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SHORT COMMUNICATION

Mother Tubers of Wild Potato *Solanum jamesii* can Make Shoots Five Times

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Abstract

Solanum jamesii (jam) is the only wild potato species with its natural range primarily within the USA. Its tubers are known to have unusual abilities to survive various environmental stresses. It has been observed during germplasm collecting that mother tubers (those that produced the plant) often appear to be as firm and viable as the new daughter tubers. This prompted investigation of whether such mother tubers can produce multiple seasons of shoots (after periods of intervening cool storage to simulate winter). We compared serial production of 20 cm shoots by the same tuber in subsequent seasons of a set of 162 jam populations to that of a diverse set of 75 populations of 25 other potato species in greenhouse cultivation at the US Potato Genebank. It was rare for tubers of any species other than jam to produce even two serial shoots. But over half of jam populations were able to produce four serial shoots (M4), and 14 populations produced five serial shoots (M5) with tubers remaining firm. When we looked for associated traits, M4 and M5 populations have no apparent single geographic origin or similarity by DNA markers. But natural origin sites for M4 and M5 populations were significantly associated with ancient human habitation. This work reports a new survival mechanism in potato by which a tuber does not expend all resources in maximizing new shoot growth, but instead presumably restocks itself to survive several seasons if all other reproductive options fail. Future work could study the physiological and genetic basis of the trait, and ways it could have practical benefit to the crop.

Keywords *Jamesii* · Mother tubers · Survival mechanism

Abbreviations

USPG US Potato Genebank
GRIN Germplasm Resources Information Network (https://npgsweb.ars-grin.gov/gringlobal/search)

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Introduction

In potato germplasm terminology, a mother tuber is the tuber which produced a plant. The new tubers produced by the plant are called daughter tubers. Mother tubers of cultivars planted for the crop are typically "spent" and not restocked from the plant they produced, but rather shrivel and die with no ability to produce more generations of viable shoots (Weeda et al. 2011). However, over many years of collecting tuber germplasm of the wild potato *Solanum jamesii* (jam), the authors have noticed that even tubers which produced a mature plant often remain as firm as daughter tubers, except with a slightly darker skin color. They are able to sprout and produce shoots and plants when brought back to the greenhouse at USPG.

We sought to characterize the ability of the same mother tuber to repeatedly produce shoots in the greenhouse environment. When this ability was observed, the assumption was that after the tuber fuels growth of a shoot, that shoot must then be quickly restocking the tuber with nutrients.

Assuming this also occurs in the wild, if continued growth is suddenly thwarted (perhaps by drought or grazing), the tuber could survive until a subsequent favorable season, even if no new daughter tubers or botanical seed propagules had been produced. Such a survival mechanism in potato has not been reported to our knowledge, and would add to the already extraordinary distinctions of jam as being able to remain dormant for many years (Bamberg 2010) and survive hard freezing temperatures (Bamberg et al. 2020).

Nutrients are translocated from the mother plant into daughter tubers via stolons. When the daughter tubers mature, the stolons senesce with the mother plant, and after dormancy is broken, they sprout to become mother tubers from which nutrients are mobilized and translocated to support the growth of a new plant.

Most potato tubers can produce sprouts, have those sprouts removed, and still have sufficient nutrients left in the tuber to sprout again even if the mother tuber appears quite flaccid.

In contrast, we sought a method that would test the ability of mother tubers to remain firm and viable as vegetative propagules, even after producing repeated generations of shoots of substantial size, implying that those tubers may have been restocked by the shoot. Observations in the wild suggest that a 20-cm-long shoot is quite sufficient to bear seeds and/or daughter tubers if conditions allow reproduction by those means (e.g., see GRIN 2023 for PI 686449).

Materials and Methods

Terminology. We adopted a standard notation for describing tubers using the letter "M" for "Mother" followed by the number indicating the serial generations of shoots which that tuber has produced. Thus, M0 is actually a daughter tuber that has produced zero shoots. M1 is the common situation observed, as when commercial "seed" tubers of cultivars produce a shoot only once. M2 tubers and beyond would be extraordinary.

