



Grass leaves as potential hominin dietary resources



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ABSTRACT

Discussions about early hominin diets have generally excluded grass leaves as a staple food resource, despite their ubiquity in most early hominin habitats. In particular, stable carbon isotope studies have shown a prevalent C₄ component in the diets of most taxa, and grass leaves are the single most abundant C₄ resource in African savannas. Grass leaves are typically portrayed as having little nutritional value (e.g., low in protein and high in fiber) for hominins lacking specialized digestive systems. It has also been argued that they present mechanical challenges (i.e., high toughness) for hominins with bunodont dentition. Here, we compare the nutritional and mechanical properties of grass leaves with the plants growing alongside them in African savanna habitats. We also compare grass leaves to the leaves consumed by other hominoids and demonstrate that many, though by no means all, compare favorably with the nutritional and mechanical properties of known primate foods. Our data reveal that grass leaves exhibit tremendous variation and suggest that future reconstructions of hominin dietary ecology take a more nuanced approach when considering grass leaves as a potential hominin dietary resource.

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1. Introduction

Diet has long been considered a prime mover in hominin evolution, but links between diet and early hominin differentiation have become more debatable as new methods and data have become available. A growing body of evidence is challenging many traditional interpretations of hominin dietary behavior (for discussion, see Ungar and Sponheimer, 2011). For instance, *Paranthropus boisei* exhibits some of the starkest morphological adaptations to diet of any known hominin species (Rak, 1988, 2014), and some have argued that its hyper-robust craniodental architecture was necessary for the habitual consumption of hard, obdurate foods such as nuts and seeds (Leakey, 1959; Tobias, 1967; Jolly, 1970; Demes and Creel, 1988; Strait et al., 2008, 2013; Constantino et al., 2010, 2011; Rak, 2014; Smith et al., 2015), yet dental microwear evidence reveals no hard-object consumption by

P. boisei (Ungar et al., 2008, 2012; Grine et al., 2012). Moreover, some argue that craniodental robusticity can result from the mechanical challenge posed by diets of tough, low quality foods requiring prolonged and repetitive loading of the chewing apparatus (Ungar and Hlusko, 2016; Daegling and Grine, 2017; see also Hylander, 1988, for earlier arguments about craniodental robusticity as an evolutionary response to repetitive loading).

Additionally, stable carbon isotope studies show that C₄ foods (i.e., foods enriched in ¹³C) became increasingly significant portions of hominin diets beginning at least 3.7 Ma—culminating with *P. boisei*, whose diet was 75–80% C₄ (van der Merwe et al., 2008; Cerling et al., 2011; Ungar and Sponheimer, 2011; Lee-Thorp et al., 2012; Sponheimer et al., 2013; Levin et al., 2015). Moreover, the degree of postcanine megadontia and mandibular robusticity exhibited by early hominin species is positively correlated with the amount of C₄ foods they consumed, suggesting that the inherent properties of these foods may have contributed to australopith craniodental adaptations (Sponheimer et al., 2013).

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Hominins may have consumed foods enriched in ^{13}C either as primary consumers of plants using the C_4/CAM photosynthetic pathway and/or as secondary consumers eating animals that consume significant quantities of C_4 vegetation (e.g., grazing ungulates such as wildebeest and zebra). However, while faunal resources were a likely source of dietary carbon, few would argue that meat consumption was a major component of early hominin diet, despite recent discoveries revealing hominin tool use before 3 Ma (McPherron et al., 2010; Harmand et al., 2015). Similarly, plants using CAM photosynthesis (e.g., succulents) were potentially consumed, but are relatively scarce within most savanna habitats. Thus, despite contributions from faunal and CAM resources, it is most likely that C_4 plants were the primary source of dietary carbon for early hominins with high C_4 isotopic signatures such as *P. boisei*, *Paranthropus aethiopicus*, and *Australopithecus bahrelghazali*.

Of the roughly 7500 species of plants that use the C_4 photosynthetic pathway, most (~80%) are monocots in the families Poaceae and Cyperaceae—tropical grasses (~4500 species) and sedges (~1500 species), respectively (Sage et al., 1999; Sage, 2004). Thus, the bulk of C_4 plant biomass available to African herbivores is located in savanna and/or wetland habitats. While definitions of ‘savanna’ can be debated, it is generally agreed upon that a mostly continuous layer of grasses is a key, if not definitive, component of savanna habitats (for discussion, see Scholes and Archer, 1997).

We are now faced with the task of determining which C_4 plants contributed to hominin diets (grasses and/or sedges) and how they were utilized. Specifically, were certain plant parts such as seeds and storage organs targeted for consumption? These questions become particularly important for species with highly derived craniodental morphology, such as *P. boisei* (Wood and Constantino, 2007; Ungar and Sponheimer, 2011; Daegling and Grine, 2017).

Grass and sedge species possess several anatomical structures that may serve as food for a consumer, including underground storage organs (USOs; e.g., tubers, rhizomes, and corms), seeds, and leaves (which include the blade, collar, and sheath). Scholars have more readily accepted some of these anatomical elements of grasses and sedges as hominin foods. For example, some (e.g., van der Merwe et al., 2008; Dominy, 2012) have argued that C_4 sedges were a likely resource because they often have relatively large USOs that are unavailable to most African herbivores. This underutilized resource would be available to hominins with rudimentary tools, such as digging sticks, and thus would have represented a novel feeding niche ripe for hominin exploitation (Hatley and Kappelman, 1980; Hernandez-Aguilar et al., 2007). Also, sedge (and other) USOs are available year-round and are often portrayed as being both nutrient-dense and mechanically suitable for hominin dental adaptations (Hatley and Kappelman, 1980; Laden and Wrangham, 2005; Dominy et al., 2008; Wrangham et al., 2009; Dominy, 2012; Lee-Thorp et al., 2012).

