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RESEARCH ARTICLE

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Evidence for human-caused founder effect in populations of *Solanum jamesii* found at archaeological sites: I. Breeding experiments and the geography of sexual reproduction

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Abstract

Premise: Plant domestication can be detected when transport, use, and manipulation of propagules impact reproductive functionality, especially in species with self-incompatible breeding systems.

Methods: Evidence for human-caused founder effect in the Four Corners potato (*Solanum jamesii* Torr.) was examined by conducting 526 controlled matings between archaeological and non-archaeological populations from field-collected tubers grown in a greenhouse. Specimens from 24 major herbaria and collection records from >160 populations were examined to determine which produced fruits.

Results: Archaeological populations did not produce any fruits when self-crossed or outcrossed between individuals from the same source. A weak ability to self- or outcross within populations was observed in non-archaeological populations. Outcrossing between archaeological and non-archaeological populations, however, produced fully formed, seed-containing fruits, especially with a non-archaeological pollen source. Fruit formation was observed in 51 of 162 occurrences, with minimal evidence of constraint by monsoonal drought, lack of pollinators, or spatial separation of suitable partners. Some archaeological populations (especially those along ancient trade routes) had records of fruit production (Chaco Canyon), while others (those in northern Arizona, western Colorado, and southern Utah) did not.

Conclusions: The present study suggests that archaeological populations could have different origins at different times—some descending directly from large gene pools to the south and others derived from gardens already established around occupations. The latter experienced a chain of founder events, which presumably would further reduce genetic diversity and mating capability. Consequently, some archaeological populations lack the genetic ability to sexually reproduce, likely as the result of human-caused founder effect.

KEYWORDS

Bears Ears, breeding system, Chaco Canyon, Escalante, founder effect, Four Corners potato, Mesa Verde, self-incompatibility, trade routes

The persistence of plant populations in fluctuating environments can depend on sexual and asexual mechanisms of reproduction. Environmental change, especially under extreme conditions of drought, temperature, and disturbance (e.g., herbivore pressure) often requires the production of diverse genotypes by means of sexual recombination (Grime, 1977; Barrett and Eckert, 1990; Goodwillie et al., 2005). Breeding systems that promote outcrossing between distinct individuals are thought to have been essential to the evolution of long-lived, geographically widespread and ecologically

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diverse taxa (Darwin, 1859; Stebbins, 1974; Karron, 1991; Silva and Goring, 2001). Under relatively stable or spatially homogenous environments, however, asexual production of ramets in the form of rhizomes, bulbs, and tubers would have competitive advantages for well-adapted genotypes, circumventing the uncertainties associated with establishment from seed when resources are limited (Grime, 1977; Silvertown, 2008; Munoz et al., 2016). Plant taxa that possess both mechanisms, such as members of *Solanum*, *Oryza*, *Dioscorea*, *Lathyrus*, *Oxalis*, *Vigna*, and Triticeae are among the most widespread, speciose, and agriculturally significant on earth.

Humans have intervened in the genus *Solanum*, taking advantage of its incredible variation among and within 111 tuber-forming species and countless landraces (Spooner et al., 2014). That variation has arisen by means of hybridization, polyploidy, and selection across vast continents, aided by an outcrossing mechanism that requires alternate forms of the *S* mating gene (Camandro et al., 2004; Dzidzienyo, 2016), as well as additional pistil and pollen factors that can inhibit pollen tube growth if two genotypes are thusly similar (Newbigin, 1993; McClure and Franklin-Tong, 2006; Lindhout et al., 2017). This gametophytic self-incompatibility (GSI) requires a population gene pool containing multiple *S* alleles and a full array of pollen and pistil factors to produce seed-containing fruits. As humans had more interest in asexual, calorie-rich tubers rather than sexual seeds, the harvest, transport, and propagation of the former could lead to reductions of the latter, especially in and around agricultural settlements (Eckert et al., 2009). Loss of the genetic variation required for sexual reproduction would be compensated by stable and favorable growing conditions for consistent and productive clonal strains. Consequently, seed-bearing fruits would become rare even in large "populations" as GSI negated pollen movement between fully functional flowers.

