



CHICAGO JOURNALS



Alternative Interpretations of Intermediate and Positive d13C Isotope Signals in Prehistoric Human Remains from Southern Mendoza, Argentina: The Role of CAM Species Consumption

Author(s): Carina Llano and Andrew Ugan

Source: *Current Anthropology*, Vol. 55, No. 6 (December 2014), pp. 822-831

Published by: [The University of Chicago Press](#) on behalf of [Wenner-Gren Foundation for Anthropological Research](#)

Stable URL: <http://www.jstor.org/stable/10.1086/678991>

Accessed: 06/12/2014 19:54

Your use of the JSTOR archive indicates your acceptance of the Terms & Conditions of Use, available at <http://www.jstor.org/page/info/about/policies/terms.jsp>

JSTOR is a not-for-profit service that helps scholars, researchers, and students discover, use, and build upon a wide range of content in a trusted digital archive. We use information technology and tools to increase productivity and facilitate new forms of scholarship. For more information about JSTOR, please contact support@jstor.org.



The University of Chicago Press and Wenner-Gren Foundation for Anthropological Research are collaborating with JSTOR to digitize, preserve and extend access to *Current Anthropology*.

<http://www.jstor.org>

Alternative Interpretations of Intermediate and Positive $\delta^{13}\text{C}$ Isotope Signals in Prehistoric Human Remains from Southern Mendoza, Argentina

The Role of CAM Species Consumption

Carina Llano and Andrew Ugan

CONICET–Laboratorio de Paleoecología Humana, Facultad de Ciencias Exactas y Naturales, Universidad Nacional de Cuyo, Padre Jorge Contreras 1300, Parque General San Martín, 5500 Mendoza, Argentina/Far Western ARG, 2727 Del Rio Place, Davis, California 95618, U.S.A. (andrew.ugan@gmail.com). 10 III 14 This paper was submitted 10 I 14, accepted 10 III 14, and electronically published 6 XI 14.

During the last several years, information from stable isotopes has been used to discuss the role of maize agriculture in prehistoric economies of southern Mendoza. Because maize is one of several sources of ^{13}C enriched carbon, a full evaluation of prehistoric diets requires data on a range of potential C_3 and C_4 plant resources. In this paper, we present stable isotope data ($N = 89$) for a suite of five previously unstudied edible cacti possessing a Crassulacean acid metabolism (CAM) photosynthetic pathway. Our results show that these plants have $\delta^{13}\text{C}$ values overlapping C_4 photosynthesizers such as maize. In order to understand their potential economic importance, we present additional procurement, processing, and nutritional data from actualistic experiments and the published literature. Using these data, we show why low levels of CAM plant consumption should be expected and how doing so may mimic a pattern of isotopically mixed diets often attributed to maize use.

The nature of late Holocene subsistence and economy, especially the role of wild resources versus domesticated corn, has been a pivotal focus of research in central-western Argentina over the last decade (Gil, Neme, and Tykot 2010, 2011 and references therein; Gil et al. 2006 and references therein). The region, centered in the southern and central province of Mendoza (fig. 1), represents an agricultural frontier. To the south, farming never took place, while to the north, domesticates such as corn played a major economic role, particularly in areas dominated by complex Andean civilizations of the last 2,000–3,000 years.

Two lines of evidence have been central to debates over the role of corn on this frontier. One is the presence of corn kernel and cob fragments from 17 archaeological sites dating

to within the last 3,000 years and concentrated along the Diamante River and the northern flanks of Cerro Nevado (fig. 1; Llano 2011 and references therein). The other is a growing set of human remains from throughout southern Mendoza exhibiting $\delta^{13}\text{C}$ values consistent with moderate to high consumption of C_4 photosynthesizing plants such as corn. Neither line of evidence has provided a clear-cut indication of the economic importance of maize.

While the macrofossils provide unambiguous proof that maize was known in southern Mendoza, the size of the samples recovered is small (131 kernels, 4 cob fragments) and in at least one instance occurs in a burial context. None of the finds are associated with evidence for storage, and sites with substantial investment in domestic architecture are rare to absent in the region. El Indigeno, a notable exception that also contains corn macrofossils, is located at over 3,000 m elevation and unlikely to have served as a residential farming base. Given abundant evidence for corn farming farther north in San Juan province and, to a lesser extent, the northern reaches of the province of Mendoza itself, a smattering of maize throughout the south of the province might be expected and simply indicate trade and interaction with more established agricultural groups elsewhere.

This inference has to be weighed against evidence for possible maize consumption seen in the bone isotope values of locally occurring human remains. In humans and other animals, bone isotope values reflect the isotopic composition of longer-term diet mediated by the metabolic pathways by which various isotopes are fixed into the tissues (Hobson and Schwarcz 1986; Kelly 2000; Koch 1998). In terrestrial settings, those dietary values are fundamentally driven by variation in plant photosynthetic pathway, which covaries with discrimination against ^{13}C (Farquhar, Ehleringer, and Hubick 1989). Cool-season grasses and more than 98% of the dicots (virtually all trees and most shrubs and herbaceous plants) use C_3 photosynthesis. This pathway discriminates heavily against ^{13}C , and C_3 plants exhibit an average $\delta^{13}\text{C}$ value of $-26.7 \pm 2.7\text{‰}$ (Cerling, Ehleringer, and Harris 1998). The C_4 photosynthetic pathway is characteristic of maize and a small array of grasses, forbs, and shrubs where daytime growing-season temperature exceeds 22°C and precipitation exceeds 25 mm (Ehleringer et al. 1997). C_4 photosynthesis discriminates less against ^{13}C , produces average $\delta^{13}\text{C}$ values of $-12.5 \pm 1.1\text{‰}$ (Cerling et al. 1998), and does not overlap the range of $\delta^{13}\text{C}$ values for C_3 plants. Modern averages are $\approx 2\text{‰}$ more negative than plants grown before fossil fuel depletion of atmospheric CO_2 (Bada et al. 1990; Francey et al. 1999; Keeling et al. 2010).

