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Authors: Kinder, David H., Adams, Karen R., and Wilson, Harry J.

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Solanum Jamesii: EVIDENCE FOR CULTIVATION OF WILD POTATO TUBERS BY ANCESTRAL PUEBLOAN GROUPS

David H. Kinder^{1*}, Karen R. Adams², and Harry J. Wilson³

The Solanaceae family of plants provides edible fruit (i.e., tomatoes, husk tomatoes, chili peppers, eggplant), tubers (i.e., potatoes), and plants used for leisure activities (i.e., tobacco) that are useful to humans. Several wild members of this family grow in the U.S. Southwest and some were eaten by the Ancestral Puebloans. We present evidence here that the Ancestral Puebloans in the Four-Corners region of the U.S. Southwest–the states of Arizona, Colorado, New Mexico, and Utah–were actively cultivating the tubers of Solanum jamesii to supplement their diets of domesticated corn (Zea mays), beans (Phaseolus sp.), and squash (Cucurbita sp.). This is supported by modern day Native American groups who have used this plant for food either now or in their recorded past. We also propose that this potato tuber was cultivated or allowed to grow in gardens or fields around some major population centers in Puebloan times and that the stands currently growing in or near some of those archaeological habitation sites are legacy stands directly descended from ancient efforts to manage the tubers for food. The plant's location at the northern limits of its current range offers support for this proposal. This potato tuber would have provided a dependable and excellent source of nutrition for the ancestral Puebloans as well.

Keywords: Solanum jamesii, wild potato, Ancestral Puebloans, cultivation

Introduction

The subsistence base of Ancestral Pueblo groups in the pre-Hispanic U.S. Southwest included a diversity of domesticated and wild plants. Although the earliest records of major crops are prone to change via new discoveries, current information suggests a number of Mesoamerican domesticates entered as separate introductions over a period of nearly two millennia (Merrill et al. 2009). The presence of maize (*Zea mays*) in the southwestern United States has been well established by multiple AMS radiocarbon dates to around 2100 cal BC. Other Mesoamerican domesticates, including squash (*Cucurbita pepo*), bottle gourd (*Lagenaria siceraria*), grain and dye amaranths (*Amaranthus cruentus, A. hypochondriacus*), common beans (*Phaseolus vulgaris*), and cotton (*Gossypium hirsutum*), entered the U.S. Southwest independently between 2000 cal BC and AD 310 (Merrill et al. 2009). For some groups in the United States, maize became a major component of subsistence soon after they acquired it, but for other groups, some time passed before maize became a major dietary resource.

³Ohio Northern University College of Business.

¹Ohio Northern University College of Pharmacy, 525 S. Main St., Ada, OH.

²Crow Canyon Archaeological Center.

^{*}Corresponding author (d-kinder@onu.edu)

Increasing reliance on domesticates can provide subsistence security and the possibility for surplus production.

Pre-contact groups in the U.S. Southwest also developed relationships with native plants that ranged from casual encouragement to management to domestication. Evidence for indigenous domesticates has been especially strong within the Hohokam culture area of central and southern Arizona (Bohrer 1991). Morphological evidence suggests domestication of native Little Barley (Hordeum pusillum) (Adams 2014; Bohrer 1984) and Mexican Crucillo (Condalia warnockii) (Bohrer 1991). Specialized pre-Hispanic fields, in conjunction with fieldside roasting pits containing charred remains, identify agave (Agave) as a major Hohokam crop (Fish and Fish 2004; Fish et al. 1985, 1992). Cool-season plants including chenopod (Chenopodia spp.), tansy mustard (Descurainia pinnata), milkvetch (Astragalus spp.), and maygrass (Phalaris caroliniana) were also locally cultivated or encouraged by the Hohokam (Bohrer 1991). The unusual geographic distribution of Agave parreyi (Minnis and Plog 1976) and cholla (Opuntia) cactus in some locations implies stand management, if not semicultivation (Bohrer 1991). Sonora panic grass (Panicum sonorum) is also considered an indigenous domesticate (Nabhan and de Wet 1984). Saltbush (Atriplex spp.), spiderling (Boerhavia L.), hog-potato (Hoffmannseggia glauca), wolfberry (Lycium pallidum), patota, groundcherry (Physalis hederifolia), dropseed grass (Sporobolus heterolepis), and ricegrass (Achnatherum hymenoides) have all been suggested as possible cultivated or tended pre-Hispanic foods (Fish and Fish 2004; Fish and Nabhan 1991; Mabry 2004). Devil's claw (Harpagophytum procumbens) is a post-contact domesticate, grown for its seed pod fibers as basketry material and for its edible seeds (Nabhan et al. 1981).

Evidence for plant management/domestication can be diverse. Morphological changes are probably the clearest evidence, when a visual change has occurred that distinguishes a domesticate from its close wild relatives. In the case of domesticated Little Barley grass (*Hordeum pusillum*), the transition from a covered to a hull-less or naked grain (caryopsis) offered a resource that required less processing time (Adams 2014). In the case of domesticated amaranth (*Amaranthus*) seeds, a thinner seed coat (testa) developed (Fritz et al. 2009) as a consequence of human selection pressures on the plants.

Other lines of evidence can be marshalled to make a case for a managed or domesticated plant (Smith 1992). One example of this includes range extensions, essentially recovering pre-Hispanic plant evidence in locations at the edge of or outside of the documented present-day geographical range of the plant (Smith 1992:45–46). Such a circumstance could indicate moving a plant from one region to another, even when no morphological changes are evident.

