Creating

anthropogenic stands of these plants would have required ancient people to make a cascade of complex decisions about field placement and preparation, seed selection and treatment, and the timing of planting, tending, and harvesting their plants under varying conditions.

The magnitude and complexity of the knowledge required to successfully raise a crop—especially from non-domesticated seed stock—can only be appreciated by attempting it with a completely unfamiliar plant. It is impossible to fully understand the historical or political ecologies of ancient eastern North American societies without understanding the constraints and potentials of their agricultural system. Here, we report the results of one year dedicated to cultivating the five lost crops, which constitutes a first step toward this goal. We would like to stress that we do not think it is possible to fully reconstruct lost traditional ecological knowledge, both practically and because such knowledge is imbedded in cultural contexts to which we will never have access. The EAC was a multispecies community consisting of people, plants, symbionts, pests, and predators. While it is impossible to interact with the human members of this community, we can gain a better understanding of their role in this lost ecosystem through experiential learning among their crops.

The experiments reported here were focused on five questions:

1. How can germination of saved seeds be maximized?
2. How might the phenological events (germination, flowering, fruiting, senescence) characteristic of these species have shaped ancient agroecologies and the scheduling of agricultural labor?
3. What are the effects of polycropping and plant density on yield?
4. What range of yields per hectare can each species produce under cultivation?

5. Are yields under cultivation different than those that have been reported for free-living populations?

These questions were explored in two experiments that we conducted at Cornell University in Ithaca, New York, from January to December in 2018.

Effects of Simulated Winter on Germination

Unlike the seeds of most domesticated plants, the seeds of wild plants often require some treatment that mimics natural processes in order to germinate (Baskin and Baskin 2014). These treatments are referred to as seed stratification. We were limited to one growing season by the circumstances of the first author's employment, so we did not have time to establish a seed bank and rely on slow waves of germination. For some crops, the initial stages of domestication may have relied on the manipulation of such natural cycles of spontaneous germination (Smith 2011). However, the domestication syndromes of many of our annual seed crops reflect selective pressures that likely arose when ancient cultivators started to save and plant seed and stopped relying on pre-existing seed dispersal mechanisms and seed maturation in the soil (Harlan et al. 1973). To cultivate our species of interest on a large scale, it was necessary to first develop methods for preparing the seeds that would result in at least some germination as soon as we planted them. This very problem would have faced ancient farmers whenever they attempted to open new fields or expand existing populations. The pilot study we conducted to develop seed treatments for the main experiment is described in the Supplement (see first two sections and Supplement Table 1; Figure 1).

Phenology and Effects of Polycropping and Plant Density on Yield

The main experiment of the 2018 growing season was designed to test the effects of polycropping and plant density