Similarly, the seeds of C_4 grasses have been proposed as a hominin food by some researchers (Jolly, 1970; Peters and Vogel, 2005). Like sedge USOs, C_4 grass seeds are perceived as nutritionally adequate and possessing physical properties (small and somewhat hard) well suited for hominin consumption. It is also worth noting that modern humans consume vast quantities of grass seed today (e.g., maize, rice, wheat) and have done so for millennia (van Oudtshoorn, 2012).

In contrast, grass leaves are not considered a viable hominin food by most because they are generally regarded as offering little nutritional value (low in protein and high in fiber) and having mechanical properties (particularly measures of toughness) that are ill-suited for hominins lacking the occlusal relief and/or hypsodonty seen in leaf-eating primates or grazing herbivores (Yeakel et al., 2007, 2014; Lee-Thorp et al., 2012; Fontes-Villalba et al., 2013; Macho, 2014). However, it is noteworthy that graminivory is

observed in other omnivorous taxa exhibiting bunodonty, such as black bears (*Ursus arctos*), which are known to eat 31 species of graminoids in Yellowstone National Park (Raia, 2004; Gunther et al., 2014).

Moreover, because C_4 grasses are generally dominant components of savanna landscapes, their leaves often represent the most abundant and accessible biomass for herbivores (Jacobs et al., 1999). Unsurprisingly, grasses represent a major source of nutrition for *Papio* living in these environments (DeVore and Washburn, 1963; Altmann and Altmann, 1973; Post, 1982; Altmann et al., 1987; Norton et al., 1987; Barton et al., 1993; Barton and Whiten, 1994; Altmann, 1998). From this standpoint, it is possible that grass leaves have been prematurely excluded from reconstructions of hominin diet by some and that, when they are considered, they are often treated as a monolithic entity in a manner that fails to account for taxonomic, seasonal, and habitat effects, which may potentially affect their nutritional and mechanical palatability (e.g., Peters and Vogel, 2005; Lee-Thorp et al., 2012; Yeakel et al., 2014; Macho, 2015).

While no one disputes that many ungulates have dental and digestive adaptations specifically enabling them to subsist on a grass-based diet (Stirton, 1947; White, 1959; Langer, 1974; Janis, 1976; Janis and Fortelius, 1988; Robbins, 2012), Poaceae are incredibly diverse, with species ranging from tree-like bamboo with woody growth to softer, strictly herbaceous and ‘carpet-like’ grasses. This suggests that we should adopt a more nuanced understanding of the diversity of consumption patterns and dietary niches adopted by primary consumers of grasses and that we reassess many assumptions about the potential role of grasses in early hominin dietary ecology.

Here, we investigate the nutritional and mechanical properties of African C_4 grass leaves. We wish to make it clear that we are not attempting to describe what hominins did, or did not, eat, we are simply interested in testing the hypothesis that grass leaves could have been a significant source of nutrition for early hominins. Moreover, we are not investigating hypotheses concerning the potential evolutionary link between australopith craniodental morphology and the consumption of grass leaves. Clearly, these are important avenues of research, but they will ultimately be of limited value if there is a lack of nutritional and mechanical data to support or reject any given hypothesis. It is the goal of this paper to begin to provide these data and to help inform future debates.

2. Methods

We collected plant samples from the Cradle Nature Reserve, South Africa (July 2014 and January 2015), and Amboseli National Park, Kenya (May 2016), from transects located in distinct microhabitats (e.g., grassland, woodland, and wetland). Microhabitats were defined according to Reed et al. (2013:Table 1.1). We sampled the most abundant grass, sedge, tree, and forb species as determined according to methods outlined in Stohlgren et al. (1995; ‘forbs’ in our study represent plants that are neither grasses, sedges, nor trees). All grass species we sampled are C_4 and sedges are mixed C_3/C_4 species. Samples were separated into their constituent organs for analyses (e.g., seed, leaf, and stem).

We grouped these samples into broad categories of potential hominin plant foods based on organs/structures known to be eaten by primates: grass leaf, sedge leaf, tree leaf, forb leaf, fruit, inflorescence (from grasses and sedges), and USOs (e.g., rhizomes, bulbs, and corms from grasses, sedges, and forbs). Here, we present mature leaf and inflorescence samples collected only during the wet season to capture nutritional values that best represent the bulk of their growth phase. Newly grown leaves (particularly among grasses) are known to be higher in protein and lower in fiber

than mature leaves (Owen-Smith, 1982; Boutton et al., 1988). Thus, we do not include data for any new growth samples we collected, to ensure that our results reflect the properties of leaves during the majority of their life cycles and when they are most abundant. Fruit and USO samples are from both wet and dry seasons as their collection is subject to availability.

