



Morphological analysis of Late Pre-Hispanic Peruvian *Chenopodium* spp.

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Abstract

Archaeologists measure features in archaeological seeds primarily to document domestication during the Neolithic period. These same methods are less frequently used to study morphological changes associated with cultural selection of landraces later in time. For example, researchers have documented domesticated forms of chenopods during the Formative period in the Andes, yet there remains very little research on postliminary chenopod morphology. In this study, I use techniques developed to understand domestication, including scanning electron microscopy, to analyse charred archaeological *Chenopodium* spp. seeds recovered from the site Ayawiri located near Puno, Peru and dated to the Late Intermediate period (AD 1100–1450), almost 4,000 years after incipient domestication of quinoa (*Chenopodium quinoa*). I found that this assemblage of chenopod seeds does not morphologically conform to modern varieties. Rather, these seeds are smaller than their modern counterparts. These findings indicate there was appreciable cultural selection of larger chenopod seed stock over the last 550 years.

Keywords Quinoa · Domestication · Andes · Late Intermediate period · Archaeobotany

Introduction

Archaeologists document morphological and micro-morphological features in archaeological seeds primarily to document domestication. They do so by measuring diachronic changes in the morphologies of seeds throughout the Neolithic period (also referred to as the Formative period in South America) (for examples of this type of research see Smith 1984; Fritz and Smith 1988; Bruno and Whitehead 2003; Willcox 2004; Fuller 2007). While this type of research provides critical insight into how humans initially established co-evolutionary relationships with plants, it is just as important to study how farmers continued to manage crop varieties later in time. Through a case study on archaeological quinoa (*Chenopodium quinoa* Willd.) dating

to over two millennia after the Formative period, I show that morphological analysis can elucidate long-term crop breeding strategies. Specifically, methods devised to study domestication can be applied to studying crop diversity, continued selection for certain traits, and seed stock management well after initial domestication of a taxon (Liu et al. 2016). This is because domestication is an on-going evolutionary process (Rindos 1984; Harris and Hillman 1989); selection for desirable traits in seed stock does not halt at the end of the Neolithic. Rather, crops continued to evolve by means of natural and cultural selection over time. Along these same lines, weeds have continued to adapt to human disturbed environments (de Wet and Harlan 1975). Indeed, across the world, selection for specific varieties continues today in the fields of traditional farmers and weeds keep evolving right alongside.

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Morphological research on archaeological seeds

Domestication and plant breeding by generations of ancient farmers made crops more congenial for humans; in other words, plants became better suited for food production and consumption that resulted in measurable changes in seed stock. For example, domestication resulted in larger seeds in many cereals and legumes because larger seeds survive

better buried deep in tilled open fields (Baskin and Baskin 2001; Fuller 2007). To study domestication syndromes, researchers primarily measure quantitative and qualitative attributes of archaeological seeds from sites throughout the Neolithic and Formative periods (for examples of this type of research on chenopods see Wilson 1981; Smith 1985a, b; Fritz 1986; Fritz and Smith 1988; Gremillion 1993a; Bruno and Whitehead 2003; Bruno 2006; Langlie et al. 2011). Indeed, documenting domestication in crops was the initial impetus for archaeobotanists to conduct morphological analysis of archaeological seeds.

Another way researchers study domestication of crops is similarly to assess the morphologies of modern seeds. They do this to look at the end-product of domestication. For example, Chiou and Hastorf (2014) measured modern chili pepper (*Capsicum* sp.) seeds to compare to archaeological specimens. Similarly, Lema et al. (2008) analysed squash (*Cucurbita* sp.) seeds. They measured micro-morphological differences in modern carbonized and uncarbonized squash seeds to distinguish if there were measurable differences between species. These studies clearly articulate significant differences in modern species, which they also assert can be used to document domestication and discern species in the archaeological record. What these studies also have in common is that they present modern specimens as a sort of idealized morphological type that all archaeological specimens are evolving towards or should conform to. In other words, ancient farmers bred these traits in their seed stock. If archaeological seeds do not conform to these proportions, then are they fully domesticated? By using modern seed specimens as a baseline, archaeobotanists (unintentionally) setup a rigid unilinear model of domestication with an end goal in mind. Our interpretations of the archaeological record, then, are distorted by implying that there is a clear evolutionary trajectory. This practice sees Neolithic period specimens somewhere along a spectrum, progressing towards modern-day seed morphologies. This leads us, myself included (see Langlie et al. 2011), to look for a specific set of characteristics that may never have been seen until the modern era. We know globalization and the industrial era wreaked havoc on native seed stocks, so these baselines may be erroneous when assessing the archaeological record.

Nonetheless, there are exceptions to these studies. For example, Willcox (2004) conducted a diachronic study on the breadth and thickness of wheat grains from Old World Neolithic sites and compared them to Chalcolithic cereal grains; however, the focus of his study was to prove domestication during the Neolithic. Rather than using modern forms, the Chalcolithic grain measurements were used as a baseline for what was considered a fully domesticated “reference set.” Willcox did not explicitly advocate establishing a pre-modern baseline, but it was a step forward in

reconceptualising the value of morphological seed analysis by archaeobotanists.

More recently, the utility of analysis of seeds after the Neolithic era is becoming increasingly popular. Ancient geneticists have a unique perspective on crop selection due to the mere fact that genes are preserved or lost in modern seed specimens. When you compare modern DNA to ancient DNA, you are assessing long-term crop selection, not just domestication. Thus, ancient geneticists have been at the forefront of studying landrace evolution through time. For example, aDNA research revealed that following the Formative period, maize (*Zea mays* L.) was exported, traded, or brought by Native Americans from Mexico to the North American southwest via a highland route about 4,000 years ago (da Fonseca et al. 2015). At the same time, maize apparently diffused northward along a lowland coastal route about 2,000 years ago. This research also demonstrated that Native Americans selected for maize drought tolerance and sugary content well after the era of incipient domestication.

On the other hand, archaeologists who study lost crops have no choice but to establish morphological thresholds for domestication status in seeds based on prehistoric assemblages. In other words, lost crops have not been cultivated in the modern era, so their domesticated forms are extinct. Subsequently, there are no modern seeds to measure; we cannot establish a baseline to compare to archaeological specimens. For example, archaeobotanists in the Old World used morphometric analysis to identify a domesticated hulled wheat variety that was grown throughout Europe and the Near East during the Neolithic and Bronze ages (Jones et al. 2000; Toulemonde et al. 2015). Research on this hulled wheat variety has focused primarily on charting the geographic diffusion and temporal presence of this crop. These data potentially provide insight into seed exchange networks, introgression, and crop breeding.