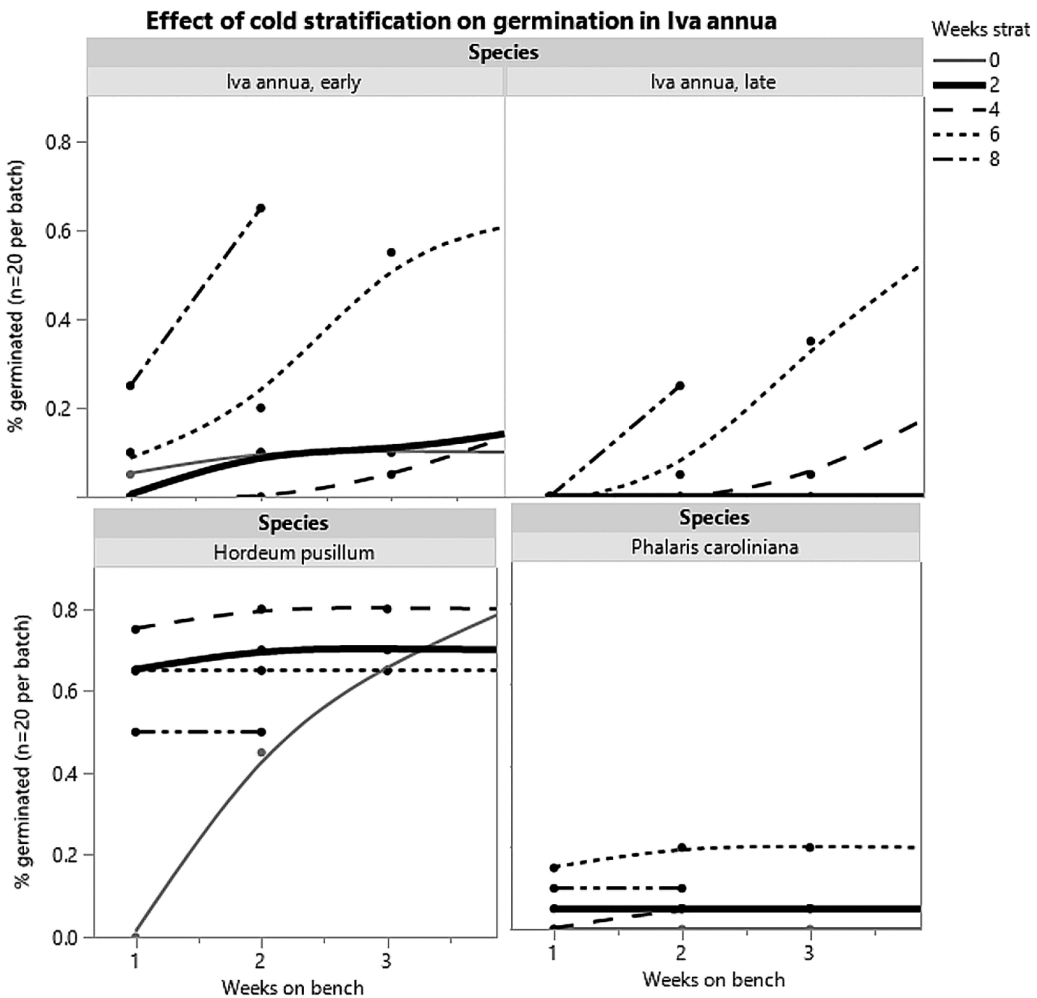


Figure 1. Results of cold stratification experiment, plotting the percentage of emerged seedlings against weeks on the mist bench. Each line represents results after a different length of cold stratification, from 0 weeks to 8 weeks. See Supplement for a discussion of methods and results.

on yield, while also collecting data on the life cycles of these five species. Historically, eastern Native American agricultural was a complex polycrop system (Fritz 2019; Mt. Pleasant 2011; Wilson 1917). Thus, although we have no record of how the lost crops were grown, it is most parsimonious to suppose that they were not grown in monocrop fields. Mueller's (2017b) experiments with erect knotweed showed that yield could be more than doubled if plants were grown at lower densities than are normally encountered naturally, suggesting that estimates of yield from harvests of

dense, free-living stands might not reflect yields under cultivation by knowledgeable farmers. If there are synergies or conflicts between these species or if increases in yield can be achieved by planting at lower densities or thinning naturally occurring stands, we assume that ancient farmers would have noticed over the course of thousands of years of cultivation. Our goal is to eventually reconstruct best practices for maximizing plant health, yield, and seed quality. This experiment is a first step towards that goal.

Methods

Using the insights gained from the exploratory germination experiment described in the Supplement, we began to prepare seed in late March. The timing of field clearance and planting was constrained by the exceptionally cold and snowy climate of Ithaca, New York. The average last frost-free day in Tompkins County, where Ithaca is located, is May 15th, so we began cold stratification of maygrass, erect knotweed, and sumpweed on March 29th, allowing at least six weeks for cold stratification. We subjected our goosefoot to a short, two-week stratification. We did not stratify the little barley seeds at all. Supplement Table 2 summarizes the provenience, seed treatment, amount of seed, and planting dates for each species.

The field was prepared by plowing and harrowing on April 27th, as soon as it was free of snow and adequately thawed. We used a randomized complete block design with three replicates for each species, for a total of 15 blocks, each of which was a 2x2 meter square. Seed batches were divided evenly by weight and planted by scattering and then pressing them into the loose soil with a tamper, which is a flat iron disk on a long pole. Each replication was subdivided into four treatments, each 1x1 meter: high, medium, and low-density monocrop, and polycrop. For the winter annual grasses, the polycrop treatment was maygrass and little barley, and for the summer annual forbs the polycrop treatment was goosefoot, erect knotweed, and sumpweed. It is possible that ancient farmers grew the summer and winter annuals together as polycrops, but we decided to isolate winter annuals and summer annuals from each other because we planned to harvest by uprooting entire plants to measure biomass. Uprooting the winter annuals in midsummer would have disturbed the summer annuals and altered the density of the plots in complex and unpredictable ways. The exact plant density for all treatments was recorded at harvest

and is summarized in Table 1. Throughout the growing season, we took data on phenology, pests, and plant growth once a week and weeded all other plants out of our test plots (but see Supplement section *Chenopodium Caveats*).

Harvests were conducted when plants had senesced or, in the case of erect knotweed and some goosefoot plants, when the first heavy snow was imminent. Harvest date(s) can be found in Table 1. For goosefoot, it was necessary to conduct three separate harvests because of variation in plant phenotypes: some plants senesced weeks before others (Table 1). For comparisons of yield, all goosefoot harvests are combined for each treatment. We hoped that these phenotypes would neatly segregate into species based on seed morphology, but this was not the case: all harvests contained low levels of honey-comb pitted seeds (see Supplement section *Chenopodium Caveats*). Plants were harvested by uprooting the entire plant and hand stripping the seeds over a tarp. Subsequently, the stripped plants were dried in paper bags for at least three days, then the remaining seeds were stripped again. Large chaff (stem fragments and adhering leaves) was removed from the seed by rubbing harvests on wire mesh, then sieving. This chaff was combined with the stripped plants for biomass weight (minus seeds/fruit). Seeds were then dried on a custom drying rack above a heat fan for three days. After drying, seeds were frozen (-4 °C) for four weeks to kill any remaining pests.

Large leaves and branch fragments were removed by sieving, but the seed was not thoroughly threshed and winnowed at this stage, complicating comparisons with modern crops. We know, from assemblages of stored seeds in rockshelter and caves, that ancient people had developed tools and methods for cleaning the seeds of these species very thoroughly. In order to make a more realistic comparison for the purposes of this analysis, we built a

Table 1. General experiments: Summary of phenology, harvest date(s), density, and yield.