Toughness was measured in the field on fresh samples using the scissors test on a Lucas Scientific FLS-I portable mechanical tester. Toughness (R) is a measure (J/m^2) of the force necessary to propagate a crack through a material (for discussion, see Lucas et al., 2012). When applicable, we performed scissors tests perpendicular to veins and/or midribs within plant tissues in order to capture maximum toughness values. For the same reason, we did not remove exocarps, sheaths, and/or rinds of organs such as fruits and USOs prior to testing. We replicated the scissors test three times per specimen and used the median value for statistical analyses. We could not test some fruit samples due to their small size and heterogeneous structural properties. We dried wet samples in the field in Excalibur® dehydrators at 40 °C, sealed dried samples in paper bags with desiccant, and exported them to the Nutritional and Isotopic Ecology Lab (NIEL) at the University of Colorado Boulder for nutritional analyses.

We present results for crude protein (CP) and acid detergent fiber (ADF) as a percentage of dry weight. We chose these measures because they are a widely used proxy for overall forage quality (Robbins, 2012; McNaughton and Georgiadis, 1986; but see discussion for the important factors such as micronutrients and water content). Crude protein was measured with a LECO® FP 528 nitrogen analyzer using the standard $\%N \times 6.25$ conversion to obtain $\%CP$. ADF was measured with an ANKOM® 2000 fiber analyzer.

We performed nonparametric comparisons using the Wilcoxon/Kruskal-Wallis test in JMP® Pro 13.0.0 (SAS Institute, 2016), as few of our datasets are normally distributed. Multiple comparisons were performed using the Steel-Dwass all pairs test.

3. Results

3.1. Nutritional data

Plant foods differed significantly in protein content ($p < 0.0001$). Grass leaves have lower protein levels than forb ($p = 0.0438$) and tree leaves ($p = 0.0397$), but higher levels than sedge leaves ($p = 0.0083$) and USOs ($p < 0.0001$; Fig. 1). Four of the five extreme outliers in the USO category are the stolons of *Cynodon plectostachyus*; the fifth is from the rhizome of *Typha capensis*. Grass leaves, fruits, and inflorescences do not differ significantly in protein content. Grass leaves exhibit a wide range of values from protein deficient (<5%) to relatively protein-rich (>15%), with some samples having higher values than the leaves of trees growing alongside them (>20%). Indeed, protein values for grass leaves span almost the entire range of all other values combined, although the distribution is bimodal with each mode normally distributed (Shapiro-Wilk test: lower mode, $p = 0.5682$; higher mode, $p = 0.7985$). The four species representing the higher cluster have mean CP as follows: *Panicum* sp. (17.4%), *Sporobolus ioclados* (19.5%), *C. plectostachyus* (20.9%), and *Setaria verticillata* (21.0%).

Grass leaves have the highest median value for ADF content (35.9%) compared to all other categories, and they are significantly higher than forb and tree leaves ($p < 0.0001$) and fruit ($p < 0.0001$; Fig. 2). However, once again, grass leaves exhibit a high degree of variation. The distribution of grass leaf ADF values is bimodal, though it is less pronounced than observed in our protein values. The four grass leaf species with the highest crude protein among grass leaves analyzed also have the lowest levels of ADF with their

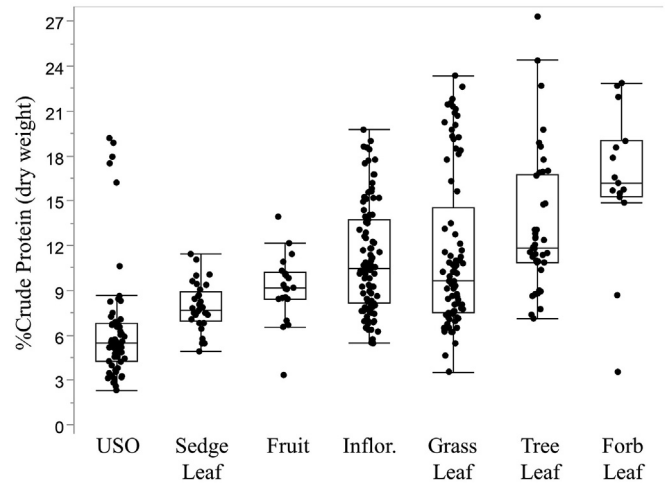


Figure 1. Crude protein content (%) of plant parts within savanna habitats known to be consumed by primates (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Categories are arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers. 'Inflor.' is the abbreviation of inflorescence.

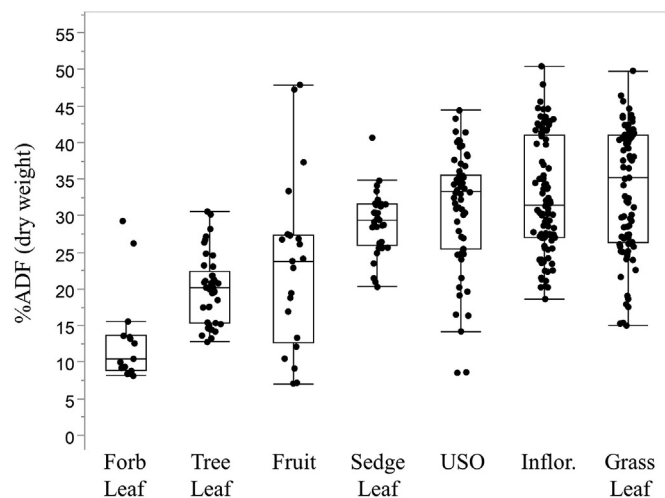


Figure 2. Acid detergent fiber content (%ADF) of plant parts within savanna habitats known to be consumed by primates (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Categories are arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers. 'Inflor.' is the abbreviation of inflorescence.

mean values as follows: *C. plectostachyus* (16.1%), *S. verticillata* (22.4%), *S. ioclados* (24.4%), and *Panicum* sp. (25.5%).