The lost crops of Eastern North America have extant feral ancestors that give us clues about their extinct domesticated relatives. Therefore researchers compare the lost crops to wild relatives in order to show morphological change associated with human selection. For example, it has been established that there are at least two varieties of *Chenopodium berlandieri* Moq. that have been documented in the archaeological record in Illinois, Kentucky, Arkansas, and the Missouri Ozarks (Fritz and Smith 1988; Gremillion 1993b; Smith and Yarnell 2009). Ongoing experiments on wild erect knotweed (*Polygonum erectum*) and analysis of archaeological specimens has elucidated how the plant was transformed through time into a delectable domesticated crop in prehistoric eastern North America (Mueller 2017).

Two recent archaeobotanical studies highlight how novel information can be gained from morphological analyses of seeds dating to after the Neolithic. Liu et al. (2016) found a decrease in grain size of several species of wheat (*Triticum*

spp.) as it spread from the Near East into China. They suggest several possibilities for a decrease in grain size including culinary preference, disease tolerance, and drought tolerance. In a similar study in the New World, Chiou et al. (2014) found considerable decreases in chili pepper seed sizes after the colonial era. They suggest there was relaxed cultural selection for large-seeded chili varieties following the Spanish conquest of South America that is attributable relaxed crop selection pressures due to population decimation and disease among the indigenous population.

Collectively, these case studies demonstrate that the same methods that we employ to study incipient domestication can be applied to study continued selection and management of crop varieties after Neolithic periods. In doing so, we may be able to pinpoint the time in prehistory when crops achieved modern proportions and morphologies, as well as management of cultivars (cultivated varieties or landraces) later in time. These methods are also well-suited for studying management of weeds during different time periods by looking at the ratio of weedy types to cultivar types. Additionally, morphological changes later in time could be traced to the introgression between crops and local wild varieties, or the selection of desired traits in cultivars such as disease or pestilence tolerance. Finally, morphological changes post-dating the Neolithic period could be associated with social or cultural interactions, socio-political transformations, seed exchange networks, or environmental changes such as drought, floods, or climate change.

Chenopods in the ancient Andes

Today, several varieties of domesticated chenopods are grown today in the Andes including numerous varieties of the globally celebrated species quinoa (*Chenopodium quinoa*) and the more drought tolerant chenopod crop called kañawa (*Chenopodium pallidicaule* Aellen). Quinoa also has a crop companion weed that is the same species but morphologically distinct known as “quinoa negra”. Quinoa and kañawa are well adapted to the inter-annual variation in the climate and the harsh ecology of the *altiplano* and were domesticated in the region approximately five and a half millennia ago (Pearsall 1992; Bruno 2006; Planella et al. 2015).

The domestication of chenopods in the south-central Andes was established by archaeobotanists who use a multivariate qualitative and quantitative approach assessing archaeological seeds (Bruno and Whitehead 2003; Bruno 2006; Langlie et al. 2011). This approach is based on chenopod studies that were initially developed by researchers working on domestication of a lost crop chenopod species in North America and relies simply on the use of measurements and assessment of attributes through low-powered binocular light microscopes (Smith 1985a, b; Fritz 1986; Fritz and Smith 1988; Gremillion 1993a; Wilson 1981).

Researchers working in both North and South America have also proven the use of scanning electron microscopy (SEM) in measuring micro-morphological attributes of seeds (Wilson 1981; Smith 1985a, b; Fritz 1986; Fritz and Smith 1988; Gremillion 1993a; Bruno and Whitehead 2003; Bruno 2006; Langlie et al. 2011). The precision afforded by SEM enables researchers to document small changes in seeds associated with the domestication processes. In the *altiplano*, these methods have been employed to study the trajectories of chenopod domestication during the Terminal Archaic and the Formative Period throughout the south-central highlands (Eisentraut 1998; Bruno and Whitehead 2003; Bruno 2006; Langlie et al. 2011). However, none of these studies looked at archaeological samples that date from after the Formative period. This means that none of these studies has looked at how farmers continued to select desirable traits and alter the morphologies of seed stock later in time.

To establish a baseline for what is considered domesticated, weedy, or wild among Andean chenopods, Bruno (2001, 2006) measured specimens of four modern varieties. The seeds she used were collected from farmers by Christine Hastorf and her students while they were carrying out archaeological investigations near Chiripa and Tiwanaku, Bolivia, over the course of several years. Bruno notes that she also collected specimens in July 2000 from Chiripa, Tiwanaku, and Achuta Grande. She notes that these specimens included two varieties of quinoa (colloquially known as “quinoa blanca” and “quinoa amarilla”). Bruno measured one modern seed of each variety. Then she charred the chenopods in a muffle furnace so that they would be comparable to archaeological specimens. Similar to studies by other researchers on chenopods (Smith 1985b; Nordstrom 1990), charring resulted in a 5% decrease in seed diameter and no change in testa thickness (Bruno 2006). Measurements of seeds provided a baseline to classify ancient Formative specimens (Bruno and Whitehead 2003). Formative period chenopods were smaller than any modern ones, but specimens possessed distinct characteristics of domestication. My colleagues and I also used Bruno’s modern baseline measurements to describe another Formative period domesticated chenopod variety from central Bolivia (Langlie et al. 2011). While these studies were initially very useful in identifying domesticated varieties in the archaeological record, it is unclear when in time chenopod seeds reached modern proportions.

What we know from this research on chenopods is that quinoa, in particular, was a staple food crop for Formative period populations residing at the ritual site Chiripa located on the southwestern shores of Lake Titicaca by 1500 BC (Bruno and Whitehead 2003), and another distinct domesticated variety was grown in the southern *altiplano* by agropastoralists living in small villages around 1200 BC (Langlie et al. 2011). As farmers intensified agricultural

production during the Formative period, the social and ritual importance of chenopods increased (Bruno and Whitehead 2003; Bruno 2014). By the Middle Horizon (AD 400–1100) power coalesced into the first local state-level urban society known as the Tiwanaku; chenopods were one of the most ubiquitous and abundant crops recovered from all archaeological contexts in the urban core of Tiwanaku (Wright et al. 2003). Chenopods continued to be a mainstay in the economy of Late Intermediate period (LIP; AD 1100–1450) domestic cuisine after the collapse of the Tiwanaku state (Langlie 2016). To date, no formal micro-morphological analysis has been undertaken on Middle Horizon, LIP, or later chenopods in the *altiplano*. What varieties or species of chenopods were eaten at Tiwanaku? How did the collapse of Tiwanaku impact the diversity of chenopod landraces? These questions will have to wait for future studies.

The aim of this study is to begin to assess cultural selection of chenopod varieties after the Formative period. This research is the first analysis of its type of Late Intermediate period chenopods in the Lake Titicaca Basin. Recently another study in Argentina examined Late Intermediate period chenopods and compared them to modern local chenopods (López and Recalde 2016), but they did not measure testa thickness. In this study, seeds from the site of Ayawiri are compared to existing datasets of *altiplano* Formative period archaeological chenopods and modern seeds. This case study links the effectiveness of using methods devised to analyse domestication of seeds to studying a broader cultural and environmental context and a longer time frame of seed stock management and cultivation practices.

