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RESEARCH ARTICLE

Seawater resistance in sweet potato (*Ipomoea batatas*) seeds: A key factor for natural dispersal from the Americas to Oceania

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Abstract

Sweet potato dispersal from Americas to French Polynesia predates known human colonization periods, therefore being a long-standing dilemma. According to recent phylogenetic studies, the most likely hypothesis to explain this migration is the sea-drift long-distance dispersal, but no research indicating the response of *I. batatas* seeds to seawater conditions have been performed so far. The aim of this study was to understand seawater resistance in *I. batatas*, an essential feature for the sea-drift natural dispersal hypothesis, thus shedding light on the historical biogeography of this species, which also has implications on human civilization history, as the archaeological presence of sweet potato in both continents has been used as an evidence of pre-Columbian contacts between ancient civilizations. The experiment consisted of submitting sweet potato seeds to seawater treatments and observing the respective germination rates after different periods of immersion. Subsequently, one-way ANOVAs were conducted to test for significant differences between groups. All seeds from the seawater immersion treatments germinated, which confirms that *I. batatas* seeds are resistant to seawater salinity for a period of 120 days. Our results support the sea-drift natural dispersal hypothesis, thus shedding light on part of the logical conditions for one of the major hypotheses on the historical biogeography of this species, which also plays an important role in the discussions related to prehistorical human mobility in Polynesian islands.

Highlights

- Several hypotheses try to explain the presence of pre-historical records of sweet potato in both the American continent and French Polynesia, ranging from hydrochory, zoochory, and anthropochory, the latter being a potential evidence of pre-Columbian contacts between native Americans and Polynesians.

- We tested the viability of sweet potato seeds following seawater immersion as a basic requirement for any biogeographical hypotheses involving sea-drift and seeds.

- All seeds within our trial germinated regardless of seawater immersion periods, corroborating modeling studies that estimate a 120-day seed dispersal period from the Americas to French Polynesia.

- The sweet potato's resistance to seawater is a novel feature we described for this species and substantially weakens a potential hindrance to the sea-drift natural dispersal hypothesis, being an important addition to biogeographical studies for this species. Plant science research can also benefit from our results due to potential agronomical advantages of salt-tolerant sweet potato seeds. Our results are neutral with regards to the hypothesis that presupposes a relationship between historical sweet potato presence in both continents and pre-Columbian human contacts. This could have occurred either with or without seed resistance to seawater.

Introduction

Sweet potato *(Ipomoea batatas* (L.) Lam.) is among the most important staple crops in the world, with an annual production of over a hundred million tons in 2016 (FAO 2016). This tuberous root probably originated in Central America (Zhang et al. 2000, Roullier et al. 2013) and was domesticated about 10,000 to 8,000 BP, being rapidly spread throughout

tropical America (Roullier et al. 2013) and elsewhere. Archaeobotanical records attest its presence in French Polynesian islands about 3,000 BP, in addition to other prehistorical sites in New Zealand, Hawaii, and Easter Island (Montenegro et al. 2008, Green 2005, Kirch 2000). This is an intriguing fact for biologists and anthropologists, as it was generally accepted that sweet potato was only introduced into these locations thousands of years later, during European expeditions (Montenegro et al. 2008, O'Brien 1972) or by Maori seafarers in New Zealand (Bassett et al. 2004).