Humans subsisting purely on C_3 plants or herbivores that feed on such plants should have bone collagen $\delta^{13}\text{C}$ values around -21.5‰ , those feeding entirely on C_4 plants and C_4 herbivores values around -7.5‰ , and those on mixed diets values somewhere in between (assuming diet-collagen discrimination of $+5\text{‰}$; Tykot et al. 2009). Because maize is by

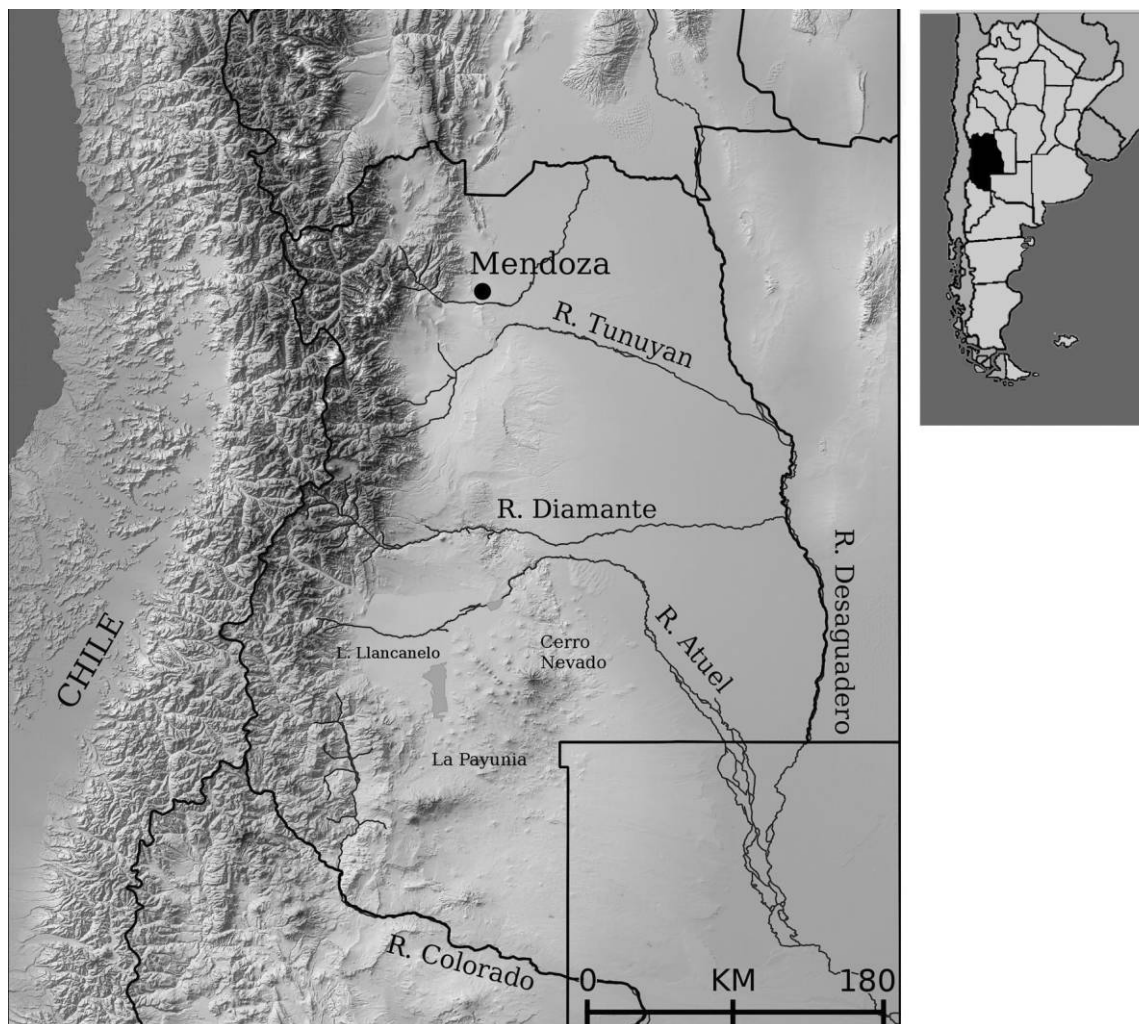


Figure 1. Map of the province of Mendoza, Argentina. A color version of this figure is available online.

far the most economically important C_4 plant in the New World, highly elevated $\delta^{13}C$ values in humans have been taken to indicate high levels of corn use and are regularly used to track the spread of maize agriculture (e.g., Schwarcz 2006; Schwarcz and Schoeninger 1991). In a sample of 86 prehistoric bone collagen samples from Mendoza (Gil, Neme, and Tykot 2011, table 1), human $\delta^{13}C$ values varied from -20.9 to -10.8 ‰, and the authors make exactly this inference: a handful of individuals with the most elevated $\delta^{13}C$ values were likely heavily reliant on maize, while in the majority of cases maize may have contributed to the diet but was never a staple (Gil, Neme, and Tykot 2011:1338).

This interpretation depends heavily on the role of wild, ^{13}C -enriched resources in the diet, however. There are a number of plants and animals in central-western Argentina that either have or may have intermediate to positive $\delta^{13}C$ values, and their incorporation in even moderate amounts would provide a fully consistent explanation for many of the “mixed

diet” signals seen in the human isotope data. Some of these are edible plants, including South American saltbush (*Atriplex lampa*) and an array of edible cacti. Others include a range of aquatic animals and small to medium sized herbivores able to feed on wild C_4 grasses common to lower elevation settings (Cavagnaro 1988). If any of these were used to complement domesticates, they could easily relegate maize contributions for all but the most positive sets of human remains from “staple” to simply “significant.”

For this reason, it is important to evaluate the full range of potential resources in terms of their possible contributions. Here we focus on one set of such resources, the cacti. In the sections that follow, we identify a suite of five edible cacti common to central-western Argentina, three with edible fruit (*Cereus aethiops*, *Maihuenia poeppigii*, and *Opuntia sulphurea*) and two with edible geophytes (*Maihueniopsis darwinii* var. *hickenii*, and *Pterocactus tuberosus*). We review data on their biology and distribution, present data on procurement and

Table 1. Stable isotope values for five edible cacti species from western Argentina

