

## THE SIGNS OF MAIZE?

### A RECONSIDERATION OF WHAT $\delta^{13}\text{C}$ VALUES SAY ABOUT PALAEODIET IN THE ANDEAN REGION

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## Abstract

Palaeodietary isotope studies have long assumed C<sub>4</sub> signals in South American archaeological populations to be due to the consumption of maize (*Zea mays*), which in turn, underlie interpretations important social processes. We presents  $\delta^{13}\text{C}$  data from wild plants (n=89) from the south coast of Peru, which may have been significant in the diets of humans and animals in the past. A combination of these with previously published results from domesticates of the Andean region (n=144) brings the proportion of C<sub>4</sub> species likely to have contributed to the human dietary isotopic signal, whether directly or indirectly, to almost one third. This undermines the widespread assumption that maize is the only plant to contribute a C<sub>4</sub> signal to diets. By considering both direct and indirect routes whereby C<sub>4</sub> plants may have contributed to the human isotopic signal we show the need for a reassessment of how palaeodietary studies are interpreted in the Andes, and perhaps elsewhere in the Americas.

Keywords: Human and animal palaeodiet; Andes; C<sub>3</sub> and C<sub>4</sub> plants; wild plant use; camelids.

## Introduction

Light stable isotopes in human bone and other remains have been used to investigate the diets of past populations across the globe for over thirty years. Yet, while the Andean region is one of humanity's rare independent hearths of agriculture and the development of 'pristine' civilisation, isotopic analyses have been, as Finucane (2007:2115) notes, rather "underutilized relative to the extent of the region's archaeological remains and the number of excavations undertaken". Isotopic techniques have considerable power to provide direct evidence about human diet in the past, and thereby, to elaborate our understanding of social, agricultural and environmental changes. In the Andes this includes a more detailed understanding of the role of maize (*Zea mays*) in social complexity in the past, cohesiveness of particular groups and how extended trade or exchange networks operated. Knowledge of the underlying ecology of both fauna and flora is fundamental to interpreting human palaeodietary information because isotopic signals from plants at the base of the food chain can contribute either directly or indirectly to the human signal. In this paper we present new data on the  $\delta^{13}\text{C}$  values of plants from the Peruvian south coast and its immediate Andean hinterlands which may have entered the human food chain in various ways. In doing so we challenge the assumption that all  $\text{C}_4$  isotope signatures in humans during Andean prehistory necessarily derived uniquely from maize.

## The Importance of Maize

The role and importance of maize in Andean prehistory are among the most investigated topics using isotope analyses (Burger and van der Merwe 1990; Finucane *et al.* 2006; Finucane 2009; Goldstein 2003; Hastorf 1991; Kellner and Schoeninger 2008). Apparently domesticated originally in Meso-America (Matsuoka *et al.* 2002), maize had, by time of the Inca Late Horizon (1476-1534 A.D.), become the most important staple crop in the Andes and of pre-eminent ritual significance. As well as being the only true American cereal, maize has long been supposed the only  $\text{C}_4$  staple crop in South America so that, in principle, isotope analyses might track precisely how and when it attained its eventual paramount importance in the Andes. That importance extended beyond subsistence, for the role of maize beer (*chicha*)

in ritualised feasting seems to have lain at the heart of Andean state formation and promulgation since at least the Middle Horizon (c. 600 - 1000 A.D.) (see for instance Godelier 1977:63-69; Goldstein 2003; Hastorf and Johannessen 1993; Isbell 1988; Valdez 2006).

Many lines of archaeological evidence have been used to track the increase of maize production and consumption under such presumed state control, including: types of ceramics associated with maize consumption (Goldstein 2003); architecture in the form of plazas and storehouses (D'Altroy 2001); (re)settlement patterns (D'Altroy and Schreiber 2004); and osteological data (Kellner and Schoeninger 2008). Isotopic evidence contributes increasingly to such interpretations, through for instance, the shift to higher  $\delta^{13}\text{C}$  values for higher status individuals (e.g. Kellner and Schoeninger 2008; Slovak and Paytan 2011; Wilson *et al.* 2007), or a difference in  $\delta^{13}\text{C}$  between the sexes (Finucane *et al.* 2006; Goldstein 2003; Hastorf 1991), and inferring past animal husbandry and manuring practices (Finucane *et al.* 2006; Finucane 2007, 2009; Horn *et al.* 2009). When carbon isotopic analysis indicates a  $\text{C}_4$  input in population where maize does not grow easily, inferences have been made about trade, tribute links and mobility (Burger and van der Merwe 1990; Slovak *et al.* 2009). These all, in turn, feed into arguments for the importance of maize and the organisation and administration needed to reinforce its role.

Notably, almost all of this research assumes that virtually the only way by which a  $\text{C}_4$  signal might arise in humans in the ancient Andes is through the consumption of maize. Although problems with this assumption are now being recognised (see Gil *et al.* 2009, 2011; Llano 2009; Turner *et al.* 2010), it nonetheless remains widespread in archaeological research, so that Burger (2012:146), for instance, can still state that "in the Andes, maize was the only  $\text{C}_4$  food in the diet ... All of the other foods consumed in the central Andes are from  $\text{C}_3$  plants". We examine here the foundation of such an assumption through a new isotopic analysis of the background ecology along the *Río Ica*: one of many rivers that drain the westward slopes of the Andes into the Pacific and which were the loci for human settlement and cultural florescence throughout prehistory on the arid Peruvian coast.