The Four Corners potato, *Solanum jamesii* Torr. (Solanaceae), is one of two tuber-forming members of the genus found in the southwestern United States. It is abundant across the Mogollon Rim of central Arizona and New Mexico (Figure 1) after monsoonal storms and is almost continuously distributed among pinyon and juniper trees in some locations (Kinder et al., 2017). Collections from this region are known to be genetically rich, with high proportions of heterozygotes and unfixed loci (Bamberg and del Rio, 2004; Bamberg et al., 2016). But northward, crossing the arid tributary basins of the Colorado River and into southern Utah and southwestern Colorado, *S. jamesii* becomes largely confined to canyon bottoms, floodplains, and slickrock drainages associated with archaeological sites (Yarnell, 1965; Kinder et al., 2017). In some cases, the association is directly with archaeological features, such as long-abandoned rock shelters, Puebloan houses, terraces, and pottery sherds. In at least one case, the association has been shown to be incredibly ancient, with starch granules extracted from grinding stones in archaeological deposits dating back 10,900 years (Louderback and Pavlik, 2017).

Although it is apparent that people have used the Four Corners potato for millennia (Louderback and Pavlik, 2017), it is not clear whether they were exploiting natural populations or decisively interacting with the species by creating outposts as reliable, local sources of food, medicine, and ceremony. Such interaction would have genetic and phenotypic consequences,

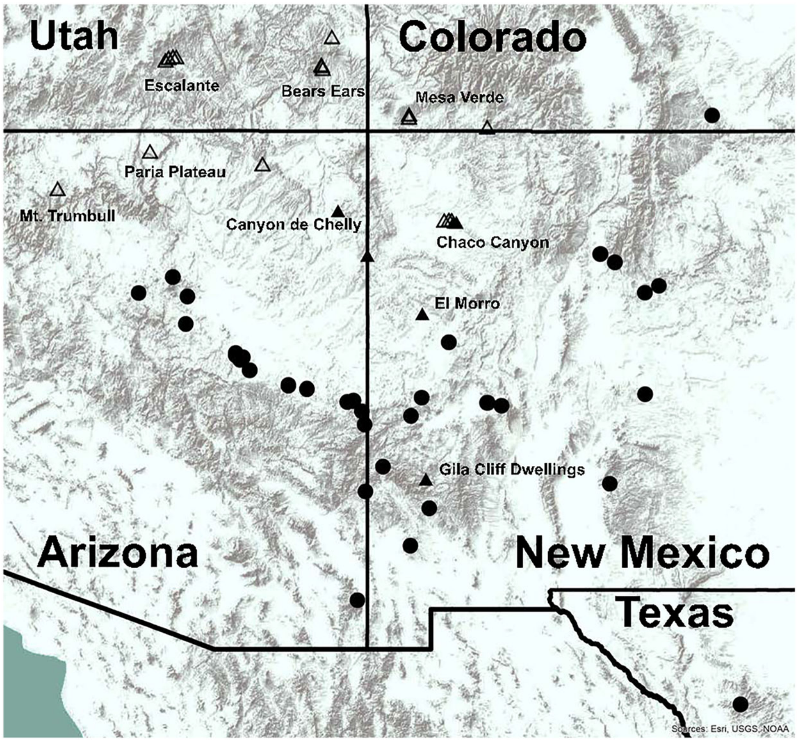

FIGURE 1 Location of *Solanum jamesii* occurrences associated with archaeological sites (triangles) and non-archaeological (circles) sites. Those observed to produce fruit are solid symbols, those without open symbols

especially if tubers had been transported and traded across the range of the species. Any one handful or satchel collected from a source population, even at the center of the range, would only contain a fraction of the genetic variation, especially if only one or a few clones were "sampled" (Ladizinsky, 1985; Serrano-Serrano et al., 2012). Any outposts established from these would thus exhibit founder effect, with low genetic variation compared to the source and possibly an incomplete array of *S* alleles and mating factors. Multiple introductions of tubers through time, however, could conceivably raise genetic variation when old occupation sites were revisited (see Bamberg et al., 2016).