General approach. We produced daughter tubers under uniform optimal screenhouse conditions. Then those tubers' ability to make shoots over serial generations in greenhouse trials was assessed, with a long (at least 10 months at 6 °C) cool storage period between each generation to simulate an overwintering phase. The diversity of potato species was surveyed by using a standard "mini-core" set composed of three populations of each of 25 representative species (see Hardigan et al. 2015 for details). This mini-core set coincidentally includes jam. The 162 jam populations held at USPG composed a second set for a concentrated survey of jam. Identities of all these populations are presented in Supplemental Table 1 with much additional origin and characterization data available to the reader through USPG website links (GRIN 2023) by searching on the 6-digit accession (PI) number.

Production of the original M0 test tubers. Twelve seedlings of each seedlot were grown in commercial potting medium in 16 cm clay pots in a screenhouse at USPG in the summer of 2018. Seeds were sown in early May, and tubers harvested in early October, with day length declining from about 16 to 11 h per day over the season. Tubers of all seedlings within populations were bulked into one paper bag. They were stored at room temperature for one day, then placed in a 6 C (43 °F) tuber storage. The size of wild species tubers ranged 1–2 cm in diameter; the cultivated species in the mini-core trial about 2–4 cm in diameter.

Testing of M0 and subsequent shoot production. In spring of 2019, the M0 daughter tubers were planted to produce their first shoots. For the 75 populations of 25 species in the min-core set, three M0 daughter tubers of each population were planted in each of 7 clay pots (~400 mL) in the greenhouse. All but two populations' tubers produced shoots whereupon those tubers became M1. Three firm M1 tubers were placed in the bottom of each well (~50 mL) of 50-well plastic plug trays.

For the test of 164 jam populations, three M0 tubers were placed in the bottom of the wells of 50-well plug trays. All but two populations produced shoots, whereupon tubers of those remaining 162 became M1. Shoots (and the potting medium) were removed from those M1, and they were returned to the same labeled well in the plug trays where they stayed throughout the yearly cycle of shoot grow-out, shoot and medium removal, and cold storage.

For both the mini-core set and the jam set, three firm M1 tubers of average size and free of any surface defects were placed in the bottom of each well in 50-well plastic plug trays in the spring, covered with potting medium, and placed in standard optimal greenhouse environment for tuber sprouting and growth at USPG. Shoots were allowed to grow to about 20 cm, which took about one month, at which time watering was stopped. The intent was to simulate an abrupt stress on the shoot, i.e., sudden total drought in the wild habitat. Mother tubers were harvested while shoots were still flaccid so the whole plug of rooted media with the three original tubers could be pulled out for examination. Thus, it was clear when the planted mother tubers were attached to a shoot they had produced, and there was no possibility that new daughter tubers had formed. Only firm tubers which had produced a shoot were replaced back into their original well, then trays were stored at room temperature for one day, then placed in cold storage until the next spring planting cycle was repeated. A population was considered able to advance to the next M generation if any