## **Isotopic Background**

Palaeodietary reconstruction using light stable isotopes is based on the principle that ‘you are what you eat’ — that molecules consumed as food are incorporated into the consumer’s body tissues so that a chemical signal, passed either unchanged, or altered in a quantifiable fashion, from food into the body can provide information on diet. The natural variation in the distribution of stable isotopes of carbon, nitrogen and sulphur throughout different ecosystems makes it possible to use them as natural dietary tracers. When interpreted in relation to the isotopic signatures of available food sources, the isotopic signature of the consumer provides an objective and *direct* measure of the diet of an individual (Ambrose 1993; Lee-Thorp 2008). The carbon isotopic signature in human and animal bone collagen reflects that of the plants at the bottom of the food chain, due to isotopic discrimination during different types of plant photosynthesis (Ambrose 1993; DeNiro and Epstein 1978; Lee-Thorp 2008). Plants that use the Calvin-Benson, or C<sub>3</sub>, pathway have  $\delta^{13}\text{C}$  values typically in the range of -33‰ to -23‰, whereas plants that use the Hatch-Slack, or C<sub>4</sub>, pathway have higher  $\delta^{13}\text{C}$  values in the region of -16‰ to -9‰ (Hatch and Slack 1966; O’Leary 1988; Sharp 2007; Tieszen and Boutton 1989). Some Crassulacean Acid Metabolism (CAM) plants, notably cacti and succulents, have carbon isotopic values that can span the range of both C<sub>3</sub> and C<sub>4</sub> plants, since they can use either the C<sub>3</sub> process or a time-separated pathway similar to that of C<sub>4</sub> plants, depending on environmental conditions. The differences seen in the plant values are passed up the food chain, with only a slight fractionation for each step of approximately +1‰, enabling reconstruction of diet (DeNiro and Epstein 1978). Carbon isotopic values can also distinguish between the intake of marine versus terrestrial foods because marine environments are enriched in <sup>13</sup>C relative to terrestrial C<sub>3</sub> ecosystems (Schoeninger and DeNiro 1984; Little and Schoeninger 1995). As with the difference in plant photosynthetic pathways, the marine/terrestrial carbon-isotopic difference is passed up the food chain, and allows us to distinguish whether humans were eating marine or terrestrial foods.

It is only by characterising and understanding the isotopic signal of the flora and fauna that constitute the region under study that we are fully able to reconstruct the diet of past populations (Llano 2009). Building such a knowledge base of the isotopic distribution in modern and palaeo-ecologies of the Andean region is still at an early stage and is, moreover, no easy matter, particularly when humans have wrought changes to them over the course of many millennia.

## **Andean Resources and Isotopic Complexity**

The Andes are one of the most topographically extreme regions on Earth. Several cordilleras run north-south down the spine of South America, rising abruptly from the arid Pacific coast up to altitudes of almost 7,000 masl, before descending to the vast, flat basin of the humid Amazon to the east. Uniquely among alpine regions, the Andes also span the Tropics. Together, these circumstances entail extreme ecological diversity, with environments able to support cultivation and significant populations even at considerable altitudes. Such diversity naturally finds expression in isotopic variations of the flora (Ambrose 1993), much of which remains to be properly investigated.

To date, only two studies exist of the isotopic values of plants across the vast area of the western slopes of the Central Andes. A seminal study by DeNiro and Hastorf (1985) analysed a group of 27 different species (together with six plants identified only to genus), comprising most of the important Andean cultivars of both the central coast and highlands of Peru. All are C<sub>3</sub> plants, apart from maize. A second important study by Tieszen and Chapman (1992) selected plants for analysis at random along a transect running from the coast to the highlands (up to ca. 4,400 masl) in the Arica area of northern Chile. Of 84 plants studied, only five belong to the C<sub>4</sub> pathway and seven to the CAM pathway. Not all of the plants in this study are identified to species level.

These two studies are invariably cited by archaeological studies using isotope analyses to justify the assumption that maize is the only C<sub>4</sub> plant of significance in the Andes (e.g. Finucane *et al.* 2006; Kellner and Schoeninger 2008). White *et al.* (2009:1528), for instance, assert that “plants in Peru are dominantly C<sub>3</sub> (DeNiro and Hastorf 1985; Tieszen and Chapman 1992) and include most wild plants and grasses, vegetable cultivars, nuts and fruits”. Yet, while most cultivated plants in the Andes may be C<sub>3</sub>, the aforementioned studies have analysed only a tiny fraction of the total native Andean wild flora. They have also included certain species which evidence suggests were introduced to the region during the post-Columbian period. Moreover, since environments of high temperature and insolation and limited water supply tend to favour plants with C<sub>4</sub> photosynthetic pathways, whereas cooler, shadier and wetter environs generally favour C<sub>3</sub>

plants (e.g. Ambrose 1993; Ehleringer and Björkman 1977), one would expect considerable variation in isotopic values within the tremendous ecological diversity between coast and sierra.

Indeed, a more recent and robust study into the background isotopic ecology of the eastern side of the Andes in the Mendoza region of Argentina suggests that the proportion of C<sub>4</sub> plants may have been under-estimated in previous isotopic studies of Andean palaeodiet. Llano (2009) analysed 65 plant species along systematic transects, including wild and domesticated plants known to be important to humans in the past because of their presence in archaeological contexts, and plants known to be important in the diets of rhea (*Rhea americana*) and guanaco (*Lama guanicoe*), two important kinds of prey for human hunters. Almost half (30 of 65) of plant species analysed in that study are C<sub>4</sub>, including species from the families of Graminae, Chenopodiaceae, Asteraceae and Amaranthaceae.

Our current lack of understanding of the isotopic variation in the background ecologies of the Central Andes hinders our ability to interpret the isotopic signals of humans in prehistory in two ways. Firstly, because it has long been recognised that any dichotomy between agriculture on the one hand, and gathering or hunting wild food sources on the other, obscures a continuum along which different forms of human food procurement actually lie. In an arid environment with an intermittent and unpredictable water supply, like the Ica Valley for instance, both archaeobotanical data and ethnographic analogy suggest that gathered wild plant foods may have comprised up to 50% of the human diet, even for fully agricultural societies (see Beresford-Jones *et al.* 2011).

Secondly, the diet of animals used for meat will, in turn, be reflected in the isotopic signal of their consumers. This indirect route of isotopic signal into human tissues is often ignored and only directly consumed foods considered (e.g. Burger 2012). While the New World offered relatively few meat-producing herd animals suitable for domestication, in the Andes domestication of camelids did provide meat as well as wool and transport, thus forming a key element of the food webs that humans created and of which they were part. Guinea pigs (*Cavia porcellus*) — scavenging animals fed on food waste from households — were ubiquitous across the whole central Andean region from the first millennia BC (Stahl 2008), providing another source of meat. Moreover, the archaeological record suggests that, aside from the

extremely rich maritime resources of the Pacific Ocean, the hunting of wild animals such as guanaco, deer (*Hippocamelus* spp. and *Odocoileus virginianus*) and various kinds of birds and the gathering of land snails (*Bostryx* sp.) in *lomas* ('fog-meadow') ecologies, also provided important supplementary protein sources in the human diet.