Several hypotheses have been put in place to explain the ancient presence of this species in Polynesia: bird dispersal; deposition over materials that eventually floated from one continent to the other; human journeys yet unrevealed by history; or marine dispersal by seeds or capsules (Jones et al. 2011). Wallin (2014) believes that the sea-drift hypothesis can be discarded, as sweet potato propagation occurs mainly through seedlings. In addition, there is a linguistic indication of potential prehistorical human contacts, as *kumar* is the Peruvian and Ecuadorian term for sweet potato, which is very close to the Polynesian words *kumara, kumala*, and *'uala* (Teresi 2003). Ancient Polynesians were eximious sailors, having discovered many Pacific islands since their arrival in the Solomon Islands about 3,100 years ago (Burley, Weisler & Zhao 2012). Such contacts would have been made through rafts that crossed the Pacific, and Heyerdahl (1973) performed the most famous experiment exploring this possibility. Based on archaeological findings of sweet potato in both regions, he and his collaborators sailed Kon-tiki, a wood raft designed as per drafts built by South American native tribes, in a successful two-month journey from South America to Polynesia. The main problem with the human-driven dispersal of sweet potato is the timing disparity between the currently available evidence. A recent study has found a common genetic ancestry between native Polynesians and Americans, but the timing of early human contacts is estimated to be around 3,000 years ago (Ioannidis et al. 2020), which is much more recent than the archaeological findings of sweet potato in both continents. After examining cultivars from South America and Oceania, Rossel et al. (2010) did not find significant genetic association among them; instead, gene flow was found between germplasm from Oceania and Mexico, and authors suggested natural dispersal as a possibility, in accordance with other investigations (Montenegro et al. 2008, Williams et al. 1990, Gichuki et al. 2003).

Muñoz-Rodríguez et al. (2018) published research results that contradict a number of hypotheses related to sweet potato dispersal to Polynesia: whole-chloroplast and nuclear genomes used to estimate divergence times between sweet potato lineages showed that this species was present in Polynesia at least 111,500 years ago, predating human colonization and refuting all hypotheses related to human dispersal of *I. batatas*. Phylogenetic analysis of 199 individuals demonstrated that this species is monophyletic, having originated by autopolyploidy from *I. trifida* about 800,000 BP. About 50,000 years later, there was an introgression event in which an *I. batatas* lineage crossed with *I. trifida* and acquired another chloroplast genome of this species. The lineage that migrated to Polynesia does not contain this *trifida*-like chloroplast, as revealed by a study on the *I. batatas* herbarium specimen collected during the legendary Captain Cook's expedition in 1779 and analyzed through genome skimming by Muñoz-Rodríguez et al. (2018). This enabled distinguishing between lineages and estimating migration periods. The authors of that study believe that long-distance dispersal (LDD) of seeds is the most satisfactory explanation for the distribution of sweet potato in pre-historical Oceanian sites.

Seed viability following saline water exposure is a long-standing research topic; it was investigated by Darwin, who conducted experiments to understand LDD of sea-drifted seeds (Guja et al. 2013, Black 2009, Darwin 1856, 1859). There have been reports of sea-drift dispersal through seeds within the *Ipomoea* genus, including species closely related to sweet potato (Muñoz-Rodríguez et al. 2018, Miryeganeh et al. 2014, Sauer 1993). Despite the lack of information about the effects of seawater conditions on sweet potato, Montenegro et al. (2008) modeled the prehistoric arrival of sweet potato in Polynesia through marine LDD, considering that the seed movements were mainly driven by the Pacific currents and the wind, and estimated that it would take approximately 120 days for the seeds to complete the journey between the American Continent and Polynesia.

Our research aimed at testing the viability of sweet potato seeds following immersion into marine water, considering that this test has not been performed yet for this species (Montenegro et al. 2008), so there is need for additional data and analyses that may bring insights to the historical biogeography of sweet potato and its potential for hydrochory, which in turn may have evolutionary and anthropologic implications.

Our hypothesis is that seawater does not prevent seed germination, thus corroborating the argument that biogeographic migration might have occurred from America to Polynesia through flotation of seeds across the ocean. This would confirm that sweet potato seeds are resistant to marine water. On the other hand, in case no seawater resistance is confirmed, the sea-drift argument for seeds reaching Polynesia by ocean floating would be questioned, unless dispersal agents responsible for LDD or the loss of salinity tolerance during the last millennia of evolution of this species were considered.