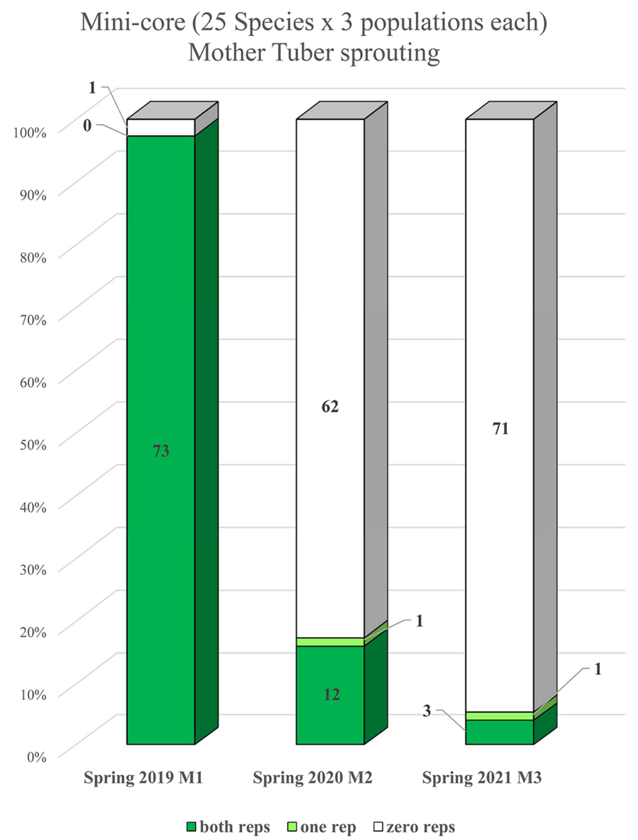

Fig. 1 Mother tuber serial sprouting potential of a spectrum of potato species tubers. Serial sprouting (of the same tuber) in duplicate trials of 75 populations of 25 species. M3 populations were *S. jamesii* 458425, 592422, 605370; and S. *pinnatisectum* 275236. See Hardigan et al. (2015) and GRIN (2023) for additional details

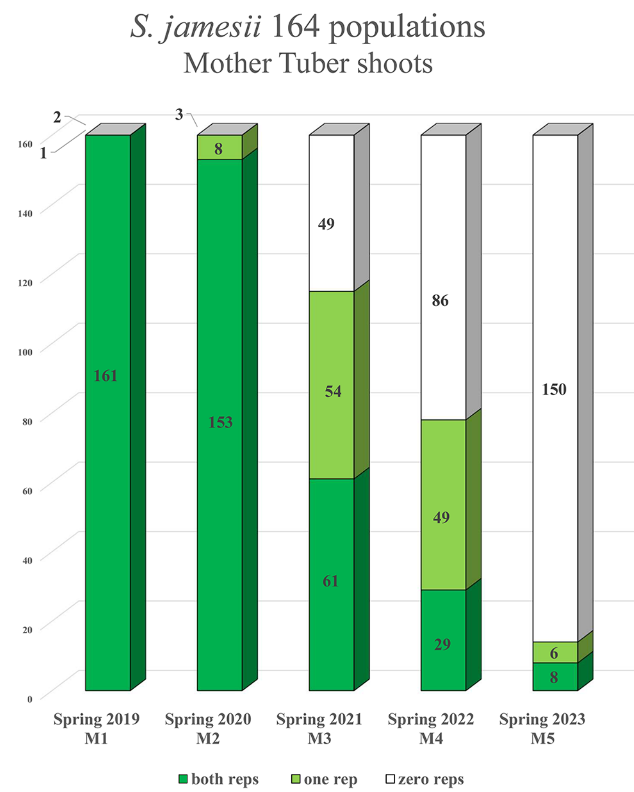

Fig. 2 Mother tuber serial sprouting potential of 164 populations of *S. jamesii.* Serial sprouting (of the same tuber) in duplicate trials. M5 populations sprouting in both reps: 458423, 592399, 595777, 595785, 605358, 612450, 612451, 676001, and in one rep: 275266, 498407, 605365, 605371, 632323, 676016. See GRIN (2023) and Supplemental data

of the three tubers advanced, and that qualitative score was recorded within two replicated sets of trays.

Assessment of jam populations that attained M4 and M5 status. Unrelated work provided AFLP marker data for many of the jam populations (Bamberg et al. 2016). This allowed comparison of populations that attained M4 and M5 status to other jam. When known, the natural origin sites of M4 and M5 jam populations were mapped to see if they originated in a common area of the jam natural range. Authors Pavlik and Louderback scored each jam population location on a 1 to 5 scale according to their knowledge of the strength of association with ancient human habitation. The criteria were: 5 = extensive dwellings and tools, 4 = dwellings and few tools, 3 = dwellings and agricultural terraces only, 2 = stone rings only, 1 = surface artifacts only, 0 = no evidence of human presence. This was done without prior knowledge of the mother tuber sprouting data.

