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ORIGINAL ARTICLE

Composition of Tubers Used by Hadza Foragers of Tanzania

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Data are presented on three edible species of tuber (*Vigna frutescens*, *Eminia entennulifa*, and *Ipomoea transvaalensis*) consumed by Hadza foragers in northern Tanzania. These species are collected almost year-round by Hadza women but previous analyses of their macronutrient composition are variable and provide results based on the analysis of whole tuber. We examined only edible portions of tuber by simulating chewing in the presence of salivary amylase and by removing from analysis the typically expectorated inedible component. Edible portions of the three peeled tubers ranged from 42.5 to 91.8 g/100 g dry wt., were low in protein (2.3–6.9 g/100 g dry wt.), and contained 19.6–26.0 g/100 g of starch. The sum of monosaccharides and disaccharides ranged from 6.2 g/100 g in the *Vigna frutescens* to 48.3 g/100 g of edible portion of *Ipomoea transvaalensis*. In addition, our analysis of 5 samples of *Vigna frutescens* had a 5-fold range in energy available to consumers, an important consideration for energetic studies. This range was due, in part, to the variation in edible portion (20.8–75.4 g/100 g of edible dry tuber). Our data, in comparison with those reported previously, show generally lower energy levels and higher levels of indigestible material for some of these tubers. These discrepancies are likely due to differences in analysis of whole tuber versus edible portion, method of measuring indigestible carbohydrate, and age of tuber.

Key Words: hunter-gatherers; East Africa; wild plant foods; *Vigna frutescens*; *Eminia entennulifa*, *Ipomoea transvaalensis*.

INTRODUCTION

Across much of Africa, the underground storage organs (collectively known as tubers) of wild plants are considered important energy sources for small groups of human foragers (Vincent, 1984) and reserve energy sources for small-scale agriculturists (Newman, 1975). These observations, coupled with the assumption that wild tubers provide high energy levels per unit time, led to recent proposals that a dependence on tubers was a significant factor in human evolution (O'Connell *et al*., 1999; Pennisi, 1999; Wood and Brooks, 1999; Wrangham *et al*., 1999). Yet, these studies probably used overinflated energy densities for wild tubers in developing their hypotheses.

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TABLE 1

Compositions of selected tubers cultivated today across Sub-Saharan Africa[1]

Common name, *Genus species*[2]	Moisture (%)	Crude protein	Fat	CHO[3]	Dietary fiber	Ash	Energy[4] (kJ (kcal)/ 100 g dry wt.)
		(g/100g dry wt.)					
Indigenous to Africa							
Yellow yam, *Dioscorea cayenensis*	67	6	< 1	80	3	—	1618 (387)
White yam, *Dioscorea rotundata*	67	7	< 1	80	3	—	1609 (385)
Elephant yam, *Amorphallus aphyllus*	71	8	1	84	5	6	1555 (372)
Hausa potato, *Solenostemon rotundifolius*	76	5	1	91	4	4	1639 (392)
Not indigenous to Africa							
Yam, *Dioscorea esculenta*	—	5	< 1	70	3	—	1622 (388)
Yam, *Dioscorea alata*	76	8	< 1	73	5	—	1601 (383)
Taro, *Colocasia esculenta*	73	7	< 1	88	4	5	1580 (378)
Cassava, *Manihot esculenta*	62	3	< 1	94	3	2	1639 (392)
Sweet potato, *Ipomoea batatas*	69	5	< 1	91	3	3	1630 (390)

Note: —, not determined.

[1] Data are rounded to the nearest whole % because the variability between samples and between studies indicated that greater accuracy was not possible.

[2] Data on yellow yam, white yam, yam (*Dioscorea esculenta*), and yam (*Dioscorea alata*) are taken from Egbe *et al.* (1984). Data on elephant yam, Hausa potato, taro, cassava, and sweet potato are taken from Leung (1968).

[3] Egbe and colleagues (1984) report starch levels but not simple sugars. Their reported starch values are placed under carbohydrate. Leung (1968) reports total digestible carbohydrate.