ID	Genus	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Weight %C	Weight %N
ASIP 259	<i>Cereus</i>	<i>aethiops</i>	-13.5	-7	51.3	2.6
ASIP 260	<i>Cereus</i>	<i>aethiops</i>	-13.4	1.6	48.6	2.4
ASIP 261	<i>Cereus</i>	<i>aethiops</i>	-13.7	2.0	46.6	2.7
ASIP 262	<i>Cereus</i>	<i>aethiops</i>	-13.2	5.6	43.8	2.5
ASIP 263	<i>Cereus</i>	<i>aethiops</i>	-13.1	8.7	43.0	3.2
ASIP 264	<i>Cereus</i>	<i>aethiops</i>	-12.4	7.0	45.8	2.1
ASIP 264	<i>Cereus</i>	<i>aethiops</i>	-12.3	10.3	46.4	2.1
ASIP 265	<i>Cereus</i>	<i>aethiops</i>	-13.5	5.1	47.8	2.6
ASIP 311	<i>Cereus</i>	<i>aethiops</i>	-13.1	1.7	51.5	3.2
ASIP 312	<i>Cereus</i>	<i>aethiops</i>	-13.2	2.5	52.0	2.5
Mean			-13.1	4.4		
SD			.5	3.5		
ASIP 293	<i>Maihuenia</i>	<i>poepigii</i>	-22.9	.1	30.7	.8
ASIP 294	<i>Maihuenia</i>	<i>poepigii</i>	-22.9	-5	39.7	.9
ASIP 295	<i>Maihuenia</i>	<i>poepigii</i>	-24.1	1.8	38.4	1.6
ASIP 296	<i>Maihuenia</i>	<i>poepigii</i>	-19.6	2.1	41.2	1.8
ASIP 297	<i>Maihuenia</i>	<i>poepigii</i>	-19.9	.7	37.9	.9
ASIP 298	<i>Maihuenia</i>	<i>poepigii</i>	-20.1	2.2	43.8	1.8
ASIP 299	<i>Maihuenia</i>	<i>poepigii</i>	-22.6	-2	39.6	1.0
ASIP 300	<i>Maihuenia</i>	<i>poepigii</i>	-21.8	.6	42.2	2.2
Mean			-21.7	.9		
SD			1.7	1.1		
ASIP 24	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.5	1.9	31.6	.6
ASIP 25	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.2	-5	36.5	.3
ASIP 29	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.5	-1.7	28.9	.3
ASIP 30	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.3	-1.6	31.8	.4
ASIP 31	<i>Maihueniopsis</i>	<i>darwinii</i>	-10.9	-7	27.2	.4
ASIP 32	<i>Maihueniopsis</i>	<i>darwinii</i>	-10.7	-6	31.7	.2
ASIP 33	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.7	-3.5	32.9	.2
ASIP 34	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.8	2.2	34.2	.2
ASIP 106	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.7	.6	35.5	.7
ASIP 106	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.9	-1	36.5	.8
ASIP 107	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.5	-3	39.8	.5
ASIP 108	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.2	-7	37.3	.6
ASIP 109	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.9	1.6	38.7	.7
ASIP 110	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.7	-2.0	38.6	1.4
ASIP 123	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.5	2.4	34.9	1.1
ASIP 124	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.4	7.5	36.9	.9
ASIP 128	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.5	-5	30.8	.3
ASIP 138	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.9	.4	36.9	.5
ASIP 139	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.0	.7	35.6	.2
ASIP 140	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.6	-1.2	35.1	.2
ASIP 141	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.6	1.3	30.3	.3
ASIP 142	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.0	1.5	39.1	.3
ASIP 144	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.7	-5	41.4	.5
ASIP 145	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.1	-8	39.3	.3
ASIP 146	<i>Maihueniopsis</i>	<i>darwinii</i>	-11.3	-1.0	41.2	.3
ASIP 287	<i>Maihueniopsis</i>	<i>darwinii</i>	-12.8	-8	38.6	.5
ASIP 288	<i>Maihueniopsis</i>	<i>darwinii</i>	-13.3	-1.0	33.8	.5
Mean			-11.8	.1		
SD			.6	2.0		
ASIP 217	<i>Opuntia</i>	<i>sulphurea</i>	-14.4	4.0	36.8	.5
ASIP 218	<i>Opuntia</i>	<i>sulphurea</i>	-13.6	4.8	53.6	2.1
ASIP 219	<i>Opuntia</i>	<i>sulphurea</i>	-13.0	.5	36.9	.6
ASIP 220	<i>Opuntia</i>	<i>sulphurea</i>	-12.2	1.6	38.0	.6
ASIP 221	<i>Opuntia</i>	<i>sulphurea</i>	-12.0	2.0	35.6	.4
ASIP 233	<i>Opuntia</i>	<i>sulphurea</i>	-13.3	3.6	36.7	.6
ASIP 234	<i>Opuntia</i>	<i>sulphurea</i>	-14.2	7.8	35.5	.8
ASIP 235	<i>Opuntia</i>	<i>sulphurea</i>	-16.0	5.4	42.3	1.3
ASIP 236	<i>Opuntia</i>	<i>sulphurea</i>	-13.6	4.0	37.6	.8
ASIP 254	<i>Opuntia</i>	<i>sulphurea</i>	-13.5	1.9	39.3	.4
ASIP 255	<i>Opuntia</i>	<i>sulphurea</i>	-24.3	11.1	40.6	2.4
ASIP 255	<i>Opuntia</i>	<i>sulphurea</i>	-12.8	8.7	39.5	.5

Table 1 (Continued)