In this study, *cultivation* is referred to as humans enhancing the survival of a plant, whereas *domestication* is the resultant morphological change of a plant in response to cultivation (Harris and Hillman 1989). Thus, plant breeding is a form of domestication where desired traits are inherited by each successive generation of seed stock managed and maintained by farmers. If we use this definition of domestication, then it seems logical to assess morphological change after the Neolithic era. *Weeds* are also the product of domestication because they are species that are adapted to thrive in anthropogenically disturbed environments (Harlan and de Wet 1965). Referred to as *crop companion weeds*, many crops have one or more weeds that followed parallel evolutionary trajectories adapting to cultivated fields in which their companion crops were sown.

The study site

In the south-central Peruvian Andes, peoples' lives were consumed by endemic warfare following the collapse of cultural hegemony of the Tiwanaku state (Stanish 2003; de la Vega et al. 2005; Covey 2008; Arkush 2011). Previous research in the Lake Titicaca Basin (Fig. 1) has documented

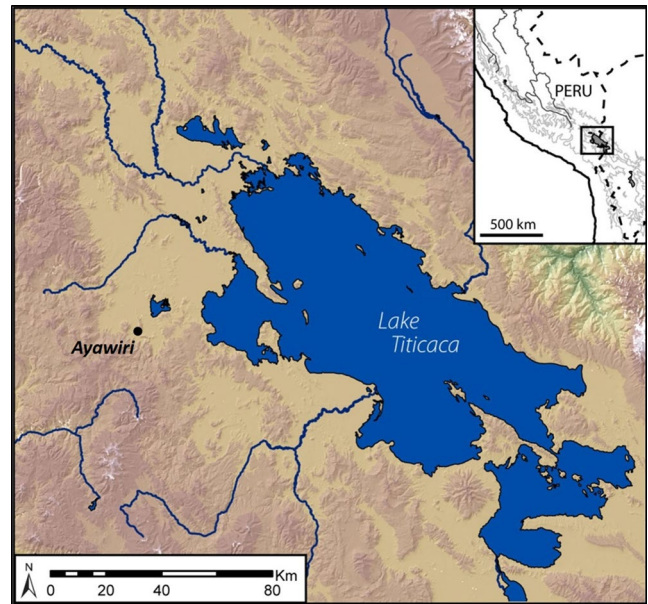


Fig. 1 Map depicting the Lake Titicaca Basin and the location of Ayawiri (rendered by E. N. Arkush)

that warfare during this time led residents in the region to relocate their residences from valley bottoms and the Tiwanaku urban core to scatter to dispersed, defensible fortified hilltop forts (Arkush 2005, 2006, 2008, 2010, 2011). At the same time, a well-documented, century-long drought certainly impacted farming strategies and threatened crop stores (Abbott et al. 1997; Thompson et al. 2000, 2003, 2006; Baker et al. 2009; Bird et al. 2011; Langlie 2016; Langlie and Arkush 2016). It has been suggested by several researchers that the drought precipitated or at least exacerbated warfare during the LIP by causing subsistence shortages throughout the highlands (Seltzer and Hastorf 1990; Stanish 2003; Calaway 2005). Nonetheless, very little research has been conducted on food and farming during the LIP in the region so we are just beginning to understand how residents adapted to this arduous time.

Ayawiri is located west of Lake Titicaca at an altitude of 4,100 m a.s.l. (Fig. 1). Carbon dates for its LIP occupation fall within the range of AD 1275 to 1500 (calibrated). From 2009 to 2014, Proyecto Machu Llaqta, directed by Elizabeth Arkush, carried out archaeological survey in the region and excavations at the site. Based on excavation data, Arkush (2017b) believes the site was rapidly abandoned around AD 1500 when aggressive Inca forces invaded the region and incorporated residents into the Inca Empire. The fortified area at Ayawiri covers over 13 hectares of the southern portion of a flat mesa (Fig. 2). The protected area of the site, located south of three stacked-stone defensive walls, includes about 120 stone-wall-enclosed compounds, within which over 670 houses and 450 small storage structures have

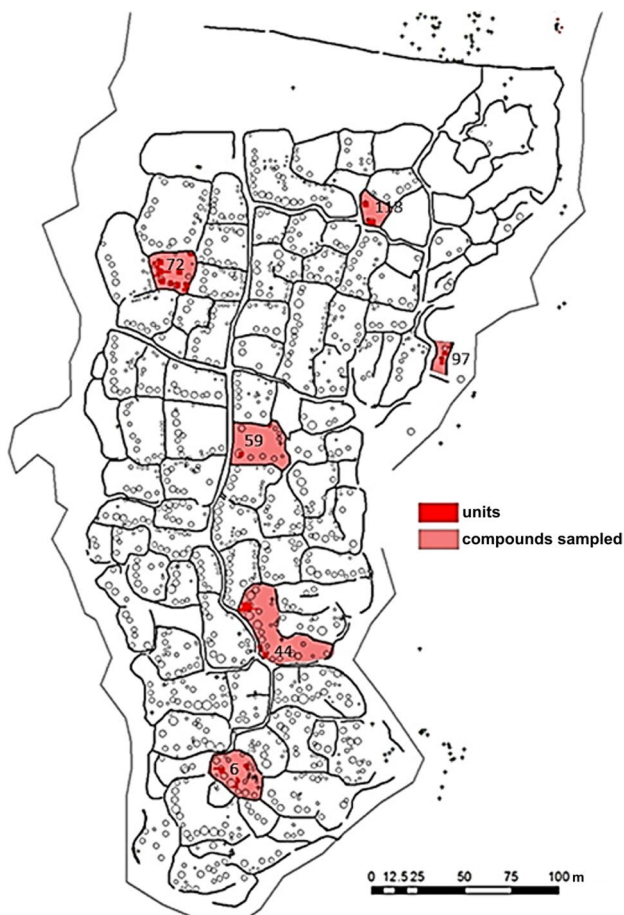


Fig. 2 Locations of excavations in the residential sector at Ayawiri (map rendered by E. N. Arkush)

been identified (Arkush 2011, 2017a). Arkush (2011) thinks upwards of 2,000 people could have lived at Ayawiri during the LIP.

Materials and methods

A total of 159 flotation soil samples, measuring approximately ten litres each, were collected at Ayawiri. In the field, these samples were processed through a modified-SMAP flotation machine. 110 flotation samples were fully sorted and analysed (for complete results of the botanical analysis see Langlie 2016). Macrobotanical samples were collected from house floors, hearths, storage pits, and middens. *Chenopodium* spp. seeds were the most abundant and ubiquitous macrobotanical remains from every context at Ayawiri. Approximately 1,035,785 chenopod seeds were identified (standardized density = 992.9 seeds/litre and 97% presence). Analysis of these palaeoethnobotanical results revealed that Ayawiri farmers were most concerned with adapting their strategies to the threat of war (Langlie 2016; Langlie and

Arkush 2016). Farmers cultivated fields near their homes and herded their llamas in nearby fields, rarely venturing far from the safety of the hillfort for subsistence needs. This ensured residents could protect their crops and livestock from the threat of enemy attack or raids. The sheer number of chenopods recovered from Ayawiri, including three caches found below house floors, gave rise to this study.