3.2. Mechanical data

Mechanically, grass leaves are significantly tougher than fruit ($p = 0.0062$), forb leaves ($p = 0.0002$), and tree leaves ($p < 0.0001$). Only USOs are significantly tougher than grass leaves ($p = 0.0175$; Fig. 3). Yet, similar to CP and ADF, grass leaf toughness values span almost the entire range of our samples (with the exception of USOs), with some having values in line with tree leaves and fruits known to be primate foods.

3.3. Summary data

Table 1 contains the summary data for all samples analyzed.

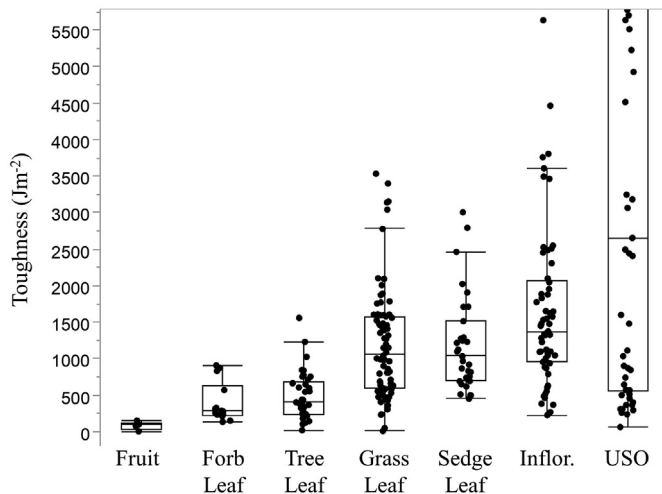


Figure 3. Toughness values (J/m^2) of plant organs within savanna habitats known to be consumed by primates (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). The y-axis has been capped at 6000 J/m^2 , as primates rarely consume foods beyond this limit. Categories are arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers. 'Inflor.' is an abbreviation of inflorescence.

4. Discussion

Grass leaves within our transects, taken as a whole, have relatively low crude protein content, high fiber content, and high toughness values. At this broad scale, common assumptions about their merit as potential hominin foods appear to be warranted. However, it is clear that grass leaves—like many plant species and plant foods commonly consumed by primates—are diverse with regard to their nutritional and mechanical properties and our data

indicate that ~25% of our samples (*C. plectostachyus*, *S. verticillata*, *S. ioclados*, *Panicum sp.*) potentially represent high-quality resources within their respective habitats. As with many other generalizations about diet and nutrition, this suggests that we rethink earlier assumptions about what constitutes a 'quality food.' Many generalizations have been made, for example, about the nutritional properties of fruit versus leaves, with fruit representing a 'high-quality' food high in easily digested mono- and disaccharides and low in fiber. Leaves, conversely, have been classically generalized as being low in simple sugars and high in fiber. Despite these assumptions (prevalent throughout the literature), nutritional analyses have revealed extreme variance in fruit and leaf nutritional composition. For example, analyses of the sugar and fiber composition of leaves and fruits consumed by catarrhines in Kibale National Park, Uganda, have demonstrated that fruit can have similar (or lower) sugars than the mean sugar value for leaves, and that the variance in monosaccharides of leaves overlaps that of fruit (Danish et al., 2006). Indeed, as more nutritionally explicit analyses are conducted on wild foods, it is increasingly evident that we should revisit all such generalizations, including those made about grasses (Simpson and Raubenheimer, 2012; Lambert and Rothman, 2015; Rothman et al., 2015).

As noted above, grass leaf is generally the most abundant plant biomass in savanna ecosystems (Jacobs et al., 1999). Thus, if we cast aside earlier generalizations made about grass leaf macronutrient composition and consider that 25% of the grass leaves within any given habitat can be palatable to species without specialized digestive strategies, this further increases their value to herbivore consumers because encounter and harvesting rates will be relatively high. At the very least, the notion that all grass leaves growing on savanna landscapes were unsuitable for hominin consumers needs reconsideration, particularly when we compare our samples with published values for other hominoid foods.

4.1. Hominoid comparisons

When we divide our samples into 'high-protein' and 'low-protein' categories based on their bimodal distribution for crude protein content, we find that our high-protein grasses (Table 1) compare very favorably against other hominoid leaf foods. In the figures below, we compare CP (Fig. 4) and ADF (Fig. 5) of the leaves consumed by gorillas from the Virunga Mountains of Rwanda and Zaire (Waterman et al., 1983); the Lopé Reserve, Gabon (Rogers et al., 1990); Bai Hokou, Central African Republic (Remis et al., 2001); and the Bwindi Impenetrable National Park, Uganda (Rothman et al., 2006). We also include data provided by Rogers et al. (1990) for leaf foods rejected by the Lopé Reserve gorillas. These comparisons reveal that our high-protein grasses have protein contents equivalent to, and in one instance higher than, the leaves consumed by gorillas (CP in high quality grass leaves is significantly higher than in the leaves eaten by the Virunga gorillas; $p = 0.0019$).

