Foraging Potential of Underground Storage Organ Plants in the Southern Cape, South Africa

Singels E. [a], Potts A.J. [b], Esler K.J. [a], Cowling R.M. [b], Marean C.W. [b] and De Vynck J. [b]

[a] Stellenbosch University

Department of Conservation Ecology and Entomology, Stellenbosch University

3001 J.S. Marais Building, Victoria Street

Private Bag X01, Matieland, 7602, South Africa

E-mail Singels E.: elzanne.singels@gmail.com

E-mail Esler K.J.: kje@sun.ac.za

[b] Nelson Mandela Metropolitan University,

Centre for Coastal Palaeoscience,

PO Box 77000, Port Elizabeth, 6031, South Africa.

E-mail Potts A.J.: potts.a@gmail.com

E-mail Cowling R.M.: richard.cowling@nmmu.ac.za

E-mail Marean C.W.: Curtis.marean@asu.edu

E-mail De Vynck J.: jandevynck@vodamail.co.za

Corresponding author: Singels E.

E-mail Singels E.: elzanne.singels@gmail.com

Phone number: +27725996636

PeerJ PrePrints | https://doi.org/10.7287/peerj.preprints.1573v1 | CC-BY 4.0 Open Access | rec: 8 Dec 2015, publ: 8 Dec 2015

Abstract

Background: 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 is no longer in existence, there is extensive ethnographic, historical and archaeological evidence of hunter-gatherers' use of such plants as foodstuffs. This is to be expected, given that the Cape supports the largest concentration of plants 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.

Methods: Here we evaluate the foraging potential of USOs by identifying how abundant edible biomass is in a coastal setting of the southern Cape, how easily it is gathered, and how nutritious it is. We staged a range of foraging events to provide an indication of the potential return rates for selected USOs when a forager is likely to be naïve about foraging for them.

Results: Nearly all of the sites sampled (83%) contained edible USOs, and the edible biomass can be highly concentrated in space. The edible USO biomass fell within the range of biomass observed in areas supporting extant hunter-gatherer communities. The six USO species we assessed for nutritional content contained between 40-228 calories/100 g. They also 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 of small stature within 2 hours.

Discussion: Thus, we demonstrate that USOs are a readily available source of carbohydrates in the southern Cape landscape and that they likely played a critical role in providing food for early humans.

Keywords

hunter-gatherer, USOs, biomass, Middle Stone Age, return rates

Introduction

[1]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 (San- Lee, 1973; Batak- Eder, 1978; Alyawara- O'Connell and Hawkes, 1981; Hiwi- Hurtado et al., 1985; Hadza- Vincent, 1985; Pintubi- Cane, 1989). As such, USO foraging has been, and remains, an important research topic in the investigation 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). 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). 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). Macro-botanical remains of USOs are rarely preserved in older sites of the Middle Stone Age (MSA), but the burnt, non-charcoal organic remains in hearths and carbonized 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

[1] Abbreviations:
USOs: Underground Storage Organs
MSA: Middle Stone Age
LSA: Later Stone Age
CFR: Cape Floristic Region
MIS: Marine Isotope Stage
ha: Hectare

glacials of the Pleistocene, especially MIS6 (~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 Agulhas Current meant that temperature differences were muted (Marean et al., 2014; Verboom et al., 2014). 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 are a reasonable analogue for those during the Pleistocene glacials such as MIS4 and MIS6.

At present, very little is known regarding the potential of USOs as foodstuff 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., In press). 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 carbohydrate (De Vynck et al., 2015b). Surprisingly, no research has been undertaken in the Cape region on the distribution, abundance and biomass of USOs, their nutritional content and an estimation of 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 (Smith et al., 1983; Hill et al., 1987; Winterhalder and Smith, 2000), 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 distribution, 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 25 m^2, 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.

Methods

Study Area

The southwestern tip of South Africa falls within a winter rainfall or Mediterranean-type climate zone (Schulze, 2008) which is characterized by warm, dry summers and cool, wet winters. The winter rainfall zone encompasses most of the Cape (or Cape Floristic Region; hereafter CFR) (Goldblatt and Manning, 2002), although the summer rainfall frequency 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 study area is 600,000 hectares, extending from Mossel Bay 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 300-500 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^{o}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 recognized by Cape botanists: strandveld, renosterveld, riparian vegetation, dune cordon, limestone fynbos and sand fynbos (Fig. 1, Fig. A.1). 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 – 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, acid, 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. Strandveld is a mosaic of subtropical thicket and fynbos elements associated with old (late Cenozoic) dune sands (Mucina and Rutherford, 2006). While Restionaceae (*Thamnochortus* spp.) are common, species richness of Proteaceae and Ericaceae is low. Owing to the low flammability of thicket species, and the low cover of other shrubs, strandveld is less prone to fire than surrounding fynbos vegetation types. The dune cordon vegetation comprises a floristically distinct form of subtropical thicket associated with recent (Holocene) marine sands that are found along a narrow coastal margin. Soils are deep but poorly developed, and highly alkaline. The associated dune thickets are not fire prone (Mucina and Rutherford, 2006). The last vegetation type, riparian vegetation, is an azonal vegetation type associated with alluvial soils, in this case fertile sandy loams, of the major rivers in the region; this vegetation comprises a tree or tall shrub component dominated by the winter-deciduous *Acacia karoo*.

Landscape-level USO richness and abundance

Sampling occurred over three months (August through October) in the spring of 2011, a time of maximum apparency of USO species in the study area (De Vynck et al., 2015b.) and elsewhere in the CFR (Johnson, 1992). In total, 100 plots of 25 m^2 were sampled, with the percentage of randomly placed plots in each vegetation type proportional to the area in which the vegetation types occur in the study area. This resulted in 15 plots in strandveld, 25 plots in renosterveld, nine in riparian vegetation, seven in dune cordon, 18 in limestone fynbos, and 26 in sand fynbos. Since the renosterveld of the southern Cape is significantly transformed by agriculture, in particular deeper soils on gentle terrain (Kemper et al., 2000), the plots in this vegetation type were generally situated on steeper slopes.

The richness and abundance of visible USO species were surveyed within each plot. Voucher specimens of each species were collected and housed in the Ria Olivier Herbarium (Nelson Mandela Metropolitan University, Port Elizabeth). For each species, the first 10-15 USOs that were found were excavated and the USO depth, length and biomass (wet weight) were recorded. These values were used to generate a mean USO biomass per species; the plot-level species abundances were multiplied by these mean values to obtain an estimate of the biomass per plot. This estimated biomass per plot was further split into separate edibility categories.

Edibility categories (edible, poisonous or unknown) were assigned to each species using the available ethnobotanical literature (Watt and Breyer-Brandwijk, 1932, 1962; Parkington, 1977; Norwood Young and Fox, 1982; Van Wyk and Gericke, 2000; Van Wyk et al., 2002). Because of their impact on humans and livestock, most poisonous species are known, but there is much less information available on the suitability of CFR USOs for human consumption. In the case of genera that are widely recorded as having edible species (e.g. *Babiana*, *Watsonia*), we categorised all species encountered as edible. In the case of genera with both edible and poisonous species (e.g. *Moraea*), we allocated to an unknown category in the absence of any records on edibility.

USO nutritional values

Of the 52 edible species, six common and widespread species were selected for nutritional analysis; these species were then also used for the naïve forager experiments (described in the next section) as we could use these data to convert USO biomass to calories. The criteria we used to select the six species were: 1) they had to be apparent and abundant in the four nature reserves – each corresponding to a different vegetation type - available to us for the experiments, 2) include some species that occur in more than one vegetation type (owing to high beta diversity, no species occur in all four vegetation types). Thus, *Cyanella lutea*, *Cyphia digitata* and *Watsonia meriana* were sampled from renosterveld in the Werner Frehse Nature Reserve (34.12ºS, 21.25ºE); *Chasmanthe aethiopica, C. digitata, C. lutea, Ferraria crispa* and *Pelargonium lobatum* from limestone fynbos in the Pauline Bohnen Nature Reserve (34.36ºS, 21.43ºE); *C. aethiopica* from strandveld vegetation in the Gouritzmond Nature Reserve (34.35ºS, 21.88ºE); and *F. crispa* and *C. aethiopica* from dune cordon in the Skulpiesbaai Nature Reserve (34.39ºS, 21.42ºE).