[4] Leung (1968) calculated energy using 11.7 kJ (2.8 kcal)/g dry wt. for protein, 16.7 kJ (4.0 kcal)/g dry wt. for digestible carbohydrate and 35.1 kJ (8.4 kcal)/g dry wt. for fat.

Variable, and sometimes inappropriate, methods have been used to measure the energy and macronutrient content of wild tubers. Further, based on unwarranted comparisons with agricultural tubers, compositional data were obtained by the analysis of whole tubers, when in fact, much of the wild tuber may not be consumed. To address these issues, we analyzed only the edible portions of selected wild tubers from East Africa as part of a larger study of foraging among the Hadza, a group living near Lake Eyasi in northern Tanzania. Wild tubers are available and eaten throughout the year by the Hadza, with the possible exception of the latest dry season and the latest wet season (personal observations 1993, 1994).

In contrast to cultivated tubers, little is known about the composition of wild tubers and there are reasons to expect that some wild species differ in composition from common agricultural varieties. Many of those used by the Hadza belong to the family Leguminosae (Vincent, 1985). In contrast, none of the agricultural tubers belong to the Leguminosae. Instead, most of the indigenous and introduced tuber species cultivated across sub-Saharan Africa today (see Table 1) belong to the Convolvulaceae. Among Hadza-collected tubers, only one species belongs to the Convolvulaceae. The unusual growth form and placement of many wild tubers as well as their

TABLE 2

Published compositions of wild tubers species collected by Hadza foragers

Hadza name *Genus species*[1] n = no. of samples	Moisture (%)[2]	Lab[3]	Crude protein	Fat	CHO	Dietary fiber	Ash	Energy[4] (kJ (kcal)/100 g dry wt.)
			(g/100 g dry wt.)					
//ekwa (*Vigna frutescens*)								
$n = 3$	70	1	7.4 ± 1.6	1.3 ± 1.1	61.3 ± 6.4	23.2 ± 6.6	6.8 ± 1.1	1166 (279) ± 121 (± 29)
$n = 6$		2	10.3 ± 4.9	—	28.9 ± 9.6	51.0 ± 6.4	—	—
Makalidako (*Eminia entennulifa*)								
$n = 1$	70	1	10.2	0.6	34.9	45.2	9.2	740 (177)
Shumuko (*Vatoraea pseudolablab*)								
$n = 4$	70	1	5.7 ± 1.0	2.6 ± 1.8	53.8 ± 5.4	24.2 ± 5.8	13.8 ± 1.8	1062 (254) ± 100 (± 24)
$n = 3$		2	7.7 ± 1.1	—	19.4 ± 6.4	27.7 ± 9.7	—	—
Do'aiko (*Vigna macrorhyncha*)								
$n = 2$	70	1	10.4	3.4	49.6	20.8	16.0	1070 (256)
$n = 2$		2	12.2	—	40.2	23.5	—	—

Note: —, not determined.

[1] Data are from Vincent (1985) and are presented as mean ± standard deviation. Energy data are recalculated on a dry weight basis.

[2] Vincent assumed an average moisture content of 70%.

[3] Samples were analyzed in two different laboratories using different methods.

[4] Energy was calculated using 11.7 kJ (2.8 kcal)/g dry wt. for protein, 16.7 kJ (4.0 kcal)/g dry wt. for digestible carbohydrate and 35.1 kJ (8.4 kcal)/g dry wt. for fat.

superficial appearances also suggest compositional divergence from cultivated ones. Most cultivated tubers grow rather superficially, whereas the majority of those harvested by Hadza women form at depths of up to 3 m. Agricultural varieties vary somewhat in superficial appearance, whereas, the appearance of different samples of Hadza tubers vary dramatically (Vincent, 1984).

The agricultural varieties are fairly constant in macronutrient composition. In contrast, wild tubers, for the most part, have unknown macronutrient compositions. Previous analyses of four species used by the Hadza produced inconsistent results (see Table 2, based on Vincent, 1985) with large intraspecies variation. Significantly, these compositional data represent the analysis of the whole tuber, which are probably of limited use because, unlike agricultural tubers, most of the wild ones are very fibrous and only partly consumed. Typically, they are chewed for 30 s–3 min and a fibrous mass, which can be quite large, is expectorated (field observations). By analyzing the total tuber, rather than limiting the analysis to the edible fraction, previous analyses may have overestimated energy and macronutrient contributions of these foods to the Hadza diet.