Our comparisons of ADF reveal a similar trend, albeit more complex (Fig. 5). Our high-protein grass leaves are significantly lower in ADF content than all categories ($p < 0.05$) except the leaves eaten by the Bwindi gorillas. Our low-protein grasses have significantly higher ADF than the high-protein grasses and the leaves eaten by the Bwindi and Lopé gorillas ($p < 0.01$), but they are not statistically different from the rejected leaf foods and the leaves eaten by the Virunga and Bai Hokou gorillas. As noted, low levels of ADF have been argued to drive food choice in some primate species and, in fact, the leaves of the eight species with the lowest ADF content within our samples are documented foods for the baboons in Amboseli (Altmann, 1998).

Table 1
Quartile values for plant samples analyzed (dry weight).^a

	N	25%	Median	75%
Grass leaf				
%CP	85	7.50	9.62	14.56
%ADF	85	26.29	35.20	40.96
R (J/m^2)	82	601.46	1064.50	1566.92
Tree leaf				
%CP	41	10.87	11.87	16.78
%ADF	41	15.38	20.20	22.46
R (J/m^2)	37	247.22	405.60	689.50
Fruit				
%CP	21	8.44	9.19	10.22
%ADF	21	12.73	23.81	27.39
R (J/m^2)	5		101.50	
Underground storage organ				
%CP	62	4.26	5.48	6.75
%ADF	62	25.45	33.36	35.63
R (J/m^2)	56	569.94	2654.32	7490.32
Sedge leaf				
%CP	33	6.94	7.69	8.87
%ADF	33	25.93	29.43	31.59
R (J/m^2)	31	696.00	1034.65	1514.45
Forb leaf				
%CP	15	15.25	16.19	19.00
%ADF	15	8.81	10.46	13.61
R (J/m^2)	14	230.32	284.72	638.25
Inflorescence				
%CP	100	8.20	10.47	13.72
%ADF	102	27.05	31.41	40.98
R (J/m^2)	61	963.85	1375.25	2073.90

^a CP = crude protein, ADF = acid detergent fiber, R = toughness.

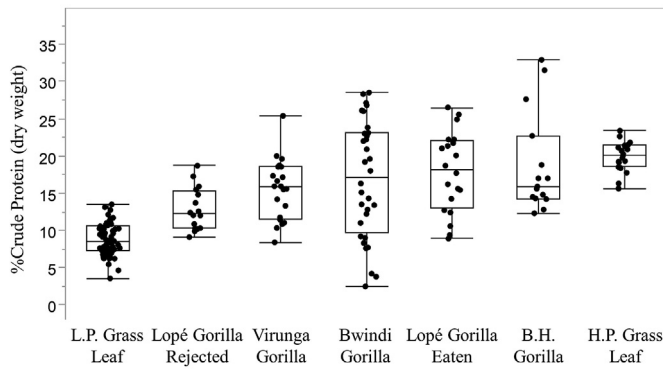


Figure 4. Crude protein (%) of low-protein (L.P.) and high-protein (H.P.) grass leaves compared to leaves eaten and rejected by gorillas arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Low-protein grasses are significantly different than all other categories ($p < 0.0001$) and high-protein grasses are significantly different than Virunga gorilla leaf foods ($p = 0.0019$) and leaves that Lopé gorillas reject (Steel-Dwass all pairs). Gorilla data from Waterman et al. (1983), Rogers et al. (1990), Remis et al. (2001), and Rothman et al. (2006).

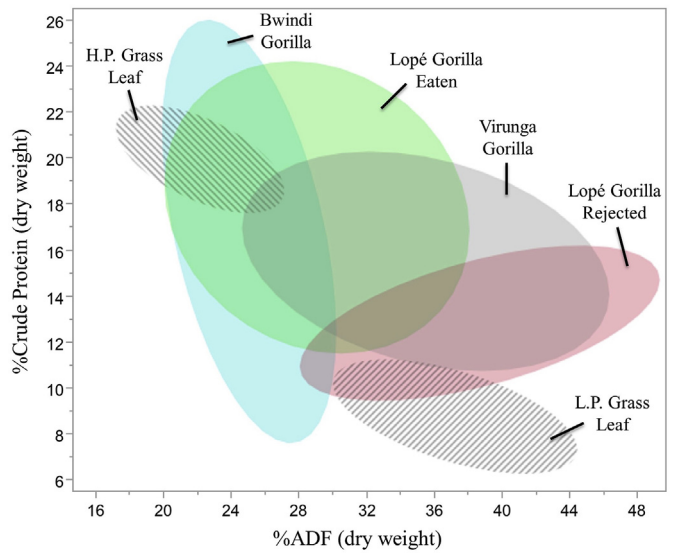


Figure 6. Protein/fiber ratios of the leaf foods of gorillas and high-protein (H.P.) and low-protein (L.P.) grass leaves. Higher protein/fiber ratio foods plot nearer to the upper left corner, foods with lower ratios plot nearer to the bottom right corner. Ellipses represent 50% of each category's distribution. Gorilla data from Waterman et al. (1983), Rogers et al. (1990), and Rothman et al. (2006). The Bai Hokou gorilla data have been omitted for clarity.

(maximum 4197 J/m^2) for tall grass leaves consumed by geladas. Presumably, hominins lacking the bilophodont dentition exhibited by cercopithecoids would have a toughness threshold considerably lower.