The nutritional content was determined by measuring the following parameters: moisture, ash, protein, carbohydrate, fat and fibre. All measurements were conducted on uncooked specimens, though we recognize that cooking likely would increase the nutritional return to a human (Carmody and Wrangham, 2009), and future work will build on this current study with cooking experiments. At least three replicates of each test were performed on each species collected during the foraging experiments. These analyses were performed in the Department of Animal Sciences, Stellenbosch University and Microchem Laboratory (Cape Town) following protocols stipulated by the Association of Official Analytical Chemists or AOAC (Nielsen, 2003). Moisture content was determined by the oven dry method (925.09, AOAC). Ash content was determined by test number 923.03, AOAC. Protein content was determined using the Kjeldahl method (955.04, AOAC). Fat content was determined by the Soxhlet test (920.85c, AOAC). Insoluble and soluble fibre content was determined by the crude fibre test (991.43, AOAC). The carbohydrate content was determined using the amyloglucosidase/α-amylase method (996.11, AOAC).

USO forager experiment

The Khoe-San descendants in the southern Cape have been influenced by agrarian technology for almost 200 years; consequently, carbohydrates based on agricultural products have replaced indigenous plants as sources of carbohydrate and the tradition of harvesting USOs has been, by and large, lost (Marks, 1972; De Vynck et al., In press). Therefore, unlike intact hunter-gatherer societies which support people with USO foraging skills (e.g. Eder, 1978; O'Connell and Hawkes, 1981; Vincent, 1985; Hurtado and Hill, 1987; Sato, 2001), we could not use knowledgeable foragers to demonstrate maximum potential return rates. Thus, in order to approximate potential return rates from USO foraging, we conducted experimental foraging events. Such foraging experiments are considered valid proxies for predicting gathering behaviour and return rates (Smith et al., 1983; Peters et al., 1984). The subjects who took part in these foraging events were women of Khoe-San origin living in towns in the southern Cape. The ethical research protocol of Stellenbosch University requires screening of studies involving human subjects by the Departmental Ethics Screening Committee (DESC) prior to any research and this study was classified as low risk for subjects. Only studies identified as having a medium to high ethics risks are referred to the Research Ethics Committee for full review.

Although the subjects had little knowledge regarding USO foraging, they were familiar with gathering resources from southern Cape vegetation (e.g. medicinal plant, leaf crop and wood harvesting). Before each foraging event, each subject was given a verbal description of the USO target species and shown a fresh sample. Each foraging event was conducted by a single forager, the starting point was pre-selected by the subject within a specific vegetation type, and the forager was restricted to a single target species. The search time to find each USO and the handling time necessary to excavate it were recorded. Each USO excavated was cleaned and weighed. The gatherer was given a digging tool in the form of a hardened stick with a digging stone (Fig. C.1). This method of harvesting USOs is a feature of cave paintings in southern Africa (Lewis-Williams, 1987), and this technology existed in the late Pleistocene (Parkington and Poggenpoel, 1971). Foraging events for target species took place in different vegetation types (described above) and seasons. Note that other than the clay-rich soils associated with renosterveld, the soils of all other vegetation types are sandy and would offer minimal resistance to digging by foragers. All sites were sampled in the wet season, when compaction of the clay-rich renosterveld sites would be relatively low, as well as in the dry season when these soils would be harder to excavate. Owing to their sandy soils, time of year is unlikely to have any impact on digging times in the other vegetation types.

For each target species, the biomass of harvested USOs was converted to calorie estimates using the species' mean nutritional values and the conversion values reported by Vincent (1985): carbohydrates = 4.03 calories per 100 g of USO, protein = 2.78 cal/100 g, and fat =

8.37 cal/100 g. Following Murray et al. (2001) and Vincent (1985), fibre content was not included in the USO calorie estimation.

Foraging events were performed on an *ad hoc* basis, based on the density of target species in each habitat. This enabled us to maximise the number of foraging events for available species in each vegetation type. Thus, these events occurred over a range of times, so as not to limit the subject during foraging (minimum=7 minutes, maximum=120 minutes, median = 22 minutes). A minimum of eight USOs had to be sampled per event. The cumulative calorie content obtained for all the USOs collected per foraging event over time was modelled using a linear regression. This was used to estimate the time taken to obtain 2000 calories for each species. If less than 2000 calories was harvested during a foraging event, the linear regression allowed extrapolation to this level. This estimate of 2000 calories is based on analyses of present-day hunter-gatherer communities and theoretical studies of prehistoric people where a diet of 1900-2000 calories per day is suggested to be sufficient to support hunter-gatherer people of small stature and high physical activity (Lee, 1968; Speth and Spielmann, 1983; Hurtado and Hill, 1989).

Results

Landscape-level richness and abundance

Our survey yielded 83 USO species from 50 genera in 17 families. Iridaceae (35 species, 42%) and Hyacinthaceae (14 species, 17%) were the most common and abundant families (See Table B.1 for a full species list). The majority of species sampled in the study possess corms (43 species, 52%), followed by bulbs (17 species, 20%), then tubers (12 species, 15%) and lastly rhizomes (11 species, 13%). More than 50% of all species found within each

PeerJ PrePrints | https://doi.org/10.7287/peerj.preprints.1573v1 | CC-BY 4.0 Open Access | rec: 8 Dec 2015, publ: 8 Dec 2015

vegetation type are considered edible. Of all 100 random plots surveyed, only 13 did not contain any edible species and these were spread across five of the six vegetation types (Table 1). Presence and abundance of USO species were found to be highly variable across the landscape, with very little consistency within or between vegetation types. This translated into a high variability of edible USO biomass among plots and vegetation types (Fig. 1, Table 1). The majority of plots had very low edible biomass (<0.5 kg per plot [<200 kg per ha]); however, in a few plots an exceptional biomass of edible USOs was found (>1.5 kg per plot [>400 kg per ha]) and these were found within four of the six vegetation types.

Of the 83 USO species found in this study, 52 were edible, 15 were poisonous and 6 were of unknown status (Table B.1). The USO edibility status, weight per species and the growing depth are shown in Fig. 2. The largest USOs usually weighed more than 100 g and belonged to 5 different USO species. Four of these species are poisonous, and one, namely *Rhoicissus digitata*, is considered edible but is not very palatable or nutritious (Fig. 2). Edible species were dominant in the 10 g to 100 g range, and the majority of USOs (edible or not) did not occur at a depth greater than 10 cm in the soil.

USO nutritional values

The nutritional value of the six USO species tested varied markedly (Table 2), where corms had the highest nutritional values observed (190-228 calories/100 g). Corms also had the lowest fibre content (3.6-9.5%) followed by rhizomes (16.1%) and tubers (18.5%). These values are equivalent to or exceed the nutritional values observed for USOs collected by extant hunter-gatherers (Table 2). These values are, however, still far below the nutritional values of a domestic species like a potato. The carbohydrate content of Cape USOs is similar to the values published for USOs gathered by extant hunter-gatherers in previous studies. . However, many of these previous studies on USO nutritional content (e.g. Eder, 1978;

Vincent, 1985; Hurtado and Hill, 1990; Youngblood, 2004) determined carbohydrate content by an array of different methods; most commonly these tests either quantified the net weight of all the other substances that make up the weight of the test matter and subtracted that from the total weight of the USO (Murray et al., 2001) or included calories or carbohydrates which are not digestible by humans. These methods are not appropriate for determining the carbohydrate content of plants as evidenced by the great variation observed between different studies (Hladik et al., 1984; Brand-Miller and Holt, 1998; Schoeninger et al., 2001). The method we employed provides a more accurate measure of the carbohydrate nutritionally available to a human.

USO forager experiment

Foraging events showed large variation in length of time and the amount of USO biomass gathered (Fig. 3). The rate of biomass accumulation varied among the species (Fig. 3, Fig. C.2, Table C.1); *Cyphia digitata* and *Cyanella lutea* had consistently lower rates of biomass accumulation when compared to the other four species (Fig. 3, Fig. C.2, Table C.1). Linear regressions adequately characterised the relationship between the cumulative edible biomass and time for each foraging events (mean [min-max] r^2 = 0.92 [0.83-0.99]; Table C.1); thus, these regressions were extrapolated to determine how much time would be required to reach the 2000 calorie threshold, assuming that the return rates remained relatively constant. The time to reach this threshold varied tremendously, from 29 minutes to over 24 hours. However, of the 26 foraging events, the rates of return for 50% of these events predict that the daily caloric requirement would be fulfilled within two hours and 26% of these events within one hour (Fig. 3, Table C.1).