To this end, we report the macronutrient composition of the edible portions, separating the inedible fraction that is normally expectorated, for three species commonly used by the Hadza. By doing this, we calculated energy contents of only the

edible portion. We also analyzed several samples of the most commonly consumed species, *Vigna frutescens* (i.e. //ekwa), in an attempt to explain the variation in previously reported compositional data.

METHODS

Field Collection

Five //ekwa tubers, cut into thin strips or small pieces, were collected during the dry season which normally extends from May to October with large interannual variation. As a time of plant food scarcity, the dry season is a major focus for our foraging study. Four of these tubers were collected during September 1993 and one in July 1997. Sixteen thin strips of a single tuber were divided into two samples consisting of eight strips each of which was analyzed separately (samples 5a and 5b in Table 4). In addition, one makaritako tuber was obtained in September 1993, and one panjuko tuber was obtained in July 1997. Tubers collected in 1993 were air-dried in the field and stored in 80% ethanol; the panjuko tuber collected in 1997 was simply air-dried in the field prior to shipment.

The tubers were collected during the Hadza daily gathering trips so that samples obtained for analysis are representative of tubers consumed by them. Sometimes the women taste and discard tubers as they are digging but we did not collect the discards. Since food is not always abundant, we could collect only limited amounts for analysis. The Hadza were continually observed during three field seasons (dry season 1993, wet season 1994, and dry season 1997) to determine the portion of food consumed and the type of preparation, if any. While the women are digging, small tubers are commonly peeled and eaten. These are chewed for up to 3 min and a fibrous residue or quid is then spit out. The majority of the tubers, however, are collected over several hours of digging, then roasted for up to 30 min over an open fire, and allowed to cool briefly. Once cool, tubers are peeled, chewed, and a quid expectorated.

To estimate the contribution of bark to the total tuber weight, three tubers (2 //ekwa and 1 panjuko) were collected during typical digging sessions, peeled, and the bark was weighed. One additional tuber was split with bark attached, dried, and weighed. In addition, to evaluate the effect of cooking on tuber weight, two tubers were weighed before and after cooking. Finally, to estimate the contribution of the inedible portion chewed with each tuber, three typical peeled //ekwa tubers were split into two roughly equal halves, one-half was chewed, the quid collected, dried and weighed. Two typical panjuko tubers were also chewed.

Laboratory Processing

Ethanol was drained from tuber samples and concentrated by roto-evaporation (Buchler Flash-evaporator, Buchler Instruments, Fort Lee, NJ). The ethanol concentrate was transferred quantitatively to a freeze-drying flask with water and lyophilized (Virtis Freezemobile-24, Virtis Co., Gardiner, NY). The whole pieces of tuber also were lyophilized to a constant weight. Tuber aliquots ($\sim$3 g dry wt.) consisted of proportional amounts of tuber and residue recovered during concentration of the ethanol.

Lyophilized tuber aliquots were rehydrated for 24 h in deionized, distilled water (60 mL) at 4°C. Rehydrated tubers were brought to room temperature, excess water was drained off and reserved, and the tuber was weighed. The drained water was combined with the tuber, water was added to bring the total to a volume of 60 mL,

and the tuber and liquid were transferred to a stomacher bag (Seward stomacher '400' bags, Catalog # 14-550-5C, Fisher Scientific, Itasca, IL). Sodium chloride (52.6 mg) was added to make a 0.015 N solution. Human salivary amylase (3 mg) (α-amylase, Type XIII-A, EC 3.2.1.1, catalog #A1031, Sigma Chemical Co., St. Louis, MO) was dissolved in 0.6 mL 0.015 N sodium chloride solution and added to the stomacher bag (Schneyer, 1956). Preliminary experiments showed that adding approximately 3.5 times more amylase had no effect on the amount of starch solubilized from the root. Samples were stomached (Stomacher Lab-Blender 400, Tekmar Co., Cincinnati, OH) for 2 min intervals and the fibrous mass was inspected visually to obtain fibers similar to the expectorated quid that were gathered in the field. Preliminary experiments, in which the fibrous mass was visually inspected at 30 s intervals during stomaching, indicated that 3–6 min of stomaching produced fibers similar to those in field-collected quids. All tubers processed for analysis were stomached for 4–6 min. After blending, samples in the stomacher bags were placed on ice for 10 min to inactivate the enzyme. The fibers were removed manually and air-dried. The remaining contents of the stomacher bag were transferred quantitatively with water to a flask, dried by lyophilization, weighed, and ground with a mortar and pestle.