Herein we examine the first line of evidence for founder effect in *S. jamesii* by conducting controlled matings between archaeological and non-archaeological populations from field-collected tubers grown in a greenhouse. In addition, we examine specimens from seven major herbaria, along with collection records from over 160 populations from across the range of the species to determine which have been previously observed to produce fruits and seeds. The purpose is to test the null hypothesis that archaeological populations at outpost locations should be able to produce fruit if crossed with other individuals from the same or different source populations. Rejection of this hypothesis would support the idea that archaeological populations lack a full complement of compatibility genes and factors, possibly as the result of human-caused founder effect. Such populations would then have been put on a path of domestication not previously documented from the southwestern United States.

MATERIALS AND METHODS

Study species

Solanum jamesii (Four Corners potato) is a tuber-forming, diploid ($2n = 24$) species that is widely distributed in central New Mexico and Arizona, with isolated populations extending north into southern Utah and western Colorado (known as the Four Corners region of North America, Figure 1) and south into northern Mexico and northwestern Texas (Heil et al., 2013; Hijmans et al., 2002).

Within the center of its distribution *S. jamesii* is closely associated with pinyon–juniper and ponderosa pine woodlands at a mean elevation of 2105 m a.s.l., but can range between 1415 and 2662 m a.s.l. overall (USDA-ARS Germplasm Resources Information Network (GRIN), 2015). Like other members of section *Petota*, it is an obligate outcrosser that requires matching of specific genetic factors (e.g., compatibility alleles and endosperm balance numbers) in order to sexually reproduce (i.e., make viable seeds in fruits) (Johnston and Hanneman, 1980). Consequently, population growth is largely driven by cloning, with prolific tubering from underground stolons that can exceed 1 m long. Tubers begin sprouting in response to monsoonal rains in late June or early July. Vegetative growth is rapid, and flowering can occur within 2 weeks. Consequently, fruit formation may start in mid to late July, but peaks in August, September, and October before frost kills the shoots. Natural dispersal of *S. jamesii* has not been studied in situ. The fruits are green berries containing high levels of the toxic glycoalkaloid solanine, which is known to be a strong inhibitor of bird and mammal seed dispersers (Cipollini and Levy, 1997; Levy and Cipollini, 1998).

As a food source for humans, *S. jamesii* is highly productive and nutritious. A single tuber grown under optimal conditions can produce over 400 tubers in as little as 4 months. The density of stems in a typical coniferous forest habitat can range from 10 to 30 per m^2, which often means hundreds to thousands beneath a single pinyon canopy. Moreover, *S. jamesii* from multiple populations has been shown to have twice the protein, calcium, magnesium, and iron content of *S. tuberosum* (Kinder et al., 2017; Burlingame et al., 2009).

It has also been observed that some populations occur within 300 m of in situ artifacts ("archaeological populations"), and with few exceptions, tend to be small in size (number of aboveground stems between 8 and 300), isolated, at the edge of the species' distribution, and associated with a wide range of vegetation types (sagebrush scrub, sycamore riparian, oak riparian, and cottonwood riparian in addition to conifer woodlands) (Bamberg et al., 2003, 2016).

Breeding experiment

Propagation of source populations

Tubers from five archaeological (A) and five non-archaeological (N) source populations were obtained directly from 2013 to 2019 field collections or from accessions stored at the U.S. Potato Genebank, Sturgeon Bay, Wisconsin (Table 1). Populations varied greatly in size based on the number of aboveground shoots observed during late summer and early fall. In all cases, attempts were made to maximize distance between collections within a population to avoid sampling from the same clones. Tubers were stored at 5°C until grown under optimal greenhouse conditions in April 2020. Propagation began with 82 tubers from 10 populations (5 A and 5 N) that averaged 71% sprouted (72% and 69%, respectively). Each sprouted tuber was planted in potting soil in a 1-gallon (3.8-L) container and watered with nutrient solution every 3 days, thus removing any resource constraints to growth, flowering, and fruiting. Flowering began in early July and crosses began on 13 July 2020.