ID	Genus	Species	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	Weight %C	Weight %N
ASIP 257	<i>Opuntia</i>	<i>sulphurea</i>	-12.8	5.2	43.9	.4
ASIP 258	<i>Opuntia</i>	<i>sulphurea</i>	-12.9	4.2	37.4	.5
ASIP 266	<i>Opuntia</i>	<i>sulphurea</i>	-13.4	4.5	40.1	.6
ASIP 267	<i>Opuntia</i>	<i>sulphurea</i>	-13.2	7.0	37.7	.5
ASIP 268	<i>Opuntia</i>	<i>sulphurea</i>	-12.9	4.7	40.4	.7
ASIP 269	<i>Opuntia</i>	<i>sulphurea</i>	-14.2	1.7	37.6	.5
ASIP 270	<i>Opuntia</i>	<i>sulphurea</i>	-13.8	10.4	27.6	.8
ASIP 306	<i>Opuntia</i>	<i>sulphurea</i>	-15.6	- .8	39.0	1.4
ASIP 307	<i>Opuntia</i>	<i>sulphurea</i>	-14.8	- .1	39.0	.8
ASIP 308	<i>Opuntia</i>	<i>sulphurea</i>	-13.0	6.0	40.2	.6
ASIP 309	<i>Opuntia</i>	<i>sulphurea</i>	-13.0	-4.8	41.6	.6
ASIP 310	<i>Opuntia</i>	<i>sulphurea</i>	-13.0	9.0	40.7	.8
Mean			-14.0	4.3		
SD			2.4	3.7		
ASIP 1	<i>Pterocactus</i>	<i>tuberosus</i>	-12.9	2.6	39.5	1.3
ASIP 2	<i>Pterocactus</i>	<i>tuberosus</i>	-12.6	3.9	36.9	1.3
ASIP 3	<i>Pterocactus</i>	<i>tuberosus</i>	-13.9	4.5	36.3	1.0
ASIP 3	<i>Pterocactus</i>	<i>tuberosus</i>	-13.6	4.7	34.3	.9
ASIP 4	<i>Pterocactus</i>	<i>tuberosus</i>	-12.0	-2.7	39.7	.3
ASIP 6	<i>Pterocactus</i>	<i>tuberosus</i>	-11.1	-1.8	39.5	.7
ASIP 7	<i>Pterocactus</i>	<i>tuberosus</i>	-11.9	-1.3	39.4	.6
ASIP 8	<i>Pterocactus</i>	<i>tuberosus</i>	-12.8	.7	37.9	1.2
ASIP 9	<i>Pterocactus</i>	<i>tuberosus</i>	-13.3	2.0	40.0	1.3
ASIP 10	<i>Pterocactus</i>	<i>tuberosus</i>	-13.3	-1.6	37.9	1.0
ASIP 11	<i>Pterocactus</i>	<i>tuberosus</i>	-11.5	.1	40.3	.7
ASIP 12	<i>Pterocactus</i>	<i>tuberosus</i>	-12.7	.0	35.2	1.0
ASIP 13	<i>Pterocactus</i>	<i>tuberosus</i>	-12.4	-1.7	34.3	.7
ASIP 35	<i>Pterocactus</i>	<i>tuberosus</i>	-12.5	-2.2	34.6	.9
ASIP 125	<i>Pterocactus</i>	<i>tuberosus</i>	-11.3	-1.2	41.3	.5
ASIP 126	<i>Pterocactus</i>	<i>tuberosus</i>	-12.2	- .3	44.3	.4
ASIP 127	<i>Pterocactus</i>	<i>tuberosus</i>	-10.5	- .9	34.2	1.1
ASIP 191	<i>Pterocactus</i>	<i>tuberosus</i>	-13.4	2.6	40.8	.8
ASIP 192	<i>Pterocactus</i>	<i>tuberosus</i>	-12.8	2.7	39.4	.6
ASIP 193	<i>Pterocactus</i>	<i>tuberosus</i>	-12.7	3.5	40.0	1.1
Mean			-12.5	.7		
SD			.9	2.4		

Note. Stable isotope values reported relative to VPDB (carbon) and AIR (nitrogen).

processing experiments relevant to assessing their potential economic importance, and provide data on their isotopic values. We show that all taxa provide moderate to high energetic returns that would have made them attractive resources when available and that they have moderate to highly positive $\delta^{13}\text{C}$ values. We conclude by discussing the potential contributions of these plants to human isotope signals from central-western Argentina and highlight areas for future research in the region and elsewhere.

Material and Methods

Cacti Characteristics and Use

The Cactaceae are a diversified group of New World plants most noted for their water-conserving morphology and photosynthetic system. The family is both interesting and challenging because of its varied morphology, adaptations to the environment, and reproductive systems (Kiesling 1984). In western Argentina, cacti occur throughout the Monte desert, with particularly cold and wind resistant taxa occurring in

the foothills and Andes to an elevation of over 4,000 m. Five specific taxa are of interest here (fig. 2; descriptions summarized from Kiesling and Ferrari 2005; Trevisson and Demaio 2006; Zuloaga, Morrone, and Belgrano 2008):

Cereus aethiops Haw. Plants that, when mature, form stately clumps of tall slender blue-green stems studded with black spines. Once the stem is 3–4 feet tall it blooms several times in the summer, producing funnel-shaped white flowers. The fruit is ovoid, dehiscent, and edible. Blooms between December and January, fruits between February and March.

Maiheunia poeppigii (Otto ex Pfeiff.) K. Schum. This plant forms dense cushions consisting of hundreds of individual segments and growing up to more than a meter in size. The species is cold-hardy and moisture resistant. Mats consist of cylindrical stems with small, succulent leaves and white spines. The flowers are large, soft, satiny, and lemon-yellow; the fruits are edible. Blooms between November and December, fruits between February and March.

Maiheuniposis darwinii (Hensl.) F. Ritter var. *hickenii* (Britton & Rose) R. Kiesling. Plant forms mats up to 80 cm



Figure 2. Five edible cacti from Mendoza, Argentina. Left to right, from top: *Cereus aethiops*, *Maihuenia poeppigii*, *Maihueniopsis darwinii*, *Opuntia sulphurea*, and *Pterocactus tuberosus*. A color version of this figure is available online.

in diameter. The stems may be very tight or loose depending on clones and form olive-green, ovoidal cladodes. Roots are enlarged and tuberous. Flowers are dirty yellow-orange, 5–6 cm in diameter. The fruits are fleshy and 4 × 2.5 cm in size, becoming yellow-orange at maturity. Both roots and fruits are edible. Blooms between November and December, fruits between February and March.

Opuntia sulphurea Gillies ex Salm-Dyck. Low-standing cactus, up to 30 cm tall. Pads more or less discoid, 10–20 cm diameter and 3 cm thick. Flowers are yellow, rarely pink, 6 cm long, and 5 cm in diameter. Fruits are ovoid-truncate, 3.5 cm diameter and yellow inside and out. Fruits are edible (pads likely so, though their use is not recorded). Blooms between October and February, fruits between April and January.

Pterocactus tuberosus (Pfeiff.) Britton & Rose. A geophytic cactus with large, tuberous roots and thin, fragile, light blue to brownish-purple stems. Stems break easily, but regenerate from the root. Flowers are a pale to deep yellow, and the stigma can go from almost white to pink or to deep red. The flowers are produced from the apex of new growth. Roots are edible. Blooms between November and December, fruits between December and January.

Ethnobotanical and archaeobotanical studies document the use of these xeric species since ancestral times in Argentina, including the use of both fruits and plants with underground organs (tubers, rhizomes, bulbs, and roots; e.g. Kiesling 1968; Ladio 2001; Ladio and Lozada 2009; Ladio et al. 2007; Martínez-Crovetto 1982, 1963; Musters 1964; Nacuzzi and Pérez de Micou 1985; Ruiz Leal 1972). Fruits are eaten raw or dried for later use. Roots were eaten raw, cooked (boiled, roasted among hot coals, cooked in animal fat), or ground and then processed into flour for making bread. Fermentation of tubers and roots was also a common practice. Acquisition involved little more than a knife or digging stick.