One variation on the range extension idea involves plants that appear to be strongly associated with archaeological sites in the U.S. Southwest, first discussed by Yarnell (1965). At times, these plants are used as site indicators, such as when wolfberry (*Lycium pallidum*) plants seem virtually confined to archaeological sites in some areas, making it relatively easy to locate the sites (San Miguel, personal communication, 2016; Yarnell 1965:671). Distinctive flora associated with archaeological sites may have more than one explanation. The plants may have been brought to the site in the past by humans and persisted there after they left,

or the plants may have simply found favorable habitat on an archaeological site. Whatever the reasons, there are three criteria that potentially indicate an ancient plant/human relationship: (1) when a plant appears to occur on and be primarily confined to archaeological sites; (2) when it appears to have had a strong association with ancient and modern indigenous groups; and (3) when it might be at the edge of or beyond its normal range. A number of plants in the Solanaceae family were considered by Yarnell (1965:664–668) to fit these criteria, including *Solanum jamesii, Solanum triflorum, Solanum elaeagnifolium, Lycium pallidum*, two species of *Physalis*, one species of *Chamaesaracha*, and *Datura meteloides*. This group of Solanaceae family plants comprises 33.3% of the 21 plants suggested by Yarnell to have been of more than casual interest to ancient groups.

Wild *S. jamesii* plants reproduce vegetatively through tubers and following pollination of the white flowers (Figure 1b) by producing fleshy tomato-like fruit with abundant seeds. The tubers, which are attached to thin underground stolons (Figure 1a), can lie dormant for up to 14 years before sprouting and developing a plant that produces more tubers (Bamberg 2010, 2014). This ability to survive poor growing conditions via dormancy would increase the plant's value to human groups. The fact that the tubers can be collected and easily transported increases opportunities for human groups to plant them in new areas.

Solanum jamesii is a perennial plant that overwinters as tubers at a range of depths below ground surface. The tubers may be close to the ground surface, but they also grow in mulch at 5 cm or greater depths. Tubers can also be attached to long stolons that follow rock cracks into deeper soils (Bamberg, personal communication, 2017). *S. jamesii* grows in fertile silty soils, typically drainages that contain silt deposits, but is not found exclusively in those areas. When information in the Germplasm Resources Information Network (GRIN 2017) database on potato populations studied by Bamberg et al. (2016:565) is examined, it is clear that populations can grow in pure sand, mulch, gravel, needles, and a range of other substrates.

Solanum jamesii are known to flower and fruit, but in the ten years that one author (DHK) has studied this potato in Mesa Verde, it has not been observed to do so. Bamberg, director of the U.S. Potato Genebank in Sturgeon Bay, Wisconsin, also mentioned this lack of fruiting (Bamberg 2010). This may be a consequence of the weather patterns where the moisture is not sufficient to allow fruiting. Typically, moisture in the form of rain is received in late July through early August, where 2–3 inches of rain may fall. No further rain is usually received, and the *S. jamesii* plants will then senesce. However, *S. jamesii* grown in containers in Ohio were found to fruit when moisture continued (either naturally or by watering) through the month of August, but did not grow if no moisture was received or given.

S. jamesii appears to be able to withstand drought conditions for several years until sufficient moisture is available for it to sprout. In the course of ten years of searching for *S. jamesii* in Chaco Canyon (South Gap area), there was a period of five years in which there were no potatoes found growing. Tubers kept in cold storage by Bamberg (2010, 2014) were found to sprout after 14 years, suggesting that dormancy is long-lived.



Figure 1. A. *S. jamesii* tubers arranged by size. Note the stolon fragments attached to some of the tubers, and B. *S. jamesii* blossom, August bloom. Decreased rainfall toward the end of summer often leads to early senescence of the plants before fruit can form. (photos by David Kinder)

This paper develops a case that a wild potato (Solanum jamesii) was cultivated for its underground tubers as a food resource by Ancestral Puebloans and that numerous modern stands of this plant in the Four-Corners region of the U.S. Southwest are legacy populations reflecting ancient management. This tuberproducing plant is often found growing in areas that have been used or presumed to have been used as ancient agricultural fields where farmers grew corn and other crops originally from Mesoamerica. We propose that these modern stands are a legacy of when wild potato plants were actively managed in or near ancient garden plots. This plant joins a growing list of wild plants that were managed or cultivated in the U.S. Southwest during the pre-Hispanic period (Adams 2014; Bohrer 1991; Fish et al. 1985, 1992). We document the distribution of wild potatoes near and within archaeological sites in the Four-Corners Region. In the next section, we describe our geographic and experimental methods for our research on the contemporary distribution of the species, which is followed by results and discussion. In addition, we provide information on the archaeobotany and ethnography of the species (Appendix A).

Methods

S. jamesii stands were located between the years 2005–2015 through reconnaissance into areas where previous reports of vouchers in herbaria or locations obtained from literature had been made. *S. jamesii* typically sprouts during and following the seasonal monsoon rains that occur during July and August, depending upon rainfall reported in the Four-Corners Region. Several archaeological site monitors reported finding the *S. jamesii* at their sites. Mesa Verde National Park and Chaco Canyon National Historic Park were accessed by permit. Canyons of the Ancients National Monument (areas around ruins and isolated canyons) were examined for the presence of *S. jamesii*. All stands were verified by Kinder.

Soil Fertility

Soil fertility can affect the ability of a plant to grow well, but also contributes to its nutritional content. The soils from sites where *S. jamesii* is found were

analyzed for standard mineral content. For comparison, soil samples were obtained from some areas where potato was not found but which coincided with habitation sites near Mesa Verde and Chaco Canyon.

Soil samples were taken near potato stands by randomly collecting material from four separate areas of a population and combining them for analysis. Depth of samples was at 12 cm, which is the approximate depth at which the potatoes are often found. Soil samples were also acquired at random places where potatoes were not present, but where they could have grown based on nearby ruins. The samples were sent to SoilTech in Bluffton, Ohio, for analysis (Table 1). The analyses were performed in a manner that provides agricultural quality information, including available phosphate (Mehlich III phosphorus), organic matter, and soil pH. Exchangeable cations were also determined, as this represents quantity available for plant growth. To determine if *S. jamesii* is limited to growing in southern Colorado/southeastern Utah, *S. jamesii* were planted in a garden near Provo, Utah, over 480 kilometers northwest of Mesa Verde National Park.