To carry out analysis of the Ayawiri chenopods, approximately 10 of the best-preserved chenopod seeds were selected from every analysed macrobotanical sample. However, when there were fewer than 10 chenopods in a sample, as many seeds as possible were analysed. Following protocols established by Bruno (2006) and Langlie et al. (2011), the seed diameter, testa thickness, testa texture, margin configuration, and beak prominence of 1,017 *Chenopodium* spp. seeds were analysed using a stereoscopic light microscope. Then, the testa thickness of 73 seeds was analysed using an SEM. These seeds were from four different contexts: two structure floors, a hearth, and a burned cache pit below a structure. SEM analysis was constrained to a sub-sample due to limited funding necessary for microscope time. A quantitative analytical procedure outlined by Bruno (2006) and Bruno and Whitehead (2003) was followed to compare seed diameter to testa thickness to further distinguish variation within the assemblage.

Measuring quantitative indices

Seed diameter

Under the selective pressures of cultivation during Formative Period, seed size of Andean chenopods has been shown to increase compared to wild species (Browman 1989, pp 143–148; Bruno 2001, 2006; Bruno and Whitehead 2003). This increase in size was the result of seedbed competition, where larger seeds out-compete smaller seeds (de Wet and Harlan 1975). Humans then harvested and sowed the larger seeds, changing the phenotype of subsequent generations of saved and sown seeds. To assess seed diameter, I used a stereoscopic light microscope with a built-in ocular micrometer and a magnification range of 10–40×. I measured the chenopod seed diameter on a horizontal plane from just adjacent to the radicle across the seed to the opposite edge (Fig. 3).

Testa thickness

The seed coat, or testa, is the membranous layer that encloses the embryo and perisperm of the seed. The testa is surrounded by a papery thin perisperm (often absent in archaeological specimens due to charring) making up the fruit wall of chenopods. It has been suggested that a decrease in relative testa thickness over time is also an indicator of human selection (Smith 1989). This idea was connected to

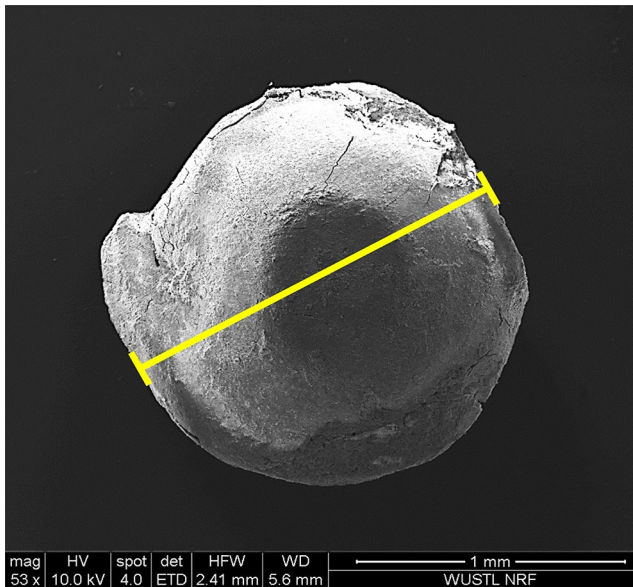


Fig. 3 SEM photograph showing where the diameter of chenopod seeds was measured

the hypothesis that the first seeds to germinate in a garden or field are ones that have thinner testae because it is easier for a radicle to bust through a thin testa. Referred to as the loss of germination inhibition (Fuller 2007), it has been suggested that this selection process took place in many crops including legumes (Plitmann and Kislev 1989) and chenopods (Fritz and Smith 1988; Bruno and Whitehead 2003). Indeed, modern testa thickness is significantly thinner in domesticated *Chenopodium* than weedy or wild varieties. Measuring a decrease in testa thickness over time has been a hallmark trait used by archaeologists to identify crop domestication. Following this line of thinking, I have also postulated that an ancient chenopod variety was domesticated based on its relative testa thickness (Langlie et al. 2011).

However, new insights and research by seed scientists deem that we re-evaluate the relationship between domestication and seed coat thickness. Growth experiments on an extinct eastern North American crop referred to as erect knotweed indicates in the wild, some plants naturally exhibit heteromorphism: one seed type sprouts quickly, where the other waits to germinate (Mueller 2017). Analysis of archaeological seeds indicates domestication resulted in a homogenous morphotype in which farmers could predict germination. Rather, in the case of erect knotweed, domestication leads to homogenous seed stock.

Research by seed scientists on quinoa also indicates that environmental conditions during embryo development impact seed dormancy and subsequently testa thickness (Ceccato et al. 2015). Under experimental conditions, quinoa testa thickness has been shown to be a product of developmental plasticity. If quinoa embryos develop under higher

temperatures and longer photoperiods (day length) then offspring have thick seed coats. If quinoa embryos develop under lower temperatures and shorter photoperiods, then offspring have thinner seed coats and lower dormancy. Thus, measuring seed coat in ancient chenopods might not give us insight into human selection for quickly germinating seeds; rather, it pinpoints the environmental conditions under which the embryo developed. These new insights mean that testa thickness probably does not predictably decrease generation after generation. Testa thickness, though, is associated with domestication. Humans sowing seeds under specific environmental conditions, as opposed to natural seed dispersal, will invariably change seed coat thickness. In natural settings chenopods seeds would disperse and embryos develop under various environmental conditions throughout the season, which should result in varying seed coat thickness of the offspring. Farmers, however, plant their fields more predictably than nature. If farmers plant seeds earlier in the season, offspring will have thicker testa. Seeds planted later in the season will have thinner testa. In a controlled setting, including ancient fields, seed coat thickness in crops should vary less resulting in reliably sprouting seeds and a homogenous harvest (Mueller 2017). On average, the seed coat of domesticated varieties should be thinner than that of weedy and wild types. Additionally, measuring seed coat thickness in palaeoethnobotanical samples is still useful because it lends insight into the environmental conditions under which seeds were sown.

To measure *testa thickness*, a sharp razor blade was used to expose a cross-section of the testa when it was not already visible. An FEI Company, Nova Nano 230 Field Emission scanning electron microscope, located in the School of Engineering at Washington University in Saint Louis, was used as well as the software measuring capabilities of this microscope to obtain testa thickness in μm (Fig. 4).