Material and Methods

Sweet potato is within *Ipomoea,* the largest genus in Convolvulaceae, a rosid clade family mostly composed of twining, herbaceous plants (Austin 1997). Sweet potato fruits are dehiscent capsules containing from 1 to 4 hard-coated seeds that weigh ~0.2g, are 3-5 mm in diameter (Monostori 2015) (Figure 1), and usually require scarification to germinate, otherwise they are viable for over 20 years (Huaman 1999, Sauer 1993, Purseglove 1968).

This research was conducted at the Evolution Lab, Department of Genetics, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, Brazil (22°42'S, 47°38'W). A hundred and twenty sweet potato seeds belonging to gene-bank-registered landraces from the Pacific coast of South America (Table 1) were provided by the International Potato Center (CIP, Lima, Peru) and imported according to Brazilian phytosanitary standards specified in Law 10711 / 2003, Decree 5153 / 2004, and Normative Instruction 25 / 2017. Upon receipt, the seeds were randomly placed in the following groups containing 3 replicates of 10 seeds each: no immersion (control group); 30-day immersion; 75-day immersion; and 120-day immersion in seawater. The different immersion periods aimed to test the maximum seawater immersion duration in which seeds are still viable, as this can help elucidate the extent of *I. batatas* seeds maritime trajectory. Replicates were used to detect statistical error, potentially caused by genetic or physiological variation among seeds and/ or uncontrollable microenvironmental variation in the experimental conditions.

In order to test seawater resistance and potential hydrochory capacity, the methodologies used by Wu (2016) and Cordazzo (2006) were adapted to this study. Because external factors such as temperature and humidity can affect seed viability (McDonald 1999, Shaban 2013), a paleoenvironmental reconstruction of conditions at the approximate time of dispersal was performed based on data available in the literature. Seawater was collected from Ubatuba, São Paulo, Brazil (23°23'S, 44°59'W), with a sea surface salinity (SSS) that ranges between 33 and 35 ppt (parts per thousand), which is similar to the salinity of most of the West coast of the American continent (NASA 2011), from where the seeds might have started drifting.
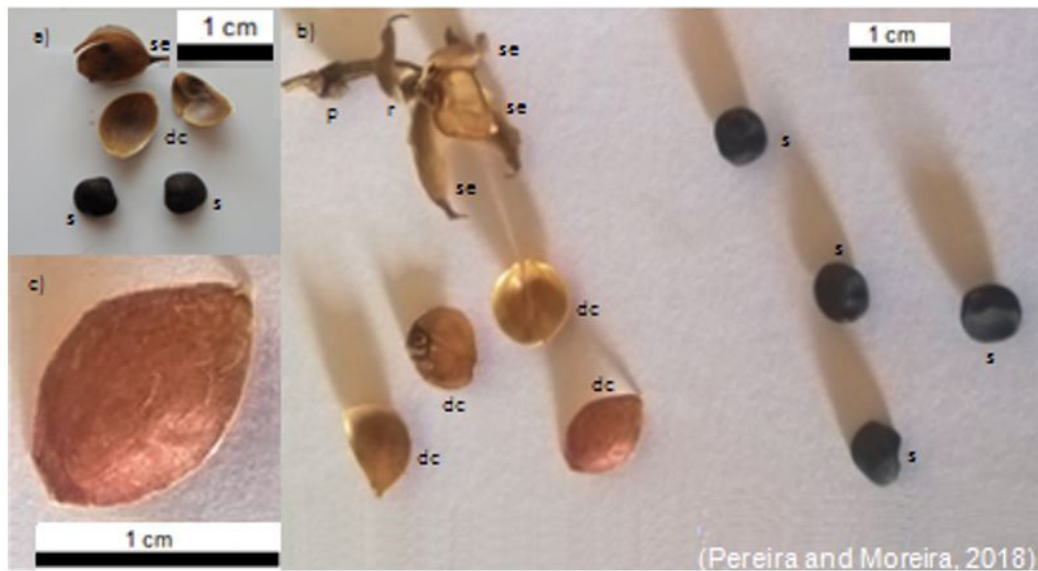

Figure 1. Sweet potato capsules and seeds. a) Dehisced capsule (dc) and two seeds (s); b) Pedicel (p), receptacle (r), sepals (se), dehisced capsules (dc), and seeds (s); c) Magnified capsule showing hairs.