Analytical Methods

The supernatant obtained by stomaching the sample was analyzed for protein, starch, and ash (Marlett, 1992). Moisture contents were calculated as the difference in weight between field-determined fresh weight and lyophilized weight measured in the laboratory. In the case of samples stored in ethanol, the total dry sample weight consisted of the lyophilized ethanol concentrate plus the lyophilized tuber. Except when noted otherwise, all analyses for protein, starch, and ash were conducted in duplicate using the dry supernatant that is equivalent to the edible portion. More detailed analyses were not possible due to insufficient sample.

Nitrogen was measured in small aliquots (25–100 mg) by a micro-Kjeldahl method (Buchi–Brinkman digestion unit model 430 and distillation unit model 320, Brinkman Instruments, Inc, Westbury, NY) (Monsma *et al*., 1992). Crude protein was estimated as the nitrogen content times 6.25. Starch was measured by an enzymatic-colorimetric method (Method 76-11; AACC, 1976) on small samples (10–100 mg). Briefly, each sample was ethanol-extracted to remove simple sugars, autoclaved to gelatinize starch, incubated with enzyme to hydrolyze starch and the liberated glucose quantitated by glucose oxidase. To determine ash, 400 mg dry aliquots were ashed (450°C, 24 h), allowed to cool, wet with concentrated nitric acid, returned to the muffle furnace overnight ($\geq$ 16 h), and brought to room temperature in a desiccator before weighing. The methods were reproducible. The means of the coefficients of variation of the eight duplicate analyses were: crude protein, 5.1%; starch, 1.3%; and ash, 6.2%.

In addition, soluble fiber was estimated by quantitating the amount of uronic acids in the supernatant using a colorimetric assay (Blumenkrantz and Asboe-Hansen, 1973) with galacturonic acid as the standard, as previously described (Marlett, 1992). Uronic acids, a measure of pectic substances, comprise 50–60% of the soluble fiber in potatoes, carrots and sweet potatoes (Marlett and Cheung, 1997). Total fiber was not determined because insoluble fiber, by definition, would not be extracted into the aqueous phase and there was insufficient sample to analyze chemically for any soluble hemicelluloses (Marlett, 1992). The fat content of the tuber and root supernatants was not determined because the amount of sample available for analysis was limited and other roots and tubers contain negligible fat (USDA, 1984). The amount of mono- and disaccharides was calculated by difference.

RESULTS

Intraspecies Variation (*Table 3*)

There was substantial variation in both the inedible and edible contents among the five individual //ekwa tubers which were analyzed. There were also slight differences between the two samples of the single //ekwa tuber. The compositions of the two pieces were consistent relative to the other four, however, and the average for the two samples of tuber number 5 was used in the following comparisons. The range for the mass of the inedible portion was 24.6–79.2 g (average of 5a and 5b) per 100 g of dry, peeled tuber. The appearance of the inedible fractions was consistent with the analytical data (see Fig. 1). Some of the fibrous material, separated after stomaching, was almost woody, whereas the inedible portion from other //ekwa samples was more pliable. It was very apparent that more edible material could be obtained by chewing some tubers rather than others.