Nutritional Content of Tubers

Representative plant parts were collected for analysis and curation. Tubers were harvested in small batches and kept together post blooming, when aboveground portions of the plant were beginning to dry (mid to late August). Nutritional content of *S. jamesii* tubers was determined by Brookside Laboratories Inc. in New Knoxville, Ohio. Several tubers weighing approximately 5 grams were sent for analysis and results were reported for the dried weight. The results reported here were converted to wet weight for comparison to literature values (see Table 2). Where multiple samples were taken from a large area (e.g., Navajo Canyon, Mesa Verde National Park), the tubers were randomly mixed for the analysis. In an attempt to determine if the nutritional content of *S. jamesii* could change under cultivated conditions, an experiment was conducted near Pleasant View, Colorado, (an area where pinto beans [*Phaseolus vulgaris*] are dryland farmed today) where containers filled with local soils were planted with tubers in the fall. Soil was amended with generic organic fertilizer, and when potatoes sprouted in mid-summer, occasional (non-measured) watering occurred.

Tuber Population Density/Nutritional Value

Efforts to determine the density of potatoes produced per 1000 cm² (about 1 square foot) were undertaken in a wild "mega population" (the term "mega population" was coined by Bamberg et al. [2016:571] following our work together in Navajo Canyon) in Mesa Verde National Park. This effort, however, was met with the realization that the wild populations would not represent what could be achieved in a cultivated setting. If the potatoes were allowed to grow randomly among other crops, an estimate of quantity that would be produced could be made. In August 2012, 20 randomly selected 1000 cm² (1 foot square) areas were chosen. The areas were near the channel of the wash in the canyon and represented some of the more visually dense stands of potatoes. Nutritive content was calculated by averaging weight per tuber. We present a potential amount of potato that could be available should it be cultivated.

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Table 1. Soil	presented fc	hectare) Sim

Location*	MEVE upper canyons	MEVE canyon bottoms	Chaco central ruins	Chaco west wash	West of MEVE	Pleasant View	Prater Canyon	Yucca House	Turkey Pen	NW Ohio soil
Total exchange capacity (M.E.)	10.3	16.8	5.5	8.0	17.2	16.2	1.3	1.9	12.1	20.6
pH soil sample	7.6	7.1	8.5	8.4	7.9	7.9	7.9	8.1	8.2	6.1
Organic matter (%)	4.68	9.33	0.37	0.42	8.57	1.39	2.22	2.53	0.58	3.90
Mehlich III phorphorous	39	83	104.5	71	112	173	142	155	50	385
Calcium	1573	2241	1559	2432	2424	3192	254	503	2434	7623
Magnesium	163	341	282	357	273	467	69	85	354	1287
Potassium	233	757	147	122	812	348	136	48	194	508
Iron	54	53	127	132	44	27	189	114	29	294
Manganese	62	70	208	156	75	93	9	ю	75	17
Copper	1.10	1.15	1.73	1.77	1.90	2.19	0.84	0.78	2.02	5.91
Zinc	1.51	4.28	2.45	2.12	4.30	1.48	21.23	3.89	1.82	3.62
* MEVE Upper canyons: Average c samples taken near Chetro Ketl and Mud Springs and Hawkins Preserve	of upper canyon bo l Casa Chiquita. Ch e. Pleasant View: so	elow step house, Lii aco west wash: sam oil from farm land s	mey Draw. MEVE ple taken from bro outh of the town o	canyon bottom ad wash west o f Pleasant View	s: average o of Peñasco Bl CO in which	f Navajo, Lo anco and no potatoes w	ong, and Rc rth of Chac ere grown.	ock Canyoi o River. We Prater Can	ns. Chaco c est of MEVI von: canvo	entral ruins: 3: average of

potato observed. Yucca House: sample taken near lower ruin, no potato observed. Turkey Pen: Turkey Pen Ruin is in NW area of Canyons of the Ancients, no potatoes observed. NW Ohio soil: sample taken from cornfield near Lima, Ohio.

1 bushel com (56#) = 25.40 (25) kilograms 1 metric ton = 39.37 (40) bushels com (56# bu) = 5.5 metric tons

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Table 2. Nutritional analysis of potatoes collected from Chaco Canyon (West valley) and Mesa Verde National Park (primarily Navajo Canyon). Comparison of *S. jamesii* to *S. tuberosum* - from review article of several sources and cultivars (Burlingame et al. 2009). All numbers are reported for wet weight of tuber. Pleasant View potatoes were grown in containers with soil from surrounding pinyon-juniper woodland. Literature values and protein determination from Burlingame et al. (2009).

	Chaco mg/100 gm	MEVE mg/100 gm	Pleasant View mg/100 gm	Literature <i>S. tuberosum</i> mg/100 gm	All potatoes (range)
Protein	4.04%	4.02%	4.60%	2.00%	(0.85-4.2 %)
Phosphorus	95	88.8	84	NA	. ,
Potassium	653	623.7	577	443	(239-694)
Calcium	26	36.3	259	10.59	(1.35-27.8)
Magnesium	37	40.26	43	20.21	(10.8–37.6)
Sulfur	50	48.6	55	NA	
Iron	3.30	2.79	1.49	1.04	(0.14 - 10.4)
Manganese	0.24	0.22	0.30	0.13	(0.05 - 0.39)
Copper	0.19	0.17	0.16	0.11	(0.05 - 0.15)
Zinc	0.80	0.85	0.90	0.41	(0.22-0.76)
Aluminum	6.63	4.88	2.47	NA	

Results

We present the results of this research first by describing the geographic locations and settings in which surveys have identified stands of *S. jamesii*. We then present results of our soil and nutritional analyses.

The Contemporary Geographic Distribution

The range of *S. jamesii* includes northern Mexico, far western Texas, much of New Mexico, southeastern Utah, and northeastern Arizona (Humans and Spooner 2001; Kearney and Peebles 1960; Welch et al. 1987). In Colorado, it occurs only in southeastern Montezuma county, plus a few other locations (Harrington 1964:485; USDA NRCS 2016). In dryer southern areas, it is found in mountainous regions where moisture is comparatively plentiful. Additional stands are known in Bandelier National Monument (NM) and in Canyon de Chelly National Monument (AZ), both with significant evidence of nearby pre-Hispanic occupation by indigenous groups. A recent map of herbaria collection materials can be found using the SEINet website (SEINet 2017). Additional information is also available in the GRIN database (GRIN 2017).