Isotope Data

Unlike the majority of plants, members of the Cactaceae rely on Crassulacean acid metabolism (CAM) photosynthesis (Osmond et al. 1973). Since plants using CAM photosynthesis can take on a range of $\delta^{13}\text{C}$ values overlapping those of both C_3 and C_4 photosynthesizers, having isotopic data on each taxon is important. For each species, we collected and dried several grams of edible tissue, either fruit or root. The material was dried in a drying oven at 65°C, then ground to a fine powder using a BioSpec Mini-Beadbeater-1 homogenizer. Individual samples were then measured into tin cups and sent to the Stable Isotope Ratio facility for Environmental Research (SIRFER) at the University of Utah for combined C and N analysis.

Sample $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were determined by flash combustion to produce CO_2 and N_2 gas and measured on a Finnigan Delta Plus mass spectrometer coupled to a Carlo Erba EA118 CHN elemental analyzer at SIRFER. Both stable isotope measurements and sample weight percent carbon and nitrogen were obtained from a single sample combustion. Standard

deviations for laboratory reference standards were 0.1‰ for carbon (measured relative to V-PDB) and 0.2‰ for nitrogen (measured relative to AIR).

These results are summarized in table 1. Mean $\delta^{13}\text{C}$ values for all taxa vary between -11.8‰ and -14.0‰ , with the exception of *Maihuenia poeppigii* (-21.7‰). Although there is substantial variation in CAM photosynthesis and CAM cycling across the many species that use it (Luttge 2004), all cacti are obligate CAM photosynthesizers. They do not cycle in and out of CAM versus C_3 photosynthesis as seen in some plants, and the degree of carbon isotope discrimination is strongly correlated with the proportion of CO_2 fixed during the day or night (Cernusak et al. 2013; Winter and Holtum 2002). The greater ^{13}C discrimination seen in *M. poeppigii* thus likely reflects increased daytime CO_2 fixation, perhaps facilitated by its distribution in cooler, higher-elevation areas of the Andes and surrounding piedmont.

Nutritional Data

In addition to isotopic data, we analyzed samples of three taxa for basic nutritional composition. Several hundred grams of *Opuntia* fruits and *Pterocactus* and *Maihueniopsis* root were collected in the field, cleaned, and frozen prior to being sent to the Center for Technological Studies, Faculty of Applied and Industrial Sciences, at the University of Cuyo. There the samples were analyzed for crude moisture, ash, dietary fiber, protein, fat, carbohydrate, and energetic content following the methods proposed by the Association of Analytical Communities (AOAC 2005). Both fruits and geophytes are carbohydrate rich, roughly 50%–75% water, and provide between 65 and 115 kcal/100 g (table 2).

Table 2 also includes published nutritional data for fruits from four related *Opuntia* taxa (nine samples total) and three fruiting columnar cacti in the same subfamily as *Cereus aethiops* (Cactoideae). The compositions of the cactus fruits are broadly similar, with digestible sugars contributing the majority of food energy. Total energetic values are also broadly similar, roughly 60 kcal/100 g (range 34–75 kcal/100 g), with variation in the estimates being tightly tied to the percent of carbohydrates and, by extension, water content of the samples. The *Opuntia sulphurea* samples stand out from all other *Opuntia* fruits due to their low water content, high digestible fiber (at 2.5 kcal/g; AOAC 2005), and correspondingly high caloric value. Given how similar the other cactus fruit data are even across subfamilies, we suggest that a mean energetic value of 60 kcal/100 g and a range of 35–115 kcal/100 g can be used to characterize unknown taxa and assign this value to our *Maihuenia poeppigii* fruit as well.

Experimental Return Rates

Estimated energetic return rates (in kcal/hr) for each cactus taxa are provided by combining the nutritional and energetic data with experimental work on collection times. Data for *Opuntia sulphurea* and *Pterocactus tuberosus* come from Llano and Ugan (2010). In each case, two to four individuals col-

Table 2. Nutritional data per 100 g edible portion of cactus fruits and geophytes from western Argentina

Taxon	Moisture	Ash	Fiber	Protein	Fat	Carbs	kcal	Source
<i>Maihueniopsis darwinii</i>	75.9	7	2.4	.5		14.2	65	This paper
<i>Opuntia sulphurea</i>	56.7	3.3	32.1	1.7	.7	5.5	115	Llano and Ugan (2010)
<i>Pterocactus tuberosus</i>	73.4	5.3	2.6	.5		18.2	81	Llano and Ugan (2010)
<i>Stenocereus griseus</i> ^a	84.1	1.1	2.7	1.1	.2	10.9	50	Bravo-Hollis and Sánchez-Mejorada (1991)
<i>Stenocereus stellatus</i> ^a	86.3	.5	.3	1	.3	11.7	53	Bravo-Hollis and Sánchez-Mejorada (1991)
<i>Hylocereus undatus</i>	84.4	.7		1.6	.6	12.7	63	FAO/Latinfoods (2002)
<i>Opuntia</i> spp. ^b	85.3	.5		.8	.1	13.3	57	FAO/Latinfoods (2002)
<i>Maihuenia poeppigii</i> ^c							60	Estimated

^a Cited in González (2006).

^b Average of nine samples from five Latin American countries.

^c Estimated energetic value given the data from Opuntioideae and Cactoideae fruits.

lected roots or fruits in a series of 30-minute foraging bouts. *Opuntia* fruits were collected by hand and *Pterocactus* roots using a simple, traditional digging stick. No gloves or other special gear were used. Roots and fruits collected during each experiment were bagged in the field and weighed upon returning to the laboratory. Return rates in kcal/hr are presented in table 3.

We also estimate returns for *Cereus aethiops* and *Maihuenia poeppigii*. These estimates use the reported or estimated energetic values from table 2 and assume yields (kg/hr) similar to the *Opuntia* experiments. Because *Maihuenia* fruits often occur in patches, collection can occur in a sustained fashion similar to the prickly pears, and we expect these estimates to be reasonably close. *Cereus* cacti, in contrast, typically occurred as isolated or sparsely distributed individuals rather than in large patches. Fruits were also quickly and easily removed. As a consequence, actual return rates may be somewhat higher than reported here, though total yields (kg) would be small.

Finally, table 3 provides new data for *Maihueniopsis* roots. As with *Cereus*, *Maihueniopsis* encounters tend to occur with isolated or sparsely distributed individuals. Eight individual cacti were collected for various analyses. The whole plant was removed in each case, and the samples weighed in the lab the same day. In four cases, we also recorded the time required to extract the plant (approximately 5 minutes per plant using simple digging sticks). Average yields are based on the weights of all eight cacti, and collection times extrapolated from the four timed experiments. Overall yields in kcal/hr are high, as one would expect given the ease of extracting the roots and their large size (750 ± 200 g/root). While sustained digging in larger patches would reduce these returns somewhat, we would expect them to remain high, competitive, and on par with returns for other large geophytes reported in the literature (e.g., Kelly 1995 and references therein).