Results and Discussion

When 75 populations in 25 representative species of the mini-core collection were tested, only 13 populations in 7 species' tubers were able to produce even one extra shoot (i.e., reach M2). This included all three representative populations of jam and *Solanum kurtzianum*, a species known to have the unusual quality of tuber frost survival (Bamberg and Lombard 2022) and two of the populations of *Solanum pinnatisectum*, a species very closely related to jam (Hardigan et al. 2015). Only jam and one tuber of one population of *S. pinnatisectum* reached M3 (Fig. 1). We concluded that survival to M3 was almost exclusively accomplished by jam, so discontinued the trial on the mini-core set.

When the set of 164 populations of jam were tested, shoot production of M0 tubers was very reliable with only 2 populations eliminated due to tubers failing to produce even one shoot. Nearly all of the 162 remaining jam reached M2 in both reps. Both reps sprouted to reach M4 for 29 populations and both reps sprouted to reach M5 for 8 populations (Fig. 2). While no side-by-side comparison could be done, and we did not measure speed of sprouting or shoot growth, there was no noticeable decline of shoot vigor over the years. Each tuber always produced a single shoot.

Previously-generated AFLP data on these jam populations (Bamberg et al. 2016) indicated over-all genetic similarity of 82%. When the similarity just among M4 jam populations and just among M5 jam populations was calculated, they were both 82%. Thus, no particular AFLP markers associated with M4 or M5 populations.

When the RANDBETWEEN function of Excel was used to pick one million sets of 14 random populations, those sets had average association with ancient habitation sites as high as the real M5 populations less than 5% of the time. This suggests that the ability of jam to have advanced mother tuber generations is associated with proximity to ancient human habitation sites. A map of the M4 and M5 jam populations with known origin locations shows they are dispersed across the natural range, but many are at sites where association with ancient human habitation is particularly strong (Fig. 3).

Conclusions and Future work. One would like to confirm these results with replication over time and with overlays of various environmental conditions– but this single test took over five years. One would also like to confirm the assumption that jam exhibits this trait in its natural environment in the wild (Fig. 4). Future work could also attempt to identify the genetic and physiological bases of the trait, which might provide some clues as to the apparent association with ancient human habitation sites. The mini-core set surveyed in this experiment is a very small representation of the whole USPG collection. More investigation could be made among the nearly 100 *S. kurtzianum* populations, since it exhibited some mother tuber potential. The genebank also has hundreds of populations of species related to jam (*S. cardiophyllum*, *S. ehrenbergii, S. lesteri, S. pinnatisectum, S. polyadenium, S. stenophyllidium, S. tarnii, S. trifidum*) which could be evaluated. Progress in hybridization of jam with cultivated forms (Bamberg et al. 2021) gives new opportunities to use jam stress tolerance mechanisms in breeding. Finally, with respect to preserving jam genetic diversity in the wild, it is reassuring to know that it can survive multiple seasons that are so unfavorable that neither seed nor typical tuber reproduction is possible.