Extensive field reconnaissance during this project has delineated the distribution of *S. jamesii* in the Four-Corners Region. Stands were located by searching areas surrounding ancient habitation sites identified on maps or readily accessible through day hikes. Four areas have been the focus of this research: Mesa Verde National Park (MEVE) and surrounding area; Chaco Canyon National Historic Park and surrounding area; Chimney Rock National Monument; and other locations, including Canyon of the Ancients National Monument and Aztec Ruins National Park.

With few exceptions, *S. jamesii* plants grow primarily in association with archaeological ruins in the Four-Corners Region (Figure 2). This is supported independently by Bamberg et al. (2003) who mapped and collected specimens for the U.S. Potato Genebank. These researchers noted that stands are often isolated, with long distances between populations, and that growth requirements include adequate soil moisture. This is supported by field observations by Kinder and field associates over a period of at least ten years (summarized below). The association of these potato populations with cultural water-impounding features (check dams, spill-overs, other water control features) and natural water-impounding features (landslides, where side-canyon drainages join main canyons, sediment within slickrock depressions) reveals how ancient groups understood the locations where potato tubers would thrive.

Mesa Verde National Park and Surrounding Areas

In the Mesa Verde area of southwestern Colorado, *S. jamesii* is found growing up to 2210 m in elevation, but no higher. It is also growing in upper drainages where check dams are plentiful—usually above formidable spill-overs. There are hundreds of check dams located near cliff dwellings and on mesa tops where crops were thought to be cultivated. Many of those check dams retain soil, and potatoes currently grow in some of those features. Multiple stands of *S. jamesii* found in Mesa Verde are shown in Figure 3.

The largest population was documented in Navajo Canyon below Chapin Mesa, where there is a large fertile area that may have been cultivated and where at least one stone check dam has been observed adjacent to the central channel. This *S. jamesii* stand is found along a length of 1600 m of the canyon, which is 60–90 m wide at its center and is considered to be a "mega-population," defined on the basis of large numbers of plants, broad spatial distribution, and genetic richness (Bamberg et al. 2016). This stand spreads from the upper end of the canyon toward the park border.

A population also occurs at a bench formed from landslide-deposited boulders at the mouth of Spruce Canyon as it opens into Navajo canyon. Additionally, on top of Chapin Mesa in the Fewkes drainage area, a small stand of *S. jamesii* grows just above the spillover near Oak Tree Ruin. The area is abundant with check dams and other water control features, as occurs for most of the potato populations in Mesa Verde National Park. In the canyon below Kiva point which is located toward the end of Chapin Mesa within the Ute Mountain Tribal Park, there is a small stand of *S. jamesii*. No other stands were found near ruins downstream on the Mancos River, presumably because of dryer conditions than at higher elevations on the Mesa.

Long Canyon (between Long and Wetherill mesas) also contains a population of potato. However, the narrowness of this canyon and the rarity of suitable habitat for the potato only allow stands that appear sporadically along an 800 m section. In the side canyon below Step House Ruin, there is a garden-like area with a stand of potatoes that is found between Wetherill Road and the mesa edge. There are check dams adjacent to the gardens and remnants of check dams in the wash area indicating past cultivation. *S. jamesii* is also found in adjacent upper side canyons.



Figure 2. Overview of S. jamesii stands found in the Four Corners.



Figure 3. Mesa Verde National Park and surrounding areas where potatoes were found. The greatest concentrations of *S. jamesii* are where the ruins are densest on Chapin Mesa and Wetherill Mesa.

Another stand occurs in Rock Canyon in the area below Long House Ruin. Rock canyon is similar to Navajo Canyon, though it has a deeper channel running through it and is at a slightly lower elevation. The potatoes found there were growing where side canyon drainage from near Long House occurs and provides greater moisture than at higher elevations in the canyon. Another stand is found in Limey Draw, which is toward the end of Wetherill Mesa almost to the Ute Tribal Park boundary. The stand occurs on silt deposits within the draw that are held in place by slickrock; there, stacked rocks suggest that, at one time, check dams were in place. These sites are shown in Figure 3.

The area surrounding Mesa Verde National Park (Figure 3) also has several populations associated with ruins. At Mud Springs, the ruins are covered with vegetation, which includes *S. jamesii*. There is evidence that a reservoir was placed in the drainage that is part of the ruin, where remnants of a check dam occur. The potatoes are found in moist soil currently held in place by the check dam with an extensive slickrock drainage above; they are also found on the bench below. Potatoes are found throughout the ruins, where they may have been protected by the architectural rubble acting as mulch by retaining moisture. The population at Mud Springs is large, as it covers at least the entirety of the ruin of about 90 m. Hawkins Preserve also contains *S. jamesii*. They are found in along the McElmo wash on the western side of the preserve near a Pueblo II ruin. *S. jamesii* are also found in slickrock areas above the wash where there are many check dams. Several additional ruins are found near Mesa Verde National Park that may have potatoes; however, we have not been able to locate any unknown populations.

Chaco Canyon National Historic Park and Surrounding Area

Chaco is an enigma as to why it was where it is, and why it has so many unique and abundant artifacts (Vivian and Hilpert 2012). It is notable that the soils in Chaco are fertile, and with water can yield crops of good quality (Wills 2012). The Chacoans manipulated their environment to utilize water and this no doubt led to production of foods for the inhabitants, but might also have produced a surplus for trade (Vivian 1992). Chaco also contains a megapopulation of *S. jamesii* in the arroyo to the west of West Mesa (Figure 4). This arroyo connects to the Chaco River and drains a substantial area to the south of the river. Potato plants grow around the shallow channel that runs through the wash and then extends for more than 3200 m. The year following the finding of this mega population only a small number of plants were observed, although they were scattered over the entire 3200 m as in the previous year.