Discussion

The CFR has the highest diversity of geophytes (herbaceous plants with USOs) in the world, with richness concentrated in the western, strongly winter-rainfall parts of the region (Procheş et al., 2005, 2006). Our tally of 83 species from the southern CFR is, nonetheless, very high for the size of the study area, by global standards (Parsons and Hopper, 2003). Of the total, 63% have USOs that are considered edible and 19% of unknown status. In this study, our goal was to develop a first assessment of the potential for USOs as a carbohydrate source for hunter-gatherers in the region, and provide some initial data for input to a paleoscape model for the south coast as described in Marean et al., 2015. While much more research needs to be done on this topic, our study provides the first data on these goals and thus is useful to researchers working on the Stone Age of this region. We found that the region's USOs provide a diverse and abundant resource that is widely, albeit patchily distributed across all the vegetation types. Furthermore, the gross return rates (not corrected for effort) on harvesting selected edible species are under some conditions sufficient to support the daily calorie demand of a hunter-gatherer with just a couple of hours of effort. Our data support suggestions (Parkington, 1977; Deacon, 1993; Marean, 2010) that USOs had the potential to contribute significantly to the diets of early modern humans of the Cape coast.

Landscape-level abundance of edible USO biomass

We found that USOs edible biomass was highly variable across the landscape with distinct coldspots of low abundance, and hotspots of high abundance distributed haphazardly with regard to vegetation type and environmental factors (unpublished data). USO biomass hotspots are common in areas which support contemporary hunter-gatherers (Vincent, 1985; Hurtado and Hill, 1987; Wrangham et al., 2009). Importantly, nearly all of the plots (83%) contained at least one edible species. This suggests that USOs would be widely available to hunter-gatherers throughout this landscape and that, with the ability to search and locate hotspots, USOs could have provided an important source of calories. This is concordant with the historical observations in this region, summarized above, that document indigenous foragers relying heavily on USOs, and the abundance of USO remains in some Holocene archaeological sites.

Comparisons of our edible biomass data with those from other studies are constrained by the different sampling strategies employed. Anthropological studies are invariably “gatherer-driven” in that biomass data are derived from the foraging of known patches of high USO abundance (hotspots) (Eder, 1978; O’Connell and Hawkes, 1984; Vincent, 1985; Sato, 2001). More rarely, biomass data are “observer-driven” in that the anthropologist undertakes the foraging of edible USOs harvested by contemporary hunter-gatherers (e.g. Youngblood, 2004). Owing to the absence of a hunter-gatherer tradition in our study area, we employed an ecological method of calculating biomass: stratified random sampling. Hence, our data are not strictly comparable to other human ecological studies and this needs to be considered when comparing our data to these studies. Nonetheless, although the average USO biomass we observed is lower than in the arid savanna habitat populated by the Hadza (Vincent, 1985), it is higher than in forest habitats occupied by the Baka (Hladik et al., 1984; Sato, 2001) (Table 3). Hotspots of USO abundance in the southern Cape – areas likely targeted by hunter-gatherers, yield biomass values in excess of 3000 kg per ha. Moreover, this biomass is readily accessible owing to the predominantly shallow USOs (and sandy soils) of the study region, in comparison to the very deep tubers, requiring much effort to extract, which are foraged by extant hunter-gatherers in many other environments (Vincent, 1985; O'Connell et al., 1999; Murray et al., 2001; Sato, 2001).

USO nutritional value

USOs gathered in contemporary hunter-gatherer communities are, in general, large tubers which are deeply buried (Hladik et al., 1984; Vincent, 1985; O'Connell et al., 1999; Sato, 2001) and are high in fibre and water content (Murray et al., 2001). In contrast, the Cape USOs are predominantly corms, comprising small packages of nutritious food that are located near the soil surface, and hence easy to extract. Comparisons of nutritional values are difficult to make owing to methodological differences. However, Cape USOs are generally equivalent to or more nutritious than USOs harvested elsewhere. Cape tubers have nutritional values similar to values for tubers reported elsewhere (Vincent, 1985; Brand-Miller and Holt, 1998).

Nutritious corms in the family Iridaceae are particularly abundant in the southern Cape and in the CFR in general (Goldblatt and Manning, 2002; Procheş et al., 2006). Corms of Iridaceae are widely documented as hunter-gatherer foodstuffs in the historical (Sparrman and Forster, 1785; Bleek and Lloyd, 1911) and archaeological literature (Deacon, 1976, 1993; Liengme, 1987; Texier et al., 2010). However, some are poisonous, thus distinguishing toxic species from edible ones would have required taxonomic skills, particularly when these differences are associated with similar-looking species (e.g. *Moraea* spp.) (Norwood Young and Fox, 1982). All Iridaceae corms are exceptionally high in carbohydrate content (up to 84%) and low in fibre content (Orthen, 2001; Dominy et al., 2008). Dominy et al. (2008) indicate that the fracture strengths of bulbs and corms are the lowest among USO types (this is due to the low fibre content) and these can be easily masticated and digested. Thus a good proportion of edible USO biomass in the southern Cape is of high quality and could provide a vast amount of energy.

USO return rate

We found that the majority of our foraging experiments would provide the daily caloric requirement in a relatively short time. The gross rates of return we observed are similar to those observed for USOs harvested by extant hunter-gatherer societies (Eder, 1978; O'Connell and Hawkes, 1981; Vincent, 1985; Cane, 1989). These return rates were obtained, despite the fact that naïve foragers were limited to foraging for one USO species, within one vegetation type. A knowledgeable forager (who is familiar with the environment as extant hunter-gatherers are) could forage optimally in the southern Cape by including multiple USO species, and such studies will be conducted in the future. This would further lower the time to gain the daily caloric requirements.

There are, however, a number of caveats associated with our return rate data. Firstly, we used staged foraging experiments which, while often the only way to investigate foraging behaviour of prehistoric humans (Peters et al., 1984; Grayson and Cannon, 1999), do over-simplify a much more complex foraging system. Secondly, we did not record time to process the USO biomass for consumption, which can be considerable for fibrous or unpalatable USOs (Milton, 1999; Carmody and Wrangham, 2009; Wrangham and Carmody, 2010). However, other than the highly fibrous rhizome of *Pelargonium lobatum* and the astringent corms of *Chasmanthe aethiopica* and *Watsonia meriana*, which would require processing to render palatable, the other species, including the tubers of *Cyphia digitata*, can be eaten raw (De Vynck et al., In press). Thirdly, the 2000 calorie daily requirement does not include the protein required for a balanced diet and normal metabolic functioning (Lee, 1968; Hurtado and Hill, 1989).

USOs as fallback foods

Pleistocene archaeological sites on the Cape south coast commonly display an abundant and diverse ungulate plains fauna that is thought to have been associated with the submerged Agulhas Bank (Klein, 1983; Parkington, 2001, 2003; Matthews et al., 2009; Marean, 2010; Faith, 2011). It has been hypothesized that the mammal fauna formed a migratory community that moved west during the winter rains and east to intercept the summer rains (Marean, 2010), and there is some support for this hypothesis in the case of the blue antelope (Tyler Faith and Thompson, 2013). Thus, the local abundance of many of the larger ungulates may have plummeted during the winter and summer months, depending upon the migration movement patterns, when populations migrated west and east and thus out of the central south coast.

Marine invertebrates, harvested from the intertidal, are also a common component of the Pleistocene archaeological sites on the south coast. Evidence for systematic mollusc exploitation has been found in MSA sites such as Pinnacle Point (PP)13B dating back to ~160 ka (Marean et al., 2007; Jerardino and Marean, 2010) and at many early modern human sites that date between 110-50 ka such as Blombos Cave (Henshilwood et al., 2001; Langejans et al., 2012), and Klasies River Mouth (Voigt, 1973; Thackeray, 1988).