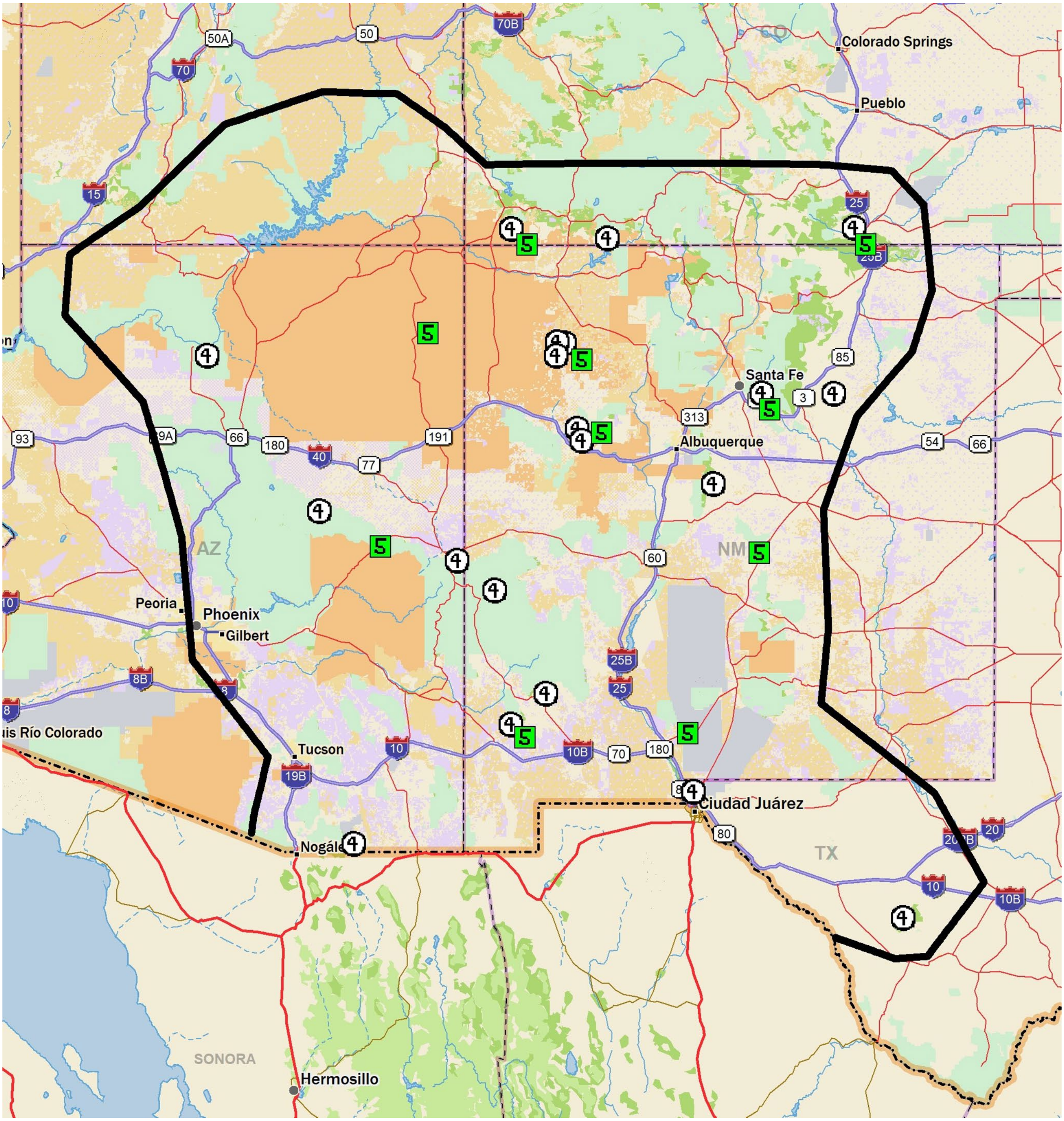

Fig. 3 Natural origin sites of *S. jamesii* M4 and M5 populations. Populations with known origin sites. Circles with "4" are (only) M4 sites; boxes with "5" are M5 sites. Black line bounds the approximate natural range of jam. Ability to produce the most years of serial sprouts is distributed across the range, but these often have a high Archeological Complexity Index of 4 or 5 (195190, 585119, 612450, 603056, 603057, 603058, 605371, 669609)

Fig. 4 *S. jamesii* in the wild showing brown mother tubers and immature white daughter tubers. PI 689431 from the banks of Cave Creek near Portal Arizona, collected after the initiation of this experiment

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s12230-023-09927-1.

Acknowledgements and Perspectives One rarely does potato germplasm research addressed by ancient philosophy. But the concept of one-chance "seeds" has been pondered for millennia as Jesus' figurative illustration that a planted seed must itself "die" in order to produce the new crop (KJV 1611). This is indeed observed with botanical seeds and typical potato tubers, but not *Solanum jamesii* mother tuber "seeds" which live on to sprout multiple times.

Declarations

Conflict of Interest The authors affirm they have no conflict of interest.

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