Another extensive potato stand grows in South Gap. This passage out of Chaco Canyon from near Pueblo Bonito has a broad wash that contains *S. jamesii* and it extends for about 1600 m from the edge of Chaco wash. More potato plants are found around Pueblo Bonito, as well as the other ruins in the center of the canyon. As with the West drainage area, potatoes do not appear to sprout every year. Only during one year (2008) was dense growth extensive, which followed a moist winter and spring.

The remaining populations in and around Chaco tend to be smaller than the two large populations just described. There is a small population in Weritos



Figure 4. Distribution of *S. jamesii* in Chaco Canyon. The largest population (mega population) is in the broad wash on the west side of the park. The park boundaries were extended on the south side in 1972 and are not shown on this map.

Rincon, which is protected from scouring winds, and around Wijiji on the north side of the canyon wall across from Chacra Mesa. Additional populations can be found in the side canyons on the north side of Chacra Mesa.

The areas where stands of *S. jamesii* are found are likely sites of intensive agricultural use and where water management was likely practiced (Vivian 1984). Only a few check dams made of stone work are found in Chaco, but evidence for using earthen works to divert or contain water for crops is present (Vivian 1992).

It is important to note that we have not encountered populations of *S. jamesii* on mesa tops. Chacra Mesa is covered by pinyon-juniper stands, indicating local moisture content greater than on other mesa tops. We have found a few check dams on Chacra Mesa, but many had lost their soils and no potato plants were observed in those areas. Potatoes, however, are found in the canyons and rincons below. The distribution is shown in Figure 4.

Chimney Rock National Monument

The Chaco outlier at Chimney Rock National Monument is located in the mountainous region of southwest Colorado. Check dams are found downslope from the ruins, but whether these check dams were used to feed a reservoir for water storage or for gardens is unknown. *S. jamesii* was observed growing near check dams as well as within architecture rubble. Given the remoteness of the site from other wild potato populations, and the elevation (2250 m) at which this site exists, it is plausible that the wild potatoes were intentionally planted.

Locations with No or Few Populations of Solanum jamesii

Despite numerous field visits to other locations, no additional populations of *S. jamesii* plants were observed. One potentially important location was Canyons of the Ancients National Monument and surrounding areas. An extensive search of archaeological sites, as well as canyons and washes, did not identify any populations. The aridness of that region might have been too great for even the drought-tolerant *S. jamesii*. We cannot discount the possibility that the residents did not grow, tend, or even encourage potato to grow in their gardens. Further, we do not know the potential impact of past and contemporary grazing on the survival of *S. jamesii*. We have observed that elk will browse the above-ground portions of wild potato plants and cattle have been grazed on western U.S. lands for quite some time (and were present during some of the searches). No wild potato stands were observed in Aztec Ruins National Park. Populations of *S. jamesii* in Utah are not common and are primarily confined to the southeastern part of the state (Bamberg et al. 2003).

Results of Experiments and Analyses

There is no striking difference between soil mineral content and mineral content in *S. jamesii* other than the experimental plot in Pleasant View. Comparing available phosphate as measured by the Mehlich III method suggests no large difference between the samples. Results for soil pH are similar. Potassium levels are much higher in Mesa Verde National Park's Navajo Canyon and Mud Springs/Hawkins Preserve soils, but potassium levels in the tubers are similar regardless of the source. Calcium levels were similar among the *S. jamesii* grown in these soils except for those taken from the Pleasant View experimental garden where the *S. jamesii* received some organic fertilizer. This difference should be further investigated to determine if this is a potential way to manipulate calcium levels in *S. jamesii*. There is a substantial difference in organic matter between the Chaco and Mesa Verde soil samples, which should not be surprising as Mesa Verde is primarily comprised of pinyon-juniper woodland and receives higher precipitation to support greater plant growth.

The results of analysis of wild collections from Chaco Canyon and tubers from the largest field present on Mesa Verde (Navajo Canyon) are presented in Table 2. In particular, calcium, potassium, magnesium, iron, copper, and zinc are important dietary trace elements. *S. jamesii* from these locations contained twice the levels of protein of modern domesticated *S. tuberosum* (russet potato), which is consumed worldwide today. Others have reported that *S. jamesii* has a reasonably high protein content of 8.0% of dry matter, the second highest out of 24 wild potatoes analyzed (Jansen et al. 2001:143). In addition, researchers noted that protein content seemed influenced by yearly growing conditions, such as higher temperatures (Jansen et al. 2001:140). All levels of minerals were as high or higher than those found in *S. tuberosum* and were within the range of other cultivars or wild potatoes analyzed by others (Burlingame et al. 2009).

Tubers ranged in diameter from about 4 mm to a maximum of 2.5 cm, averaging about 1 cm. Potatoes from the Pleasant View experiment were of similar size to those seen in the wild in New Mexico and Colorado. *S. jamesii* sprouted and grew in the summer of 2012 and all but one plant was harvested for tubers. In 2013,

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the potatoes left in the ground sprouted again in June. This is in contrast with the usual sprouting period for *S. jamesii* in southwestern Colorado following the start of monsoon rains of July. This experiment suggests that tubers can sprout and grow significantly farther north than the current known range of the species. Bamberg (personal communication, 2017) also reports that *S. jamesii* have survived in an outdoor garden in NE Wisconsin for over 20 years, sprouting every year, flowering, drawing pollinators, and producing seeds that look normal. However, it is not known if *S. jamesii* would successfully reproduce only by seedlings in these northern locations if, for some reason, the tubers were decimated.

In the Navajo Canyon mega-population at Mesa Verde National Park, numbers of *S. jamesii* tubers in a 930 cm² ranged from 7–20, with an average of about 13 tubers. The average weight of the tubers was 1.3 gm/tuber; 17 gm of tubers could be gotten from 930 cm² of soil, or, for a 9 m² plot, 1.7 kg could be obtained using these conservative estimates. In modern times, an average medium russet potato is 100 gm or about 77 calories/100 gm (Navarre et al. 2009). Under ideal conditions, the *S. jamesii* potato tuber could have contributed significant carbohydrates, along with other nutritional components, to the diet of the Ancestral Puebloans.