In another study designed to contribute to the building of the paleoscape model, De Vynck et al. (2015a) used experienced foragers of Khoe-San descent and showed exceptionally high peak return rates (~4,500 kcal hr-1) from the Cape south coast intertidal under ideal harvesting conditions (spring tides). However, owing to tidal constraints, and the fierce sea conditions experienced there, harvesting was only possible for 10 days a month, for 2-3 hours on each day; lowest returns were recorded in winter and spring – a time of strong winds and high seas – and highest returns in summer and autumn, when sea conditions were calmer (de

Vynck et al., 2015b). During the MSA the species representation of the molluscs suggests that they are only collecting primarily during the spring tides (Marean et al., 2014).

Consequently, there would have been periods of various lengths – ranging from days to weeks – when hunter-gatherers during the Pleistocene would not have been targeting migratory prey and/or marine molluscs. Particularly "protein-deficient" times would have been during times when the migrations were gone and the tides were in a neap phase when collecting returns were low. De Vynck et al. (2015a) suggest that during the winter and early spring months there was a scarcity of protein but an abundance of carbohydrates. At these times, hunter-gatherers would have been dependent on smaller animals, such as the smaller-bodied antelope and mammals and reptiles of the Cape flora, and may have had to rely to a greater degree on the carbohydrates afforded by the USOs studied in this research.

Under conditions of high sea level, for example during the peak of Marine Isotope Stage 5e when the sea level was up to 5-6 m higher than it is today (Hearty et al., 2007), and during the Holocene when the sea level reached its modern configuration in South Africa (Ramsay and Cooper, 2002), the large herds of grazing ungulates on the Paleo-Agulhas plain would have been permanently removed as a food source. The MIS5e peak high sea level archaeological record on the south coast is not well resolved at this time (Marean et al., 2014), but there is a rich record of Holocene occupation during the Later Stone Age. These occupations document a subsistence focus on small animals of the Cape flora with very rare exploitation of large grazing ungulates combined with exploitation of marine molluscs that eventually displays patterns interpreted to show very intensive collection (Marean et al., 2014) and indications of resource depletion (Klein and Steele, 2013). Scavenged Cape fur seals and scavenged marine birds are abundant components of the diet, and overall there is a pattern suggesting people foraging very intensively for low-ranked food resources (Marean et al., 2014). As discussed above, there is also ample evidence for USO exploitation in the

Holocene from both archaeological sites and ethno-historic observations. At these times of relative food scarcity, plant carbohydrates, especially USOs, may have comprised a significant portion of dietary intake, which would categorise them as a staple fallback food (Marshall and Wrangham, 2007). It is interesting to note that the small body size associated with Khoe-San people appears during the Holocene (Stynder et al., 2007; Kurki et al., 2012; Pfeiffer, 2012) when the large mammals were absent as prey.

Conclusions

The southern Cape comprises a vegetationally complex landscape that supports a rich flora of nutritious and forager-accessible USOs, most of which are cormous species belonging to the Iridaceae family. Globally, this USO composition is a unique feature. Edible USO biomass shows high variation within and between vegetation types. While almost all sites sampled included some edible biomass, a few were associated with hotspots where biomass exceeded 3000 kg per ha. While nutritional content did not differ markedly from values reported for USOs harvested by contemporary hunter-gatherers, most southern Cape USOs can be eaten raw, which is not the case for the fibre-rich tubers that predominate records of use elsewhere. Furthermore, USOs show high gross return rates based on calories. Overall, our preliminary study suggests that USOs of the southern Cape could have supported the carbohydrate needs of a hunter-gatherer community during some times of the year, and could also be used as a fall-back food. More experimental research is required to assess the caloric returns from USOs and aboveground carbohydrates in comparison to those from preferred foodstuffs such as shellfish and game.

Acknowledgements

We acknowledge the following sources of funding: National Research Foundation (Grant number: 73664, CPR 2010030500009965) (RMC and KJE), Fynbos Forum (ES), Claude Leon Foundation (AJP), the Oppenheimer Memorial Trust (RMC), National Science Foundation (BCS-0524087, and BCS-1138073) (CWM), the Hyde Family Foundation (CWM), The Templeton Foundation (CWM), and the Institute of Human Origins at Arizona State University (CWM). We thank CapeNature for permission to collect flora specimens (permit number: 0028-AAA007-0006). Kim Hill has provided helpful comments and discussion. Corli Witthuhn provided valuable guidance to complete the nutritional analysis.

References

Barrow, J., 1801. An account of travels into the interior of southern Africa, in years 1797 and 1798. Cadell and Davies, London.

Bleek, W.H.I., Lloyd, L.C., 1911. Specimens of Bushman folklore. George Allen & Company, London.

Branch, G.M., Branch, M., 1992. The living shores of southern Africa. Struik Publishers, Cape Town, South Africa.

Brand-Miller, J.C., Holt, S.H.A., 1998. Australian Aboriginal plant foods: a consideration of their nutritional composition and health implications. Nutrition Research Reviews. 11, 5–23.

Cane, S., 1989. Australian Aboriginal seed grinding and its archaeological record: A case study from the Western desert. In: Harris, D.R., Hillman, G.C. (Eds.), Foraging and Farming. Unwin Hyman, London, pp. 99–119.

Carmody, R.N., Wrangham, R.W., 2009. The energetic significance of cooking. Journal of Human Evolution. 57, 379–391.

Cowling, R.M., 1992. The ecology of Fynbos: nutrients, fire and diversity. Oxford University Press, Cape Town.

Cowling, R.M., Holmes, P.M., 1992. Endemism and speciation in a lowland flora from the Cape Floristic Region. Biological Journal of the Linnean Society. 47, 367–383.

De Vynck, J.C., Anderson, R., Atwater, C., Cowling, R.M., Fisher, E.C., Marean, C.W., Walker, R.S., Hill, K., 2015. Return rates from intertidal foraging from Blombos Cave to Pinnacle Point: understanding early human economies. Journal of Human Evolution.

De Vynck, J.C., Cowling, R.M., Potts, A.J., Marean, C.W., 2015a. Seasonal availability of edible underground and aboveground carbohydrate resources to foragers on the Cape south coast, South Africa. PeerJ PrePrints.

De Vynck, J.C., Van Wyk, B.-E., Cowling, R.M., 2015b. Indigenous edible plant use by contemporary Khoe-San descendants of South Africa's Cape south coast. South African Journal of Botany.

Deacon, H.J., 1976. Where hunters gathered: a study of Holocene Stone Age people in the Eastern Cape. South African Archaeological Society, Claremont.

Deacon, H.J., 1979. Excavations at Boomplaas cave- a sequence through the upper Pleistocene and Holocene in South Africa. World Archaeology. 10, 241–257.

Deacon, H.J., 1989. Late Pleistocene palaeoecology and archaeology in the southern Cape, South Africa. In: Mellars, P., Stringer, C. (Eds.), The Human Revolution. Princeton University Press, Princeton, pp. 547–564.

Deacon, H.J., 1993. Planting an idea: an archaeology of Stone Age gatherers in South Africa. South African Archaeological Bulletin. 48, 86–93.

Deacon, H.J., Deacon, J., 1999. Human beginnings in South Africa: Uncovering the secrets of the Stone Age. David Philip Publisher, Cape Town.

Deacon, H.J., Geleijnse, V.B., 1988. The stratigraphy and sedimentology of the main site sequence, Klasies River, South Africa. The South African Archaeological Bulletin. 43, 5–14.

Deacon, J., 1984. Later Stone Age people and their descendants in southern Africa. In: Klein, R.G. (Ed.), Southern African Prehistoric and Paleoenvironments. A.A. Balkema, Rotterdam/Boston, pp. 220–328.

Dominy, N.J., Vogel, E.R., Yeakel, J.D., Constantino, P., Lucas, P.W., 2008. Mechanical properties of plant underground storage organs and implications for dietary models of early Hominins. Evolutionary Biology. 35, 159–175.

Eder, J.F., 1978. The caloric returns to food collecting: Disruption and change among the Batak of the Philippine tropical forest. Human Ecology. 6, 55–69.

Faith, J.T., 2011. Ungulate community richness, grazer extinctions, and human subsistence behavior in southern Africa's Cape Floral Region. Palaeogeography, Palaeoclimatology, Palaeoecology. 306, 219–227.

Goldblatt, P., Manning, J., 2002. Plant diversity of the Cape region of southern Africa. Annals of the Missouri Botanical Garden. 89, 281–302.