To understand fully the isotopic signal of humans in prehistory we need to explore the isotopic variation within the full range of plants, both wild and domestic, that could contribute to human isotopic signals either directly or indirectly through the animals they consume. This paper analyses a more complete range of securely identified native flora that might have contributed to the human food chain, thereby establishing an ecological baseline for the Ica Valley, against which isotopic data from human remains may be interpreted.

## **Materials and Methods**

Our study area was the Department of Ica, on the south coast of Peru. The majority of plant material used in this study comes from the South Coast of Peru collection held at the Herbarium of the Royal Botanic Gardens Kew, (RBG Kew) London. These voucher specimens were collected according to Kew Herbarium collecting protocols (see Bridson and Forman 2010). They were subsequently identified in the Herbarium of RBG Kew, where uniquely large comparative collections, comprehensive taxonomic literature and a hub of specialists allow for a high level of species identification and, of special relevance to this study, insights into plant distribution and ecological phytogeography.

Collections were made between July 2002 and August 2008 from locations across the Department of Ica (including the Pisco, Palpa and Nazca watersheds) and into the lower western edge of the Department of Ayacucho (see Figure 1 and Beresford-Jones 2005; Whaley *et al.* 2010a; Whaley *et al.* 2010b). More specifically, collection localities included the Ica Valley and its ephemeral tributaries and *quebradas* (ravines) of the inter-Andean valleys; the riparian basins along the course of the *Río Ica* itself, including dry forest, agricultural fields and wetlands; *lomas* vegetation from the Lomas de Ullujaya y Amara rising to



almost 1,000 masl; and xerophytic cactus scrub from the dry western Andean foothills up to 2,000 masl (see Whaley *et al.* 2010a:fig. 2). The total flora of the South Coast of Peru collection currently comprises 480 identified plant species in 64 families. Nearly one third of this recorded flora of Ica is represented by plants of the grass (Gramineae) and legume (Leguminosae) families, and over half by these and four other families: Compositae, Solanaceae, Malvaceae and Cyperaceae (see Whaley *et al.* 2010a:table 1).

[Place Figure 1 around here]

Of this collection, 89 species were selected for isotopic analysis (see Table 1) because they were judged likely food or forage — eaten by humans and/or livestock and wild animals in ethnobotanical observations in Ica. The analysis excludes the most obvious Andean domesticates (such as maize) which have already been extensively analysed (DeNiro and Hastorf 1985; Tieszen and Chapman 1992). The part of the plant sampled for isotopic analysis depended on the quantities of parts (i.e. flower, seed or leaf) available. Ten additional samples of the cultivar *kiwicha* (*Amaranthus caudatus*), and six of *Atriplex rotundifolia* (a south coast endemic) were also analysed in order to investigate intra-species isotopic variation. These additional samples of the *Atriplex* and three of the *Amaranthus* were also from RBG Kew collections but from locations beyond the Ica Valley from mountainous and coastal regions of Peru and Argentina. The remaining *Amaranthus* specimens were collected in several locations in Peru in 2010.

Most samples from plant specimens (65%) were powdered using a ball mill into a fine homogenous powder to attain an average isotopic signal of the plant. The remaining samples were not powdered but sufficient material (e.g. leaf, seed or stem) cut from the plant specimen. Small amounts (approximately 0.8 mg) of the powdered or cut plant material was weighed into tin capsules. One sample of *Vallesia glabra* had glue adhering from its mounting as a botanical specimen. To remove this the sample was heated in sequentially in water, acetone, water, methanol and then water at 40°C, before being dried in an oven at 75°C to remove the solvent, before being powdered and prepared for isotopic analysis.

All samples were analysed in duplicate using a Costech elemental analyser coupled in continuous-flow mode to a Thermo Finnigan MAT253 mass spectrometer at the Godwin Laboratory, University of

Cambridge. Carbon isotopic ratios were measured on the delta scale in comparison to the international standard VPDB, in units of 'permil' (Hoefs 1997). Repeated measurements on international and in-house standards showed that the analytical error was <0.2‰.

Statistical analysis of our results show that the samples analysed are not normally distributed. Therefore we shall treat this data as non-parametric in our analysis.

## Results

We analysed 89 plant species, with  $\delta^{13}\text{C}$  values ranging from -30.8‰ to -11.9‰ (see Table 1 and Figure 2). Photosynthetic pathways had previously been identified for 58 of the species analysed (Batanouny *et al.* 1988; Beuning and Scott 2002; Cavagnaro 1988; Collins and Jones 1986; DeNiro and Hastorf 1985; Doliner and Jolliffe 1979; Hesla *et al.* 1982; Llano 2009; Mulroy and Rundel 1977; Raghavendra and Das 1978; Sage *et al.* 2007; Schulze *et al.* 1996; Smith and Brown 1973; Tieszen and Chapman 1992; Wang 2004; Watson and Dallwitz 1994). The remainder were classified as  $\text{C}_3$  or  $\text{C}_4$  according to their isotopic values.  $\delta^{13}\text{C}$  values for  $\text{C}_3$  species (n=49) ranged from -30.8‰ to -21.6‰, with a median value of -26.8‰ and IQR of 3.0‰. The  $\text{C}_4$  range was -19.3‰ to -11.9‰, with a mean of -13.9 and IQR of 3.0‰ (n=38). Those species which lie on the boundary between  $\text{C}_3$  and  $\text{C}_4$ , (i.e. those with values of -21.6‰ and -19.3‰) have previously had their photosynthetic pathways identified in the literature so that we were confident of our assignment of the remainder based on isotope value alone. We classified any species belong to the Cactaceae family as CAM plants if the pathway had not been previously identified. The two CAM species analysed had  $\delta^{13}\text{C}$  values of -14.4‰ and -13.7‰. Of all the species analysed in this study 55% were  $\text{C}_3$ , 43%  $\text{C}_4$  and 2% CAM.

[Place Figure 2 around here]

Because all the samples used here are from modern sources, we did not correct their  $\delta^{13}\text{C}$  values to account for modern atmospheric  $\text{CO}_2$  levels (Marino and McElroy 1991). While this will make some small

difference when comparing the plant isotopic baseline to archaeological data, it does not affect our purpose here to examine relative proportions of C<sub>3</sub> and C<sub>4</sub> plants.