Figure 7 shows the toughness values recorded for our low and high protein grasses compared with those for the leafy vegetation consumed by chimpanzees from Kibale National Park, Uganda (Vogel et al., 2008); orangutans from the Ketambe Research Station, Sumatra (Vogel et al., 2014); and gorillas from the Bwindi Impenetrable and Mgahinga Gorilla National Parks in Uganda (Elgart-Berry, 2004). There are no significant differences in toughness between the leaves of our high-protein grass samples and the leaves eaten by chimpanzees, gorillas, and orangutans.

4.2. Primate grass consumption

The vast majority of primate species, including those used for comparison above, do not rely on grasses as a major source of

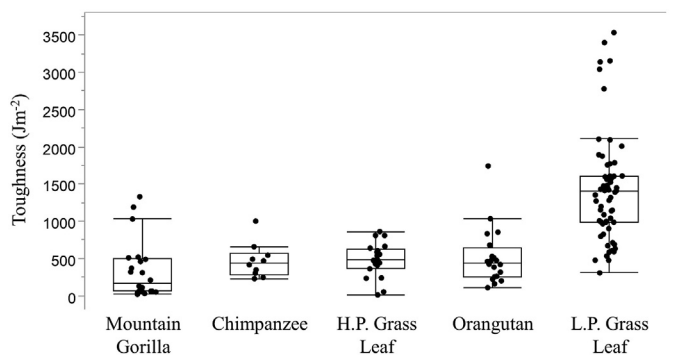


Figure 7. Toughness values of grass leaves compared to the values for leaves consumed by chimpanzees, gorillas, and orangutans arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers. Low-protein (L.P.) grasses have values significantly higher than all other categories ($p < 0.0001$ for all comparisons; Steel-Dwass all pairs).

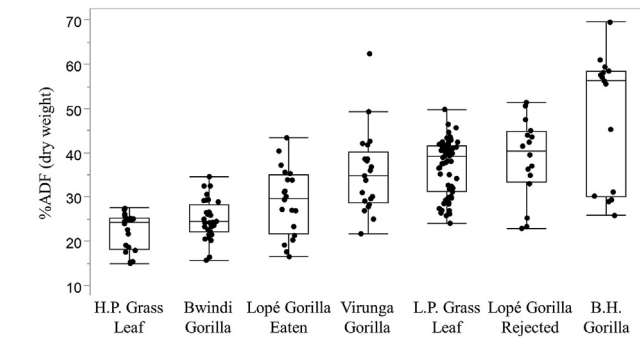


Figure 5. Acid detergent fiber content (%ADF) of high-protein (H.P.) and low-protein (L.P.) grass leaves compared to leaves eaten and not eaten by lowland and mountain gorillas arranged in ascending order by mean value. Boxes represent the 25th–75th percentiles, the lines within them are the medians, the whiskers show data within 1.5 times the interquartile ranges, and the dots outside of the whiskers are outliers (Wilcoxon/Kruskal-Wallis test, $p < 0.0001$). Low-protein grass ADF values are significantly higher than high-protein grasses ($p < 0.0001$), Bwindi gorilla leaf foods ($p < 0.0001$), and Lopé gorilla leaf foods ($p = 0.0029$). High-protein grasses are significantly different than the leaves that Lopé gorillas reject ($p = 0.0004$), leaves Lopé gorillas eat ($p = 0.0410$), Virunga gorilla leaf foods ($p < 0.0001$), and Bai Hokou gorilla leaf foods ($p < 0.0001$; Steel-Dwass Method). Gorilla data from Waterman et al. (1983), Rogers et al. (1990), Remis et al. (2001), and Rothman et al. (2006).

The ratio of protein to fiber content (protein/fiber) has been proposed as a useful index to gauge the palatability of vegetation for primates (Milton, 1979; Barton et al., 1993; Chapman et al., 2002). Figure 6 combines the data from Figures 4 and 5 to create a spatial representation of these ratios for each food category. As can be seen, high protein/fiber grasses skew higher in nutritional space compared to most gorilla foods, whereas our low protein/fiber grasses only intersect with the leaf foods rejected by the Lopé gorillas.

Toughness can also influence dietary selection for primates and other mammalian herbivores (O'Reagain and Mentis, 1989; O'Reagain, 1993; Hill and Lucas, 1996; Wright, 2005). For instance, O'Reagain (1993) found that the acceptability of grass leaves to grazing sheep at the Dundee Research Station, South Africa, was inversely correlated with tensile strength. Venkataraman et al. (2014) recorded a mean fracture toughness of 2686 J/m^2

nutrition mainly due to the fact that most primates live in forested environments where grasses are less abundant, if present at all. Yet, even when grasses are present they are rarely a preferred food. For example, the Fongoli chimpanzees of Senegal that inhabit woodland savanna generally eat few grasses despite their ubiquity within their habitat (Sponheimer et al., 2006). Chimpanzees in Kibale National Park, Uganda, are known to consume the pith of elephant grass (*Pennisetum purpureum*) when preferred fruits are unavailable, but grass leaves are rarely, if ever, eaten (Wrangham et al., 1991, 1998; Conklin-Brittain et al., 1998).