Grayson, D.K., Cannon, M.D., 1999. Human paleoecology and foraging theory in the Great Basin. In: Models for the Millennium: Great Basin Anthropology Today. University of Utah Press, Saltlake, pp. 141–151.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., 1997. Hadza women's time allocation, offspring provisioning, and the evolution of long postmenopausal life spans. Current Anthropology. 38, 551–577.

Hawkes, K., O'Connell, J.F., Blurton Jones, N.G., Alvarez, H., Charnov, E.L., 1998. Grandmothering, menopause, and the evolution of human life histories. Proceedings of the National Academy of Sciences of the United States of America. 95, 1336–1339.

Hearty, P.J., Hollin, J.T., Neumann, a. C., O'Leary, M.J., McCulloch, M., 2007. Global sea-level fluctuations during the Last Interglaciation (MIS 5e). Quaternary Science Reviews. 26, 2090–2112.

Henshilwood, C.S., Sealy, J.C., Yates, R.J., Cruz-Uribe, K., Goldberg, P., Grine, F.E., Klein, R.G., Poggenpoel, C., Van Niekerk, K.L., Watts, I., 2001. Blombos cave, southern Cape, South Africa: Preliminary report on the 1992 - 1999 excavations of the Middle Stone Age levels. Journal of Archaeological Science. 28, 421–448.

Hill, K., Kaplan, H., Hawkes, K., Hurtado, A.M., 1987. Foraging decisions among Aché hunter-gatherers: New data and implications for optimal foraging models. Ethology and Sociobiology. 8, 1–36.

Hladik, A., Bahuchet, S., Ducatillion, C., Hladik, M.C., 1984. The tuberous plants of the central African rain-forest. Revue d'Ecologie (la Terre et la Vie). 39, 249–290.

Hurtado, A.M., Hawkes, K., Hill, K., Kaplan, H., 1985. Female subsistence strategies among Ache hunter-gatherers of eastern Paraguay. Human Ecology. 13, 1–28.

Hurtado, A.M., Hill, K., 1987. Early dry season subsistence ecology of Cuiva (Hiwi) foragers of Venezuela. Human Ecology. 15, 163–187.

Hurtado, A.M., Hill, K., 1989. Experimental studies of tool efficiency among Machiguenga women and implications for root digging foragers. Journal of Anthropological Research. 45, 207–217.

Hurtado, A.M., Hill, K., 1990. Seasonality in a foraging society: variation in diet, work effort, fertility, and sexual division of labor among the Hiwi of Venezuela. Journal of Anthropological Research. 46, 293–346.

Janssen, M.A., Hill, K., 2014. Benefits of grouping and cooperative hunting among Ache hunter-gatherers: Insights from an agent-based foraging model. Human Ecology. 42, 823–835.

Jerardino, A., Marean, C.W., 2010. Shellfish gathering, marine paleoecology and modern human behavior: Perspectives from cave PP13B, Pinnacle Point, South Africa. Journal of Human Evolution. 59, 412–424.

Johnson, S., 1992. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. Journal of Ecology. 81, 567–572.

Kemper, J., Cowling, R.M., Richardson, D.M., Forsyth, G., McKelly, D., 2000. Landscape patterns and their correlates in a fragmented ecosystem: South Coast Renosterveld, South Africa. Austral Ecology. 25, 176–186.

Klein, R.G., 1983. Palaeoenvironmental implications of Quaternary large mammals in the Fynbos region. Fynbos Palaeoecology: a preliminary synthesis. 75, 116–138.

Klein, R.G., Steele, T.E., 2013. Archaeological shellfish size and later human evolution in Africa. Proceedings of the National Academy of Science. 110, 10910–10915.

Kurki, H.K., Pfeiffer, S., Stynder, D.D., 2012. Allometry of head and body size in holocene foragers of the South African Cape. American Journal of Physical Anthropology. 147, 462–471.

Laden, G., Wrangham, R.W., 2005. The rise of the hominids as an adaptive shift in fallback foods: Plant underground storage organs (USOs) and australopith origins. Journal of Human Evolution. 49, 482–498.

Langejans, G.H.J., van Niekerk, K.L., Dusseldorp, G.L., Thackeray, J.F., 2012. Middle Stone Age shellfish exploitation: Potential indications for mass collecting and resource intensification at Blombos Cave and Klasies River, South Africa. Quaternary International. 270, 80–94.

Lee, R.B., 1968. What hunters do for a living, or, how to make out on scarce resources. In: DeVore, I., Lee, R.B. (Eds.), Man the Hunter. Aldine, Chicago, pp. 30–48.

Lee, R.B., 1973. Mongongo: The ethnography of a major wild food resource. Ecology of Food and Nutrition. 2, 213–307.

Lewis-Williams, J.D., 1987. A dream of Eland: an unexplored component of San shamanism and rock art. World Archaeology. 19, 165–177.

Liengme, C., 1987. Botanical remains from archaeological sites in the Western Cape. In: Parkington, J., Hall, M. (Eds.), Papers in the Prehistory of the Western Cape, South Africa. Oxford: Archaeological Report International Series 332(i), Oxford, pp. 237–261.

Marean, C.W., 2010. Pinnacle Point Cave 13B (Western Cape Province, South Africa) in context: The Cape Floral Kingdom, shellfish, and modern human origins. Journal of Human Evolution. 59, 425–443.

Marean, C.W., Anderson, R.J., Bar-Matthews, M., Braun, K., Cawthra, H.C., Cowling, R.M., Engelbrecht, F., Esler, K.J., Fisher, E., Franklin, J., Hill, K., Janssen, M., Potts, A.J., Zahn, R., 2015. A new research strategy for integrating studies of paleoclimate, paleoenvironment, and paleoanthropology. Evolutionary Anthropology: Issues, News, and Reviews. 24, 62–72.

Marean, C.W., Bar-Matthews, M., Bernatchez, J., Fisher, E., Goldberg, P., Herries, A.I.R., Jacobs, Z., Jerardino, A., Karkanas, P., Minichillo, T., Nilssen, P.J., Thompson, E., Watts, I., Williams, H.M., 2007. Early human use of marine resources and pigment in South Africa during the Middle Pleistocene. Nature. 449, 905–908.

Marean, C.W., Cawthra, H., Cowling, R.M., Esler, K., Fisher, E., Milewski, A., Potts, A., Singels, E., De Vynck, J., 2014. Stone age people in a changing South African greater Cape Floristic Region. In: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), Ecology and Evolution of Fynbos: Understanding Megadiversity. Oxford University Press, Oxford, pp. 164–199.

Marks, S., 1972. Khoisan resistance to the Dutch in the seventeenth and eighteenth centuries. The Journal of African History. 13, 55–80.

Marlowe, F.W., Berbesque, J.C., 2009. Tubers as fallback foods and their impact on Hadza hunter-gatherers. American Journal of Physical Anthropology. 140, 751–758.

Marshall, A.J., Wrangham, R.W., 2007. Evolutionary consequences of fallback foods. International Journal of Primatology. 28, 1219–1235.

Matthews, T., Marean, C., Nilssen, P., 2009. Micromammals from the Middle Stone Age (92-167 ka) at Cave PP13B, Pinnacle Point, south coast, South Africa. Palaeontologia Africana. 44, 112–120.

Milton, K., 1999. A hypothesis to explain the role of meat-eating in human evolution. Evolutionary Anthropology: Issues, News, and Reviews. 8, 11–21.

Mucina, L., Rutherford, C.M., 2006. The vegetation of South Africa, Lesotho and Swaziland. South African National Biodiversity Institute, Pretoria.

Murray, S.S., Schoeninger, M.J., Bunn, H.T., Pickering, T.R., Marlett, J.A., 2001. Nutritional composition of some wild plant foods and honey used by Hadza foragers of Tanzania. Journal of Food Composition and Analysis. 14, 3–13.

Nielsen, S.S., 2003. Food analysis, 3rd ed. Kluwer Academic/ Plenum Publishers, New York.

Norwood Young, M.E., Fox, F.W., 1982. Food from the veld: Edible wild plants of southern Africa botanically identified and described. Delta Books LTD, Johannesburg.

O’Connell, J., Hawkes, K., 1981. Alyawara plant use and optimal foraging theory. In: B, W., Smith, E.A. (Eds.), Hunter-Gatherer Foraging Strategies. University of Chicago Press, Chicago, pp. 99–125.