### *Intra-species Isotopic Variation*

From the specimens analysed for intra-species variation, eleven samples of *Amaranthus caudatus* seeds had  $\delta^{13}\text{C}$  values that varied between -11.8‰ and -14.3‰. Seven samples from leaves of *Atriplex rotundifolia* had  $\delta^{13}\text{C}$  values that varied between -10.7‰ and -15.6‰ (see Table 2).

## **Discussion**

### *A Synthesis Between New and Published Data*

We can produce a more complete picture of the isotopic background of the western flanks of the south-central Andes in Pre-Columbian times by combining our new data from the Ica Valley with those of two existing published studies (DeNiro and Hastorf 1985; Tieszen and Chapman 1992). Tieszen and Chapman's data is from Arica, Chile, in the Atacama desert, some 700 km south of our study area, but nonetheless broadly complementary to our data because of similarities between the respective ecologies (Tieszen and Chapman 1992). DeNiro and Hastorf's analyses meanwhile provide data on many of the important crop plants of the Andean region (DeNiro and Hastorf 1985). While some samples in this study are from plants grown in the USA where growing conditions may produce somewhat different  $\delta^{13}\text{C}$  values to those of plants grown in the Andes, such differences would be very unlikely to confuse overall classifications as either C<sub>3</sub> or C<sub>4</sub>.

The total synthesised dataset comprises 144 different plant species. Where analysis of a plant species is duplicated across several studies we have used their mean value (see Table 1). Mean species  $\delta^{13}\text{C}$  values range from -30.8‰ to -10.7‰, encompassing C<sub>3</sub>, C<sub>4</sub> and CAM plants (see Figure 3). The range for

all C<sub>3</sub> plants (n=96) is -30.8‰ to -21.9‰, with a median of -25.7 and IQR of 3.0‰. The range of all C<sub>4</sub> plants (n=41) is -19.3‰ to -11.8‰, with a median of -13.8 and IQR of 3.0‰. The range of CAM plants (n=7) is -14.4‰ to -10.7‰ with a median of -13.2 and IQR of 3.7‰.

[Place Table 1 and Figure 3 around here]

Strikingly, all species within a family, or indeed even genus, do not necessarily share the same photosynthetic pathway. For instance, our data (see Table 1) shows both C<sub>3</sub> and C<sub>4</sub> fixation present in the genus *Cyperus* (and see also Hesla *et al.* 1982) within Cyperaceae: a family whose systematics are presently subject to ongoing revisions, especially in South America. This has also been noted for several genera in both Chenopodiaceae and Amaranthaceae (Kadereit *et al.* 2003). All of which serves to underline the importance of using taxonomically verified plant collections in isotopic analyses.

Each of the three isotopic studies synthesised here represent the isotopic background signals of western Andean flora in different ways because they each focus on particular plant groups and associations. Taken together they offer a more complete view, not only of the plants grown in the Ica valley, but also of economically important highland plants. Many of these, such as the Andean potato (*Solanum tuberosum*), were and are successfully propagated on the coast, while others may have been traded, exchanged or otherwise moved between different ecotones. There is copious evidence that the tremendous Andean topography drove such movements of products as various “institutions of Andean complementarity” (Salomon 1985:520) unfolded to harness the tremendous ecological diversity encountered within relatively short distances. Furthermore any analysis of the isotopic variation within an ecological background needs also to include the many so-called ‘wild plants’ that contributed more significantly to the diet, even of fully agricultural societies, than has been hitherto recognised in Andean studies.

A number of plants in the previously published Andean isotopic analyses have been stripped out of our synthesis here — eleven from Tieszen and Chapman’s (1992) and two from DeNiro and Hastorf’s (1985) study — some because they were introduced to the Andean region during historical times and are therefore not pertinent to the Pre-Columbian period; or, because they have been defined using names which are reclassified by botanists so that we cannot be sure of their species identity (see Table 3) for discarded

species). The botany of this vast and diverse region is itself an incomplete and ongoing matter of study. Misidentification and synonymy are recurrent problems, especially in certain families. Furthermore some large genera include undescribed, or poorly resolved, species. In short, the inclusion of either exotic or misidentified plants skews any interpretation of ancient background ecology and, consequently, palaeodiet.

[Place Table 3 around here]

We discuss next the implications of these results for understanding the isotopic signature of the Andean background ecology, and consider what they may mean for observed C<sub>4</sub> signals in humans. In doing so we consider how C<sub>4</sub> signals from a variety of food resources may be incorporated into human tissues through both direct and indirect routes.

### *The C<sub>4</sub> Signal in Andean Ecology*

Each photosynthetic pathway is represented in the combined dataset of plant species as follows: C<sub>3</sub> 67% (n=96); C<sub>4</sub> 28% (n=41); CAM 5% (n=7). Thus species belonging to the C<sub>4</sub> pathway make up almost one third of the total species analysed.

The occurrence of C<sub>4</sub> plants in the families of Gramineae, Amaranthaceae, Chenopodiaceae and Cyperaceae (see Table 4) is of particular interest because they each contain important edible species for humans as well as animals. Gramineae, the single most significant family in the flora of Ica, is composed of 75% C<sub>4</sub> species and 25% C<sub>3</sub> species in the combined data (n=40).

[Place Table 4 around here]

Our focus here is the terrestrial resources that may result in a C<sub>4</sub> isotopic signal in human tissues, but this may be complicated by the consumption of marine resources which can yield similar  $\delta^{13}\text{C}$  values. The Pacific coastline here has one of the world's richest marine ecosystems that provided the subsistence foundation of the earliest complex societies and continued to be important throughout prehistory (Moseley 1975; Quilter and Stocker 1983). While it lies beyond our scope here, it is worth noting that marine and

terrestrial components of a diet can be discriminated between by using nitrogen and sulphur isotope analysis (e.g. Goldstein 2003; Horn *et al.* 2009; Tomczak 2003).

### *Intra-species Variation*

Extreme climate conditions — such as the hyperaridity of the lower Ica Valley coast — can influence  $\delta^{13}\text{C}$  values in plants, so that these may vary between plants of the same species grown under different regimes of insolation and water availability. Ancient archaeobotanical remains may likewise show isotopic variations from modern reference materials if they grew under different ecological or climatic conditions. Our data from collections of *Amaranthus caudatus* and *Atriplex rotundifolia* in several different locations show intra-species variations which likely reflect precisely such variations in local ecological conditions (see Table 2 and Figure 4). Yet these variations are too small to confuse the broad classification of a plant's particular photosynthetic pathway (Tieszen and Boutton 1989).