The range for soluble fiber varied directly with the size of the edible fraction. Tuber sample 1, which had the highest fraction of edible material (75.4 g/100 g of dry peeled tuber), also had the largest amount of pectin (2.3 g/100 g), whereas tuber sample 5 had the lowest pectin content (0.2 g/100 g, average of 5a and 5b) and edible yield (20.8 g/100 g). The range in the edible carbohydrate contents agreed inversely with the inedible portions. Among the 5 //ekwa tubers, the range for starch was from 5.0 g/100 g (average of 5a and 5b) in the sample with the largest inedible fraction to 51.1 g/100 g in the sample with the smallest inedible fraction. The range for mono- and disaccharides was 2.7–10.7 g/100 g. There was a slight range in ash content (3.2–7.2 g/100 g dry tuber) and in crude protein content (3.3–6.2 g/100 g dry tuber), but little variation among moisture contents which were consistently high ($> 75\%$) in the 5 //ekwa tubers. In total, these variations in composition resulted in a 5-fold range in energy density among these 5 //ekwa tubers from a low of 255 kJ (61 kcal)/100 g dry wt. (average of 5a and 5b) to a high of 1104 kJ (264 kcal)/100 g dry wt.

TABLE 3

Variation in composition of //ekwa (*Vigna frutescens* A. Rich.) from East Africa[1]

Sample[2]	Moisture %	Edible portion[3]	Crude protein	Starch	Simple sugars[4]	Pectin	Ash	Energy[5] (kJ (kcal) /100 g dry wt.)
		(g/100 g dry, peeled tuber)						
1	—	75.4	4.2	51.1	10.7	2.3	7.2	1104 (264)
2	83.4	42.8	4.4	25.8	6.2	0.5	5.8	610 (146)
3	75.1	45.1	3.3	35.1	2.7	0.8	3.2	686 (164)
4	76.5	28.6	4.2	12.8	7.2	0.4	3.9	405 (97)
5a	75.8	19.5	5.6	4.9	3.3	0.2	5.4	230 (55)
5b	75.8	22.2	6.8	5.0	4.9	0.3	5.2	280 (67)

Note: —, not determined.

[1] Data are the mean of duplicate analyses.

[2] 5a and 5b represent two separate preparations of the same tuber; 1–5 are preparations of different tubers.

[3] Edible portion is that fraction of the tuber solubilized by stomaching hydrated sample in the presence of salivary amylase.

[4] The fraction containing monosaccharides and disaccharides was determined by difference.

[5] Energy was calculated using 16.72 kJ (4 kcal)/g dry wt. for protein and digestible carbohydrate.

FIGURE 1. Examples of inedible material recovered after stomaching various wild tuber samples. Some of the material is more flexible than others. This material is similar in appearance to that expectorated as quids by the Hadza after chewing for 30 s–3 min (field observations). Based on our laboratory results, these quids contain, in all likelihood, adherent edible fractions, especially starch, but are largely inedible fiber.

Interspecies Comparison (*Table 4*)

Edible portion: The fraction of each tuber that was edible also varied substantially among the three species that we analyzed. Using the average of the 5 //ekwa tubers, the two legume species (//ekwa and makaritako) were $\leq 50\%$ edible, whereas the non-legume, panjuko, was $> 90\%$ edible. These data corroborate field observations. Three //ekwa tuber samples, chewed in the field, and dried as quids had quid weights that accounted for 26%–42% ($n = 3$: 26%, 35%, and 42%) of the expected dry weight of a tuber assuming a 70% moisture content. In contrast, two panjuko samples produced virtually no quid at all. Cooking of two //ekwa tubers had no discernible effect on the amount of tuber expectorated as a quid.

The edible fraction of these tubers was even smaller when the contribution of bark to the total mass is considered. Two //ekwa tubers, prepared in the field, had bark weights that accounted for 23% and 24% of the total fresh weight of the tuber; one panjuko tuber was 29% bark. Makaritako has a superficial appearance similar to //ekwa and also has a substantive covering of bark, although weights were not measured directly.