Nonetheless, there are primate species that rely heavily on grass as a source of nutrition. It has long been known that many baboon populations consume almost all parts of various grass species: seeds, stem bases, rhizomes, and leaves (DeVore and Washburn, 1963; Altmann and Altmann, 1973; Post, 1982; Altmann et al., 1987; Norton et al., 1987; Barton et al., 1993; Barton and Whiten, 1994; Altmann, 1998). For example, during the Amboseli dry seasons, baboons utilize the stem bases and rhizomes of many grass species, but in the weeks after the rains when the grass is in flush, their diet (adults and juveniles) consists of 90% grass leaves (Dougall et al., 1964; Altmann and Altmann, 1973). Altmann (1998:82) noted that the fresh leaves of *S. verticillata* are a “baboon favorite” and listed many of the species we sampled as being major sources of nutrition for Amboseli baboons, including *C. plectostachyus*, *Cynodon dactylon*, *S. ioclados*, and *Sporobolus spicatus*. Similarly, Barton et al. (1993) and Barton and Whiten (1994) observed baboons in Laikipia, Kenya, spending 10.7% of their average monthly feeding time on the grass leaves of *C. dactylon*, *C. plectostachyus*, and *Pennisetum* spp. With the exception of *Pennisetum*, which we did not sample, all of the above grasses are relatively high in protein with low toughness values compared to many of the other plant tissues in our study.

Also, the gelada, whose diet is often dominated by grass leaf (~90%), clearly demonstrates that large-bodied primates can subsist on grasses (Crook and Aldrich-Blake, 1968; Dunbar and Dunbar, 1974; Dunbar, 1976; Iwamoto, 1979; Fashing et al., 2014).

4.3. The dietary value of grasses beyond their mechanical and nutritional properties

Poaceae are the fourth largest plant family globally and roughly a tenth of all grass species occur in eastern and southern Africa (van Outshoorn, 2012). The dominance of grasses in many savannas can be seen when measures of net primary production (NPP) are compared. Grasses often double aboveground NPP compared to trees, particularly in nutrient rich savannas where grass NPP represents two thirds of total NPP. While there is considerable morphological variation among grass species, leaf tissue generally accounts for over 50% of the aboveground biomass (O'Reagain, 1993). In this sense, it is not surprising that 75–90% of the large mammal biomass living in savanna habitats is supported by grass (Owen-Smith and Danckwerts, 1997).

Altmann (1998) noted that *C. dactylon*, a major food resource for the baboons of Amboseli, is not only valuable from a nutritional standpoint, but also because it is a rhizomatous grass that occurs in thick ‘carpets’ across large stretches of ground. As such, encounter and harvesting rates are high leading to high energetic yield per invested harvesting time. *Sporobolus spicatus*, another species of great importance to both the baboons of Amboseli and Laikipia, forms thick mats in saline soils and is similarly dominant in areas where it is found. In fact, the two wetland transects we sampled in Amboseli are differentiated by the fact that one is bordered by *S. spicatus* and the other by *C. dactylon* mats.

The fact that *C. dactylon* and *S. spicatus* are known to be major baboon foods is telling in light of the fact that, among our samples,

they do not fall within the distribution of high-protein grasses. That being said, these two species (along with *Dactyloctenium aegyptium*) have the highest protein/fiber ratios within our low-protein category and their consumption by baboons is likely a function of availability as much as it is a result of their inherent nutritional and mechanical properties. It is worth noting that many of our high-protein grasses are the dominant grasses within their respective transects, at least seasonally.

4.4. Grass consumption and dental morphology

It can be argued that specialized dentition with high occlusal relief and pronounced shearing crests is necessary for the efficient and effective comminution of leaves (Lucas, 2004; Atkins, 2009; Ungar, 2010). Indeed, colobine primates (which can be leaf-eating specialists) exhibit ‘blade-like’ teeth (Kay, 1975; Lucas, 2004; Atkins, 2009; Ungar, 2010). Gelada teeth exhibit increased hypsodonty compared to *Papio*, their more generalist sister taxon, and this dental morphology is diagnostic for *Theropithecus* in the fossil record (Eck and Jablonski, 1984; Leakey, 1993).

However, current research is beginning to investigate whether the lack of occlusal relief necessarily indicates a lack of tough, leafy foods in their diets. Winchester et al. (2014) argued that increases in enamel thickness and megadontia are functionally equivalent to hypsodonty in that the increased absolute amount of enamel similarly resists wear over the course of an animal's lifetime. Moreover, australopith dental morphology may be the result of the genetic inability to adopt hypsodonty over a relatively short period of evolutionary time (Grine et al., 2012; Ungar and Hlusko, 2016; Daegling and Grine, 2017). Ungar and Hlusko (2016:29) noted that the dental adaptations seen in the robust australopiths (molar inflation and thickened enamel) could represent “the evolutionary path of least resistance,” arguing that an adaptive shift toward hypsodonty would have required a higher degree of genetic restructuring for such a radical reorganization of dental morphology. Indeed, temporal lags between behavioral shifts and morphological adaptations are seen in other clades such as the East African proboscideans. The fossil record shows a clear and profound dietary shift to C₄ grass dominated diets among late gomphotheres and early elephants ~8 Ma and yet significant increases in lamellar number and hypsodonty do not appear until ~5 Ma (Lister, 2013, 2014; but see Jardine et al., 2012, for discussion of how dietary grit, rather than grass itself, may have selected for mammalian hypsodonty).

What is more, Rabenold and Pearson (2011) examined the phytolith content in the diets of several primates and used the data to predict the molar enamel thickness needed to adequately resist dental attrition. When they compared their predicted values with the observed enamel thickness, they found a strong correlation ($R^2 = 0.87$), suggesting that a diet focused on plants with high phytolith content (such as the leaves of grasses) may have selected for the hyperthick dental enamel found in species such as *P. boisei*.