Crosses

Given that we could not be certain that tubers from a single source population came from different clones, only source populations were considered independent replicates for each type of cross. Each source was designated a source symbol (e.g., Anc = North Creek Shelter source, Table 1). Multiple plants (e.g., Anc1, Anc2, etc.) and pollen transfers between flowers within each source population were treated as repeated attempts at each type of cross (self, outcross within a population [W], outcross between populations

TABLE 1 Population sources for tubers used in breeding experiments for *Solanum jamesii*. A = archaeological, N = non-archaeological source populations, source symbol abbreviations as shown in parentheses

A vs N	Tuber collection	Location	Est. pop. size	Collection year	No. plants	Source symbol
A	North Creek (nc) Shelter A, Escalante	Garfield Co., Utah	475	2019	4	Anc
A	Oak Clone (oc), Escalante	Garfield Co., Utah	10,000	2018	6	Aoc
A	Potato Amphitheater (pa) 5, Bears Ears	San Juan Co., Utah	336	2018	6	Apa
A	Paria Plateau (pp) 30, Vermillion Cliffs	Navajo Co., Arizona	1000	2018	5	App
A	Lower Navajo (ln) Canyon, Mesa Verde	Montezuma Co., Colorado	10,000	2015	6	Aln
N	West Magdelena (wma) 342a	Socorro Co., New Mexico	10,000	2015	6	Nwma
N	West Magdelena (wmb) 342b	Socorro Co., New Mexico	10,000	2015	5	Nwmb
N	State Route (sr) 41, 2	Socorro Co., New Mexico	10,000	2015	6	Nsr
N	Nelson Reservoir (nr)	Apache Co., Arizona	no data	1995*	7	Nnr
N	Picnic Creek (pc) 505	Apache Co., Arizona	1,000	2015	4	Npc

TABLE 2 Summary of crosses performed for breeding source populations of *Solanum jamesii*. See Table 1 for source symbol abbreviations

	Replicates		Repeats			Replicates		Repeats		
Type	**Stigma**	**Pollen**	**No. plants**	**No. flowers**	**No. fruits**	**Stigma**	**Pollen**	**No. plants**	**No. flowers**	**No. fruits**
Self	Anc	Anc	4	15	0	Nwma	Nwma	5	17	0
n **= 5**	Aoc	Aoc	5	13	0	Nwmb	Nwmb	4	13	0
	Apa	Apa	5	9	0	Nsr	Nsr	4	15	1
	App	App	5	23	0	Nnr	Nnr	6	33	1
	Aln	Aln	2	9	0	Npc	Npc	4	18	1
		Sums	**21**	**69**	**0**		**Sums**	**23**	**96**	**3**
Outcross (W)	Anc	Anc	3	7	0	Nwma	Nwma	5	17	0
n **= 4 or 5**	Aoc	Aoc	3	12	0	Nwmb	Nwmb	2	8	0
	Apa	Apa	1	2	0	Nsr	Nsr	5	15	0
	App	App	5	19	0	Nnr	Nnr	4	19	0
						Npc	Npc	4	16	1
		Sums	**12**	**40**	**0**		**Sums**	**20**	**75**	**1**
Outcross (B)	Nsr	Anc	3	10	1	Aln	Nwma	2	6	5
n **= 7 or 8**	Npc	Anc	3	13	1	Aoc	Nsr	5	19	16
	Nsr	Aoc	4	10	1	Anc	Nsr	1	3	1
	Nnr	Aoc	6	30	0	App	Nsr	4	24	19
	Nsr	Apa	5	22	2	Anc	Nnr	6	22	18
	Npc	Apa	3	8	0	App	Nnr	5	31	29
	Nnr	App	6	27	2	Apa	Npc	5	13	11
	Nwma	Aln	2	8	6					
		Sums	**32**	**128**	**13**		**Sums**	**28**	**118**	**99**

[B]). Repeated attempts ensured that a particular cross would not fail because of inadequate pollen load on the stigma, indelicate handling of flowers or other uncontrolled factors that inhibited seed and fruit formation.

We began the breeding experiments with the following types of crosses (Table 2): (1) Self cross—pollen transfers among flowers on the same individual plant of a source population (e.g., Anc1 × Anc1, Nsr1 × Nsr1), (2) outcross

W—pollen transfers between flowers on different individual plants from within the same source population (e.g., Anc1 × Anc2), (3) outcross B—pollen transfers between flowers on individuals from different source populations (e.g., Anc1 × Nsr1).