Table 1. Varieties of the sweet potato seeds used in the experiment, their accession numbers, DOI (Digital Object Identifier), origin and quantities.

Accession Number	DOI	Origin	Variety	Number of Seeds
CIP 420187	10.18730/3ZPG	PER	Conchucano	9
CIP 420695	10.18730/4FA=	PER	Morado	9
CIP 420724	10.18730/4G7V	PER	Chilpe Grande	8
CIP 421792	10.18730/5F5J	PER	Japones	9
CIP 421830	10.18730/5G7F	PER	Lenguatino	8
CIP 421837	10.18730/5GDN	PER	Camote Uva	9
CIP 421861	10.18730/5H47	PER	Morado Sies Meses	9
CIP 421889	10.18730/5HSW	PER	Amarillo Claro	9
CIP 421892	10.18730/5HTX	PER	Trujillano	9
CIP 421909	10.18730/5JB9	PER	Zapallo	8
CIP 421950	10.18730/5KJB	PER	Tres Mesino	9
CIP 421952	10.18730/5KMD	PER	Blanco Huayro	8

As an attempt to keep seawater as close to natural conditions as possible, while avoiding immersed seed contamination due to the presence of potential marine microbes within the collected seawater, seawater was sterilized by a microwaving technique according to Keller et al. (1988), as other sterilization procedures can interfere significantly with the physicochemical properties of ocean water (Andersen 2005). Although we recognize that in natural conditions seeds which undergo hydrochory are exposed to and need to overcome seawater microbial contamination before reaching new landscapes, testing antimicrobial resistance in sweet potato seeds is out of the scope of this research, which specifically aims to test seawater resistance. Nine laboratory glass bottles were filled with 0.5 L of seawater and each of them was placed in a 700-W microwave oven for 10 minutes, minimum time required for sterilization (Keller et al. 1988). The following interruption times (after heating began) were considered to manually agitate the liquid and allow the contents and temperature to homogenize: 1.5 min, 3 min, 5 min, 8 min, and 10 min. This is required because microwaves reach different areas of the bottle in an uneven manner, leading to temperature gradients, and manual agitation was proven to fix such disparities and provide for complete sterilization (Keller et al. 1988). Each group of seeds was placed into the sterilized bottles filled with seawater, covered with sterilized cotton plugs to prevent microbial contamination from air movement, and stored in a sterilized chamber at 25-27 °C, which is the approximate mean annual temperature for most of the geographic areas between Mexico and French Polynesia (Levitus et al. 2005). These parameters consider that during the end of the marine isotope stage (MIS) 5e, or MIS 5.5, also called the last interglacial period (LIG), temperatures were similar to today (McKay et al. 2011, Dutton & Lambeck 2012), with a 12-hour photoperiod as the trajectory was along the Equator. The paleoenvironmental parameters used to test seawater resistance in *I. batatas* are summarized in Table 2. To prevent stagnation and simulate wave movements (Cordazzo 2006), agitation was performed by manually shaking the bottles on a daily basis. Also, the amount of seeds that remained floating or sank was noted, in addition to observations on the general aspect of the seeds, such as development of mold.

One week after the start of the experiment, a fungus infection was detected in about 5% of the immersion groups, apparently of endogenous origin. These were discarded and contents of each bottle were treated with 50 mg of nystatin (0.1% concentration) (Zanotti et al. 2012, Luz 2008) to prevent further contamination.

