



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

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