[Place Table 2 and Figure 4 around here]

For instance, the standard deviations<sup>1</sup> observed in our data of  $\pm 0.7\text{‰}$  ( $1\sigma$ ) for *Amaranthus caudatus* ( $n=11$ ) and  $\pm 1.7\text{‰}$  ( $1\sigma$ ) for *Atriplex rotundifolia* ( $n=7$ ), are too small to obscure the definition of these plant species as  $\text{C}_4$ . These relatively modest isotopic variations are similar to the variations of up to 2‰ shown for maize grown under different environmental conditions (Tieszen and Fagre 1993a), and well within the  $\pm 5\text{‰}$  seen with ecological difference in other studies (e.g. Körner *et al.* 1988; Sparks and Ehleringer 1997; van de Water *et al.* 2002; Vitousek *et al.* 1988; Vitousek *et al.* 1990; Wang *et al.* 2008).

### *Indirect Consumption of $\text{C}_4$ Plants - Animals in the Food Chain*

Isotopic signals in human tissues are, in part, derived from the consumption of animals, so that  $\text{C}_4$  signals in humans may be attributable to the  $\text{C}_4$  component of the diet of those animals. The meat of

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<sup>1</sup> The data from the intra-species results is normally distributed, using a Kolmogorov-Smirnov test *Amaranthus caudatus*  $D(11)=0.10$ ,  $p>0.05$  and for *Atriplex rotundifolia*  $D(7)=0.16$ ,  $p>0.05$ , hence the use of parametric statistics here.

domesticated llama (*Lama glama*) and alpaca (*Vicugna pacos*) and hunted wild camelids together with guinea pigs and wild deer as well as bird species offered valuable sources of protein to past human societies. All of these animals may have consumed C<sub>4</sub> plants whose presence in today's ecologies and the archaeobotanical record attest to the likelihood of their incorporation in prehistoric food chains.

*Camelids.* Our understanding of the full range of ecologies across which the herding of domesticated camelids was practised in the past is still limited (Thornton *et al.* 2011). Today most takes place in specific types of pasture at altitudes above 3,800 masl. Yet models of Andean ecological complementarity hinge on the movement of camelids (Murra 1985) and patterns of transhumance between *lomas* and other much higher altitude ecotones that are still followed today (Flores Ochoa and MacQuarrie 1994). There is a considerable body of evidence for the presence of domesticated camelids on the coast in the pre-Columbian past.

Llamas are well adapted to coastal living (Wheeler 1995). Today, for instance, several generations of llamas have been raised with no signs of physiological stress in the Samaca Basin almost at sea level (pers. comm. Alberto Benavides G.). There is overwhelming archaeological and ethnographical evidence for presence of domesticated camelids on the coast and highland foothills (i.e. below 2,500 masl) (for example see Lozada *et al.* 2009; Shimada and Shimada 1985; Wheeler *et al.* 1992). Data from  $\delta^{34}\text{S}$  and  $\delta^{18}\text{O}$  analyses of archaeological camelid teeth supports the idea that camelids were raised on the coast (Horn *et al.* 2009). Camelid bone collagen and wool keratin with  $\delta^{13}\text{C}$  values ranging from -17‰ to -9‰ from a number of pre-Columbian coastal sites (DeNiro 1988; Horn *et al.* 2009; Verano and DeNiro 1993) suggests that these camelids had C<sub>4</sub> components to their diets, while those from Middle Horizon and early colonial sites at 2,500 m suggest exclusive or partial C<sub>4</sub> diets (Thornton *et al.* 2011). This is unsurprising given the abundance of C<sub>4</sub> grasses, chenopod and amaranth species, as well as CAM cacti (discussed further below) in our data from the Ica coast.

The majority of plants identified as C<sub>4</sub> in this study are from the Gramineae family. Several of these are recorded as being used for fodder for modern camelid herds, including *Distichia spicata*, *Atriplex*

*atacamensis*, *Aristida adscencionis* and *Sporobolus virginicus* (Baaijens and Veldkamp 1991; Brack Egg 1999; Holden 1991). The latter species is identified at a *lomas* site in the Chilca valley, on the north coast, dating to 7700-5000 B.P. (Weir and Dering 1986), although identification to species was tentative for the majority of specimens. On the south coast, wild grasses have been recovered archaeologically from sites in the Samaca and Ullujaya basins in the lower Ica valley, especially from Late Nasca (c.440-600 A.D.) and Middle Horizon deposits (Beresford-Jones *et al.* 2011). The archaeobotanical evidence has identified material belonging to *Cenchrus*, *Setaria* and *Eriochloa* all of which are exclusively C<sub>4</sub> genera (Smith and Brown 1973; Watson and Dallwitz 1994). Cook and Parrish (2005) record various grasses in the archaeobotanical remains from Callango, Ica Valley although not to genus. Nine out of the eleven grass species identified at Cahuachi and other Nasca period sites (Piacenza 2005) are C<sub>4</sub> (Smith and Brown 1973; Watson and Dallwitz 1994)(see also Table 1); and these too include those grasses commonly used today as fodder (Brack Egg 1999). Only two of these grasses might plausibly be found in archaeological contexts because they were used in construction — caña brava (*Gynerium sagittatum*) and *Phragmites australis* — although both are also used for fodder (Brack Egg 1999; USDA, ARS, National Genetic Resources Program 2012; Whaley *et al.* 2010b).

Other plant species also are likely to contribute to this C<sub>4</sub> signal. We have, for instance, observed guanaco in the Lomas de Ullujaya browsing on *Suaeda foliosa* (Chenopodiaceae), an unusual C<sub>4</sub> plant, confined to *lomas* locations on the south coast of Peru (and see Squeo *et al.* 2006 and Schulz *et al.* 2011 for Chilean examples). *Atriplex* spp. are also useful fodder (El Shaer 2006), almost certainly browsed by deer and guanaco as they migrate down the ephemeral streams along which *Atriplex* grows. Foddering llamas on maize after harvest is observed ethnographically (McCorkle 1987) and has been proposed to account for C<sub>4</sub> signals in archaeological camelid bones at high altitudes (Burger and van der Merwe 1990; Finucane *et al.* 2006) because above 3,000 masl C<sub>3</sub> plants predominate across those parts of the Andes that have so far been investigated (Tieszen and Boutton 1989).