O’Connell, J.F., Hawkes, K., 1984. Food choice and foraging sites among the Alyawara.

Journal of Anthropological Research. 40, 504–535.

O'Connell, J.F., Hawkes, K., Blurton Jones, N.G., 1999. Grandmothering and the evolution of Homo erectus. Journal of Human Evolution. 36, 461–485.

Orthen, B., 2001. A survey of the polysaccharide reserves in geophytes native to the winter-rainfall region of South Africa. South African Journal of Botany. 67, 371–375.

Parkington, J., 2001. Mobility, seasonality and southern African hunter-gatherers. The South African Archaeological Bulletin. 56, 1–7.

Parkington, J.E., 1977. Soaqua: Hunter-fisher-gatherers of the Olifants River valley Western Cape. South African Archaeological Society. 32, 150–157.

Parkington, J.E., 2003. Middens and moderns: shellfishing and the Middle Stone Age of the Western Cape, South Africa. South African Journal of Science. 99, 243–247.

Parkington, J.E., Poggenpoel, C., 1971. Excavations at de Hangen, 1968. The South African Archaeological Bulletin. 26, 3–26.

Parsons, R.F., Hopper, S.D., 2003. Monocotyledonous geophytes: comparison of south-western Australia with other areas of mediterranean climate. Australian Journal of Botany. 51, 129–133.

Peters, C.R., O'Brien, E.M., Box, E.O., 1984. Plant types and seasonality of wild-plant foods, Tanzania to southwestern Africa: Resources for models of the natural environment. Journal of Human Evolution. 13, 397–414.

Pfeiffer, S., 2012. Conditions for evolution of small adult body size in southern Africa. Current Anthropology. 53, 383–394.

Procheş, Ş., Cowling, R.M., Du Preez, D.R., 2005. Patterns of geophyte diversity and storage organ size in the winter-rainfall region of southern Africa. Diversity and Distributions. 11, 101–109.

Procheş, Ş., Cowling, R.M., Goldblatt, P., Manning, J.C., Snijman, D.A., 2006. An overview of the Cape geophytes. Biological Journal of the Linnean Society. 87, 27–43.

Ramsay, P.J., Cooper, J.A.G., 2002. Late Quaternary sea-level change in South Africa. Quaternary Research. 57, 82–90.

Sato, H., 2001. The potential of edible wild yams and yam-like plants as a staple food resource in the African tropical rain forest. African Study Monographs. 26, 123–134.

Schapera, I., Dapper, O., ten Rhijne, W., Grevenbroek, J.G., Farrington, B., 1933. The early Cape Hottentots, described in the writings of Olfert Dapper (1668), Willem Ten Rhyne (1686) and Johannes Gulielmus de Grevenbrock (1695). Van Riebeeck Society, Cape Town.

Schoeninger, M.J., Bunn, H.T., Murray, S.S., Marlett, J.A., 2001. Composition of tubers used by Hadza foragers of Tanzania. Journal of Food Composition and Analysis. 14, 15–25.

Schulze, R., 2008. South African atlas of climatology and agrohydrology. Water Research Commision Report, Pretoria, South Africa.

Smith, E.A., Bettinger, R.L., Bishop, C.A., Blundell, V., Cashdan, E., Casimir, M.J., Christenson, A.L., Cox, B., Dyson-Hudson, R., Hayden, B., Richerson, P.J., Roth, E.A., Simms, S.R., Stini, W.A., 1983. Anthropological applications of optimal foraging theory: a critical review (and comments and reply). Current Anthropology. 24, 625–651.

Sparrman, A., Forster, G., 1785. A voyage to the Cape of Good Hope: towards the Antarctic polar circle, and round the world: but chiefly into the country of the Hottentots and

Caffres, from the year 1772, to 1776., Vols I and. ed. Cape Town: Van Riebeeck Society., Cape Town.

Speth, J.D., Spielmann, K.A., 1983. Energy source, protein metabolism, and hunter-gatherer subsistence strategies. Journal of Anthropological Archaeology. 2, 1–31.

Stynder, D.D., Ackermann, R.R., Sealy, J.C., 2007. Craniofacial variation and population continuity during the South African Holocene. American Journal of Physical Anthopology. 134, 489–500.

Texier, P.-J., Porraz, G., Parkington, J.E., Rigaud, J.-P., Poggenpoel, C., Miller, C., Tribolo, C., Cartwright, C., Coudenneau, A., Klein, R., Steele, T., Verna, C., 2010. A Howiesons Poort tradition of engraving ostrich eggshell containers dated to 60,000 years ago at Diepkloof Rock Shelter, South Africa. Proceedings of the National Academy of Sciences of the United States of America. 107, 6180–6185.

Thackeray, J.F., 1988. Molluscan fauna from Klasies River, South Africa. The South African Archaeological Bulletin. 43, 27–32.

Thunberg, C.P., 1795. Travels in Europe, Africa, and Asia, Made Between the Years 1770 and 1779; in Four Volumes: Containing travels in the empire of Japan, and in the islands of Java and Ceylon, together with the voyage home. F. and C. Rivington, London.

Tyler Faith, J., Thompson, J.C., 2013. Fossil evidence for seasonal calving and migration of extinct blue antelope (hippotragus leucophaeus) in southern Africa. Journal of Biogeography. 40, 2108–2118.

Van Wyk, B.-E., Gericke, N., 2000. People's plants: A guide to useful plants of southern Africa. Briza Publications, Pretoria.

Van Wyk, B.-E., Van Heerden, F., Van Oudtshoorn, B., 2002. Poisonous plants of South Africa. Briza Publications, Pretoria.

Verboom, G.A., Archibald, J.K., Bakker, F.T., Bellstedt, D.U., Conrad, F., Dreyer, L.L., Forest, F., Galley, C., Goldblatt, P., Henning, J.F., Mummenhoff, K., Linder, H.P., Muasya, a. M., Oberlander, K.C., Savolainen, V., Snijman, D. a., Niet, T. Van Der, Nowell, T.L., 2009. Origin and diversification of the Greater Cape flora: Ancient species repository, hot-bed of recent radiation, or both? Molecular Phylogenetics and Evolution. 51, 44–53.

Verboom, G.A., Linder, H.P., Forest, F., Hoffmann, V., Bergh, N.G., Cowling, R.M., 2014. Cenozoic assembly of the Greater Cape flora. In: Allsopp, N., Colville, J.F., Verboom, G.A. (Eds.), Fynbos: Ecology, Evolution, and Conservation of a Megadiverse Region. Oxford University Press, Oxford, pp. 93–118.

Vincent, S., 1985. Plant foods in savanna environments: A preliminary report of tubers eaten by the Hadza of Northern Tanzania. World Archaeology. 17, 131–148.

Voigt, E.A., 1973. Klasies River Mouth: an exercise in shell analysis. Bulletin of the Transvaal Museum. 14, 14–15.

Watt, J.M., Breyer-Brandwijk, M.G., 1932. The medicinal and poisonous plants of southern Africa: Being an account of their medical uses, chemical composition, pharmacological effects and toxicology in man and animal., 1st ed. E. & S. Livingstone, Edinburgh.

Watt, J.M., Breyer-Brandwijk, M.G., 1962. The medicinal and poisonous plants of southern and eastern Africa. E. & S. Livingstone Ltd, London.

Wheeler, R., Mackowiak, C., 1996. Proximate composition of CELSS crops grown in NASA's biomass production chamber. Advances in Space Research. 18, 43–47.

Winterhalder, B., Smith, E., 2000. Analyzing adaptive strategies: Human behavioral ecology at twenty-five. Evolutionary Anthropology Issues news and reviews. 9, 51–72.

Wrangham, R.W., Carmody, R., 2010. Human adaptation to the control of fire. Evolutionary Anthropology: Issues, News, and Reviews. 19, 187–199.

Wrangham, R.W., Cheney, D., Seyfarth, R., Sarmiento, E., 2009. Shallow-water habitats as sources of fallback foods for hominins. American Journal of Physical Anthropology. 140, 630–642.

Youngblood, D., 2004. Identification and quantification of edible plant foods in the upper (Nama) Karoo, South Africa. Economic Botany. 58, 43–65.