Species	Emergence noted	Flowering (range)	Fruiting (range)	Senescence (range)	Harvest date	Treatment	Mean density (plants/m ²)	Mean yield (g/m ²)	Estimated mean yield (hg/ha)
<i>Hordeum pusillum</i>	May 24	June 29–Oct 31	July 3–Nov 11*	Alive as of May 2019	July–Nov	Mono	153	---	---
						Poly	199	---	---
<i>Phalaris caroliniana</i>	May 30	June 12–Oct 31	July 3–Nov 11*	Aug 1–Nov 11*	July–Nov	Mono	11	---	---
						Poly	10	---	---
<i>Chenopodium</i> sp.	June 8–Sep 19	July 25–Oct 17	Aug 15–Nov 11	Sep 19–Nov 11	Oct 5–7	Mono	104	74 +/-31	7400 +/- 3110
					Oct 30	Poly	56	106 +/-48	10600 +/-4750
					Nov 11				
<i>Iva annua</i>	June 25–August 15	Sep 19–Oct 3	Sep 26–Nov 7	Oct 31–Nov 7*	Oct 22	Mono	1	---	---
						Poly	1	---	---
<i>Polygonum erectum</i>	June 8	June 22–Oct 31	July 3–Nov 11	Nov 6–Dec 15*	Nov 7^	Mono	41	83 +/-30	8300 +/- 3000
						Poly	34	38 +/- 30	3800 +/-3000
Polycrop combined						Poly	92	143 +/-42	14300 +/-4200

*Last formal observation of the plants.
+End of range beyond harvest based on observation of plants of the same species in other experiments in the same field.
^Three of nine replications were harvested on Oct 24, see “Variability in yield,” in Results section for discussion.

small seed vacuum winnower based on an open-source plan by Real Seeds². We threshed and winnowed all batches of erect knotweed and goosefoot by rubbing against wire mesh and between gloved hands, then running the batches through the winnower at least four times. Sieving, threshing, and winnowing took approximately 60 woman-hours, roughly three times the amount of time it took to harvest. To estimate yields in terms that could be compared to other crops, we first extrapolated hectograms per hectare (hg/ha) from our measurement of kilograms per square meter (kg/m²). Ultimately, we had adequate germination and reproduction in two species (erect knotweed and goosefoot) to estimate yields. For yield comparisons, we first ran an ANOVA to ascertain if variances were significantly different. If they were not, we used a two-tailed t-test. If variances were significantly different, we used a Welch's t-test to compare means. Analysis was conducted in JMP and results are presented as p-values in text.

Results

Winter Annual Grasses

Failure to reproduce (little barley) or poor germination (maygrass) prevented us from obtaining yield data on these species, but we nonetheless gained several insights into the logistics of their cultivation. Both the little barley and the maygrass germinated despite being planted in early May, when both would normally be fully mature plants. Their life cycles continued to be extraordinary throughout the growing season (Table 1). The little barley quickly formed a dense and homogenous mat that rarely needed to be weeded (Figure 2A-B). Very few of them ever flowered or produced seed—in some replications, no plants did so. The little barley also never senesced in the fall. Surprisingly, as of May 4th, 2019, a full year after planting, these little barley plants were still alive and looked much the same as they had since midsummer of 2018

(Figure 2B). That mature little barley can overwinter in western New York is unexpected because: 1) little barley in an annual plant that normally senesces in early summer after an approximately seven-month life cycle; and 2) it occurs less commonly in the northern Plains and the northeast than in the rest of the country, which made us think it might be somewhat cold sensitive. According to the United States Department of Agriculture Plant Guides, domesticated winter barley varieties (*Hordeum vulgare*) are sensitive to extreme cold and cannot survive temperatures below -8 °C, which regularly occurred in Tompkins County over the winter of 2018-19. Little barley is thus significantly hardier than its eastern hemisphere cousin.

These results strongly suggest that ancient farmers could have planted this species in autumn without being concerned about cold sensitivity, and that obtaining a second crop in the summer or fall would not have been possible unless domesticated populations with different photoperiodism existed. Little barley germinates readily with no seed treatment and quickly forms a near-impermeable mat. Of the five species, it was the only one that was able to compete with field weeds like *Digitaria* sp. and *Plantago* sp. without our assistance in this seed bed setting (Figure 2A-B). For ancient farmers, it may have served the dual purpose of providing grain in the spring and keeping fields clear of other, more troublesome plants before the summer annuals were established.

Germination of maygrass was very low and the plots required considerable labor to keep them free of competing weeds (Table 1). The maygrass plants growing among the dense little barley appeared to be just as healthy as those in monocrop plots and the polycrop plots required a lot less labor to keep clear, suggesting that this polycrop treatment warrants further investigation. Flowering and fruiting of maygrass occurred almost two months later than it does in populations Mueller has observed