These observations are all in line with Thornton *et al.*'s (2011) comprehensive review of modern camelid isotopic data from both western and eastern sides of the Andes. This shows a trend of increasing camelid  $\delta^{13}\text{C}$  values with decreasing altitude, and supports a general picture of predominately C<sub>3</sub> vegetation



at high altitudes, with increasing occurrence of C<sub>4</sub> plants with lower altitudes. Local variation in the background isotopic signatures of the flora that prevail across these vast areas remain to be investigated in any detail. Panarello and Fernández (2002), for instance, record localised C<sub>4</sub> pastures of *Muhlenbergia* sp., *Pennisetum chilensis* and *Sporobolus rigens*, at high altitudes in the *puna* (high altitude plateau) of Jujuy, Argentina, although it is not known if these are anthropogenic in origin.

The remains of guanaco are a feature of various archaeological sites in the Andes, including on the coast (Reitz 1988). Guanaco move seasonally between two distinct Andean habitats; the inter-Andean *quebradas* and the *lomas* ecosystems of the coast (pers. comm. Jane Wheeler). By contrast the much smaller vicuña (*Vicugna vicugna*) follow far less mobile lifeways and live only at high altitudes where C<sub>3</sub> vegetation predominates (Tieszen and Boutton 1989), especially the C<sub>3</sub> grass genus *Stipa* spp. According to Cajal (1989) grasses represents 87%, and shrubs and cacti 13% of the diet of guanaco, although forbs are also thought to contribute up to 44% of the diet in spring. Guanaco are known to browse on Cactaceae (Knight Piésold Consultores S.A. 2003), many of which have a  $\delta^{13}\text{C}$  value within the C<sub>4</sub> range due to the arid regions where they grow (see Table 1).

All of these considerations are potentially further complicated by the movement of goods and animals between different altitudes for which there is so much evidence in the ancient Andes. Most of these movements were articulated by llama caravans, which entail animals feeding on a variety of plants across different ecosystems. Late Horizon llama bones from Machu Picchu, for instance, show a range of  $\delta^{13}\text{C}$  values from -20.0‰ to -10.6‰ suggesting precisely such a wide ranging diet (Turner *et al.* 2010).

*Other Terrestrial Meat Sources.* Other potential terrestrial sources of meat in the Andes included domesticated guinea pigs and wild deer. The former are often fed kitchen scraps and so their isotopic signatures are likely to reflect human diets. Archaeological data from Conchopata in the Ayacucho highlands show a wide range of  $\delta^{13}\text{C}$  values for guinea pigs (Finucane *et al.* 2006) in which high C<sub>4</sub> signals are again interpreted as evidence of maize consumption. However, we show shortly there are a number of

other possible C<sub>4</sub> sources which may be consumed by humans and then by way of scraps to guinea pigs, thereby entering the food chain twice — once directly and once indirectly.

There are two genera of deer in the Andes: *Hippocamelus* spp. of the high sierra and white tailed deer (*Odocoileus virginianus*) of the coast. Rostworowski (1981) reports that the meat of the former, like that of the wild vicuña, has a disagreeable flavour due to its diet of *ichu* grass (*Stipa ichu*). The coastal *Odocoileus*, by contrast, is regarded as highly edible. Although today restricted mainly to the inter-Andean valleys (Emmons 1990), early Spanish chronicles report that coastal woodlands once teemed with *Odocoileus* (see for instance Cieza de León [1553] 1955:203). Deer and deer hunting are depicted in the iconography of various coastal cultures, most notably Moche (100-800 A.D.), and *Odocoileus* remains are identified in coastal zooarchaeological assemblages (Reitz 1988). Isotopic analyses of deer have not yet been carried out in the Andes but, especially on the coast, their diet might reasonably be expected to approximate to that of the coastal guanaco and to include seasonally a significant C<sub>4</sub> component.

Finally, land snails (*Bostryx* sp.) are a conspicuous feature of many archaeological midden deposits on the south coast of Peru. These snails were gathered in lomas ecologies (see Beresford-Jones *et al.* 2011; Golte 2009:fig 6.19), where various C<sub>4</sub> plants likely comprised their fodder, mostly notably the shoots of *Atriplex* spp., in which we observe them aestivating in the Lomas de Ullujaya.

In sum there is a wealth of evidence that, in the past, C<sub>4</sub> plants likely comprised a significant proportion of the diets of wild and domesticated camelids and other animals such as guinea pig and deer. That proportion will have varied depending upon animal movement and the seasonal availability of C<sub>4</sub> and C<sub>3</sub> plant fodder, but may well have contributed some significant C<sub>4</sub> isotopic signal to human consumers of these animals in the past.

#### *C<sub>4</sub> Foods - Direct Consumption*

*‘Wild’ Plants.* While the majority of archaeological Andean populations investigated through isotopic analyses were agriculturalists, the potential contribution of wild plants to their diets should not be ignored. This is true everywhere but nowhere more so than on the arid and semi-arid western slopes of the Andes, firstly because the water sources upon which irrigation agriculture depends are highly seasonal and erratic, and secondly because a particularly high proportion of its desert flora is edible by humans (see Beresford-Jones 2011).

Both archaeobotanical and ethnographic evidence attest to the importance of gathered wild plant resources in the Ica Valley (see Beresford-Jones *et al.* 2011). Based on that evidence, we have argued elsewhere that even the fully agricultural pre-Hispanic societies of the south coast of Peru relied on gathered wild plants for up to half of their diet: an estimate reflected in almost all the available archaeobotanical data from the south coast of Peru (see Beresford-Jones 2011; Cook and Parrish 2005; Piacenza 2005; Roque *et al.* 2003; Silverman 1993). The most important of these edible wild plant food resources come from the families of Leguminosae, Solanaceae, Cyperaceae, Cactaceae, Chenopodiaceae and Amaranthaceae: all of which are represented in our isotopic analyses presented here. Of these, the latter four families all include important C<sub>4</sub> or CAM species.