Measuring qualitative indices

Testa texture. Testa texture has been shown to co-vary with domestication status of Andean chenopod seeds (Eisentraut 1998; Bruno and Whitehead 2003; Bruno 2006). Domesticated quinoa has a smooth texture, whereas weedy and wild forms generally have textured and pitted testa surfaces (Bruno 2006). It is believed that the absence of texture in quinoa is related to its thinner seed coat (Wilson 1981). The testa texture was assessed using a stereoscopic light microscope and seeds were categorized based on three testa textures including *smooth* (lacking texture), *reticulate* (web-like), and *canaliculated* (channeled lengthwise or grooved), following Bruno (2006).

Margin configuration. A change in margin configuration has been shown to accompany changes in chenopod seed diameter and testa thickness (Smith 1984; Gremillion

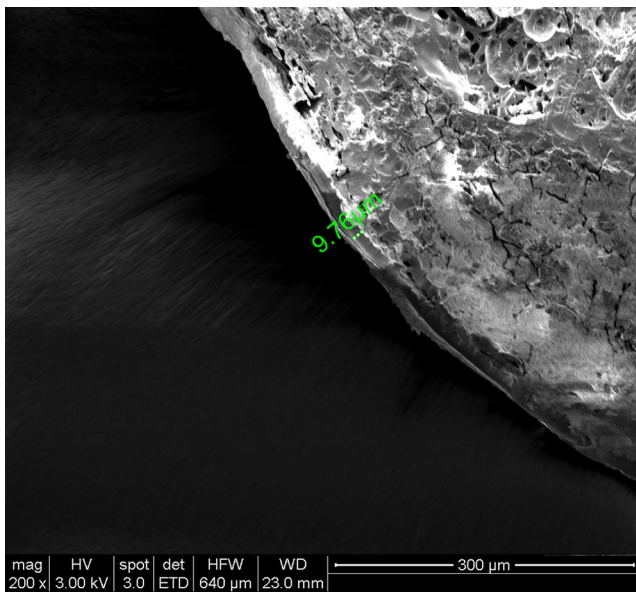


Fig. 4 SEM image of an Ayawiri archaeological example of the measurement of the thickness of a chenopod testa (9.76 μm)

1993b; Bruno and Whitehead 2003; Bruno 2006, 2008; Langlie et al. 2011). The margin configuration is described by turning a chenopod seed on its side and assessing the shape of the seed's cross-section (Fig. 5). In cross-section, thick seed coats compress the embryo and perisperm of wild and weedy chenopods, whereas thinner seed coats of domesticated chenopod varieties restrict the embryo and perisperm less. As a result, plumping of the embryo and perisperm in

domesticated varieties causes a rounded-to-truncate margin configuration in domesticated Andean chenopods (Bruno and Whitehead 2003; Langlie et al. 2011; López and Recalde 2016). The margin configuration was assessed using a stereoscopic light microscope. The seed was flipped on its side, the shape of its cross-section examined, and categorized into one of four margin configurations including *biconvex* (the two planes of the seed are convex coming to a point along the periphery where they meet), *equatorially banded* (the testa is compressed so the embryo looks like a band encircling the perisperm in cross-section), *rounded*, and *truncate* (squared off) (after Bruno and Whitehead 2003) (see Fig. 5).

Beak prominence. Beak prominence has also been shown to increase in domesticated chenopods because the embryos are restricted less by their thinner seed coats (Asch and Asch 1985; Gremillion 1993b). Beak prominence is how far the radicle extends beyond the periphery of the seed (Gordon 2006; Langlie et al. 2011). Following the same four categories of beak prominence established by Gordon (2006) in her assessment of Mesoamerican chenopods and used by Langlie et al. (2011) to assess Andean chenopods, in this study seeds were categorized as having beaks that are *very weak* (does not extend past the periphery of the seed), *weak*, *prominent*, and *very prominent* (points outward from the periphery of the seed) (see Fig. 6). Beak prominence was assessed using a stereoscopic light microscope.

While seed diameter was visible on every specimen, it was not always possible to distinguish margin configuration, seed coat texture and beak prominence due to taphonomic processes. When seeds were puffed due to conditions of the

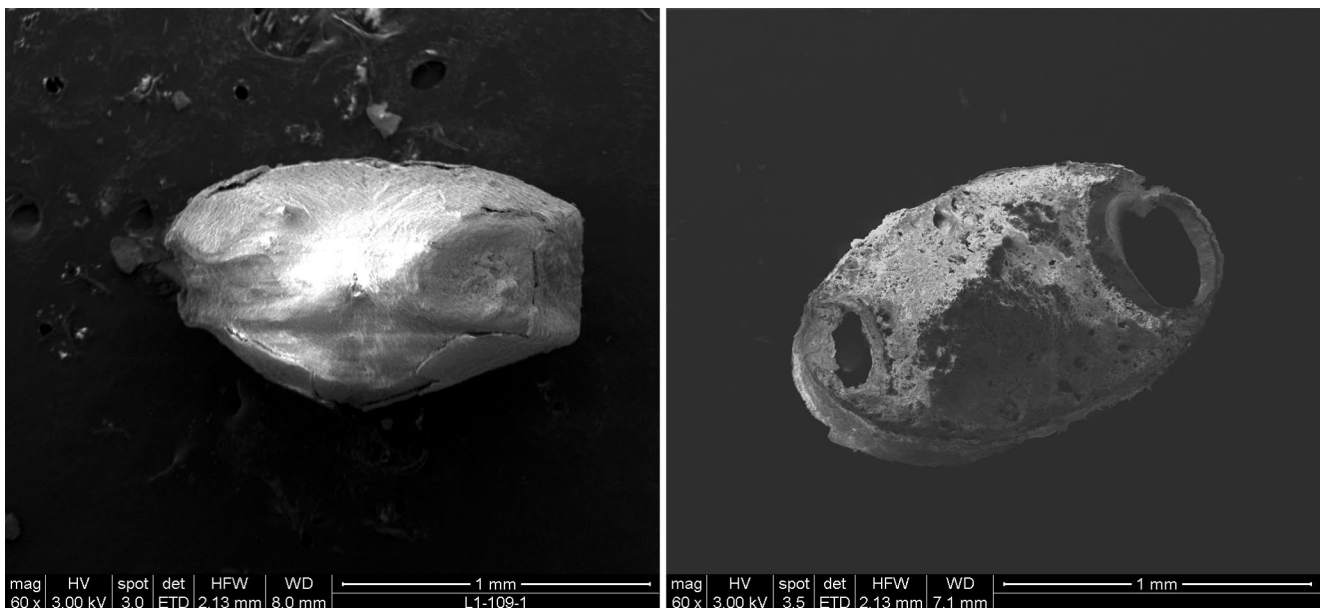


Fig. 5 SEM images of examples of the margin configuration of an Ayawiri truncate chenopod (left) and a rounded margin configuration (right) of a seed that has been sliced with a razor blade to expose its testa thickness