Macronutrient composition: There was little variation in protein, starch, and ash contents among the three tuber species analyzed, but a large amount of variation in mono- and disaccharide levels and in soluble fiber. The range for crude protein content was 2.3–6.9 g/100 g, for ash contents it was 5–6 g/100 g, and for starch

TABLE 4

Edible portion and macronutrients of selected tubers from East Africa

Hadza name[1] *Genus species*	Moisture %	Edible portion[2]	Crude protein	Starch	Simple sugars[3]	Pectin	Ash	Energy[4] (kJ (kcal) /100 g dry wt.)
		(g/100 g dry, peeled tuber)						
//ekwa *Vigna frutescens*	77.7 ± 3.8	42.5 ± 20.9	4.5 ± 1.1	26.0 ± 18.2	6.2 ± 3.1	0.8 ± 0.8	5.1 ± 1.6	610 (146) ± 322 (± 77)
Makaritako *Eminia entennulifa*	79.9	56.9	6.9	19.6	23.2	1.3	5.9	832 (199)
Panjuko *Ipomoea transvaalensis*	85.9	91.8	2.3	23.9	48.3	11.8	5.5	1246 (298)

Note: [1] Data are the mean of duplicate analyses, except for //ekwa data which are mean ± standard deviation of the analyses of five different tubers (see Table 3).

[2] Edible portion is that fraction of the tuber solubilized by stomaching hydrated sample in the presence of salivary amylase.

[3] The fraction containing monosaccharides and disaccharides was determined by difference.

[4] Energy was calculated using 16.72 kJ (4 kcal)/g dry wt. for protein and digestible carbohydrate.

contents it was 19.6–26 g/100 g dry, peeled tuber. In contrast, the amount of mono- and disaccharides varied from a low of around 6 g/100 g dry wt. in //ekwa to a high of almost 50 g/100 g dry wt. in panjuko. The value for makaritako was 23.2 g/100 g dry wt., almost directly in between the two extremes. Pectin levels also varied; //ekwa and makaritako levels were similar at about 1 g/100 g dry wt., but the panjuko, which had the highest amount of edible weight, contained almost 12 g pectin in the edible portion per 100 g dry wt. of peeled tuber. These compositional variations resulted in a 3-fold difference in energy content across species, from a low of 610 kJ (146 kcal)/100 g dry wt. for //ekwa, on average, to a high of 1246 kJ (298 kcal)/100 g dry wt. for panjuko. The energy in makaritako, with 832 kJ (199 kcal)/100 g dry wt., was between these two extremes.

Moisture: All species analyzed in the laboratory had consistently high ($\geq$ 75% total weight) moisture contents. This corroborated field observations where two tuber samples (one //ekwa and another tuber that is similar to shumuko), dried in the field with bark removed, showed a weight loss of 70%. One //ekwa sample, dried with the bark attached, had a 65% weight loss. Cooking had no effect on tuber weight.

DISCUSSION

Our most important finding is that the amount of edible fraction varied substantially within and between tuber species. Across the five //ekwa tubers analyzed, the edible fraction shows a range from a low of around 20% to a high of 75% which is reflected in a 5-fold difference in the energy provided by them. Independent of season and presence of above-ground foliage, Hadza women use the same sites for digging up //ekwa, and they did not appear to discard tubers on the basis of size. This suggests that the age of the tuber may be an important factor where the older tubers have a higher fraction of inedible material. The similarity between the two samples of //ekwa tuber 5 suggests that the major source of variation is between and not within individual tubers. Although we analyzed only uncooked tubers, our field observations on quid size suggest that cooking does not account for variation reported here or previously.

It is difficult to compare directly the analytical data presented here with those published previously (Vincent, 1985). The earlier analyses were performed on the total peeled tuber, whereas we analyzed only the edible portion. In addition, the methods used previously were different from our own. For fiber analysis (see Table 2), Laboratory 2 in Vincent's study used the neutral detergent fiber method (NDF) (Van Soest, 1963) which incorporates some of the starch in the fraction measured as fiber (Marlett, 1990) and thus, would inflate the fiber results. But, at the same time, the NDF procedure fails to include soluble fiber (Marlett, 1990). Thus, the fiber results from Laboratory 2 are similar to the values for the inedible portion that we measured in some of our tuber samples, but this comparability is for erroneous reasons. The data in Vincent's study from Laboratory 1, which used the crude fiber method, are more comparable to our own, because this method recovers most of the cellulose, the likely major constituent of the quid. Our value for the inedible fraction of makaritako also is similar to that reported by Vincent's Laboratory 1. The difference between the inedible fraction of //ekwa between the data sets probably indicates that the three //ekwa samples analyzed by Vincent had low amounts of inedible material and were most similar to our single //ekwa sample that was 75% edible.