Newly opened or unopened flowers receiving pollen were emasculated by removing the stamens and petals, exposing the pistils. Pollen was released from stamens using a mid-C tuning fork onto a piece of clean paper. The paper was then spread evenly over the receiving stigma. A labeled, fine-mesh bag was placed over the pollinated stigma, and all tools were then cleaned and sanitized. These were performed between 13 July and 5 August 2020, interspersing cross types among the flowers available at any point in time. Consequently, the number of replicates and repeats (plant or flowers) could vary as the floral season progressed and the number of available flowers fluctuated.

Fruits were left to mature and collected when the peduncle senesced and could be easily removed or fell off on its own. All fruits were dried in paper bags at room temperature.

Geography of fruit production

Population database

Field surveys and collections of *S. jamesii* began in 1992 (U.S. Potato Genebank) and have extended through 2020 (U.S. Potato Genebank and University of Utah). The current U.S. Potato Genebank database for *S. jamesii* records the species at 162 georeferenced locations and includes observations of habitat, population size and condition, tuber collections, and the presence of flowers and/or fruit. Repeated visits to these locations have resulted in 243 population-specific observations, especially at archaeological sites throughout the range. Sites were subsequently sorted into archaeological vs. non-archaeological and fruit observed or not observed during the surveys.

Herbaria survey

Seven major herbaria within and beyond the Four Corners region were visited between 2014 and 2020 to examine every available specimen of *S. jamesii*. These included Garrett (UT-Botany); Intermountain (USU-UTC); Deaver (ASC); University of New Mexico (UNM-Vascular Plants); Brigham Young University, S.L. Welsh (BRY-V); Royal Botanic Gardens Kew (KEW); British Museum of Natural History (NHM). We examined 250 specimens, with one fruit occurrence added to the population database.

We also examined records and photographs (if available) of specimens of *S. jamesii* for occurrences of fruit available on the Consortium of Intermountain Herbaria (https://intermountainbiota.org/portal/collections/index.php), which included 17 institutions: ARIZ; ASU-CCH; ASU-Seeds; BLM-BLMGJFO; BLM-NM; COCO; COLO-V; CS; ENMU; FLD; GCNP; Harvard; KAIB; MABA-Plants; MESA; MNA; NAVA; NHI; NMC; NMNHI; NPS-MEVE; NPS-PISP; SJNM; SNM; SUU; SWRS; USFS-COC; USFS-GILA; USFS-SWRH; USFS-TEUI; UVSC; WSCO; YU; ZNP. This search resulted in an additional 206 specimens, adding three fruit occurrences to the database.

On average, 86% of all collection records were made during the phenoperiod for fruiting (August through October) and georeferenced occurrences of flowering and fruiting were mapped using ArcGIS Pro 10.8 (ESRI, Redlands, CA, USA) using the U.S. Geological Survey topographic base map.

RESULTS

Breeding experiment

A total of 34 crosses within and between source populations, 136 crosses within and between individual plants, and 526 crosses between flowers were made over 23 days during the peak floral display of *S. jamesii*. Archaeological populations did not produce any fruits when selfed or outcrossed between individuals from the same source (Table 2). A weak ability to self or outcross within populations was observed in non-archaeological populations, but was not statistically significant. Outcrossing between archaeological and non-archaeological populations, however, produced fully formed, seed-containing fruits, especially if non-archaeological populations were the pollen source. Cursory examination indicated that pollen grains from both A and N populations were capable of rapid and robust tube growth in vitro.

The asymmetry of A × N and N × A outcrosses between populations (B) was by a factor of 6.2, with the mean ± SD probabilities of flowers producing fruit 0.771 ± 0.198 and 0.134 ± 0.253, respectively (Table 3). This difference was

TABLE 3 Probability of fruit formation (fruit/flower ratio) for replicate self- and out-crossed (W = within source population, B = between) *S. jamesii*. A = archaeological, N = non-archaeological source populations

	Selfs		**Outcrosses**			
	A × A	**N × N**	**A × A (W)**	**N × N (W)**	**N × A (B)**	**A × N (B)**
	0	0	0	0	0.1	0.846
	0	0.067	0	0	0.1	0.842
	0	0.056	0	0.189	0.0454	0.333
	0	0.030	0	0	0	0.818
	0	0	0	0	0	0.792
					0.0741	0.936
					0	0.833
					0.750	
Mean	0.000	0.031	0.000	0.038	0.134	0.771
SD	0.000	0.031	0.000	0.085	0.253	0.198