Several species of Cyperaceae (‘sedge family’) have starchy rhizomes which have provided valuable food for humans in the past in various parts of the world in the past, including in the Andean region (Brack Egg 1999). Various sedges have been identified in the Andean archaeobotanical record (Roque *et al.* 2003; Towle 1961; Weir and Dering 1986), including in human coprolites (Holden 1991). Our Ica Valley isotopic data shows that the Cyperaceae family includes both C<sub>3</sub> and C<sub>4</sub> edible species, such as *Cyperus oderatus* and *Cyperus rotundus* (both C<sub>4</sub>) and *Schoenoplectus americanus* (C<sub>3</sub>).

Cactaceae are CAM plants which might also contribute to what may be interpreted as a C<sub>4</sub> signal for they can use different photosynthetic pathways depending on water availability and evaporation rates. In very arid conditions, such as that of the south coast of Peru, cacti are likely to have  $\delta^{13}\text{C}$  values closer to that of C<sub>4</sub> plants than C<sub>3</sub> (Eickmeier and Bender 1976). Of the cacti collected by Tieszen and Chapman (1992), for instance, five out of six of those growing in dry regions up to 4,340 masl had isotopic values similar to

those of C<sub>4</sub> plants. Of the seven CAM plants in our synthesis here, all fall within the C<sub>4</sub> range of  $\delta^{13}\text{C}$  values, reflecting the arid environment that they grew in. Cacti have been identified in archaeobotanical assemblages (Weir and Dering 1986) and, since many have edible fruits, likely contributed to human dietary signals in prehistory. Indeed today the communities of the inter-Andean valleys and *quebradas* of Ica gather wild cacti fruit (Whaley *et al.* 2010b), which are seasonally an important component of local diet. In the *quebradas* (800–1,200 masl) *Neoraimondia arequipensis* is particularly appreciated for its sweet magenta red fruits. Most of the south coast *Haageocereus* spp. and *Cleistocactus acanthurus* also have edible fruits. At higher elevations (2,500–3,200 masl) the large fruits of *Corryocactus brevistylus* are an intensively gathered food resource for humans, for instance in the Comunidad de Larimate, Ayacucho, as well as an important source of food and moisture for guanaco (Knight Piésold Consultores S.A. 2003).

[Place Figure 5 around here]

Finally we must consider various plants of Amaranthaceae ('amaranth family'), and Chepodiaceae ('goosefoot family'), both now sometimes subsumed under Amaranthaceae (APG 1998; Judd *et al.* 1999), which are represented in many archaeobotanical assemblages from the region (*inter alia* Beresford-Jones *et al.* 2011; Cook and Parrish 2005; Piacenza 2005; Weir and Dering 1986). These plants are colonists of freshly disturbed ground and are therefore classic indicators of the clearances and ecological disturbances that go hand in hand with human activities such as agriculture, just as suggested by pollen records from the region (Beresford-Jones *et al.* 2009). They are generally adapted to habitats such as warm temperate and tropical grasslands, savannas, sand dunes, salt marshes and deserts all of which are generally rich in C<sub>4</sub> plants and members of these families have evolved C<sub>4</sub> photosynthesis independently at least thirteen times (Kadereit *et al.* 2003).

The ethnobotany of various arid American ecologies has documented both the seeds and foliage of various wild species, which are palatable, high in vitamins and relatively high in protein, as providing valuable food for humans (Altieri *et al.* 1987; Hodgson 2001; Nabhan 1985). Indeed, millennia of human-plant interactions have led to the domestication of a number of important so-called 'pseudo-cereals' from these families in the Andes such as quinoa (*Chenopodium quinoa*). Distinguishing between the

archaeobotanical remains of wild and domesticated varieties within (and even between) these is far from straightforward and has only recently been properly addressed (Bruno 2006), so that some previous identifications to species level remain uncertain.

This may be important because different species of Chenopodiaceae and Amaranthaceae show both C<sub>3</sub> and C<sub>4</sub> isotopic signatures (see Table 1), including C<sub>4</sub> species that are known ethnobotanically as wild foods in Peru and elsewhere such as *Amaranthus hybridus* and *Amaranthus spinosus* (Brack Egg 1999; United States Department of Agriculture 2011). Plants of the genus *Atriplex* (saltbush, Amaranthaceae) are halophytes that aggregate salt in their leaves whilst remaining palatable and are widely used as food for humans and browsing animals in many parts of the Americas (see for example Castetter and Underhill 1935; Little and Schoeninger 1995; Minnis 1989). *Atriplex rotundifolia*, for instance, is endemic to south coast Peru and used as food, largely as a condiment (Whaley *et al.* 2010b). *Atriplex* spp. are all C<sub>4</sub> (Kadereit *et al.* 2003).

*Kiwicha*. One of the Andean domesticated pseudo-cereals and the only domesticated *Amaranthus* species (Brack Egg 1999) is *kiwicha* (*Amaranthus caudatus*). As documented by Turner *et al.* (2010) and confirmed here, *kiwicha* is C<sub>4</sub>. Described by the United States National Research Council (1989) as a ‘staple grain’ of pre-Columbian populations *kiwicha* has similar but smaller seed grains to the domesticated chenopod quinoa. *Kiwicha* grows well both at altitude in the sierra and on the coast and is also a source of fodder for animals (Brack Egg 1999). It is highly nutritious, containing high levels of the indispensable amino acid lysine as well as calcium, phosphorous, iron, potassium, zinc, vitamin E and B (Brack Egg 1999:26). Significantly, for our considerations here, its protein content is between 13-19%, higher than that of maize (Brack Egg 1999; Food and Agriculture Organization of the United Nations 1992; Gross *et al.* 1989; National Research Council 1989; United States Department of Agriculture 2011).

### *Considerations of Protein Routing*

Reconstructions of past diets using isotopic data naturally entails an awareness of the particular fraction of diet that is recorded isotopically in the consumer’s body tissues and which are subsequently

analysed. For instance, body tissue proteins (such as bone collagen and hair keratin) are preferentially composed of the protein component of diet (known as ‘protein routing’), and so their isotopic signal is biased towards that of dietary protein, whereas the carbon in the mineral fraction (hydroxyapatite) of bone and teeth isotopically represents the whole diet (Ambrose 1993; Ambrose and Norr 1993; Froehle *et al.* 2010; Jim *et al.* 2004; Tieszen and Fagre 1993b). For diets where sufficient levels of protein are consumed, the carbohydrate and lipid macronutrient fraction of the diet will be underrepresented isotopically in body proteins. However, in diets deficient in protein, carbon from carbohydrate and lipid sources will contribute to the synthesis of protein to compensate for this shortfall (Ambrose 1993; Ambrose and Norr 1993). Whilst protein routing is not of concern for the reconstructions of mono-isotopic palaeodiets, it becomes significant when protein and carbohydrate components differ isotopically, as would be the case for example if C<sub>3</sub> protein and C<sub>4</sub> carbohydrate were being consumed.