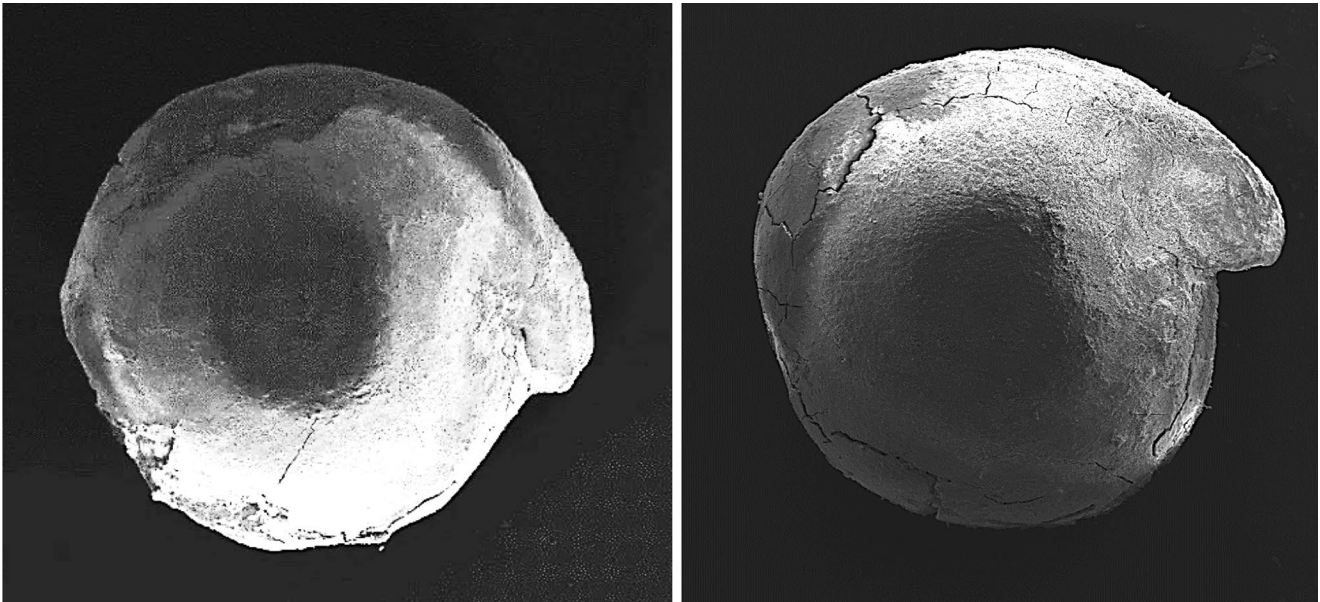


Fig. 6 SEM images of examples of Ayawiri chenopods with a weak beak (left) and a very prominent beak (right)

fire in which they were carbonized, the margin configuration was often distorted to the point where I did not feel 100% confident in its original configuration. Smith (1985b) noted that in his analysis of archaeological chenopods from eastern North America that the perisperm swelled, “popped”, and the testa ruptured, often along the margin of the fruits due to substantial charring. Nonetheless, he was still able to observe many morphological features of distorted seeds including margin configuration and seed coat thickness. In this study, seeds lacking a wholly intact testa, or that were poorly preserved, did not have a distinguishable seed coat texture. Sometimes the beak was broken off some specimens, so it was not possible to assess beak prominence. Even when the testa was just partly broken off some specimens, it was still possible to determine how far the radicle extended past the perimeter of the seed as long as the embryo was still attached to the perisperm. I observed as many attributes as I could in each seed.

It is worth noting that for the qualitative portion of this analysis, it was often hard to distinguish between the margin configuration shape and testa texture options. There are three reasons why this was probably so difficult. First, charring and puffing distort these features to varying degrees, but many seeds were in good shape. Researchers have carried out carbonization experiments on chenopods, but they did so under the controlled burning conditions of a muffle furnace (Smith 1985b; Nordstrom 1990; Bruno 2006). While these studies mention a rate of 5% shrinkage, they do not mention the impact of charring on testa texture. Furthermore, I suspect under less controlled burning conditions that qualitative features of seeds may distort. Second, the analysed features

are not discrete attributes; rather, phenotypic change is the result of evolution over time. It would thus be unsurprising to have intermediate morphological types. Third, chenopod plants are wind pollinated (Wilson 1990), so introgression between wild, weedy, and cultivated species could have an impact on seed morphology. Breeding and introgression processes could be responsible for ambiguity and overlap in these morphological features. In other words, these categories should be thought of as a continuum, morphing over generations from one shape to another through natural and cultural selection. This makes sense since human selection occurs over time and this process results in small incremental phenotypic change.

Results

The mean diameter of the 997 chenopods seeds measured in this study is 1.16 mm ($\sigma = 0.4$, min = 0.4 mm, max = 2.0 mm). However, seed diameter is strongly bimodal (Fig. 7). Due to poor preservation of morphological traits, I could only determine the margin configuration and the testa texture of 456 chenopod seeds (Fig. 8). From the chenopods for which both these traits could be distinguished, 92% have a smooth testa texture with a rounded or truncate margin configuration ($n = 419$).

The beak shape of 723 chenopods could be determined (Table 1). Of the seeds with intact beaks, 58% have prominent beaks and 29% have weak beaks.

The mean testa thickness of the 73 chenopods examined with a SEM is 8.5 μm ($\sigma = 5.8$ μm , min = 2.2 μm ,

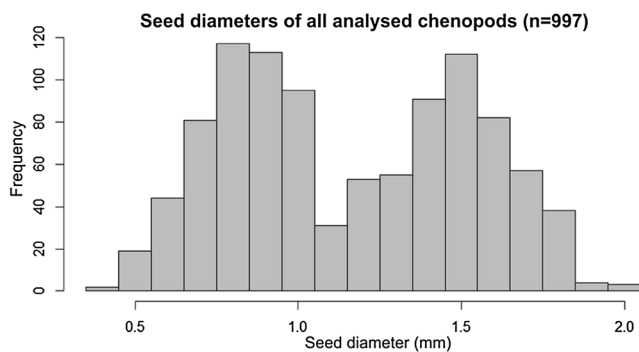


Fig. 7 Histogram of the seed diameter of Ayawiri chenopods

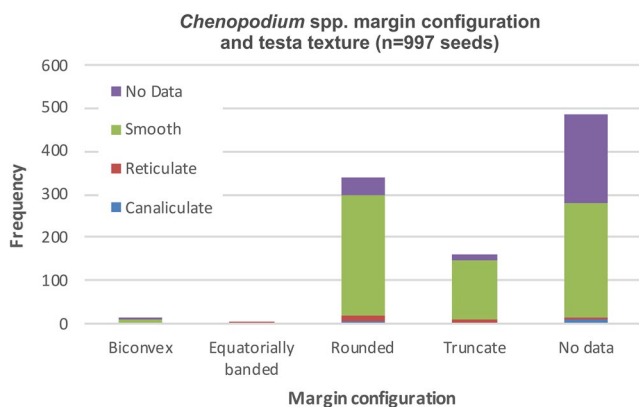


Fig. 8 Bar graph of the margin configurations compared to testa texture for Ayawiri *Chenopodium* sp. seeds

Table 1 Summary of the beak shape for Ayawiri *Chenopodium* spp. seeds

Very prominent	Prominent	Weak	Very weak	No data	Total
68	419	210	26	274	997

max = 36.8 μm). When the ratio of the testa compared to the seed diameter of chenopod seeds has been plotted (following Bruno 2006) there are two distinct clusters that generally correspond to the two clusters based on seed diameter size evident in Fig. 7.