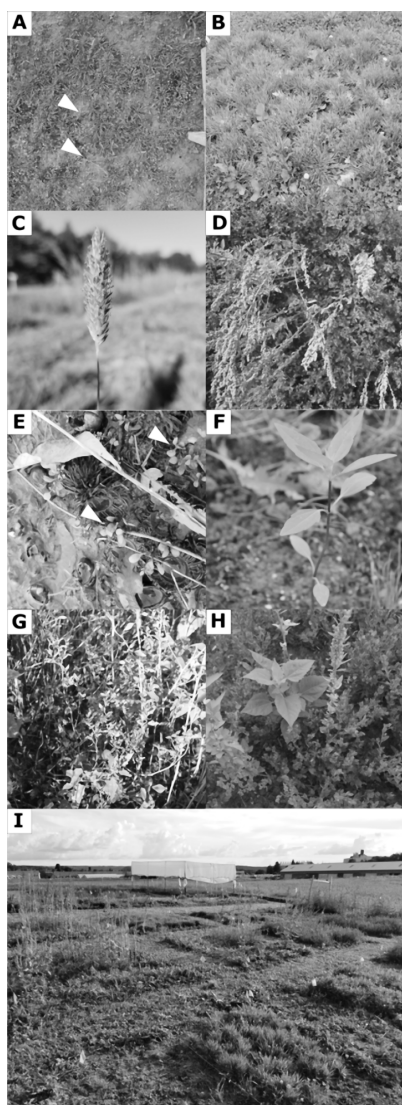


Figure 2. **A)** A representative little barley/maygrass polycrop treatment on July 3, arrows pointing out two maygrass plants; **B)** the same plot as (A) in May 2019 after overwintering; **C)** “resurrection maygrass,” inflorescence, sprouted from seemingly senesced plant, flowering on September 16; **D)** a representative goosefoot and erect knotweed polycrop treatment on September 12, with erect knotweed in the understory and flowering goosefoot plants in foreground; **E)** sumpweed seedlings (pointed out with white arrows) emerging in standing water in Arkansas on February 24, 2019; **F)** late summer sumpweed seedling in our experiment, August 22; **G)** erect knotweed growing in the understory of goosefoot and sumpweed in Kentucky, October 9, 2017; **H)** goosefoot, sumpweed, and erect knotweed polycrop in our experiment, August 22; **I)** A view of the entire experimental area, September 16, 2018.

in Arkansas, Mississippi, and Missouri: we harvested most of the seeds at the end of July (Table 1). We expected this delay, given the late planting and the fact that the experiment was located almost 4° of latitude north of the northern extent of maygrass’ natural range in west-central Missouri.

After we harvested the mature seed heads at the end of July, most of the maygrass plants appeared to be senescing but, by the end of August, they had started to flower again (Figure 2C). We referred to this phenomenon as “resurrection maygrass,” and obtained just as much seed from this second round of reproduction as from the first. These results suggest that, unlike little barley, maygrass could have been grown as a winter or summer annual, and that it may have been possible to obtain more than one harvest from the same plants in a growing season, as has been suggested previously (Cowan 1978). This, perhaps, explains why maygrass is found at archaeological sites far north of its natural range (Fritz 2014): if it could not be planted as a winter annual because of cold sensitivity, it could have been grown as a summer annual instead in these regions. However, we have not yet investigated the winter hardiness of maygrass planted in the fall, so this remains an open question.

Summer Annual Forbs

Sumpweed

Germination of sumpweed was very low (Table 1). We had at most three plants in a treatment, and many treatments had no plants. As a result, we do not provide an estimation of sumpweed yields and, in the following discussion, “polycrop treatment” refers to erect knotweed and goosefoot, rather than all three species. We suspect that the poor germination of the sumpweed was due to lack of adequate and consistent soil moisture in the spring. A sump is defined as a hollow or depression where water collects. As the common name suggests, this species is often found in seasonal wetlands and floodplains (Asch

and Asch 1978; Yarnell 1978). Mueller has only observed sumpweed in dense stands growing on riverbanks, backwater lakes, bison wallows, or in dry creek beds or ditches that are sometimes flooded, and it can survive complete inundation as a seedling (Figure 2E). Our experiment was conducted on top of a hill, and we suffered a late spring drought. Lending further support to this explanation, during an uncommonly wet August and September, we observed several sumpweed seedlings germinating in our plots (Figure 2F).

Goosefoot and Knotweed

We were able to obtain yield data for two of the five species from the experimental plots: erect knotweed and goosefoot. Our polycrops were inspired by the association of some free-living populations of these plants, such as those pictured in Figure 2G. The comparison between monocrop and polycrop treatments at first suggests a trade-off for ancient farmers: for goosefoot, yields were higher in the poly-

crop treatments (though not significantly so, two-tailed t-test, $p = 0.112$), whereas, for erect knotweed, they were significantly higher in the monocrop treatments (two-tailed t-test, $p = 0.005$; Figure 3). This is probably because these species have very different growth habits. Goosefoot usually has few lateral branches and the maximum plant height per treatment averaged 1.24 m by late summer. Erect knotweed is highly branched and its average maximum plant height by later summer was only 0.43 m (measurements for the week of September 19, see also Figure 2D,H). Thus, by the time these plants are producing seed, goosefoot plants are not competing for light with erect knotweed, but benefit from erect knotweed crowding out the seedlings of tall plants that could otherwise compete. Erect knotweed, on the other hand, is shaded by goosefoot, especially late in the season. If the seeds of both crops were considered equally desirable, or if goosefoot was more desirable than erect knotweed, then there was no trade-off: the polyculture was significantly

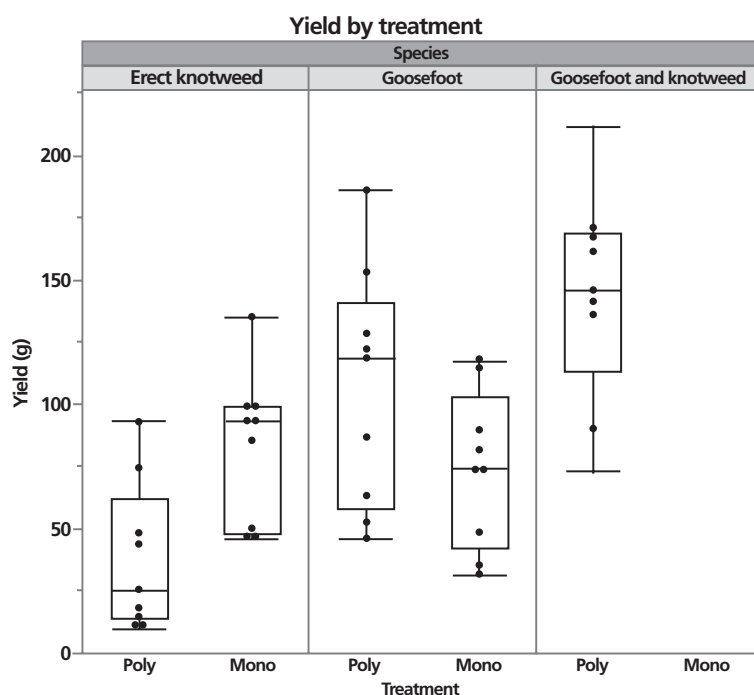


Figure 3. Boxes visualize the median and interquartile range. Comparison of yields by treatment. Each point represents the yield for one 1 m² replication.

