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Jeff D. Leach

Kristin D. Sobolik

Wright State University - Main Campus, kristin.sobolik@wright.edu

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Review Article

High dietary intake of prebiotic inulin-type fructans in the prehistoric Chihuahuan Desert

Jeff D. Leach^{1*} and Kristin D. Sobolik²

¹Paleobiotics Laboratory, 2401 Burgundy Suite 7, New Orleans, LA 70117, USA

²Department of Anthropology and Climate Change Institute, 5773 S. Stevens Hall, University of Maine, Orono, ME 04469, USA

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Archaeological evidence from dry cave deposits in the northern Chihuahuan Desert reveal intensive utilisation of desert plants that store prebiotic inulin-type fructans as the primary carbohydrate. In this semi-arid region limited rainfall and poor soil conditions prevented the adoption of agriculture and thus provides a unique glimpse into a pure hunter–forager economy spanning over 10 000 years. Ancient cooking features, stable carbon isotope analysis of human skeletons, and well-preserved coprolites and macrobotanical remains reveal a plant-based diet that included a dietary intake of about 135 g prebiotic inulin-type fructans per d by the average adult male hunter–forager. These data reveal that man is well adapted to daily intakes of prebiotics well above those currently consumed in the modern diet.

Inulin: Agave (*Agave lechuguilla*): Prebiotics: Prehistory

Advances in molecular microbiology continue to further our understanding of the role of intestinal microbiota in modulating aspects of our postnatal development, adult physiology and overall health and wellbeing^(1–3). Throughout human evolution, microbial growth via hydrolysis and fermentation of undigested exogenous carbohydrates has been critical to maintaining the dynamic ecological equilibrium between various micro-organisms in the gastrointestinal tract⁽⁴⁾. Though poorly understood, our so-called ‘westernised’ diet⁽⁵⁾, which is dominated by easily digested carbohydrates, may be influencing host–microbe symbiosis through a quantitative reduction in the structural and chemical diversity of undigested carbohydrates^(6–8).

Since it was discovered that mammalian digestive enzymes could not hydrolyse β -glucosidic bonds found in some carbohydrates, such as inulin-type fructans⁽⁹⁾, these oligosaccharides and polysaccharides have emerged as prebiotics, able to escape metabolism in the upper intestine and selectively stimulate the growth and metabolic activity of beneficial bacteria (for example, bifidobacteria and lactobacilli), while suppressing the growth of less desirable micro-organisms⁽¹⁰⁾. Improving the microbial balance of our westernised guts through the prebiotic effect can result in a wide range of physiological benefits to the host, including reduced gut infections, improved lipid metabolism, improved mineral absorption, enhanced immunomodulation and reduced risk of carcinogenesis⁽¹¹⁾. However, initial faecal microbiota

composition, dosage and duration of dosage, as well as the physio-chemical structure of the substrate, can have measurable outcome on the prebiotic effect^(12–14).

Current daily intake of prebiotic fructo-oligosaccharides in the USA is 1–4 g, and 3–11 g in Western Europe⁽¹⁵⁾. Prebiotics are formulated into an increasing number of foods and embraced by dietitians⁽¹⁶⁾, but little is known about dietary intake of prebiotic carbohydrates by ancestral populations. Said differently, were prebiotics part of the nutritional landscape upon which our organic human–microbiota symbiosis was selected? While prebiotic plant foods have been available throughout human evolution, advances in technology have increased consumption within the last 40 000 years^(7,17). Unique archaeological preservation in the arid regions of the Chihuahuan Desert provide a glimpse into dietary intakes of prebiotics that far exceed those consumed by modern man.

Prehistoric diet of the Chihuahuan Desert

In the semi-arid northern Chihuahuan Desert, near the modern town of Del Rio (TX, USA) archaeological research over the last four decades has revealed an extraordinary well-preserved prehistoric record dating back over 10 000 years⁽¹⁸⁾. Erosion and down cutting of the limestone canyons and plateaus have created numerous overhangs, rock shelters, and caves of stratified layers of faunal and botanical remains, human skeletons and mummies, archaeological cooking features and

* Corresponding author: Dr Jeff D. Leach, fax +1 504 373 5213, email jeff@paleobioticslab.com

an unparalleled collection of desiccated human faeces (coprolites) in deposits often metres deep. Though rainfall was limited, three rivers in the area provided a water supply that supported a diversity of plants and wildlife.