Based on these data, there are clearly at least two distinct types of chenopods at Ayawiri. In this paper, the large type is referred to as Ayawiri Chenopod Type #1 (n = 43) and the smaller type as Ayawiri Chenopod Type #2 (n = 30). To evaluate whether seed diameter and testa thickness are statistically different between these two types, a two sample Welch's *t*-test was run twice. First, it was tested whether seed diameter was significantly different between the two chenopod types. Then, whether testa thickness was different between the two types. Both seed diameter ($t = -29.003$,

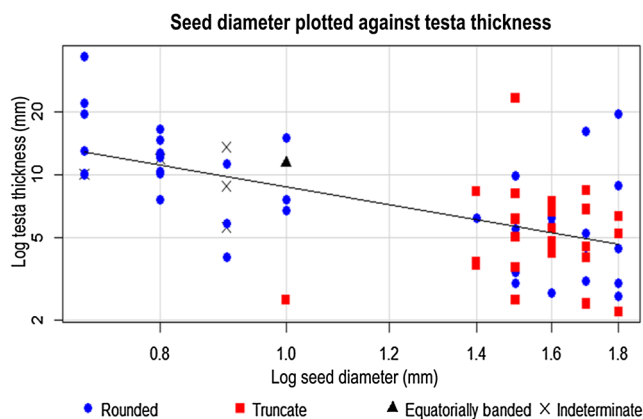


Fig. 9 Scatterplot and regression line of log testa thickness compared to log diameter of Ayawiri chenopod seeds (n = 73). The margin configuration is also plotted on this graph

$df = 69$, $p < 0.001$) and testa thickness ($t = 4.277$, $df = 47$, $p < 0.001$) are significantly different at the 0.05 level. These tests confirm that Chenopod Types #1 and Type #2 are from populations that have discretely different mean seed diameters and testa thicknesses. However, a Pearson *r* test indicates that an increase in chenopod seed diameter is only moderately correlated with a decrease in testa thickness ($r = -0.60$ based on log of seed diameter and log of total testa; also see Fig. 9 regression line). Figure 9 also indicates that Ayawiri Type #1 has a predominantly truncate margin configuration, whereas Ayawiri Chenopod Type #2 is predominantly rounded.

Comparing chenopods through time

To shed further light on these two varieties, it is useful to compare the Ayawiri chenopods with other local studies of ancient and modern chenopods in the *altiplano* (Table 2). Most of the Ayawiri chenopods have a rounded (n = 347) to truncate (n = 162) margin configuration, which previous studies indicate is associated with domesticated crop varieties. Based on margin configuration alone, there are a few specimens that may be wild or weedy types (n = 12 with a biconvex margin, and n = 1 with an equatorially banded margin).

Almost all the seeds in this study have a smooth testa texture. Based on other studies, this could indicate the Ayawiri specimens are quinoa. As previously noted, I think different burning conditions have the potential to distort testa texture. Therefore, having a smooth testa texture could simply mean seeds were distorted. It is also possible that in the archaeological past, there was more variation in testa texture of chenopods due to introgression between weedy, wild and domesticated varieties.

Table 2 Summary of the morphological features of *altiplano* chenopods

	Age	Margin	Testa texture	Beak prominence	Seed diameter (mm)	Testa thickness (μm)
Quinoa ^a	Modern	Truncate	Smooth	Prominent ^d	1.6–2.2	1.2–3.75
Quinoa Negra ^a	Modern	Biconvex ^e	Reticulate	Weak ^d	1.4–1.6	22–51
Kañawa ^a	Modern	Round	Canaliculate	Prominent ^d	0.8–1.4	4.2–7.5
Paiko ^a	Modern	Round	Punctate	Very weak ^d	0.7–1.2	11–14.5
Ayawiri #1	LIP (AD 1100–1450)	Round ^e	Smooth	Prominent ^b	1.4–1.8 ^f	2.2–23.2
Ayawiri #2	LIP (AD 1100–1450)	Truncate ^e	Smooth	Prominent ^e	0.7–1 ^c	8.8–16.4
Chiripa ^b	Middle Formative (800 BC–AD 100)	Truncate ^e	Smooth ^e	Not evaluated	1.2–1.6	3.75–31
Chiripa ^b	Early Formative II (1000–800 BC)	Biconvex ^e	Reticulate ^e	Not evaluated	0.8–1.4	14.5–34
Chiripa ^b	Early Formative I (1500–1000 BC)	Truncate ^e	Smooth ^e	Not evaluated	0.9–1.2	3.5–34
La Barca ^c	Early Formative (1500–800 BC)	Biconvex ^e	Reticulate ^e	Very prominent ^b	0.9–1.1	3.5–12.4

^aBruno 2006^bBruno and Whitehead 2003^cLanglie et al. 2011^dDetermined by Langlie based on analyses of modern specimens^eSpecimens are predominantly this shape and size, although there is some variation within each sample population^fBased on sample selected for SEM

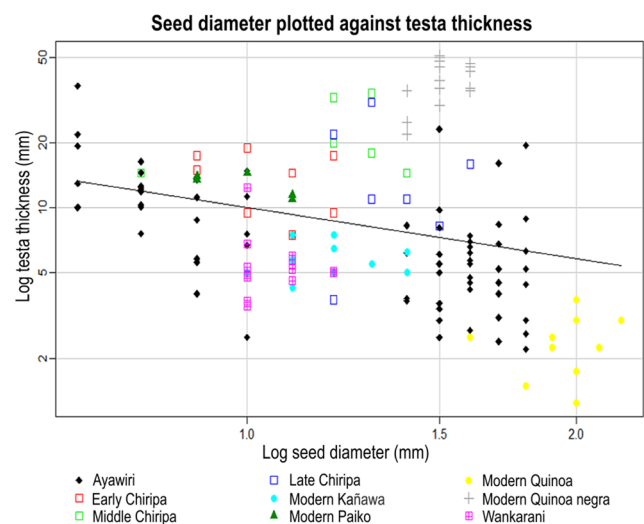
Modern chenopods were assessed to determine beak shape and these findings are included in Table 2. An image from Bruno and Whitehead (2003, Fig. 6B) indicates that quinoa negra at Chiripa also had a weak beak. Like other domesticated chenopod varieties of the past and present era, the Ayawiri chenopods generally have prominent beaks, providing further support they are crop varieties. These findings also indicate that an increase in beak prominence likely goes hand-in-hand with other domestication syndrome features in Andean chenopods.