Discussion

This project has provided a case study supporting the addition of *S. jamesii* to the growing list of wild plants managed by human groups in the U.S. Southwest in ancient times. Use of Solanaceae plants in the U.S. Southwest has been documented by the presence of seeds, pollen grains, and other microremains such as phytoliths and starch grains often found on grinding tools (see Appendix A). The stands of *S. jamesii* found in proximity to ancient ruins provide the primary evidence that they have been managed by those groups. Supportive evidence includes the presence of S. jamesii tubers in one bowl associated with a burial in Chaco Canyon, plus there is a report that potato tubers were found in Betatakin in Navajo National Monument (Appendix A). Unlike other plants that have been domesticated, it is currently impossible to say if any morphological changes occurred in S. jamesii over time, due to their scarcity in archaeological sites in part because of their fragile nature. However, the distribution of large contemporary potato stands in areas that are rich in archeological sites, such as Mesa Verde, Chaco Canyon, and other areas, supports their use as food either by cultivation or encouragement through plant tending.

Genetic analysis of potato markers such as AFLPs (Amplified Fragment Length Polymorphisms) can address whether changes occurred under human management. Generally, the longer a species has been growing in one area, the more opportunities there are for genetic variations to emerge that are unique to that population. However, if isolated populations of a species are combined by importing that species from several different isolated locations to one area (such as a village field) and allowed to cross pollenate, the population will show the aggregate of the populations brought together. The genetically diverse wild potatoes found in Mesa Verde's Navajo Canyon encompass over 80% of the AFLP markers known in the species (Bamberg and del Rio 2016; Bamberg et al. 2016). This could be an indication that tubers collected elsewhere were "brought home" to be planted in the canyon. It has been proposed that the Inca were collecting

to be planted in the canyon. It has been proposed that the Inca were collecting food crops to test in their terraced gardens at Machu Picchu, which would then make the plants brought in that were allowed to cross pollinate an ancient genebank or experiment station for testing different varieties of Solanaceous crops (Bamberg and del Rio 2005).

When Solanum jamesii tubers are planted and tended (e.g., loosening soil, adding nutrients, watering), they become larger than those harvested from the wild and have increased calcium and potassium content, as demonstrated in the Pleasant View experiment above. S. jamesii is a diploid (2N) species and another wild tuber-producing potato in the U.S. Southwest, S. fendleri, is a tetraploid (4N) species (Bamberg et al. 2016:571). A doubling of chromosome numbers during meiosis or mitosis could potentially lead to larger plants and their parts, something that would have immediately been noticed and appreciated by human groups. A closely related wild potato over 1600 kilometers south of the United States border in Mexico, S. cardiophyllum, has rare large tuber mutants that could conceivably transfer genes for large size to S. jamesii (Bamberg, personal communication, 2017). Researchers are finding that S. jamesii hybrids can make tubers in the range of 100 times the size of wild tubers, potentially a "game changer" in terms of food provision (Bamberg et al. 2017). Mesa Verde National Park is on the Northern Edge of S. jamesii's range today (USDA NRCS 2016), but an experimental planting in the north in a colder climate (Provo, Utah) demonstrates that people could have moved S. jamesii northward during prehistory. Indeed, Mesa Verde and Chaco Canyon inhabitants are thought to have carried on a robust trade even with people of Mesoamerica, where chocolate (Theobroma cacao) (Crown and Hurst 2009) and the Red Macaw are found.

In addition, *S. jamesii* has a strong ethnographic record of use by indigenous groups today, as discussed in Appendix A and by Ortman (2012). A review of those groups shows that most report using *S. jamesii* as a food source. Often the reports include the information that it is eaten with a mineral clay to lessen a bitter taste, while at other times the report is that the tubers were dried prior to consumption (Moerman 1998). Ancestral Puebolans were already agriculturalists whose farming practices would have facilitated cultivation or management of a wild resource where they would have selected for certain characteristics of that plant.

As a potential legacy plant near and within ancient habitation sites and agricultural fields, *S. jamesii* offers several advantages. These include its reproduction as a tuber that can be easily carried from one place to another. The tubers also provide high nutritional value, which includes a significant quantity of starch, and, in particular, trace minerals such as calcium and potassium. Protein content for this potato is comparable to that of other wild and modern potato cultivars, such as *S. tuberosum*. The tuber can remain dormant for up to 14 years during drought and, if planted or allowed to grow in an Ancestral Puebloan garden, farmers could have dug and consumed the tubers even if it had not sprouted. Thus, it could have been used when maize or other cultivated crops failed.

Various glycoalkaloids are present in most potatoes, including *S. jamesii* (Savarese et al. 2009). These compounds impart a bitter taste to the tubers. The degree of bitterness is related to the glycoalkaloid content. While one might expect the glycoalkaloid content to be problematic for those who consume *S. jamesii*, methods of preparation mentioned above would neutralize the effects, such as using the mineral clay to prevent the alkaloids from being absorbed following eating. The quantity of the glycoalkaloid that is necessary to cause significant toxicity is not well described for humans. Cases of glycoalkaloid poisoning are few for *S. tuberosum*, and no quantity of potato ingested or quantity of glycoalkaloid present in those potatoes has been reported.

Conclusion

Members of the Solanaceae family provided nutrition to the early Ancestral Puebloan diet, as evidenced by the presence of seeds in fire pits and middens and by pollen grains and other microremains preserved on grinding stones and in pottery containers (Appendix A). This research adds the association of modern stands of Solanum jamesii plants with archaeological sites as another line of evidence for past use. It is likely that these plants were cultivated along with other domesticated Mesoamerican crops, both to increase their quantity and to have ready access to them. For dense human populations, the food value can be considerable. Because the tubers are able to survive underground during long periods of drought or cold, S. jamesii provides a reliable subsistence resource for human groups. The likelihood that it was cultivated is supported by the presence of extensive modern stands in and near Ancestral Puebloan ruins, especially in the arid Chaco Canyon and Mesa Verde National Park areas. Chimney Rock in southcentral Colorado is a Chaco outlier which also has potatoes that grow in check dam areas, as well as among the ruins. Given the distance from other potato stands, and Chimney Rock's montane location, it is quite likely that the potato was introduced, which is consistent with cultivation. Further evidence comes from S. jamesii tubers in one bowl in a Chaco Canyon burial and the recovery of potato "roots" (likely tubers) at Betatakin some distance away. Ancestral Puebloan populations appear to have considered wild potatoes as both a food and an important ceremonial item.