Discussion and Conclusion

Of the five edible cacti species considered here, four have stable isotope values that clearly overlap the range of C_4 plants

such as maize: *Cereus aethiops* ($\delta^{13}C = -13.1$), *Maihueniopsis darwinii* ($\delta^{13}C = -11.8$), *Opuntia sulphurea* ($\delta^{13}C = -14.0$), and *Pterocactus tuberosus* ($\delta^{13}C = -12.5$). These are also modern values, and affected by the large amounts of ^{13}C -depleted CO_2 introduced into the atmosphere since the industrial revolution. Accounting for this difference implies prehistoric $\delta^{13}C$ values about 2‰ more positive than modern, so between -12.0 ‰ and -9.8 ‰. With an average prehistoric C_3 dietary $\delta^{13}C$ value of -24.5 ‰, a CAM $\delta^{13}C$ value of -13 ‰, and a diet-collagen offset of $+5$ ‰, expected human collagen $\delta^{13}C$ would be between -18.9 ‰ and -17.2 ‰ if cacti contributed as little as 5%–20% of dietary carbon. This assumes that the cacti are the only source of enriched carbon, and if so they would account for the dietary signature of almost a third of the individuals reported for west-central Argentina (Gil, Neme, and Tykot 2011; table 1).

The preferential routing of proteins to bone collagen formation (Ambrose and Norr 1993; Fogel and Tuross 2003; Froehle, Kellner, and Schoeninger 2010; Howland et al. 2003; Jim et al. 2006; Schwarcz 2000; Tieszen and Fagre 1993) and the low protein content of the edible fraction of these cacti might bias these estimates. However, using bone apatite $\delta^{13}C$ values, which reflect whole diet (Ambrose and Norr 1993; Kellner and Schoeninger 2007; Schwarcz 2000), and assuming a 10.1‰ apatite-diet spacing (Fernandes, Nadeau, and Grootes 2012), produces similar results. Expected human apatite values would be between -13.8 ‰ and -12.1 ‰, accounting for between 14% and 39% of the individuals. Similar isotope values have been attributed to similar patterns of resource use among archaic hunters and gatherers of the American Southwest (Chisholm and Matson 1994). While these values are very general and will vary to some degree given specifics such as protein routing, collagen versus apatite signals, exact discrimination values, and so on, the potential contribution of cacti clearly remains important.

Assessing just how large a contribution cactus may have made is more difficult. Botanical studies in the region have focused on issues of taxonomy and distribution (Kiesling 1968, 1971, 1975, 1984, 2003; Kiesling and Ferrari 2005).

Table 3. Experimental return rates for five edible cacti taxa from western Argentina

Taxon	kg/hr	kcal/kg	kcal/hr	Notes
<i>Cereus aethiops</i>	1.8	600	1,080	Estimated returns
<i>Maihuenia poeppigii</i>	1.8	600	1,080	Estimated returns
<i>Maihueniopsis darwini</i> ^a	9	650	5,850	Average of 4 time trials, 8 sample weights
<i>Opuntia sulphurea</i> ^a	1.8	1,150	2,070	Average of 4 trials
<i>Pterocactus tuberosus</i> ^a	1.05	810	850	Average of 6 trials

^a Data from Llano and Ugan (2010).

There are no quantified data on the natural density or productivity of these taxa, little in the way of descriptive commentary, and there are also the potential impacts of domestic cattle and goats to consider in some parts of the region. These problems are most severe for *Maihuenia* fruits and especially *Maihueniopsis* roots.

While we lack quantitative information on *Pterocactus tuberosus*, our own experience is that they occur in sparse to moderately dense (5–10 plants/100 m²) patches. Kiesling (1968) describes encountering dense patches of these cacti as well, and notes that under favorable precipitation regimes they can reproduce twice per year (R. Kiesling, pers. comm.). While the edible roots of these cacti are smaller than those of *Maihueniopsis*, their total yields and dietary contribution may well be higher.

Finally, there are *Cereus aethiops* and *Opuntia sulphurea*. Again, few data are available on these taxa specifically. However, there is an abundance of data on their near relatives, many of which were extremely important to Native Americans in the past and remain actively cultivated today (Nobel 2002). All prickly pear (*Opuntia* sp.) fruits and pads are edible. Plants typically yield between 20 and 40, 200 g pads per plant, with several fruits per pad (Myers 1998). Commercial *O. ficus-indica* in San Juan, Argentina, produce 60 fruits on mature plants (Caloggero and Parera 2004), and commercial yields can be in the range of five tons per hectare (Inglese, Basile, and Schirra 2002). *O. sulphurea* is found throughout the Monte desert of southern Mendoza, often in large stands, and while macrobotanical remains of fruits are rare, we expect it to have been an important and widely utilized resource. While *Cereus* and other columnar cacti are found throughout the region today, they do not occur at the densities of confamilials exploited by the Seri Indians and other indigenous peoples of northern Mexico and the American Southwest (e.g., Felger and Moser 1977). Lacking evidence to the contrary, we assume that these cacti were similarly scarce in the past and that their fruits represented welcome but intermittent additions to the diet.

Given data from actualistic experiments on return rates, all of the cacti analyzed should have been exploited when available. Four would have enriched human collagen $\delta^{13}\text{C}$ values, mimicking the effects of maize and confounding efforts to determine contributions of this important domesticated to prehistoric diets. Exactly how much of a contribution the cacti

might have made to the diet remains unknown due to the lack of clear data on either modern or prehistoric abundances. We looked at the effects of a hypothetical contribution of 5%–20% of diet to human isotopic signatures and would suggest that those values serve as a fair starting point. Based on the limited published information on these cacti and their relatives, as well as our experience searching for and extracting them, a long-term contribution in the 5%–10% range would seem a reasonable, conservative estimate, with most of that contribution coming from the more productive *O. sulphurea* and *P. tuberosus*. Doing so would elevate human $\delta^{13}\text{C}$ signatures and reduce or eliminate the amount of maize (or other C₄ plant) consumption implied. As a consequence, the amount of maize implied by these positive values may well be less than once believed, particularly where the archaeological record indicates only a moderate reliance on domesticates. This has implications for how human isotope data are interpreted both in central-western Argentina and in analogous circumstances in arid environments elsewhere.

Acknowledgments

We would like to thank Adolfo Gil, Gustavo Neme, the Museo de Historia Natural de San Rafael, and FACA-Universidad Nacional de Cuyo for their support of this project. Partial funding was provided by NSF Grant 0754353.