After the immersion periods, scarification procedures were performed as per Lebot (2009), using sand paper for 2 minutes and distilled water for a 6-hour soaking. Germination was tested in Petri dishes containing filter paper and distilled water. The seeds that germinated were counted and germination rates were calculated. Binomial error distribution and one-way ANOVA tests were performed using R software for the different immersion regimes and replicates in order to test potential statistical differences among groups regarding germination performance. The following parameters have been used: cumulative seed germination percentage (G_{max}), representing the total seeds germinated at the end of the trial (Cabra-Rivas & Castro-Díez 2016), and Timson germination index (TGI),

Table 2. Paleoenvironmental parameters used to test seawater resistance in *I. batatas* seeds. The laboratory conditions reproduced the estimated paleoconditions, which are similar to current environmental conditions, according to the "Value" column.

Parameter	Value	Paleoenvironmental Proxy	Reference
Period	~111,500 BP	• Molecular clock	Muñoz-Rodríguez *et al.*, 2018
Trajectory	Mexico – French Polynesia (5,200 km)	• Phylogenetic relationships among *I. batatas* varieties	Rossel *et al.*, 2010; Muñoz-Rodríguez *et al.*, 2018
Temperature	25-27 °C	• Luminescence of speleothems • Mg/Ca ratios in foraminifera • Alkenone unsaturation ratios (i.e., U37 k)	Dutton & Lambeck, 2012 Levitus *et al.*, 2005
Photoperiod	12h		Levitus *et al.*, 2005
pH	8.03	• Boron isotopes ($\delta^{11}B$) in biogenic carbonates • pCO_2 carbon isotopes of marine molecular biomarkers or carbonate in pedogenic minerals, or from stomatal density in leaves • CO_3^{-2} from foraminiferal shell weights and B/Ca ratios in foraminifera	Pelejero *et al.*, 2010 Key *et al.*, 2004
Sea Surface Salinity (SSS)	33-37 ppt	• Coral Sr/Ca • Coral $\delta^{18}O$	NASA, 2011 Asami *et al.*, 2013 Hay *et al.*, 2006

calculated as ΣG/T, where G refers to the percentage of seeds germinated per day and T refers to the germination period (Damalas et al. 2019).

Results

Throughout a 12-day germination period, 100% of both the immersed and control-group seeds germinated (Figure 2). A binomial error distribution test was conducted and confirmed that the sweet potato germinability in our study is within the 95% germinability rate estimated in previous studies (Lebot, 2009; P_{binom} = 1; number of successes = 76; within -3SD of 66.5 and +3SD of 77.9).

A one-way ANOVA compared the TGI between the seeds submitted to different immersion periods, all of which contained 3 petri dish replicates each (Table 3). The TGI data conformed with ANOVA assumptions, such as normality, confirmed by a Shapiro-Wilk test. With a p-value of 0.445, the ANOVA results did not show significant differences in overall germination success between seeds immersed in seawater for 30, 75, or 120 days and control group seeds, which were not immersed in seawater (Table 4).