more productive than either monocrop overall (Welch's t-test, $p = 0.003$; Figure 3). The polycrops were also easier to maintain than goosefoot alone, and about the same amount of work as erect knotweed alone, because erect knotweed (like little barley) tends to crowd out other plants once it is established (Figure 2A, D, H).

The results of our analysis of the effects of plant density on yield were less dramatic. In the monocultures, plant density was not strongly correlated with goosefoot yield, at least not at the relatively low densities (compared to natural stands) that occurred in our experiment ($R^2 = 0.06$). The relationship between yield and density is much stronger in monocrops of erect knotweed ($R^2 = 0.70$): replications with more plants were consistently higher yielding, with the densest plot (70 plants/ 1m^2) yielding the most seed. This result is somewhat surprising, since a previous experiment with erect knotweed indicated that lower density planting increased yield (Mueller 2017b). We can only surmise that plant densities in our experiment did not reach levels at which crowding would begin to depress yield and, thus, variation in yield was caused by other factors. If this is true, then it might be possible to achieve higher yields by increasing plant density above the maximum densities in these experiments for these two species. There was no apparent relationship between overall plant density and overall yield in our polycrop treatments ($R^2 = 0.0002$). This is likely influenced by the fact that goosefoot seed makes up more of the total seed mass in these plots and there was less of an effect from density on goosefoot yields.

Yield Comparison with Free-Living Plants

We compared our yields to those reported by Smith (1992) for free-living goosefoot and found that cultivated goosefoot was, on average, slightly higher yielding than Smith's free-living harvests. The mean estimated yield for all of Smith's populations ($n = 15$) was 8833 hg/ha, while

the mean estimated yield for our experiment was 9005 hg/ha. Neither variances nor means were significantly different (ANOVA, $p = 0.927$; two-tailed t-test, $p = 0.923$). However, if we break down Smith's data further, it becomes clear that cultivated populations and free-living populations occupying certain kinds of anthropogenic environments are consistently higher yielding than free-living populations occupying other kinds of habitats. We have made an attempt to group yield estimates from Smith's (1992) survey locations into habitat types that may be illustrative (Figure 4). One single plant is an outlier with respect to both datasets. This is Smith's #91, a single plant that he found growing in a "creek bottom vegetable garden" (Smith 1992:169) in Pike County, Ohio in November of 1985. This was a very large and highly branched individual, occupying a 1.5m^2 area. The next six highest yield estimates all come from plants occupying newly created dirt piles or growing along roadsides, situations that mimic a clearing created purposefully by a cultivator. The lowest yielding populations are from the most naturalistic settings: vacant lots, overgrown fields, riverbanks, and floodplain forests. The main advantage we gave our cultivated plants was relief from competition with other plants by constant weeding. The data from the free-living plants supports the conclusion that this simple (though time consuming) activity makes a difference in terms of yield. Additionally, the lowest yielding of Smith's (1992) populations came from the understory of a floodplain forest. Both Smith (1992) and Mueller have frequently found goosefoot growing in partial or full shade. However, the creation of clearings large enough to grow plants in full sun seems to be necessary to achieve high yields for this species.

Yield Comparison with Domesticated Crops

Why were the lost crops abandoned? This question is unresolved, but one possi-

ble answer is that when locally adapted maize landraces were developed by farmers in eastern North America, they were much higher yielding than the lost crops. We compared our estimated yields to data from a previous study on maize yields using traditional landraces and agricultural methods. In this study, an open-pollinated white flour corn, obtained from a Kanien’kehá:ka (Mohawk) seed keeper, was cultivated by hand in mounds using methods that were common across much of eastern North America when European colonists arrived (Mt. Pleasant 2015). This maize was grown at different densities as either a monocrop or in the traditional three sisters polycrop (maize, beans, and squash) in two different soil types near Ithaca, New York (Mt. Pleasant and Burt 2010). Yields reported in this study were converted from bushels/acre to hg/ha, assuming 56 lbs/bushel, a

standard conversion, for comparison to our data. The mean yield for goosefoot and erect knotweed in our polycrop treatment is significantly lower than that for traditionally grown maize (Welch’s t-test, $p > 0.001$), but, surprisingly, the ranges overlap (Figure 5).