References Cited

- Ambrose, Stanley, and Lynette Norr. 1993. Experimental evidence for the relationship of the carbon isotope ratios of whole diet and dietary protein to those of bone collagen and carbohydrate. In *Prehistoric human bone: archaeology at the molecular level*. J. Lambert and G. Grupe, eds. Pp. 1–37. New York: Springer-Verlag.
- AOAC. 2005. *Official methods of analysis of AOAC International*. 18th edition. Gaithersburg, MD: AOAC International.
- Bada, Jeffrey, Richard Peterson, Arndt Schimmelmann, and Robert Hedges. 1990. Moose teeth as monitors of environmental isotopic parameters. *Oecologia* 82:102–106.
- Bravo-Hollis, H., and H. Sánchez-Mejorada. 1991. *Las cactáceas de México*. 2nd edition. México D.F.: Universidad Nacional Autónoma de México.
- Caloggero, Silvina, and Carlos A. Parera. 2004. Assessment of prickly pear (*Opuntia ficus-indica*) varieties and their possible planting systems. *Spanish Journal of Agricultural Research* 2(3):401–407.
- Cavagnaro, Juan Bruno. 1988. Distribution of C₃ and C₄ grasses at different altitudes in a temperate arid region of Argentina. *Oecologia* 76:273–277.
- Cerling, Thure E., Jim R. Ehleringer, and John M. Harris. 1998. Carbon dioxide starvation, the development of C₄ ecosystems, and mammalian evolution.