The number of floating seeds was noted. At the beginning of the experiment, 9 seeds, or 30% of the 30-day immersion group, were floating (Figure 3), being 2 from replicate #1, 1 from replicate #2, and 6 from replicate #3. They appeared to be trapped in air bubbles, and all of them sank following agitation and did not float again throughout the experiment. By the end of the experiment, no seeds were floating.
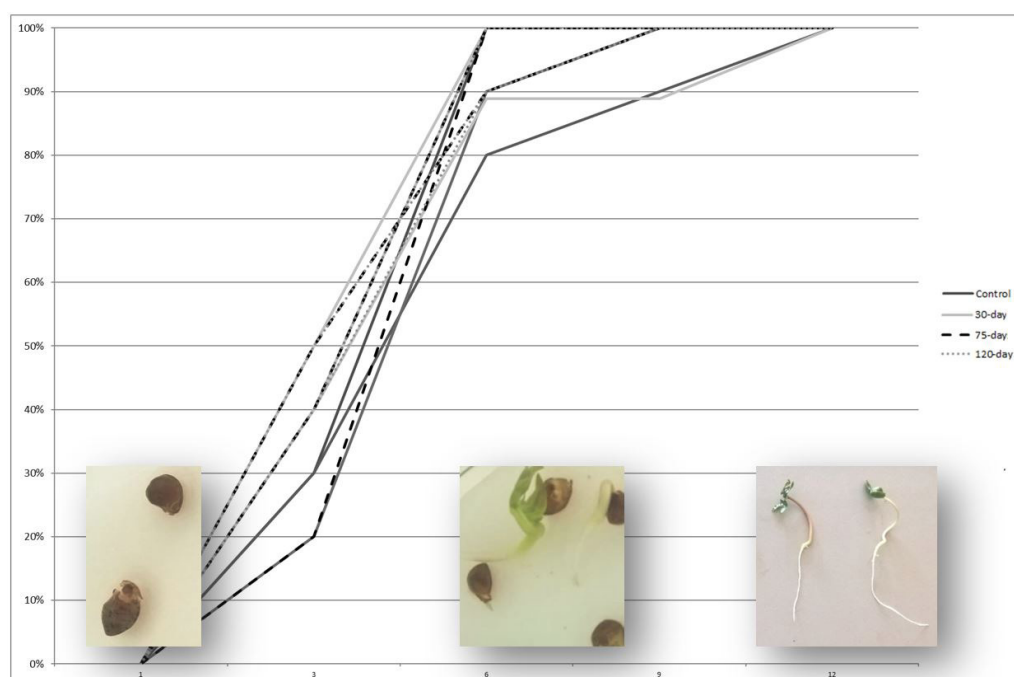

Figure 2. G_{max} (cumulative germination percentage) for control and seawater immersion treatments, during 12 days following the end of each treatment period. Each line represents a replicate. Pictures represent germination progress at the correspondent time slots of the table.

Table 3. Results calculated for cumulative seed germination percentage (Gmax) and Timson germination index (TGI) in sweet potato seeds submitted to seawater and control (no immersion) treatments.

Immersion regimen	Treatment groups	# of seeds	Gmax	TGI
No immersion	Control 1	10	100%	33%
	Control 2	10	100%	30%
	Control 3	10	100%	25%
Seawater immersion	30-day 1	8	100%	38%
	30-day 2	9	100%	26%
	30-day 3	8	100%	35%
	75-day 1	8	100%	35%
	75-day 2	9	100%	30%
	75-day 3	9	100%	34%
	120-day 1	7	100%	33%
	120-day 2	7	100%	34%
	120-day 3	9	100%	35%

Table 4. One-way ANOVA conducted to analyze the relevance of different seawater immersion periods on Timson germination index (TGI) in sweet potato seeds. No significant differences were observed between immersion regimes in terms of germination performance.

Response variable	*Explanatory variable*: Seawater immersion				
	Degrees of Freedom	Sums of Squares	Mean Squares	F value	P-value
TGI	3	0.04195	0.001398	0.99	0.445
Residuals	8	0.011293	0.001412		

Figure 3. A floating seed is indicated by the arrow in one of the bottles.

Discussion

Sweet potato has been one of the most important cultivated plants to human populations for about ten thousand years (Roullier et al. 2013), dating back to the origins of agriculture; despite its importance, the origin and biogeography of this species is just starting to be better understood. Research that brings new insights on sweet potato origin, domestication, and dispersal is not only interesting because it helps to solve a long-standing puzzle — namely, how sweet potato reached the Polynesian islands from America — but are also valuable because they help understand how plants evolved and colonized different areas of the planet. Moreover, findings related to sweet potato biogeography may shed light on human civilization history and on hypotheses of pre-historic contacts between Polynesians and Americans following sea crossings.