There is much overlap in seed diameter in modern and ancient chenopod varieties from the Andes (Nordstrom 1990; Bruno and Whitehead 2003; Bruno 2008; López and Recalde 2016). This demonstrates that seed diameter alone is insufficient in the Andes to distinguish weeds from crops. The range of both Ayawiri Chenopod Type #1 and #2 overlaps with modern and ancient wild, weedy, and cultivated species. If we are to assume that these chenopods are crop varieties, then the entire range of Ayawiri Chenopod Type #1 is smaller than the range of modern quinoa; however, the average mean diameter of Ayawiri Chenopod Type #1 is slightly larger than Early Formative period chenopods found at Chiripa. The mean diameter of Ayawiri Chenopod Type #2 is also slightly smaller than modern kañawa.

Ayawiri Chenopod Type #1 seeds have testae thicknesses consistent with both quinoa and kañawa. Ayawiri Chenopod Type #2 seeds have testae thicknesses within the range of wild chenopods such as paiko, but they mostly do not have testae thicknesses as great as the crop companion

weed quinoa negra. Only one chenopod has a testa thickness within the range of that of the weed quinoa negra.

Figure 10 illustrates the ratio of testa thickness compared to seed diameter of all chenopods analysed for these variables in the *altiplano*. Ayawiri Chenopod Type #1 has a smaller diameter and thicker testa than modern quinoa, but is also larger in diameter and has a slightly thinner testa than Formative period chenopods. These findings indicate that the dimensions of Ayawiri Chenopod Type #1 are about halfway between Formative period quinoa and modern

**Fig. 10** Scatter plot and regression line of testa thickness and seed diameter of ancient and modern *altiplano* chenopods

quinoa. Ayawiri Chenopod Type #2 has a small seed diameter and thicker testa than kañawa and even the wild species paiko. These findings indicate that Ayawiri Type #2 is smaller than any archaeological variety identified as a crop, but most closely resembles kañawa.

Discussion and conclusions

Chenopod seeds with morphological features of the weed quinoa negra (thick testa, equatorially banded) were identified in less than 1% of the samples analysed. At Formative Period Chiripa, Bruno and Whitehead (2003) found higher amounts of quinoa negra in early contexts and lower amounts in later contexts. They suggest this indicates that Chiripa residents later in time meticulously weeded their fields, coinciding with agricultural intensification. The low incidence of quinoa negra type seeds in Ayawiri samples also indicates residents were probably carefully weeding their fields. It is also possible that camelids and humans may have been eating the quelites (or leaves) of quinoa negra before these plants went to seed.

Based on multiple qualitative and quantitative measurements, Ayawiri Chenopod Type #1 closely resembles quinoa. It has a rounded to truncate margin, a smooth testa texture, a prominent beak, and a low testa thickness to seed diameter ratio. Though Ayawiri Chenopod Type #1 is smaller than modern quinoa, the mean diameter is only slightly larger than archaeological quinoa specimens from the region dating to the Formative period.

Ayawiri Chenopod Type #2 has a higher testa thickness to seed diameter ratio, with truncate margin, and prominent beak. These features most closely resemble both kañawa and wild chenopods. Notably, there was a large quantity of this charred chenopod type in the cache below a house floor. This contextual information rules out the possibility that the chenopods entered the archaeological record at Ayawiri through utilitarian use or as llama forage or fodder charred and preserved through dung burning. Rather, this was likely an intentionally burnt cache of stored seed. These contextual data in concert with morphological analyses indicate that Ayawiri Chenopod Type #2 was probably kañawa. The abundance of burnt stores of this crop at Ayawiri could mean that farmers were intentionally planting drought-tolerant kañawa to cope with climate change. Indeed, climate scientists have documented a drought in local palaeoclimate proxies (Thompson et al. 2000, 2003, 2006; Calaway 2005; Baker et al. 2009; Bird et al. 2011). Nonetheless, this kañawa is still smaller than its modern relative.

There is overlap between many of the morphological features of the different types of archaeological chenopods in this study. Chenopods are wind-pollinated, so introgression between different varieties and wild varieties could have

occurred frequently. There are also pronounced disparities between these LIP chenopods and modern seeds. This could be a product of the aforementioned environmental plasticity in chenopods (Ceccato et al. 2015). In the past, it is possible that farmers planted their seeds earlier or later in the planting season resulting in less homogenous seed stock. Along the same lines, Bruno and Whitehead (2003) note sharp distinctions between Formative Period quinoa and modern specimens. They attribute this difference to human selection over time, implicitly occurring after the Formative period. However, the Ayawiri LIP chenopods do not conform to modern proportions. Both varieties of Ayawiri chenopods are smaller than their modern counterparts.

Archaeobotanical research in Peru on chili peppers indicates that modern seeds are smaller than pre-Hispanic seeds, indicating relaxed cultural selection in the modern era (Chiou et al. 2014). Researchers suggested that this trend is linked to historic population decimation of indigenous people and Spanish Colonial reformations in agricultural practice. In the case of chenopods, it seems the opposite: historic-era changes in agricultural practice are linked to intensified cultural selection pressures on quinoa varieties. In other words, cultural selection postdating the LIP resulted in the sharp disparities in morphological features between LIP and modern chenopods. Modern varieties are under cultural selection by industrial farming and global market forces. Farmers in the historic era may have sought to grow larger and quicker germinating seeds in order to sell quinoa as a cash crop that was competitive with Old World crops made available during the Colonial era. Marketing a homogenous and larger-seeded variety might have made quinoa more competitive against crops such as wheat and rice. Perhaps the current international export market preference caused these differences. *Quinoa real* is the variety marketed most commonly in grocery stores around the globe today (Jacobsen 2011) and is produced and sold in bulk. How much has the market demand driven morphological homogenization and increase in size in chenopod varieties available today? With the current data available, and a limited baseline, we can only begin to build hypotheses about the causes and pace of changes in chenopod morphology through time. Regardless of industrial and market selection pressures on seed stock, there are still at least 195 quinoa varieties grown in the Lake Titicaca Basin (Andrews 2017). Above all, this study urges the need for further analysis of chenopods throughout the prehistory and history of the Andes to better understand selection for such a plethora of quinoa varieties in the modern era.

One important finding of this research is that modern chenopods do not provide a comparative baseline or reference set for what we consider to be fully domesticated in archaeological contexts. An increase in seed size and decrease in testa thickness seems to be a drawn-out process that took

several millennia, only reaching modern morphologies since the historic era. Studying the morphological attributes of archaeological seeds after the Neolithic should not simply be done to provide a reference set or baseline for studying domestication. Rather, measuring morphological changes in seeds after the Neolithic gives insight into the selection pressures landraces were under and subsequently the cultural preference and breeding strategies of past farmers. Studies of this nature drive home the need for conducting more morphological studies of crop landraces in the Andes and elsewhere.

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