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Appendix A

Evidence for Cultivation of Wild Potato Tubers by Ancestral Puebloan Groups The Archaeological Record of Solanaceae Use

In the U.S. Southwest, ancient groups utilized numerous plants in the Solanacae family. A good example of this is the genus *Physalis* (husk tomato,

ground cherry). The widespread archaeological record of *Physalis* seeds/fruit indicates usage in a range of locations in New Mexico, Arizona, and Colorado and includes evidence of charred and uncharred seeds in storage and hearth contexts and within human coprolites as direct evidence of consumption (Adams 1988:365; Huckell and Toll 2004). Archaeological evidence is supported by frequent references to *Physalis* in the historic record of plants important to indigenous groups. For example, fruits of at least five species of *Physalis* were eaten fresh or cooked by groups from Isleta, Zuni, and Hopi Pueblos, as well as by Navajo groups and people living in Chihuahua, Mexico (summarized in Adams 1988:362–363).

Evidence of other plants in the Solanacae family has also preserved in archaeological sites. The archaeological record of wild tobacco (*Nicotiana*) seeds and other plant parts is extensive (Adams 1990; Adams and Toll 2000; Adams et al. 2015); tobacco likely represented both ritual/ceremonial and personal use. In addition, nightshade (*Solanum*) seed and tuber evidence, wolfberry (*Lycium*) seeds and fruit, and Jimsonweed (*Datura*) seeds have all been documented (Huckell and Toll 2004).

At least two examples of tuber preservation in U.S. Southwest archaeological sites are known. An early report is of a preserved *Solanum jamesii* tuber within a bowl associated with a burial from Pueblo Bonito in Chaco Canyon, NM (Judd 1954:62–63). It is possible that the tubers were included as food for the deceased during the afterlife. Although no photos or descriptions of the Chaco Canyon tubers were provided, they were identified as *S. jamesii* by Frank A. Thackery of the U.S. Department of Agriculture, who collected modern specimens and grew them out in both southern Arizona and California and reported finding up to 100 tubers on a single plant that received irregular irrigation (Judd 1954:63). The second report, from Betatakin in Navajo National Monument, AZ, indicated the presence of "edible roots, such as a species of wild potato that grows abundantly in canyons of the Kayenta district" (Judd 1931:66). Identifications of Betatakin plant specimens were made by D. N. Shoemaker of the Bureau of Plant Industry, U.S. Department of Agriculture (Judd 1931:66), who perhaps should have used the term "tubers" instead of "roots."

Identifying Seeds

The morphological and size differences in Solanaceae family seeds make it possible to tell some of them apart when recovered from an archaeological site. A photo of a number of seeds representing five genera (*Capsicum*, *Datura*, *Lycium*, *Physalis*, and *Solanum*) reveals these differences visually (Supplementary Figure 1). Generally, the seeds of *Capsicum* and *Datura* are larger and/or have different surface traits/textures than smaller wedge-shaped *Lycium* seeds. Flat, slightly asymmetrical seeds of four different *Physalis* species are fairly similar to each other. Seeds of *Solanum* species vary in size from larger *Solanum elaeagnifolium* seeds (mean length of 2.88 mm) to smaller *S. jamesii* seeds (mean length of 1.21 mm). In fact, *Solanum jamesii* seeds are essentially the smallest seeds of all those examined and compared here. Additional photos of four species of *Solanum* (*S. douglasii*, *S. jamesii*, *S. stoloniferum* [formerly *S. fendleri*], and *S. triflorum*) seeds

from plants in the University of Arizona Herbarium also display size and shape variability (Supplementary Figure 2), especially evident in a table of seed measurements (Supplementary Table 1).

Direct comparisons of ancient charred seeds in U.S. Southwest archaeological sites to this range of Solanaceae family seeds commonly shows that a designation of *Physalis* type matches well in terms of shape and size. However, the role of shrinkage during burning of Solanaceae family seeds has not been fully evaluated via controlled burning experiments, adding a potential source of size and morphological overlap between taxa when ancient specimens are charred.

Recognizing Geophytes

A geophyte is defined as "a perennial plant that bears its overwintering buds below the surface of the soil" (Gove 1986:950). Botanists characterize geophytes as those vascular plants that survive unfavorable periods by dying back to underground storage organs such as rhizomes, tubers, corms, or bulbs (Parsons 2000:39; Raunkiaer 1934; Rees 1989). Reliance on underground storage organs is common the world over, illustrated by a list of domesticated geophytes (Supplementary Table 2). *S. jamesii* tubers have been recently shown to be extraordinarily freeze tolerant (Bamberg et al. 2017).

Some wild plant tubers or tuber-like geophytes in the U.S. Southwest of interest to historic groups are listed in Supplementary Table 3. There is a high possibility that ancient groups knew of and utilized some or all of these resources as well. The extensive ethnographic record of *S. jamesii* use will be elaborated below.

Morphological and anatomical criteria used to recognize these different types of geophytes have been previously published (Adams 2013:Table 7). Distinguishing the different geophytes within archaeological sites can be difficult, especially when parts are burned and broken. As a general rule, recognition of bulbs, such as from onions and other members of the lily family (Liliaceae), appears easier than recognizing tubers or other less distinctive parts, unless preservation is excellent or plant parts are recovered within vessels or other storage features. Stem tubers and root/stolon tubers come in a wide range of shapes and sizes, but the presence of nodes (locations where stem/leaf growth begins) in stem tubers usually distinguishes them from root tubers, which lack nodes (Esau 1977).

