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Foraging potential of underground storage organ plants in the southern Cape, South Africa

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ABSTRACT

Underground storage organs (USOs) serve as a staple source of carbohydrates for many hunter-gatherer societies and they feature prominently in discussions of diets of early modern humans. While the way of life of hunter-gatherers in South Africa's Cape no longer exists, there is extensive ethnographic, historical, and archaeological evidence of hunter-gatherers' use of USOs. This is to be expected, given that the Cape supports the largest concentration of plant species with USOs globally. The southern Cape is the location of several Middle Stone Age sites that are highly significant to research on the origins of behaviourally modern humans, and this provided the context for our research. Here, we evaluate the foraging potential of USOs by identifying how abundant edible biomass is in the southern Cape, how easily it is gathered, and how nutritious it is. One hundred 5 × 5 m plots were assessed in terms of USO species and abundance. Nearly all of the sites sampled (83%) contained edible USOs and some had high concentrations of edible biomass. Extrapolating from these sites suggests that the edible USO biomass falls within the range of biomass observed in areas supporting extant hunter-gatherer communities. The nutritional content for six USO species was assessed; these contained between 40 and 228 calories/100 g. Furthermore, foraging events were staged to provide an indication of the potential return rates for the same six USOs. The target species grow near the soil surface, mostly in sandy soils, and were gathered with minimal effort. Some 50% of the foraging events conducted yielded enough calories to meet the daily requirements of a hunter-gatherer within two hours. In conclusion, we demonstrate that USOs are a readily available source of carbohydrates in the southern Cape landscape and, therefore, there is a strong possibility that USOs played a critical role in providing food for early humans.

1. Introduction

Hunter-gatherers depend on plants harvested in their natural habitat for their carbohydrate intake. Plants with underground storage organs (USOs) are generally rich in carbohydrates and are a significant component in the diet of many hunter-gatherer societies across a variety of environments (Alyawara—O'Connell and Hawkes, 1981; Batak—Eder, 1978; Hadza—Vincent, 1985; Schoeninger et al., 2001; Hiwi—Hurtado et al., 1985; Pintubi—Cane, 1989; San—Lee, 1973). It has been suggested that USO foraging was an important factor in the evolution of early *Homo* and that this adaptive shift to a high caloric diet contributed to the evolution of a large brain (O'Connell et al., 1999; Pennisi, 1999; Laden and Wrangham, 2005; Ungar et al., 2006; Perry et al., 2007; Wrangham et al., 2009). As such, USO foraging has been, and remains, an important research topic in investigations of human origins (Hawkes et al., 1997, 1998; O'Connell et al., 1999; Laden and Wrangham, 2005; Marlowe and Berbesque, 2009; Wrangham et al., 2009; Hardy et al., 2015; Schnorr et al., 2015). In the Cape Floristic Region (CFR) of South Africa, the remains of USOs have been commonly found in Holocene deposits of archaeological sites (Parkington and Poggenpoel, 1971; Deacon, 1976, 1984, 1993). Historical evidence also supports the importance of USOs in the diet of CFR hunter-gatherers (Sparrman and Forster, 1785; Thunberg, 1795; Barrow, 1801; Bleek and Lloyd, 1911; Schapera et al., 1933). Macrobotanical remains of USOs are rarely preserved in older sites of the Middle Stone Age (MSA), but the burnt, non-charcoal organic

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remains in hearths and carbonised lenses have been interpreted as extensive USO use (Deacon, 1979, 1989; Deacon and Geleijnse, 1988; Deacon and Deacon, 1999). It has been hypothesised that the abundant and diverse USO flora of the Cape south coast (Procheş et al., 2006), together with the juxtaposition of a rich and abundant marine invertebrate fauna (Branch and Branch, 1992), would have facilitated the persistence of humans on the Cape south coast during the cold glacials of the Pleistocene, especially Marine Isotope Stage (MIS) 6 (~195–123 ka; Marean, 2010), which yields one of the richest records for the behaviour of early modern humans (Marean et al., 2014).

While glacial climates of the Cape south coast were colder than those of the Holocene, the tempering influence of the Agulhas Current meant that temperature differences were muted (Marean et al., 2014; Verboom et al., 2014). While the floristic composition of the vegetation types sampled in this study almost certainly changed in response to Pleistocene climate forcing, it is likely that their overall distribution, controlled as it is primarily by edaphic factors (Bergh et al., 2014), did not change significantly from the present. Moreover, data from dated molecular phylogenies shows that diversification of USO lineages continued throughout the Pleistocene on the southern Cape coast and elsewhere in the CFR (e.g., Verboom et al., 2009). Consequently, we think that current patterns of USO abundance and diversity in these vegetation types are a reasonable analogue for those during the Pleistocene glacials such as MIS4 and MIS6. However, we cannot say the same of the Paleo-Agulhas Plain that would have been exposed to various extents during glacials; this was an entirely novel habitat in terms of Cape ecosystems, which supported large herds of grazers (Marean, 2010) and likely consisted of fertile soils (Cawthra et al., 2015).