TABLE 4 Probabilities of source populations, individual plants and individual flowers contributing to fruit formation in *S. jamesii*. Success index is the sum

Type	Stigma × Pollen	*P* (source pop)	*P* (plants)	*P* (flowers)	Index
self	A × A	0.00	0.000	0.000	0.00
	N × N	0.60	0.13	0.03	0.76
outcross	A × A (W)	0.00	0.00	0.00	0.00
	N × N (W)	0.200	0.100	0.040	0.340
	N × A (B)	0.750	0.406	0.102	1.258
	A × N (B)	1.000	1.000	0.742	2.742

statistically significant using a two-sample *t*-test assuming unequal variances ($t = 5.47$, df = 13, $P < 0.001$). High probabilities (≥0.82) were achieved in all archaeological populations as long as they were the stigmatic recipients. There was no apparent difference between non-archaeological pollen donors as all were capable of affecting a high degree of fruit output. The probabilities of all other crosses producing fruit were negligible.

Successful fruit output in this breeding experiment depended most upon outcrosses between source populations, with a probability range of 0.75 to 1.00 regardless of pollen contributor (Table 4). All A × N (B) plants were successful (compared to 0.41 for N × A (B)). The sum of these probabilities is a relative success index indicating almost universal success (2.7/3.0) for virtually any A × N (B) cross. Subsequent germination tests on 29 seeds (treated with 2000 ppm GA3) from six N × A fruits showed 58.6% germination.

Geography of fruit production

The U.S. Potato Genebank/University of Utah database records a total of 248 observations of *S. jamesii* populations from 162 locations across the range. When combined with the herbaria survey, there were 45 non-archaeological populations observed with fruit, 26 archaeological populations with no fruit observed, and six archaeological populations observed with fruit (Figure 1). Archaeological populations with no fruit were observed an average of 3.0 times (flowering years), while those with fruit were observed an average of 1.7 times during the surveys. The latter were either from the central range of the species (El Morro and Gila Cliff Dwellings) or from outposts of Puebloan habitations to the north (Canyon de Chelly, Chaco Canyon and Window Rock). Chaco Canyon had at least six, rather isolated occurrences—three with fruit and three without (two of each observed during the same flowering year). No in situ fruiting populations have been observed north of 36.2° latitude (Canyon de Chelly) despite having almost 30 known occurrences in that region.

DISCUSSION

The Four Corners potato, *Solanum jamesii*, has a gametophytic self-incompatibility breeding system that is common among other members of the genus. Breeding between individuals from within the same source populations, however, is no better than selfing with respect to fruit formation. This is not simply a function of population size (if measured by the number of aboveground shoots), nor the sole result of cloning (distances between tuber samples in a population were greater than 10 m). Successful sexual reproduction requires outcrossing between geographically and presumably genetically distant populations, at least as structured by this experiment.

Source populations associated with obvious archaeological features such as Puebloan habitations, agricultural terraces, storage granaries, petroglyphs, stone tools, pottery, and debitage could not self or outcross with others in the same population or provide pollen that readily affected fruit formation in flowers of non-archaeological populations. Reversing the cross by transferring non-archaeological pollen onto archaeological stigmas produced fruit an average of 77% of the time, with a maximum of 94%. The cause of this female fertile asymmetry is not known, but it is likely that a host of pistil and pollen molecular factors beyond the *S* mating allele mechanism are involved (Lindhout et al., 2017).

The geographic analysis of survey records and herbarium specimens reveals that populations in central Arizona and New Mexico are much more likely to produce fruit than those elsewhere, whether they are archaeologically associated or not. Most occur at intermediate elevations along the long arc of the Mogollon Rim, although fruiting sites have been noted in southern Arizona and New Mexico, as well as northwestern Texas. Northward, the six sampled occurrences at Chaco Canyon are both with and without fruit. These occurrences are associated with drainage features adjacent to Ancestral Puebloan archaeology and separated by 2–3 km of intervening desert scrub vegetation (Kinder et al., 2017). This suggests that gene flow might be spatially restricted on a relatively small scale, although more observations during wetter summers might prove otherwise. Other long-inhabited sites, such as Canyon de Chelly and Window Rock, also had occurrences with fruit, the former found in still-cultivated fields, while the latter probably extirpated by recent changes in land use. But it is probably true that in situ sexual reproduction in *S. jamesii* is very rare compared to clonal growth, even under the best genetic circumstances. Fruit formation has only been observed in 51 of 162 occurrences, with minimal evidence of constraint in some locations by monsoonal drought, lack of pollinators, or the spatial separation of suitable partners.