Is there any reason to pursue the re-domestication of the lost crops? Quinoa (*Chenopodium quinoa*) and buckwheat (*Fagopyrum esculentum*) are the extant crops that are most closely related to goosefoot and erect knotweed, respectively. We obtained the most recent global average yield data for these crops from the Food and Agriculture Organization of the United Nations (FAO 2019), in order to gain a rough idea of the potential of the lost crops by comparison (Figure 5). The average yield for buckwheat was somewhat higher than the average yield for erect knotweed, while the average yield for quinoa

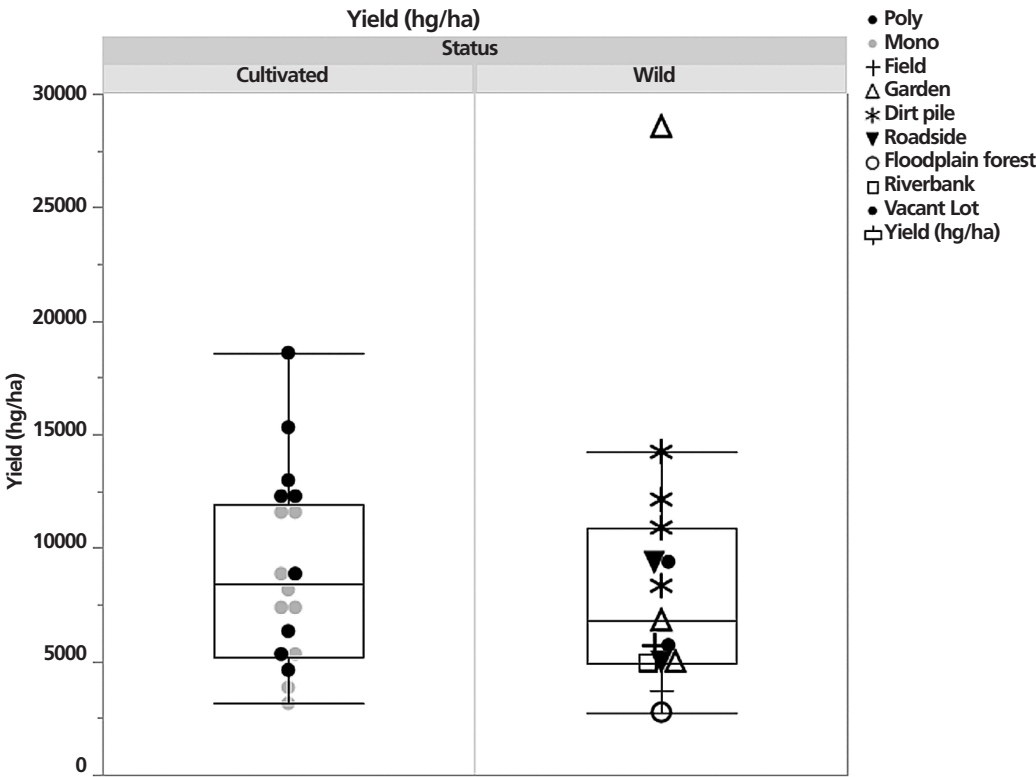


Figure 4. Boxes visualize the median and interquartile range. This figure uses data reported in Smith (1992:Table 7.2) to compare yields from free-living (uncultivated) goosefoot to those from our experiment.

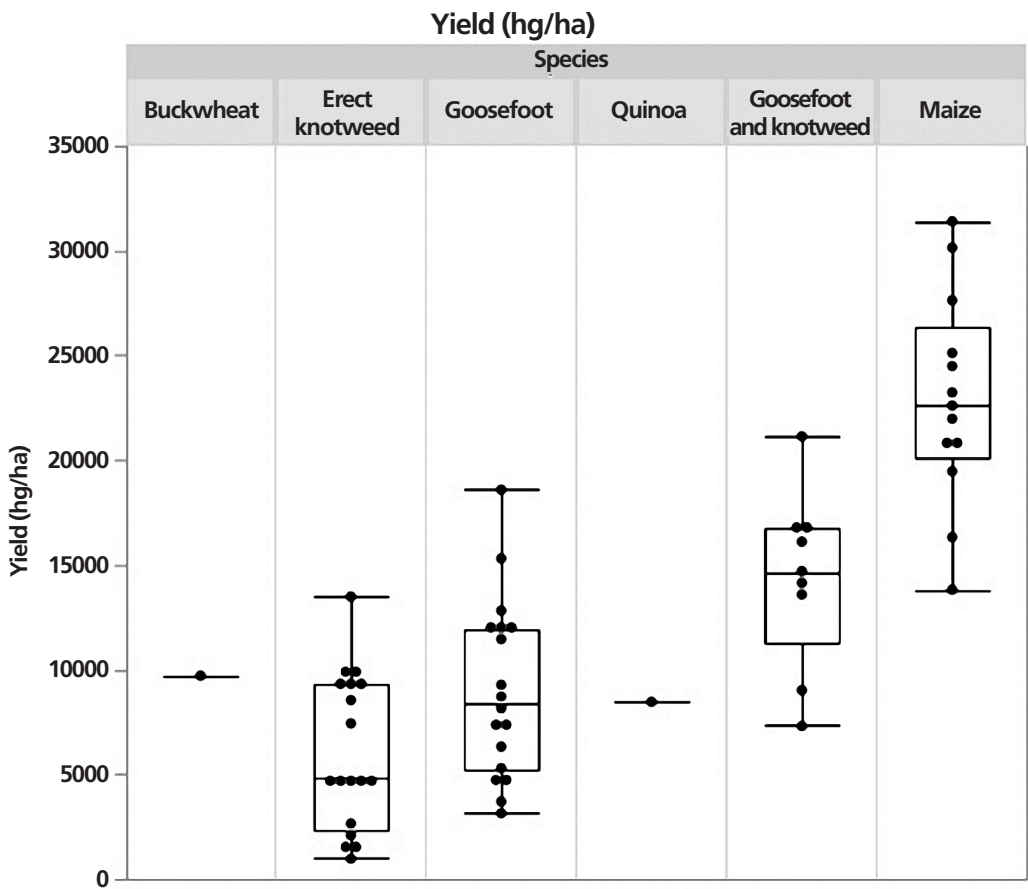


Figure 5. Comparison of monocrop and polycrop treatments in our experiment with domesticated crops. Boxes visualize the median and interquartile range. Values for buckwheat, quinoa, and sunflower are global averages for 2017 from FAOSTAT (FAO 2019). Maize yields are from Mt. Pleasant and Burt (2010), converted from bu/acre assuming 56 lbs/bushel.

was almost identical to our extrapolated yields for goosefoot.