At present, very little is known regarding the potential of USOs as foodstuffs in the Cape. A study of the existing ethnobotanical knowledge of the area has identified many potentially important plant species that provided carbohydrates for human use, including USOs (De Vynck et al., 2016a). In addition, with the exception of the mid-summer and early autumn months, USOs of the Cape south coast have structures (e.g., leaves, flowers, dried stems) that are visible to foragers, thereby affording a reliable source of carbohydrates (De Vynck et al., 2016c). Surprisingly, no research has been undertaken in the Cape region on the distribution, abundance, and biomass of USOs, their nutritional content, or an estimation of the nutritional return rates of foraging. Our study, albeit preliminary, is the first attempt to address these research gaps in an area notably important for the evolution of behaviourally modern humans (Marean et al., 2014).

The research goal guiding this study is the development of a paleoscape model of the Cape south coast that can be used to better understand hunter-gatherer adaptations in that region so as to elucidate the rich record there for modern human origins. A paleoscape model is a computer model of the spatial and temporal distribution of resources and their foraging returns, including food, water, raw materials, etc. Such a model can then be forced to change in response to climate and environmental change to re-project the distribution of resources. Computer agents simulating hunter-gatherers can be added to the model to then study how they would use these environments and from that make predictions that can be compared to the archaeological records. The behaviour of these agents is guided by principles grounded in optimal foraging theory following prior applications to humans (Hill et al., 1987; Winterhalder and Smith, 2000; Smith et al., 2012) and can be tested via application to modern hunter-gatherer behaviour, some of which has been accomplished (Janssen and Hill, 2014). The overall rationale, theory, and workflow are described in Marean et al. (2015). The model requires input on the spatial and temporal distributions and return rates of all the major food resources in this region. Acquiring such data is a major longitudinal research effort, and our strategy is to build the needed data up incrementally and publish those data when attained so they are available to other researchers, since it is impossible to accomplish it all in one study. This study was designed to provide preliminary input for the model on the USO resource base of the Cape south coast.

First, we investigated the distribution of edible USOs on the Cape south coast by randomly locating 100 plots of 5 × 5 m, stratified according to major vegetation type. These data provided us with a landscape-level assessment of the richness and biomass of edible USOs potentially available to a forager. However, edible biomass is not in itself a clear indication of the nutritional content of USOs, so we also investigate this for six of the most abundant species. Lastly, we set up a ‘naïve forager’ experiment where a subject searches and excavates USOs from a predetermined set of species, one species at a time. We found that edible USOs are widely distributed through the landscape, they can be highly abundant locally, they are nutritionally valuable, and that an extremely naïve forager could obtain sufficient edible USO biomass to meet daily energy needs.

2. Methods

2.1. Study area

The southwestern tip of South Africa falls within a winter rainfall or Mediterranean-type climate zone (Schulze, 2008) that is characterised by warm, dry summers and cool, wet winters. The winter rainfall zone encompasses most of the Cape (or CFR; Goldblatt and Manning, 2002), although the frequency of summer rainfall increases as one moves east. Our study area is situated on the southern Cape coast of South Africa, which is in the transitional zone between the strictly winter rainfall zone (to the west) and the summer rainfall zone (to the east). The size of the study area is 600,000 ha, extending from Mosselbay in the east to the Breede River in the west (107 km east–west axis), and from the coastline to the foot of the Langeberg–Outeniqua mountains (47 km north–south axis; Fig. 1). The annual rainfall over the study area ranges from 300 to 500 mm per year (Schulze, 2008), with a general pattern of increasing rainfall as one approaches the higher ground on its inland margin. Freezing temperatures are seldom recorded and absolute maxima seldom exceed 30°C.

Like other parts of the CFR, this region has a high diversity of vegetation types and, owing to high beta diversity, a large number of plant species (Cowling, 1992; Cowling and Holmes, 1992). Mucina and Rutherford (2006) describe 14 vegetation types in the area associated with four biomes. We collapsed these vegetation types into six major units widely recognised by Cape botanists: strandveld, renosterveld, riparian vegetation, dune cordon, limestone fynbos, and sand fynbos (Fig. 1; Supplementary Online Material [SOM] Appendix A, Figure A1). Renosterveld occurs on relatively fertile, clay-rich soils derived from shale and mudstone (Mucina and Rutherford, 2006); it is a fire-prone, evergreen shrubland with an understory of grasses and a high biomass and diversity of USO species (Procheş et al., 2006). Renosterveld of the Cape south coast (south of Langeberg and Riviersonderend Mountains) is considered a distinct type with a high abundance of largely C4 grasses and between 50% and 70% plant cover (Mucina and Rutherford, 2006). Fynbos is the most widespread vegetation of the CFR and—like renosterveld—is a fire-prone evergreen shrubland; it is associated with nutrient-poor, sandy soils (Mucina and Rutherford, 2006). Limestone fynbos grows on shallow, alkaline sands derived from late Cenozoic limestones, whereas sand fynbos is associated with deposits of leached, acidic, wind-blown sands. While appearing similar in structure, these two fynbos forms have highly distinct flora, and we therefore treated them as different vegetation types.