The data for carbohydrate in //ekwa from Laboratory 1 in Vincent's study are similar to the sum of monosaccharides, disaccharides, and starch in our //ekwa tuber

which has the highest amount of edible fraction. Our makaritako result is also similar to her makaritako value from Laboratory 1. The data from Laboratory 2, which are lower, are less comparable since what was measured as NDF probably incorporates starch in the absence of a starch extraction step (Marlett, 1990) as noted previously.

Our method of protein analysis is the same as Vincent's Laboratory 1 and our results are generally comparable to Laboratory 1. In contrast, Vincent's Laboratory 2, on average, reports higher values using the ninhydrin amino acid method rather than Kjeldahl crude protein, even though it is not consistent across individual samples. Since ninhydrin measures free amino groups and some amino acids have more than one free amino group, it is possible that the difference reflects the lack of application of a normalization factor to the ninhydrin data. All of the ash analyses used similar methods and the overlap in ranges in the two data sets suggests that the concentration of ash in the whole tuber is similar to that in the portion solubilized by salivary amylase and stomaching.

Assuming that the data from Vincent's Laboratory 1 are legitimately comparable to ours, two major differences appear between the two sets of data. First, it appears that Vincent did not sample tubers with the amount of compositional variation as those eaten by the Hadza we followed. Since she did not sample tubers with fiber levels similar to those of our inedible fraction, her energy estimates are consistently higher than ours. Second, by analyzing the complete tuber rather than just the edible portion, the data presented by Vincent probably overestimate the energy typically provided by these tubers. We show a range across three tuber species of 610–1246 kJ (146–298 kcal)/100 g dry tuber, whereas the range across three out of four of the species analyzed by Vincent was 1062–1166 kJ (254–279 kcal)/100 g dry tuber.

In comparing these data with those published for peeled cultivated tubers (see Table 1), several points of divergence can be noted. First, the peeled cultivated varieties are completely edible. Second, the level of dietary fiber is quite low in the cultivated tubers. Our results indicate that the more commonly consumed Hadza tubers (e.g., //ekwa) can consist of up to 80% inedible material and other tubers with low amounts of inedible material can contain significant soluble fiber levels. Concomitantly, the absolute amount of digestible carbohydrate (starch, monosaccharides, and disaccharides) in the Hadza tuber is much lower than in the agricultural varieties, even though the relative amount (i.e., digestible carbohydrate as percent of edible) is similar. This translates into much lower energy returns from each kilogram of collected Hadza tuber when compared to the cultivated varieties. Cultivated ones average close to 1650 kJ ($\sim$400 kcal)/100 g dry wt., whereas the Hadza tubers average less than 1250 kJ ($\sim$300 kcal)/100 g dry wt. and are close to 825 kJ ($\sim$200 kcal)/100 g dry wt. if panjuko is not included.

CONCLUSIONS

At best, the Hadza tubers provide approximately half the energy of cultivated tubers while requiring what can, at times, be enormous energy investments by the Hadza women. Based on the average of the five //ekwa samples we analyzed, a 1 kg tuber contains only 80 g of edible dry fraction yielding about 400 kJ ($\sim$100 kcal). The panjuko tuber sample, which had the highest edible fraction, contains 184 g edible dry fraction per kilogram yielding 2291 kJ (548 kcal). In contrast, we expect that 1 kg of an indigenous cultivated tuber contains, on average, 270 g of edible dry fraction yielding 4335 kJ (1037 kcal) based on an average $\pm$ standard deviation ($n = 4$) of 1605 $\pm$ 36 kJ (384 $\pm$ 8.5 kcal)/100 g dry wt.). The data most comparable to our own in the previous study of Hadza tubers (Laboratory 1 in Vincent, 1985) overestimate energy

density because the study analyzed the inedible as well as the edible fraction, analyzed tubers with limited compositional variation, and did not analyze soluble fiber (i.e., pectin) levels. Our data, when compared with those on cultivated varieties and the previous study, raise questions concerning the validity of emphasizing the calories provided by this resource in human evolution models.

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