Recent sweet potato research shows that the presence of this species in different continents can no longer be used as evidence for pre-historic human voyages between America and Polynesia, as DNA data shows that *I. batatas* dispersal occurred at least 111,500 years ago, long before humans occupied both areas, that is, ~16,000 years BP for America and ~3,000 years BP for Polynesia (Andrew 2008, Matisoo-Smith et al. 1998), with natural dispersal being the most probable explanation for sweet potato distribution (Muñoz-Rodríguez et al. 2018). Nonetheless, according to Montenegro et al. (2008), there is no information in literature "on how capsule contact with salt or fresh water might affect seed viability", which makes estimates on "how long a capsule could remain afloat and still produce viable seeds" difficult . Our seawater tolerance results fulfill these gaps in the literature, as we confirm that 100%

of the tested seeds were able to germinate following ocean water exposure, which indicates potential for marine LDD. In addition, other *Ipomoea* species have floating seeds that can survive after being in the seawater for over 90 days (Muñoz-Rodríguez 2018, Miryeganeh et al. 2014). Animal-aided dispersal is another possibility, but no bird species travelling from America to Polynesia have been identified so far (Montenegro et al. 2008, Bulmer 1966, Zhang et al. 2004). Although sea-drift LDD seems to be the most reasonable dispersal method for this species, further evidence related to the timing of migration needs to be gathered. The divergence periods considered in the present work were estimated by Muñoz-Rodríguez et al. (2018), but some of the angiosperm fossil samples used as reference for calibrations might be younger than the actual age of the nodes they were supposed to calibrate, which in turn determined divergence periods. According to Muñoz-Rodríguez et al. (2018), the estimates of sweet potato age would be biased toward younger ages, thus not interfering with the main evidence for pre-human migration of sweet potato to Oceania. Nonetheless, for the purposes of the present study, a different migration period could represent different environmental conditions, such as temperature and seawater parameters, that should have been applied to the seeds being tested.

Regarding seed floating capacity, our experiment showed that some *I. batatas* seeds floated but sank following agitation, being able to float again when attached to an air bubble. Air bubbles integrate sea foams, a global phenomenon that may last up to a few days and consists of enriched material originated mainly from seaweed and phytoplankton being whisked with ocean water following agitation by waves and wind (Schilling & Zessner 2011). Our experiments show that sweet potato seeds might have been transported by sea foams for a limited period of time, considering the lifetime of sea foams and the density of sweet potato seeds. Seeds presenting similar shape, volume and mass as *I. batatas* have a density of ~1.35 g.cm^{-3}, which is higher than seawater density (1.025 g/cm^{-3}), thus being negatively buoyant (Ruiz-Montoya et al. 2012). Despite their lack of long term floating capacity, very small and light seeds such as *I. batatas* can be mobilized from the bottom of shallow seawaters even under moderate wave events (Ruiz-Montoya et al. 2012), and once back in the water column they can be carried by currents, animals, air bubbles, tree bark, or other natural debris. Mats of floating debris could actually have carried other sweet potato parts, such as tubers or capsules (Montenegro et al. 2008).

Another possibility is that capsules carried their seeds to Polynesia, as they float in water (Lebot 2009, Montenegro et al. 2008) due to the presence of hairs (Boland 2014; Figure 1c). In addition, the capsules provide protection to seeds against external agents, such as salinity and sources of contamination. Our research did not test capsules due to their unavailability and because *I. batatas* capsules are dehiscent, which means that during their journey in the seawater, capsules would likely dehisce as soon as they mature, thus releasing seeds into the sea. Such capsules mature between 4-6 weeks following pollination (Lebot 2009), which would not provide enough time for the closed capsule to complete the trajectory from America to Polynesia. Nonetheless, wild populations of *I. batatas* var. *apiculata* found in Mexico have indehiscent capsules, which have not opened or sank when floated in saline water for many days, and their seeds were still viable following saline water exposure (Lebot 2009, McDonald and Austin 1990). Thus, it is possible that the variety that made its way to Polynesia had indehiscent floating capsules, especially because this variety is found in Mexico, which is the most probable place of origin for *I. batatas* dispersal to Polynesia according to recent DNA analyses (Rossel et al. 2010, Muñoz-Rodríguez et al. 2018).