Variability in Yield

A glance at the yield columns in Table 1 reveals that yields for erect knotweed and goosefoot in our experiment were quite variable between replications. To take the most extreme example, the mean and standard deviation for erect knotweed yield within polycrop treatments are nearly equal. We need more data to more accurately estimate mean yield, especially because we are extrapolating from small areas to large areas, which increases any small error in the mean enormously. Because of the small sample size, our current means are influ-

enced by possible outliers. For example, we harvested erect knotweed from three of the polycrop treatments two weeks earlier than the rest of the erect knotweed plants (Oct 24 vs. Nov 7). These were three of the four lowest yielding erect knotweed replications overall. We include these data in our analysis because they represent possible outcomes of cultivating erect knotweed (if you harvest it too soon), but we do not think such yields would have been typical for knowledgeable cultivators. Similarly, Halwas and Worley’s (this issue) common garden experiments with goosefoot revealed that garden placement is an extremely important variable determining yield. In this experiment, one garden site

had an average yield of 261 hg/ha, an order of magnitude lower than our yields, while the other garden averaged 13,253 hg/ha, higher than our average for polyculture plots (Figure 4). Considerations of yield and knowledge of these species' reaction norms to different growth environments would have shaped decisions about where to live and where to grow crops, as well as how to schedule yearly labor.

Discussion

Implications for Agricultural Practice in Eastern North America

Here, we briefly summarize novel insights into ancient agricultural practice gleaned from this study:

1. The assumption that these crops would have been grown as polycultures, which, until now, has been based upon analogy with historical Native American crop systems and the presence of mixed assemblages of these species in storage contexts in the archaeological record, is also supported by our data. A polyculture of goosefoot and erect knotweed produces more food in the same area than either of these crops can produce when grown alone. Polycultures of maygrass and little barley and of goosefoot and knotweed were easier to maintain than monocultures of maygrass or goosefoot, because little barley and erect knotweed form closed canopies that reduced new seedling germination (Figure 2A, D). In both cases, this is similar to the later three sisters polyculture, in which squash was used to reduce weed pressure around mounds containing maize and beans. There are many possible permutations of polyculture within this agricultural system that remain to be investigated.
2. Seed treatments are necessary to induce germination in sumpweed, erect knotweed, and maygrass. For ancient cultivators to introduce these species to newly opened fields or gardens, they would have needed to either understand their germination requirements or possess domesticated varieties that germinated more readily. It is possible that germination inhibitors were reduced or eliminated by cultivation of pre-existing populations before farmers started to open new fields. But if people did expand populations of plants with wild-type germination inhibitors, then their recalcitrance could presumably be overcome by planting seed in the fall or late winter, although this would expose planted seeds to a host of risks, including pathogens, predation, and removal by spring floods. Another option would be to intentionally place seed stock in a cold, moist location during the winter, as we did in our germination experiment. There is ample archaeological evidence that seeds were sometimes stored in subterranean pits (Powell 2000). In at least two cases, this storage method resulted in the sprouting of ancient erect knotweed fruits (Mueller 2017c). The evolution of uniform and immediate germination in domesticated annuals is perhaps the single most important domestication trait from a logistical standpoint, and has received less attention in the archaeological record than changes in seed dispersal (e.g., shattering) and seed size.
3. Little barley is winter hardy even at high latitudes, and produces very few seeds when planted in the spring. We conclude that it was likely an obligate winter annual and that ancient farmers would have planted it in the late autumn. However, we did have a few plants

that produced seeds even when planted in the late spring. These rare variants could have been selected by ancient farmers to develop populations of little barley that could be grown as summer annuals.

4. Our observations of maygrass indicate that it could be grown as a summer annual if seed treatments to induce germination were better understood. Our maygrass plants also produced a second crop of seeds in the fall, which has never been observed in free-living populations, but might have been typical of cultivated maygrass in ancient fields.
5. The germination rate for sumpweed seeds was very low in our hilltop field during an unusually dry spring. Coupled with Mueller's observations of free-living and cultivated populations elsewhere, this suggests that sumpweed must be cultivated in soil that is consistently wet during the late winter and spring. Ancient cultivators may have been constrained in their choices of field placement for this crop to low, swampy, or seasonally inundated locations, as the common name suggests. This requirement may have prevented ancient farmers from growing sumpweed in polyculture with others of the lost crops. Alternatively, this limitation could have provided an opportunity for selection under cultivation, where more drought tolerant individuals were selected to develop populations that could be grown in dry fields or gardens with the other members of the crop complex.