Efforts to identify broken and charred fragments of geophytes are most advanced in archaeobotanical research that focuses on central Texas. Early efforts resulted in identifications made to broad taxonomic levels, such as "Liliaceae type bulb" and "storage root type" (Dering 1997). The "storage root type" could conceivably include enlarged root and/or stem parts of plants in more than one plant family, including the Solanaceae. Additional efforts went on to include gathering modern samples of many bulb-producing taxa, charring them, and then photographing/describing their distinctive outer bulb epidermal patterns under the Scanning Electron Microscope (Dering 2003). These efforts identify broken and charred fragments of geophytes and need to incorporate the range of geophytes known to or suspected of providing food resources to human groups in the U.S. Southwest. One example of unidentified charred "tuberous roots" comes from an archaeological site along the La Plata River in southern Colorado (Morris 1939). A number of charred specimens that appear to have eyes, scales, and clear points of attachment to stems (Morris 1939:Plate 99d) were preserved at Site 22, occupied during Basketmaker III times (\sim AD 500–700). These do not conform to the appearance of *Solanum jamesii* tubers and other possibilities include the sedge family (Cyperaceae) tubers or possibly large reedgrass (*Phragmites*) rhizomes.

Distinguishing Solanaceae Pollen Grains, Phytoliths, and Starch Microremains

Palynologists often record Solanaceae family pollen grains within archaeological sites. Gish (2000) and Cummings (2000) developed approaches for determining the presence of tobacco (*Nicotiana*) pollen grains from archaeological contexts, including assessment of the risks of modern contamination by archaeologists who smoke. Holloway and Dean (2000) and Gish (2000) also studied the pollen morphology of numerous additional Solanaceae plants within the U.S. Southwest, which indicate overlap and suggest that *Solanum* pollen grains are generally indistinguishable from those of *Physalis* (Holloway and Dean 2000:222) or from those of *Capsicum, Physalis, Chamaesaracha,* and *Margaranthus* (Gish 2000:255). All agree that the pollen grains of the *Datura* plant are among those most easily recognized.

Phytoliths and starch microremains are two additional parts that can sometimes be used to identify plants utilized in prehistory. Although some Solanaceae plant parts and tissues like leaf epidermis, xylem elements, and trichomes can form phytoliths when soluble silica polymerizes within and around such structures (Mercader et al. 2009; Morris et al. 2009), these phytoliths are not considered diagnostic of the Solanaceae (Piperno 2006). The starch microremains (granules) in potato members of the Solanaceae are generally distinguished on the basis of their large size, eccentric hila, and pronounced lamellae. Some large S. jamesii starch granules may be distinguished from S. tuberosum (the modern domesticated potato from South America) by the presence of a distinctive fissure running from the hilum toward the distal end of the granule (Louderback et al. 2016). A study of starch microremains from a range of geophytes in the early village site of Jiskairumoka, in the Titicaca Basin of southern Peru, included wild and domesticated potatoes (Solanum), plus a number of other useful tubers (Rumold and Aldenderfer 2016). This comparative study provided background for identifying cultivated potato starch from Late Archaic–Early Formative (~3400 cal BC to 1600 cal BC) periods. In the American Southwest, it is unknown if the tuber starch granules of wild Solanum jamesii can be distinguished from those of wild Solanum fendleri.

Ethnographic Record of S. jamesii Use

Ethnobotanical information obtained over the past century reveals a great interest in *S. jamesii* tubers by Native Americans. Sources are from the Hopi

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(Whiting 1939), Tewa (Robbins et al. 1916), and Navajo (Vestal 1952), among many who reference the use of the wild potato as a food eaten with "Indian clay." The Hopi used the potato by boiling and eating it, sometimes with the magnesia clay found in the southwest (Whiting 1939). The Isleta and Western Keres (Acoma, Laguna) (Swank 1932) also used the potato for food and it is listed for the western Keres as a starvation food consistent with the ability of this plant to lay dormant for a considerable amount of time (White 1945). The Tewa (Robbins 1916) are also known to have eaten these tubers.

It is interesting to note that the Ramah Navajo boiled the tuber with clay, but also stored the tuber for the winter by first sun drying and placing them in a pit (Vestal 1952). The use of clay with this potato has been mentioned as a means to counter the bitter taste from glycoalkaloids present in *S. jamesii*, as well as other wild potatoes (Savarese et al. 2009). While these glycoalkaloids are mildly toxic (Friedman et al. 2003; Johns and Duquette 1991), various animal models indicate that levels found in the *S. jamesii* would not be toxic for humans, which is supported by modern Native American consumption of the potato. Additionally, the divalent metal ions (Mg²⁺. Ca²⁺) in the clay likely chelate the alkaloids (clay contains magnesium, nickel, other divalent ions) to eliminate the bitter taste associated with the potato (Johns and Duquette 1991). Clay might also be thought of as a condiment by adding a salty taste. Eating clay or other minerals with foods is a common practice, particularly when various minerals can contribute to the nutritional status of the people (Johns and Duquette 1991).

One important aspect of *S. jamesii* collection relates to method(s) of harvest. One of our anonymous reviewers stressed that use of a wooden digging tool is common among Rio Grande Pueblo farmers. Dirt is loosened and, as tubers are collected, any "eyes" (stem buds) remaining in the soil will develop into plants. In this manner, harvest reduces competition among tubers and ensures planting of the next generation, as it would be nearly impossible to collect every available tuber fragment. Farmers would even spread remaining tuber fragments and/or intentionally bury some of them. When digging tubers, one can distinguish the following types: current season tubers; mother tubers that produced the current plant; and tubers produced in previous season(s) but that have not yet sprouted (Bamberg, personal communication, 2017).

Ortman (2012) has argued, based along linguistic lines, that the people of Mesa Verde abandoned that area and assimilated into the Pueblo groups along the Rio Grande, rather than establishing a separate settlement and maintaining their traditions. The pueblos along the Rio Grande (Tanoan/Keres speaking groups) are likely to have incorporated use of some plants and foods of the Four Corners into their own subsistence diet and activities. Historic use of *S. jamesii* may have a deep pre-Hispanic history (Wolfea et al. 1985).

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