Figures

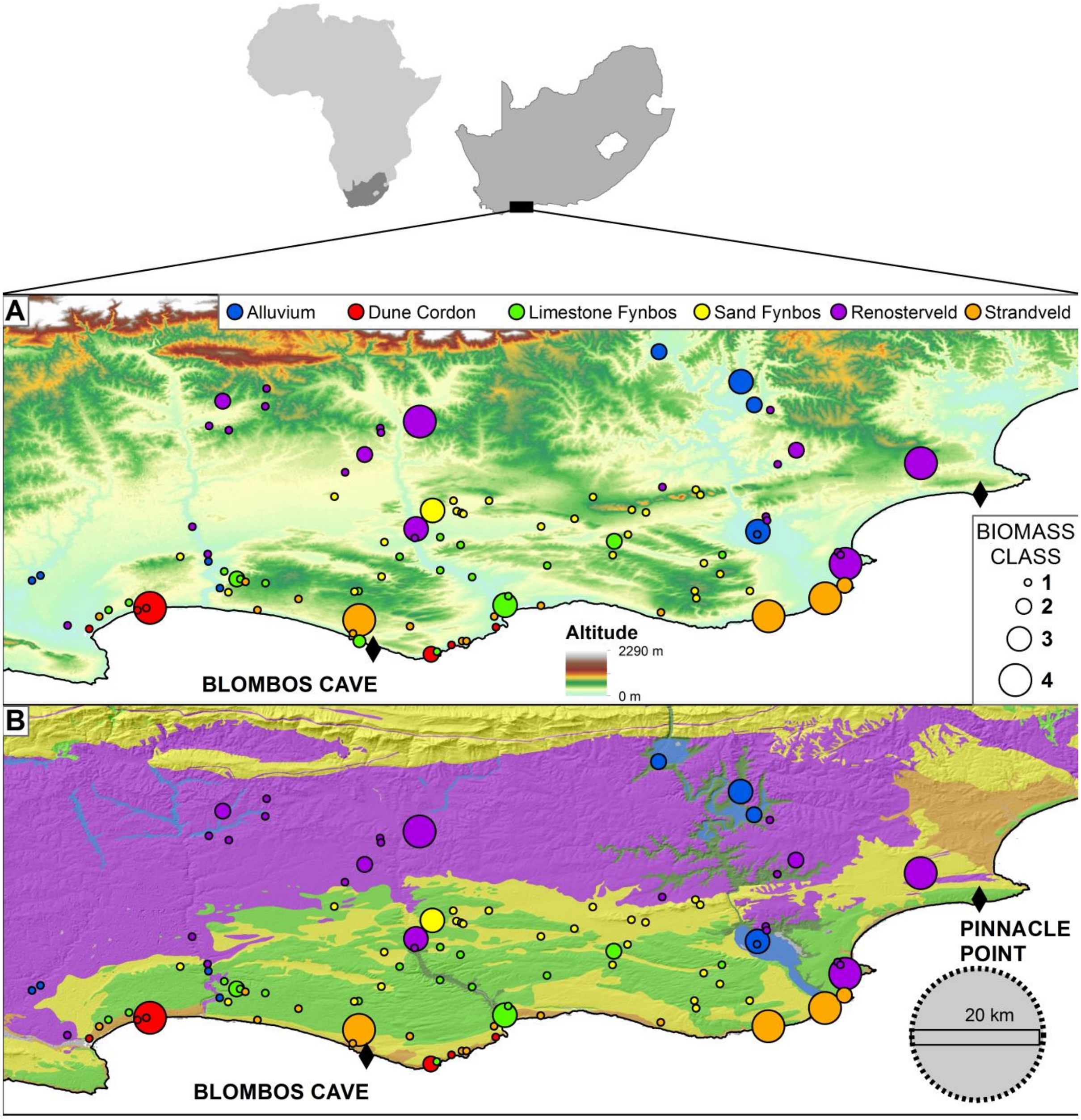


Figure 1. The distribution of edible underground storage organ biomass per 25 m^2 plot across the study region on the southern Cape coast of South Africa. Biomass is represented by four classes (1:0.0-0.5 kg, 2:0.5-1.0 kg, 3:1.0-1.5 kg, 4: >1.5 kg). The position of the plots is shown relative to (A) a digital elevation model of the study area, and (B) the vegetation as mapped by Mucina and Rutherford (2006). Note that colours correspond to the vegetation

types used for the symbols, except for Albany Thicket – dark green – which was not sampled in this study.

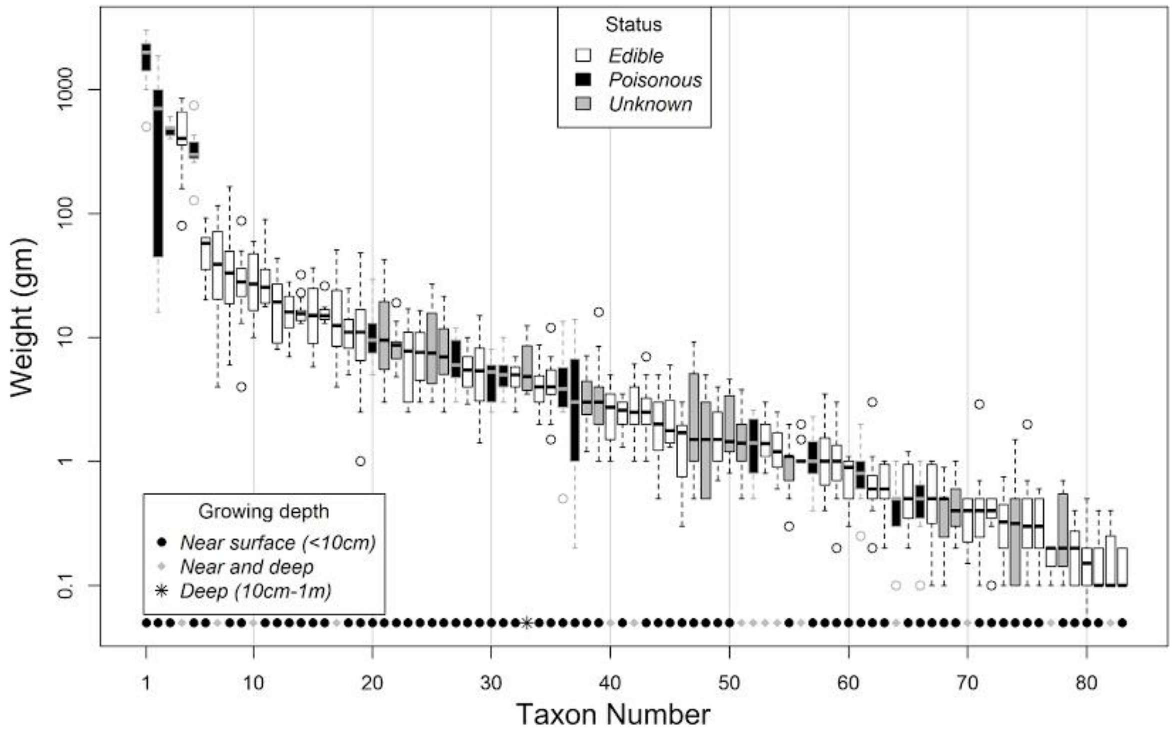


Figure 2. The weight distribution (shown on a log-scale) of the underground storage organs from 83 species including the edibility status and growing depth. Species are labelled as follows: 1:*Crossyne guttata*; 2:*Drimia fosteri*; 3:*Brunsvigia orientalis*; 4:*Rhoicissus digitata*; 5:*Haemanthus coccineus*; 6:*Chlorophytum crispum*; 7:*Pelargonium lobatum*; 8:*Pelargonium triste*; 9:*Cyphia digitata*; 10:*Ferraria crispa*; 11:*Satyrium carneum*; 12:*Albuca fragrans*; 13:*Watsonia meriana*; 14:*Watsonia fergusoniae*; 15:*Albuca maxima*; 16:*Pelargonium rapaceum*; 17:*Cyphia phyteuma*; 18:*Chasmanthe aethiopica*; 19:*Satyrium longicolle*; 20:*Ledebouria revoluta*; 21:*Lachenalia rubida*; 22:*Massonia echinata*; 23:*Trachyandra ciliata*; 24:*Trachyandra revoluta*; 25:*Lachenalia sp. 2*; 26:*Wachendorfia paniculata*; 27:*Eriospermum lancifolium*; 28:*Albuca flaccida*; 29:*Trachyandra falcata*; 30:*Dipcadi viride*; 31:*Eriospermum pubescens*; 32:*Watsonia fourcadei*; 33:*Bonatea speciosa*; 34:*Gladiolus floribundus*; 35:*Satyrium corrifolium*; 36:*Eriospermum cordiforme*; 37:*Ledebouria valifolia*; 38:*Tulbaghia alliacea*; 39:*Holothrix burchellii*; 40:*Babiana ringens*; 41:*Tritonia crocata*; 42:*Freesia leichtlinii*; 43:*Babiana patula*; 44:*Freesia caryophyllacea*; 45:*Cyanella lutea*;