Yield Potential of the Lost Crops

It is truly remarkable that the yields of two non-domesticated species are comparable to the average yields for their most

closely related crop relatives. Equally surprising, the productivity of goosefoot and erect knotweed grown in polyculture is higher than the average productivity of either buckwheat or quinoa, and our range of yields for this polyculture overlaps with the range of productivity of traditionally cultivated maize, one of the highest yielding crops. In assessing the import of these results, it is important to keep in mind that we were completely inexperienced in the cultivation of these species, to the extent that we were only successful enough in our first year to obtain any yield data for two of the five species we attempted to cultivate. We did not grow sunflower or native eastern North American squashes, two other members of the pre-maize crop complex. In other words, our polycrop yield estimate reflects less than one third of the potential yields of this crop system, before the domestication of any of these species, when cultivated by total neophytes with no guidance from expert farmers. We also experienced a very difficult growing season. The following summary draws from US National Climate Report for 2018 (NOAA 2019). The coldest April in the past 20 years, coupled with the largest area of snow cover in the contiguous United States, prevented us from preparing the field or planting until well into May. This was followed by record-breaking heat and below average precipitation in May and June, when the seeds were germinating and the seedlings were most vulnerable. October was the sixth wettest on record, and November precipitation was well above average in New York state. This delayed the senescence of the plants and made harvesting and drying seed challenging. The combination of our lack of skill and the unfavorable weather makes us very confident that these yields can be improved upon significantly in future experiments.

With respect to the comparison with maize, it is clear that as a single crop maize has the potential to be more productive than cultivated, non-domesticated erect knot-

weed or goosefoot, but not massively so. In the hands of more skilled cultivators, it is possible that either of these lost crops could have been as productive as the maize landraces available to ancient farmers. When maize arrived in eastern North America, it was likely not as productive as the landrace used by Mt. Pleasant and Burt (2010), which had benefited from an additional millennium of selection by farmers in this region, while, by that time, farmers already had developed domesticated subspecies of erect knotweed and goosefoot that were presumably more productive and/or easier to cultivate than the free-living populations we grew. Of course, the Native American crop systems that replaced the EAC were not maize monocultures, and also included yields from other crops. Mt. Pleasant and Burt (2010) concluded that, even though their monocultured maize was slightly higher yielding than the maize grown in the polyculture treatments, the three sisters polyculture was higher yielding overall than maize alone. Still, our data calls into question explanations of EAC abandonment that rely on the assumed, but never demonstrated, vast superiority of maize over previous crops—at least in terms of yield. It is certainly possible that maize was easier to harvest, process, or cook, or that it was simply considered tastier.

Turning to the comparisons with quinoa and buckwheat, the fact that non-domesticated plants are capable of producing yields comparable to their domesticated relatives complicates many of our assumptions about the importance of domestication to the development of early agriculture. These results suggest that the practice of cultivation may have been more important than the presence of domesticated seed stock for increasing food supplies at the dawn of agriculture. The higher yields of cultivated goosefoot and goosefoot in gardens and openings, compared to goosefoot in more naturalistic settings, also suggest that simply attending to wild plants can increase yield significantly, before any

selection for domesticated populations has occurred. These results testify to the deep ecological knowledge of ancient Indigenous people, who domesticated two such productive plants from the thousands of seemingly similar candidates. As *de novo* domestication becomes an increasingly popular idea for addressing food insecurity and adapting to climate change (Zsögön et al. 2017), it would be a terrible waste not to first consider plants that were domesticated by such knowledgeable actors and successfully grown as crops for thousands of years.

Direction for Future Research

Although these experiments have yielded many insights into the potential of these species as crops, we failed to answer several of our initial research questions. We did not obtain yield estimates for maygrass, little barley, or sumpweed, and we were not able to discover effective seed treatments to induce germination in maygrass and goosefoot. We did not assess the effectiveness of planting seeds at different times of the year. Without these data, our reconstructions of the yield potential and yearly schedule of this agricultural system remain incomplete. It is not surprising that we were unable to master the cultivation of these five species in one year. Agriculture is a highly complex knowledge system, and farmers add and remove new species from their farms with care and small-scale experimentation. It is unlikely that any ancient person ever obtained the seeds of these five crops from the wild and started growing them all together the next year. The archaeological record indicates that this agricultural system coalesced gradually, beginning around 4000 years ago, with the domestication of squashes, sunflowers, sumpweed, and goosefoot, and culminated in a highly diverse crop complex, including the other three lost crops, by around 2000 years ago (Mueller 2018). Before any of these plants entered a field system like ours (if they ever did), they were likely observed, harvested, and encouraged in

their natural habitats for many years, if not centuries. Our experiences also suggest that obtaining seed is merely a necessary pre-condition for raising a crop. Without guidance from experienced cultivators, success is not likely and best practices need to be painstakingly developed over the course of many growing seasons. Thus, the movement of knowledgeable people likely accompanied any successful movement of crops across ancient landscapes.

We stress this difference in our experience versus the experience of ancient cultivators for two reasons. First, the conclusions of this paper, especially our reports of yields and qualitative remarks on labor, should not be taken as representative of the experiences of ancient farmers with these plants. It would be very surprising if they were not able to achieve greater yields with less effort, given the disparity in knowledge between us and them. Second, we would like to encourage more widespread experimentation with these and other crop progenitors. Every interaction we have had with these plants has raised new and fruitful questions about the process of domestication, the dynamics of agroecosystems, and the lived experience of early farmers.

Notes

¹ In the context of this study, free-living denotes not intentionally cultivated (Wilson 1990). Following Wilson, we use free-living rather than wild for two reasons: 1) we do not know if free-living populations are truly wild or partly or wholly feral descendants of cultivated populations; and 2) these plant populations are growing in anthropogenic ecosystems. Within the mid-continental core area where these crops were once grown, and where these surveys were conducted, there are arguably no non-anthropogenic ecosystems. ² <http://www.realseeds.co.uk/seedcleaner.html>.

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