The assumption is usually made that because plant sources are relatively low in protein they will be under-represented in collagen, whereas animal foods which are high in protein will dominate the collagen isotopic value and thereby obscure any signal from plants. Different plants do of course have different protein contents. Maize, for instance, has a low protein content and has been shown to contribute significantly to consumer collagen only in circumstances of protein deficiency in diet (Ambrose 1993; Ambrose and Norr 1993; Tieszen and Fagre 1993b). *Kiwicha* — an alternative C<sub>4</sub> plant source in the human diet — is relatively high in protein and so would consequently be more likely to register isotopically in bone collagen. Theoretically then, in diets with sufficient protein levels, *kiwicha* will contribute significantly more to bone collagen than will maize, and thereby disproportionately to any C<sub>4</sub> signal, with respect to their relative quantities in the diet.

## Conclusions

Llano (2009:133) rightly warns that “our capacity to reconstruct the diet [of past populations] is limited by our knowledge of the abundance and distribution of C<sub>3</sub> and C<sub>4</sub> photosynthetic pathway plants and of the fauna associated with them”. The vast Andean region spans topographical extremes and tropical, sub-

tropical and temperate environments, all of which entail extreme ecological diversity. Such diversity will naturally find expression in the isotopic variations of its flora, much of which remains to be properly investigated in the present. Moreover, great changes have been wrought in Andean vegetation associations by their long undergone interactions with humans, not least the introductions of non-native plants: processes of change which accelerated greatly following the cataclysmic first encounter between the Old and New Worlds in the 16<sup>th</sup> Century.

We have sought to make a contribution here by augmenting the results of the two existing studies of western Andean plant isotopes with our own analyses of 89 plants from the South Coast Peru collection at RBG Kew: a securely identified herbarium collection from the Ica Valley, mostly collected between sea-level and 2,000 masl. These plants were selected because ethnobotanical observations in the region lead us to believe that they might make some contribution to human or animal diet. For to understand the isotopic signal of humans in prehistory we need to explore the isotopic variation within the full range of plants, both wild and domestic, that could contribute to human isotopic signals either directly, or indirectly through the animals they consume. Isotopic studies in the Andes, and elsewhere in the Americas, have in their interpretations of past diets sometimes glossed over the potential subtleties and complications which may arise through these different routes into the human food chain.

Indeed, it turns out that almost one third of the total flora of 144 plants in our synthesised dataset of food and fodder plants of the western slopes of the south-central Andes show  $\delta^{13}\text{C}$  values indicative of C<sub>4</sub> or CAM photosynthetic pathways. These include many plants in the Gramineae, Cyperaceae, Cactaceae, Chenopodiaceae and Amaranthaceae families that are potentially important food sources either for humans, or for the animals they hunted or herded in the past including wild and domesticated camelids, guinea pigs and deer. This set of C<sub>4</sub> plants included the domesticated amaranth *kiwicha*, an important Andean pseudo-cereal crop and one with a particularly high protein content: reflected accordingly in the body tissue proteins (such as bone collagen and hair keratin) of any ancient consumers.

Our measure of one third C<sub>4</sub> plants in the background isotopic signal of human direct and indirect plant consumption thus undermines the assumption currently made in many interpretations of Andean

isotopic results: namely that maize is the *only* significant potential source of *any* C<sub>4</sub> signal in ancient human or camelid remains. The prevalence of C<sub>4</sub> photosynthetic pathways is well known to increase in the flora of arid and semi-arid ecologies. Such ecologies were the locus of the florescence of many complex ancient societies in various parts of the New World including the coast of Peru, parts of the Mexican highlands and the North American southwest. In all these places, then, the idea that any C<sub>4</sub> signal in humans must *necessarily* arise from maize consumption may need to be examined more critically — upon the foundation of a much more comprehensive understanding of the isotopic variation inherent in these various background ecologies. Given the ritual and subsistence significance accorded to maize, the only true cereal crop of the Americas, this is potentially a matter of wide importance to our archaeological interpretations.

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## Tables and Figure Captions

Table 1. List of the synthesised species data used in this article.

<sup>a</sup>Data from Brack Egg (1999); USDA, ARS, National Genetic Resource Program (2012)

<sup>b</sup> Agricultural margin includes irrigated areas and canals, paths and field borders; *quebradas* are the lower sections of inter-Andean immersing on the coastal plain; ephemeral streams (*huaycos*) are sporadic, seasonal streams that may flow for only a few days and traverse the rocky outwash deltas from *quebradas*.

<sup>c</sup> Those pathways in bold have been identified previously in the literature and relate to the samples analysed by this study only.

<sup>d</sup>1=authors; 2=Tieszen & Chapman (1992); 3= DeNiro & Hastorf (1985).

Table 2. Location and mean  $\delta^{13}\text{C}$  data of the *Amaranthus caudatus* and *Atriplex rotundifolia* samples used to investigate intra-species variation.

Table 3. Species discarded from Tieszen and Chapman's (1992) and DeNiro and Hastorf's (1985) Studies.

Table 4. Proportion of  $\text{C}_3$  and  $\text{C}_4$  plants in families important in the consideration of direct and indirect consumption.

Figure 1. Map of the Ica Region, south coast Peru showing the provinces from which plant collections were made for the RBG Kew South Coast Collection (see Table 1).

Figure 2. Mean carbon isotope distribution of species (n=89) analysed in this study.

Figure 3. Distribution of species mean  $\delta^{13}\text{C}$  values (n=144) from this study and the published data (Tieszen and Chapman 1992, DeNiro and Hastorf 1985).



Figure 4. Intra-species  $\delta^{13}\text{C}$  variation with altitude of *Amaranthus caudatus* (n=9) and *Atriplex rotundifolia* (n=6).

Figure 5. Examples of  $\text{C}_4$  and CAM plants that are edible by humans and animals.