Detailed paleodietary studies^(19–23) demonstrate that these prehistoric populations consumed a wide variety of plants, animals and other resources including prickly pear, agave, mesquite, sotol, acorns, walnut, berries, pecan, acacia, onion and other geophytes, rodents, turtle, fish, rabbits, hares, insects, birds, reptiles and deer. Analysis of well-preserved faunal and macrobotanical remains from excavated rock shelters and caves reveals a broad-spectrum diet of wild plants and predominately small animals for the entire 10 000-year record. Among the consumed plants, the desert succulents *Agave lechuguilla* (agave), *Dasyliirion* sp. (sotol) and *Opuntia* sp. (prickly pear) were heavily utilised, along with *Allium drummondii* (onion), *Yucca* sp. (yucca) and *Prosopis* sp. (mesquite). No evidence of agriculture is present in the area, owing to limited rainfall, high evaporation rates and poor soil conditions.

Of particular interest are agave, sotol and onion, all three of which store inulin-type fructans as the major carbohydrate^(15,24–25). The epidermal tissue (hearts) of agave and sotol were harvested in large quantities and processed in rock-lined earth ovens heated with fuel wood and cooked for >40 h. The cooked material is eaten immediately, or pounded into sheets, dried and stored for later consumption⁽²⁶⁾. The moist cooking environment of the earth oven reduces the plants' toxicity and improves the nutritional profile⁽²⁷⁾. Evidence of these massive cooking facilities dots the arid landscape and the remains (leaf bases, fragments) of agave and sotol are well-represented in cultural layers in caves throughout the region⁽²⁶⁾. Wild onion was cooked and eaten, but also consumed raw.

Stable carbon isotope analysis on skeletal material recovered from various deposits in the area suggested that between 45 and 68 % of the diet may have been derived from C4 and other plants that utilise crassulacean acid metabolism (CAM) photosynthetic pathways, with the CAM plant agave making the greater contribution⁽²⁸⁾. Note that plants CAM photosynthetic pathways leave distinct ¹³C signatures in the tissues of the animals that consume them.

Analysis of 359 human coprolites dating throughout the 10 000-year sequence from various cave deposits supports the widespread consumption of agave, sotol and onion, as undigested fragments and DNA remnants of these plants are identified from these well-preserved samples⁽²⁹⁾.

Available evidence (macrobotanical, cooking features, stable carbon isotopes, coprolites) across multiple excavated rock shelter and cave sites suggests that agave, sotol and onion were dietary staples, with agave and sotol contributing significantly more energy. These data suggest that 60–80 % of the energy was provided from plant resources. For the present paper, it will be assumed that only 50 % of the diet (carbohydrate + protein + fat) was derived from plants and that conservatively 20 % of the energy from this plant proportion of the diet was derived from the carbohydrate portion (fructan) of agave, sotol and onion. The fructan fraction (DM) of agave and sotol is 65–70 % (dry weight) and 41–88 % for onion^(15,26). All three plants were available throughout the year and agave and sotol can be considered

the primary carbohydrate source in the diet. Note that yucca and prickly pear were also heavily utilised and contain small amounts of inulin-type fructans, but will not be considered in the following discussion.

If it is assumed that an adult male hunter–forager from this desert population consumed on average 11 297 kJ (2700 kcal)/d⁽³⁰⁾, then 5648 kJ (1350 kcal)/d were derived from plants and, of that, the three fructan plants contributed 1130 kJ/d (270 kcal). The much larger size of agave and sotol, and overall abundance on the landscape, compared with the small bulbs of wild onion from the region (*Allium drummondii* Regel.), along with the archaeological evidence, suggests that agave and sotol may have collectively contributed up to 80–90 % of the inulin-type fructans in the diet.

The fructans in agave and sotol consist of a linear and linear and branched mixture of $\beta(2 \rightarrow 1)$ and $\beta(2 \rightarrow 6)$ linkages with a degree of polymerisation (DP) range of 3–32^(24–25). Agave and sotol fructans have been categorised as graminans and branched neo-fructans⁽²⁵⁾. The prebiotic effect of species of agave and sotol has recently been demonstrated⁽³¹⁾. The fructans of species of modern onions have a lower molecular weight, with a DP of about 3–10⁽³²⁾.

As mentioned, agave and sotol were cooked in earth ovens for >40 h before consumption. The cooking of these desert succulents is supported by the presence of massive accumulations of thermally altered stones known as burned rock middens, some measuring 5–20 m in diameter, representing hundreds of cooking events per facility. Experimental data suggest that while the initial heating of the stones within the earth ovens reached temperatures of 300°C, the food 'packages' only achieved peak temperatures ranging from 90 to 106°C for a proportion of the entire cooking period⁽³³⁾. Temperatures of 100°C have been shown to degrade inulin by about 7–10 %^(34–35).