Montenegro et al. (2008) modeled a 120-day journey from Peru to French Polynesia for *I. batatas* capsules, but as new DNA evidence show that Mexico is the most probable departure point for the capsules or seeds, the trajectory could be reduced in about 1,000 km, which, depending on the currents, could significantly reduce the time taken to reach Polynesia. Additional modeling would be required to understand the new journey duration, providing input for future seawater testing experiments, but any journey lasting 120 days or less would be possible according to our results, as all seeds germinated across all immersion groups (30 days, 75 days, and 120 seawater immersion days). Archaeological remains of sweet potato found in Hawaii (Horrock & Rechtman 2009) corroborate a potential dispersal from Mexico to French Polynesia, as Hawaii is in the same approximate longitude as Polynesia. Our results, which demonstrate that: 1) germination rates are of 100% across all immersion and control groups; 2) seawater does not impair germination parameters such as germination speed or success rates, confirm the hypothesis that seawater does not prevent seed germination, further corroborating the argument that biogeographic migration might have occurred from America to Polynesia through flotation of seeds across the ocean.

As there is no indication of the exact time of sweet potato dispersal to Polynesia, it is not possible to be sure of the temperature the dispersed seeds were submitted to during the journey. Because of that, our experiment was conducted using the current mean annual temperatures for the tropical Pacific area, which were similar to global temperatures about 111,500 BP. Additional studies could test sweet potato seeds resistance across gradients of temperature, salinity, and pH, as such physical conditions vary along

the way from Americas to Polynesia and our study measured mean values for each parameter. Because there is no specific information for salinity at the estimated time of dispersal (111,500 BP) in the literature, estimated mean salinities at ~197,000 BP were used (Asami et al. 2013), and potential deviations from the actual salinity *I. batatas* seeds were exposed to have to be considered. More exact previsions regarding the dispersal timing of *I. batatas* to Polynesia would also allow more precise estimations of environmental conditions at the time of dispersal, such as salinity, temperature, photoperiods, and potential organisms that may have been dispersal agents.

Considering the dispersal timing provided by Muñoz-Rodríguez et al.(2018), the most probable currents that might have carried sweet potato seeds across the Pacific are the California and the Equatorial currents, as thermohaline circulation is primarily related to sea salinity and temperature (Rahmstorf 2006), in addition to sea levels (NOAA 2005), which were not too different from nowadays. As with the other environmental factors, in the case that the time of dispersion was different, sea level and currents might have been different as well, affecting the duration of the journey undertaken by sweet potato. It is also important to note that our research focused on potential abiotic stress factors for the immersed seeds, whereas in actual dispersal conditions many biotic factors might have played a role in the journey of *I. batatas* to Polynesia. *I. batatas* seeds susceptibility to both abiotic and biotic constraints could be tested in future studies with daily seawater change, avoiding the need to sterilize the seawater used in the treatments.

The origins and geographic distribution of sweet potato have interesting implications for plant science and anthropological fields of study. Our results are an important addition to this discussion: with a germination rate of 100% following seawater soaking, one potential obstacle to the sea-drift natural dispersal hypothesis is removed. Plant science implications include our novel observation that sweet potato seeds are salt-tolerant. Our findings, together with genetic and archaeological results from previous research (Williams et al. 1990, Gichuki et al. 2003, Montenegro et al. 2008, Rossel et al. 2010, Jones et al. 2011, Muñoz-Rodríguez et al. 2018), corroborate the idea that long-distance water dispersal is viable for sweet potato, further weakening correlations between the presence of this vegetable in Americas and Oceania and pre-Columbian civilization contacts. After all, it is a possibility that, for sweet potato, the eminent Kon-Tiki vessel might have been a small, rare but otherwise sturdy seed.

Acknowledgments

Data Availability Statement

Raw data were generated at the Evolution Lab, Piracicaba Campus, University of Sao Paulo. Derived data supporting the findings of this study are available from the corresponding author GCXO on request.

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