- Philosophical Transactions of the Royal Society B: Biological Sciences* 353:159–170.
- Cernusak, Lucas A., Nerea Ubierna, Klaus Winter, Joseph A. M. Holtum, John D. Marshall, and Graham D. Farquhar. 2013. Environmental and physiological determinant of carbon isotope discrimination in terrestrial plants. *New Phytologist* 200:950–965.
- Chisholm, Brian, and Richard Ghia Matson. 1994. Carbon and nitrogen isotopic evidence on Basketmaker II diet at Cedar Mesa, Utah. *Kiva* 60(2): 239–255.
- Ehleringer, Jim R., Thure E. Cerling, and Brent R. Helliker. 1997. C₄ photosynthesis, atmospheric CO₂, and climate. *Oecologia* 112:285–299.
- FAO/Latinfoods. 2002. *Tabla de composición de alimentos de América Latina*. <http://www.rlc.fao.org/es/conozca-fao/que-hace-fao/estadisticas/composicion-alimentos>.
- Farquhar, Graham, Jim Ehleringer, and Kerry T. Hubick. 1989. Carbon isotope discrimination and photosynthesis. *Annual Review of Plant Physiology and Molecular Biology* 40:503–537.
- Felger, Richard S., and Mary B. Moser. 1977. Columnar cacti in Seri Indian culture. *Kiva* 39(3–4):257–275.
- Fernandes, Ricardo, Marie-Josée Nadeau, and Pieter M. Grootes. 2012. Macronutrient-based model for dietary carbon routing in bone collagen and bioapatite. *Journal of Archaeological and Anthropological Sciences* 4(4):291–301.
- Fogel, Marilyn, and Noreen Tuross. 2003. Extending the limits of paleodietary studies of humans with compound specific carbon isotope analysis of amino acids. *Journal of Archaeological Science* 30:535–545.
- Francey, R. J., C. E. Allison, D. M. Etheridge, C. M. Trudinger, I. G. Enting, M. Leuenberger, R. L. Langenfelds, E. Michel, and L. P. Steele. 1999. A 1000-year high precision record of δ¹³C in atmospheric CO₂. *Tellus Series B-Chemical and Physical Meteorology* 51(2):170–193.
- Froehle, Andrew, Corina Kellner, and Margaret Schoeninger. 2010. Focus: effect of diet and protein source on carbon stable isotope ratios in collagen; follow up to Warinner and Tuross (2009). *Journal of Archaeological Science* 37(10):2662–2670.
- Gil, Adolfo, Gustavo Neme, and Robert Tykot. 2010. Isótopos estables y consumo de maíz en el centro occidente argentino: tendencias temporales y espaciales. *Chungara, Revista de Antropología Chilena* 42(2):497–513.
- . 2011. Stable isotopes and human diet in central western Argentina. *Journal of Archaeological Science* 38:1331–1340.
- Gil, Adolfo, Robert Tykot, Gustavo Neme, and Nicole Shelnut. 2006. Maize on the frontier: isotopic and macrobotanical data from central-western Argentina. In *Histories of maize multidisciplinary: approaches to the prehistory, biogeography, domestication, and evolution of maize*. J. Staller, R. Tykot, and B. Benz, eds. Pp. 199–214. New York: Academic.
- González Cruz, Irma. 2006. Desarrollo y aplicación de procesos tecnológicos para la elaboración de conservas a base de pitaya (*Stenocereus spp.*) de la región Mixteca. Thesis, Universidad Tecnológica de la Mixteca, Huajuapán de León, Oaxaca.
- Hobson, Keith, and Henry Schwarcz. 1986. The variation in ¹³C values in bone collagen for two wild herbivore populations: implications for paleodiet studies. *Journal of Archaeological Science* 13:101–106.
- Howland, M., L. Corr, S. Young, V. Jones, S. Jim, N. Van Der Merwe, A. Mitchell, and R. Evershed. 2003. Expression of the dietary isotope signal in the compound specific δ¹³C values of pig bone lipids and amino acids. *International Journal of Osteoarchaeology* 13(1–2):54–65.
- Inglese, Paolo, Filadelfio Basile, and Mario Schirra. 2002. Cactus pear fruit production. In *Cacti: biology and uses*. P. Nobel, ed. Pp. 163–184. Berkeley: University of California Press.
- Jim, Susan, Vicky Jones, Stanley H. Ambrose, and Richard P. Evershed. 2006. Quantifying dietary macronutrient sources of carbon for bone collagen biosynthesis using natural abundance stable carbon isotope analysis. *British Journal of Nutrition* 95(6):1055–1062.
- Keeling, R. F., S. C. Piper, A. F. Bollenbacher, and S. J. Walker. 2010. Monthly atmospheric ¹³C/¹²C isotopic ratios for 11 SIO stations. In *Trends: a compendium of data on global change*. Oak Ridge, TN: Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy. <http://cdiac.ornl.gov/trends/co2/iso-sio/iso-sio.html>.
- Kellner, Corina, and Margaret Schoeninger. 2007. A simple carbon isotope model for reconstructing prehistoric human diet. *American Journal of Physical Anthropology* 133(4):1112–1127.
- Kelly, Jeffrey F. 2000. Stable isotopes of carbon and nitrogen in the study of avian and mammalian trophic ecology. *Canadian Journal of Zoology* 78:1–27.
- Kelly, Robert. 1995. *The foraging spectrum: diversity in hunter-gatherer lifeways*. Washington, DC: Smithsonian Institution Press.
- Kiesling, Roberto. 1968. Cactaceas y suculentas Mexicanas. *Órgano de la Sociedad Mexicana de Cactología, A.C.* 13(2):35–38.
- . 1971. Dos nuevas especies de *Pterocactus* (Cactaceae). *Boletín de la Sociedad Argentina de Botánica*. 14(1–2):111–116.
- . 1975. Los géneros de cactaceae en Argentina. *Boletín de la Sociedad Argentina de Botánica* 16(3):197–227.
- . 1984. Estudios en cactaceae en Argentina: *Maihueniopsis* y *Tephrocactus* y géneros afines (Opuntioideae). *Darwiniana* 25(1–4):171–215.
- . 2003. *Flora de San Juan, República Argentina*. Vol. 2. Buenos Aires: Estudio Sigma.
- Kiesling, Roberto, and Omar Ferrari. 2005. *100 cactus Argentinos*. Buenos Aires: Editorial Albatros.
- Koch, Paul L. 1998. Isotopic reconstruction of past continental environments. *Annual Review of Earth and Planetary Sciences* 26:573–613.
- Ladio, Ana. 2001. The maintenance of wild edible plant gathering in a Mapuche community of Patagonia. *Economic Botany* 55(2):243–254.
- Ladio, Ana, and Mariana Lozada. 2009. Human ecology, ethnobotany and traditional practices in a rural population of the Monte region, Argentina: resilience and ecological knowledge. *Journal of Arid Environments* 73(2): 222–227.
- Ladio, Ana, Mariana Lozada, and Mariana Weigandt. 2007. Comparison of traditional wild plant knowledge between aboriginal communities inhabiting arid and forest environments in Patagonia, Argentina. *Journal of Arid Environments* 69:695–715.
- Llano, Carina. 2011. Aprovechamiento de los recursos vegetales entre las sociedades cazadores-recolectores del sur de Mendoza. PhD thesis, Universidad Nacional de Comahue, Centro Regional Universitario Bariloche.
- Llano, Carina, and Andrew Ugan. 2010. Rendimiento económico de plantas silvestres del sur de Mendoza: valores nutricionales, costos de manejo e interpretación del registro arqueológico. In *Tradiciones y transformaciones en Etnobotánica*. M. L. Pochettino, A. H. Ladio, and P. M. Arenas, eds. Pp. 44–48. La Plata: CYTED.
- Lüttge, Ulrich. 2004. Ecophysiology of crassulacean acid metabolism (CAM). *Annals of Botany* 93:629–652.
- Martínez-Crovetto, Raul. 1963. *Las noticias etnobotánicas de Augusto Guimard*. Primer Congreso de Área Araucana Argentina. Pp. 29–41. Comisión Nacional Ejecutiva del 150° Aniversario de la Revolución de Mayo, Buenos Aires, Argentina.
- . 1982. Breve panorama de las plantas utilizadas por los indios de Patagonia y Tierra del Fuego. *Suplemento Antropológico: Universidad Católica de Asunción* 17(1):61–97.
- Musters, George. 1964 (1871). *Vida entre Patagones*. Buenos Aires: Ed. Solar.
- Myers, Claudia. 1998. *Specialty and minor crops handbook*. Davis: Division of Agriculture and Natural Resources, University of California.
- Nacuzzi, Lidia, and Cecilia Pérez de Micou. 1985. Los recursos vegetales de los cazadores de la cuenca del Río Chubut. *Cuadernos del Instituto Nacional de Antropología* 10:407–423.
- Nobel, Park S. 2002. *Cacti: biology and uses*. Berkeley: University of California Press.
- Osmond, C. B., W. G. Allaway, B. G. Sutton, J. H. Troughton, O. Queiroz, U. Lüttge, and K. Winter. 1973. Carbon isotope discrimination in photosynthesis of CAM plants. *Nature* 246:41–42.
- Ruiz Leal, Adrian. 1972. *Flora popular Mendocina*. Deserta III, Contribuciones del Instituto Argentino de Investigaciones de Zonas Áridas, Mendoza, Argentina. Buenos Aires: Departamento Impresiones de FECIC.
- Schwarcz, Henry P. 2000. Some biochemical aspects of carbon isotopic paleodiet studies. In *Biogeochemical approaches to paleodietary analysis*. S. H. Ambrose and M. A. Katzenberg, eds. Pp. 189–209. New York: Kluwer Academic.
- . 2006. Stable carbon isotope analysis and human diet: a synthesis. In *Histories of maize multidisciplinary: approaches to the prehistory, biogeography, domestication, and evolution of maize*. J. Staller, R. Tykot, and B. Benz, eds. Pp. 315–321. New York: Academic.
- Schwarcz, Henry, and Margaret Schoeninger. 1991. Stable isotope analysis in human nutritional ecology. *Yearbook of Physical Anthropology* 34:283–321.
- Tieszen, Larry, and Tim Fagre. 1993. Effect of diet quality and composition on the isotopic composition of respiratory CO₂, bone collagen, bioapatite, and soft tissue. In *Prehistoric human bone: archaeology at the molecular level*. J. Lambert and G. Grupe, eds. Pp. 121–156. New York: Springer-Verlag.
- Trevisson, Marcelo, and Pablo Demaio. 2006. *Cactus de Córdoba y el centro de Argentina*. Buenos Aires: LOLA.

- Tykot, Robert, Fernanda Falabella, María T. Planella, Eugenio Aspillaga, Lorena Sanhueza, and Cristian Becker. 2009. Stable isotopes and archaeology in Central Chile: methodological insights and interpretative problems for dietary reconstruction. *International Journal of Osteoarchaeology* 19:156–170.
- Winter, Klaus, and Joseph A. M. Holtum. 2002. How closely do the $\delta^{13}\text{C}$ values of crassulacean acid metabolism plants reflect the proportion of CO_2 fixed during day and night? *Plant Physiology* 129:1843–1851.
- Zuloaga, Fernando, Osvaldo Morrone, and Manuel Belgrano. 2008. *Catálogo de las plantas vasculares del Cono Sur* (Argentina, Sur de Brasil, Chile, Paraguay y Uruguay). Monographs in Systematic Botany of the Missouri Botanical Garden, Vol. 107. Buenos Aires: Missouri Botanical Garden Press.