4.5. Digestive constraints on the consumption of grass leaf

Though there are exceptions, the majority of mammalian grazers have specialized digestive systems that enable them to extract energy from the structural carbohydrates found in plant cell walls using both autoenzymatic and alloenzymatic processes. While we will never fully know the digestive capabilities of extinct hominins, the ‘funnel-shaped’ australopith torso has been argued to indicate a larger gut, and thus the ability to consume more difficult-to-digest (higher fiber) plant foods compared to *Homo* (Aiello and Wheeler, 1995). While the specialized, multichambered stomachs of the colobines are clearly adaptations that aid fiber

fermentation, other non-colobine primates have an excellent capacity for so-called hindgut fermentation. Chimpanzees, for example, are considered ‘high fermenters’ of fiber (particularly hemicelluloses) among the hominoids (Conklin-Brittain et al., 2006) and it is probably fair to assume that ancient hominins had some ability to extract energy from dietary fiber. Regardless, many of the grasses we examined are relatively low in ADF and when protein/fiber ratios are taken into account, it becomes clear that many grass leaves fall within the ranges of non-grass leaf foods consumed by other hominoids (Fig. 6).

4.6. Future considerations

We recognize that levels of protein and fiber alone do not dictate food choice in herbivores and that the nutritional quality of any potential food is more difficult to quantify. Other macronutrients such as non-structural carbohydrates (e.g., starches, sugars) and lipids, as well as water content and essential minerals such as calcium, phosphorous, and sodium, are important factors to consider when assessing the potential value of any given food resource (Sniffen et al., 1992; McDowell and Valle, 2000). Nutritional quality is also impacted by antifeedants such as lignin and tannins, plant secondary metabolites (true toxins), and biogenic silica that can both impede nutrient uptake and cause toxic effects for herbivore consumers (Robbins, 2012; Reed et al., 2000). Grass leaves, while generally lower in secondary compounds than tree leaves, can accumulate high amounts of silica in their leaf tissues (Coughenour, 1985) and can increase concentrations in response to grazing pressure (Jones and Handreck, 1967; Van Soest and Jones, 1968). Future research should attempt to account for as many of these variables as possible in order to obtain a more accurate picture of dietary quality.

Furthermore, the effects of season and habitat play a role in determining the nutritional and mechanical properties of plant foods throughout their life cycle. Here, the bulk of our data is from plants collected during the wet season (see Methods). Any assessment of the potential for plant foods to act as staple components of diet need to incorporate these spatial and temporal effects, notably the tendency for the nutritional quality of leafy vegetation in savanna habitats to decline during dry seasons (Owen-Smith, 1982; Boutton et al., 1988; Cooper et al., 1988; Georgiadis and McNaughton, 1990). Seasonal effects on leafy vegetation are among the reasons that USOs are often argued to have been important foods for hominins, because they are thought to be relatively resistant to temporal fluctuations in nutritional quality (Laden and Wrangham, 2005). However, it must be noted that ‘USO’ is a somewhat artificial category considering the wide range of forms that underground storage organs can take (e.g., fleshy, starch filled tubers vs. tough rhizomes), and further study requires separating USOs into multiple categories. From a spatial perspective, habitat differences at both the local and regional level almost certainly affect the nutritional and mechanical properties of vegetation and this may be particularly important for our understanding of hominin dietary ecology. It is conceivable that the different carbon isotopic compositions of *P. boisei* and *Paranthropus robustus* (for discussion, see Sponheimer et al., 2013) are the result of nutritional and mechanical differences between the available C₄ vegetation within their respective habitats. Though we suspect that this might be the case, our understanding of the paleolandscapes on which these hominins lived and, particularly, the mechanical and nutritional properties of the available vegetation, is not sufficiently advanced at this point to address this question.

5. Conclusion

Stable carbon isotope analyses have revealed that C₄ foods were consumed by many hominin species and it is a fair assumption that

the bulk of those resources came in the form of plant tissues. Early hominins were likely to be generalist feeders that opportunistically consumed resources based on their seasonal availability (Knott, 2005).

The USOs of C₄ sedges and C₄ grass seeds were almost certainly part of the broader hominin dietary repertoire just as they are for baboons today (Jolly, 1970; Norton et al., 1987; Altmann, 1998; Dominy et al., 2008). However, a combination of the limited seasonal availability of grass seeds, the lack of dental microwear evidence supporting USO consumption, and their nutritional/mechanical properties reported here, make it unlikely that they could solely account for all of the C₄-derived carbon in high-C₄ species like *P. boisei*. Our data show that grass leaves should not be treated as a ‘one size fits all’ category as many are less tough, higher in protein, and lower in fiber than other potential plant foods on some savanna landscapes. This, coupled with their great abundance, means we should not summarily exclude grass leaves from reconstructions of hominin diets. Indeed, we know of no living large-bodied mammal (excepting carnivores that prey heavily on grazing herbivores) with a C₄ isotopic signature like the one seen in *P. boisei* that does not eat grass leaf extensively, if not exclusively. It is not clear to us that hominins are exceptions to this mammalian rule. Regardless, if we hope to build better models of early hominin dietary behavior, the inherent variation of grass leaf properties (and of other potential foods), as demonstrated here, needs to be considered.

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