Why would some archaeological populations be able to produce fruit and others not? Those that do produce fruit are positioned along well-known trade and pilgrimage routes, extending from the Rio Grande Valley, through the Mogollon Rim to Chaco and beyond to Mesa Verde and the San Juan Basin (Colton, 1941; Malville and Malville, 2001;

Hull et al., 2014; Friedman et al., 2017). Salt, ceramics, shells, turquoise, obsidian, cacao, and scarlet macaws are among the valuable and exotic goods that moved through the extensive Chacoan (pre-Chacoan?) network (Baldwin, 1972; Riley, 1975; Crown and Hurst, 2009; Arakawa et al., 2011; Washburn et al., 2011; Watson et al., 2015). We suggest that nutritious, easily transported tubers of *S. jamesii* joined this procession, moving north and west and carrying highly biased gene pool samples, a fraction of which became established at distant habitation sites. If, in some places, the introduction of these tubers was a singular event, the result would be a strong founder effect and low genetic variability. Persistence then depended exclusively on cloning. In other places, such as Chaco Canyon, multiple introductions over long periods eventually brought a fuller compliment of genes, thus allowing sexual reproduction. Bamberg et al. (2016) report that tuber collections of *S. jamesii* from Mesa Verde capture 82% of the total genetic variation of the species, a "mega-population" that could represent the potato gene bank of its day. However, despite multiple attempts over many years, no in situ fruiting specimens have been collected or observed from Mesa Verde (Bamberg et al., 2016; Kinder et al., 2017). It is unlikely that this limitation was environmental because monsoonal precipitation during seven of the 10 years of contiguous observation (2005–2015) had been above the 90-year mean for the region (WRCC Western Regional Climate Center, 2013). In four of those same years, monsoonal precipitation was 157% of the mean. When grown ex situ, however, and mixed with plants from Chaco Canyon and abundant pollinators, Kinder et al. (2017) found that Mesa Verde tubers could produce fruit. Unfortunately, we did not have enough flowering material to confirm Mesa Verde fruiting with an Aln × Aln (W) cross (Table 2).

West of Mesa Verde are some of the most isolated populations of the species. Near the summit of Mount Trumbull in western Arizona plants grow near a stone hunting blind. On the Paria Plateau, several thousand stems can be found intermingled with abundant pottery sherds, but no fruits have been observed. Multiple occurrences in and around Escalante, Utah (once known as Potato Valley) and within Bears Ears National Monument, Utah have not produced fruit despite having large populations and up to 7 years (2013–2020) of in situ observation (monsoonal precipitation in 5 years above the 106-year mean, three of which exceeded 183% of that mean). However, in previous work at the U.S. Potato Genebank, plants that originated from archaeological sites in Utah (other than those tested here) were able to produce fruit after sib mating. Therefore, archaeological populations could have different origins at different times—some descending directly from large genepools to the south and others derived from gardens already established around occupations. The latter were within a chain of founder events, which presumably would further reduce genetic diversity and mating capability.

Consequently, the null hypothesis is rejected, and we conclude that some archaeological populations, especially those in northern Arizona and southern Utah, lack the genetic ability to sexually reproduce, likely as the result of human-caused founder effect.

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AUTHOR CONTRIBUTIONS

B.M.P.: conceptualization, formal analysis, investigation, methodology, writing and editing of original draft; M.B.: investigation, greenhouse experiments; J.B.: data curation, investigation, review and editing of drafts; A.d.R.: data curation, investigation, review and editing; D.K.: investigation, review and editing; L.A.L.: funding acquisition, investigation, review and editing.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.prr4xgxm5 (Pavlik and Louderback, 2021).

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