The degradation of inulin-type fructans is critical, as heat creates lower-molecular-weight fractions (mono- and disaccharides) and breaks the β -bonds that make the fructan unavailable to enzymic hydrolysis in the upper gastrointestinal tract. Once degraded and the β -glycosidic bonds were broken, the carbohydrate is digested and absorbed in the small intestine and unavailable for microbial fermentation and therefore does not contribute to the prebiotic effect. For the purpose of the present paper, a degradation of 25 % will be assumed for pit-baked fructans, more than double the published rate.

Of the 1130 kJ (270 kcal)/d contributed by agave, sotol and onion, 283 kJ (68 kcal) (25 %) would have been provided by the degraded fructans at a rate of 16.74 kJ/g (4 kcal/g), following standard conversion rates for digested carbohydrates⁽³⁶⁾. However, since selective anaerobic hydrolysis and fermentation is necessary to salvage energy from undigested fructans, an energy contribution of 6.28 kJ/g (1.5 kcal/g) is applied for those byproducts utilised by the host for energy⁽³⁷⁾. Therefore, the remaining 847 kJ (202 kcal) not provided by the degraded fructans would be contributed by 135 g prebiotic inulin-type fructans per d.

Concluding remarks

Well-preserved archaeological remains from the northern Chihuahuan Desert reveal that prehistoric populations relied

heavily on desert plants that store inulin-type fructans for over 10 000 years. Evidence for the intensive use of these prebiotic plants is provided by extant cooking features, macrobotanical evidence, stable carbon isotope analysis of human remains and preserved human coprolites.

Conservative estimates of the contribution of inulin-bearing plants in the diet suggest that the average male hunter–forager from this population would have consumed about 135 g prebiotics per d, and adult females about 108 g/d (based on about 20 % less energy). The absolute dietary intake of prebiotic inulin-type fructans would have no doubt fluctuated from day to day and season to season, but does illustrate the highest reported intake of any prehistoric or modern population in the literature.

When the non-starch polysaccharides (for example, cellulose, hemicellulose, lignin) from agave, soto, onion and the other dozens of plants from the diet are considered, the overall dietary intake of fibre from all sources ranges from about 150 to 225 g/d for an adult male. Further, when all fermentable substrates, such as NSP, resistant starch, unabsorbed sugars, dietary protein, gut secretions, mucus, and sloughed epithelial cells entering the large intestine⁽³⁸⁾ on a daily basis are considered, a significantly greater proportion of basal energy needs was provided from the large intestine for this prehistoric population than is observed among modern, westernised populations. A greater energy contribution from fermentation products would have resulted, along with the minimally processed diet in general for this prehistoric population, in less need for the hormone insulin to be secreted.

Even though about 135 g/d is difficult to comprehend in the context of our modern diet, it is also useful to remember that the total dietary fibre component for this prehistoric population, as with most ancestral groups⁽³⁹⁾ before the widespread adoption of agriculture, was characterised by an extraordinary diversity of fibre sources that were linear and branched and low and high molecular weights. This is the nutritional landscape upon which our genome and symbiotically evolved microbiome were selected.

The implications of the evolutionary role of prebiotics in modern human health and wellbeing are unknown. It is clear from the archaeological data, such as those presented here, and from the ecological distribution of fructans-bearing plants throughout the planet's diverse environs, that ample opportunities to include such non-digestible carbohydrates in diet existed throughout the evolution of our genus. It is against this evolutionary backdrop that makes the physiological parameters, which define a prebiotic, most interesting.

As advances in metagenomics expand our understanding of the complex interaction between host genome and the microbiome and how they contribute to normal physiology and predisposition to disease⁽⁴⁰⁾, the modulating effects of dietary inputs on microbiota will receive greater attention. The accumulating physiological health benefits observed for prebiotics should come as no surprise when you consider the nutritional landscape upon which co-evolution between microbial communities and their human hosts took place. With total dietary intake of 'fibre' in the USA averaging < 20 g/d, from a remarkably limited number of sources⁽⁴¹⁾, there should be no doubt that our so-called 'westernised diet' of highly processed carbohydrates and reduced quantity and diversity of fermentable substrates has resulted in a nutritional

state that may be causing measurable shifts in bacterial species in the microbiome⁽⁴²⁾.

An evolutionary perspective on prebiotics may result in the rediscovery of mixtures of polymers of varying chain lengths that attenuate human disease and contribute to a sense of wellbeing. That said, it may be appropriate for prebiotics to be a public health term supported by dietary guidelines to promote consumption of plants and functional foods that provide substrates for the growth of beneficial intestinal flora.

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