46:*Ixia flexuosa*; 47:*Lachenalia bulbifera*; 48:*Lachenalia pustulata*; 49:*Satyrium stenopetalum*; 50:*Lachenalia sp. 4*; 51:*Moraea inconspicua*; 52:*Moraea flaccida*; 53:*Moraea fugax*; 54:*Babiana tubiflora*; 55:*Bulbinella caudafelis*; 56:*Freesia alba*; 57:*Wurmbea marginata*; 58:*Gladiolus sp. 1*; 59:*Watsonia coccinea*; 60:*Chlorophytum undulatum*; 61:*Moraea polyanthos*; 62:*Watsonia aletroides*; 63:*Tritonia squalida*; 64:*Androcymbium eucomoides*; 65:*Romulea rosea*; 66:*Lapeirousia pyramidalis*; 67:*Cyperus esculentus*; 68:*Holothrix mundii*; 69:*Moraea tripetala*; 70:*Ixia micrandra*; 71:*Gladiolus cunonius*; 72:*Hesperantha juncea*; 73:*Watsonia laccata*; 74:*Empodium gloriosum*; 75:*Oxalis pes-caprae*; 76:*Geissorhiza aspera*; 77:*Gladiolus rogersii*; 78:*Spiloxene flaccida*; 79:*Gladiolus involutus*; 80:*Gladiolus stellatus*; 81:*Oxalis polyphylla*; 82:*Oxalis obtusa*; 83:*Moraea setifolia*.

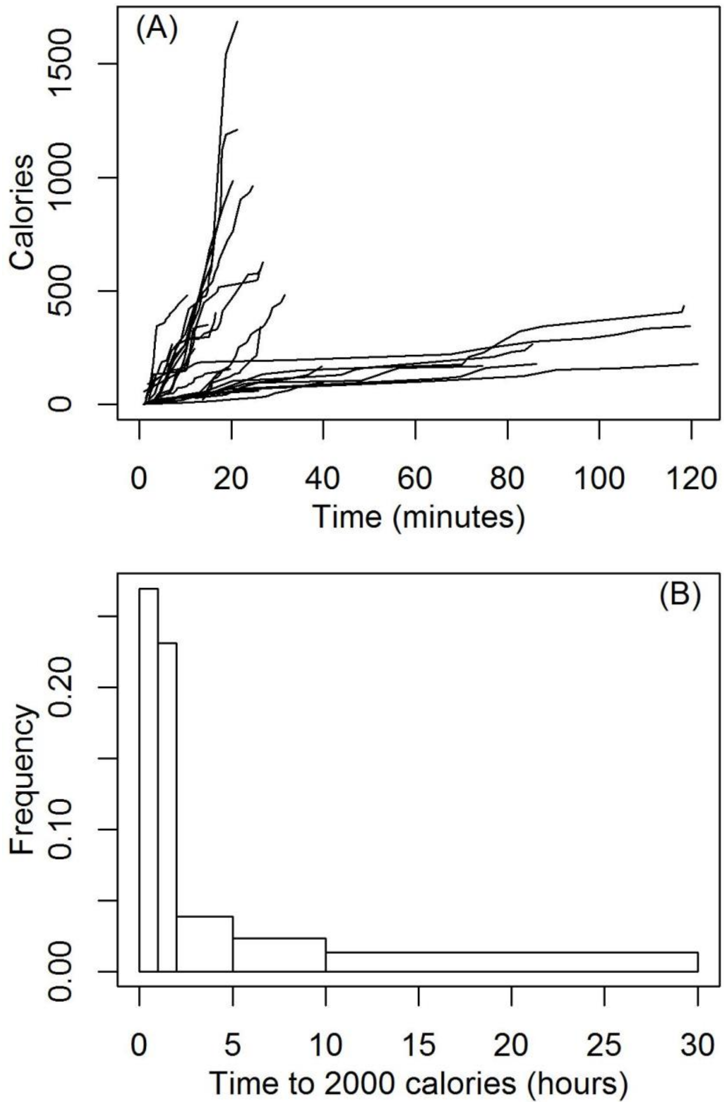


Figure 3. Underground storage organ foraging by a naïve gatherer. (A) The cumulative caloric return over time per foraging event. Each foraging event handicapped the forager to a single species and vegetation type. (B) The estimated time to obtain 2000 calories (the average daily nutritional requirement for a hunter-gatherer) based on linear regression extrapolation. See Fig. C.2 for further information.

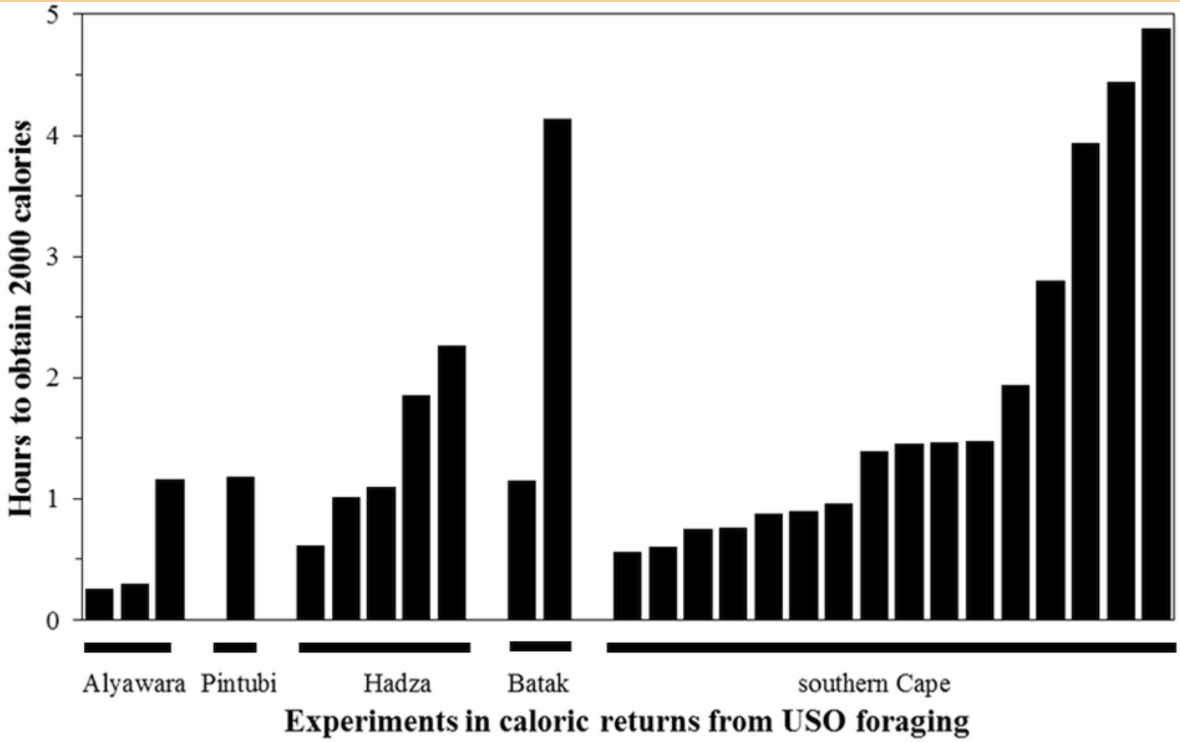
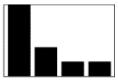
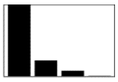
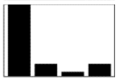
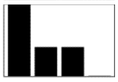
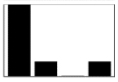
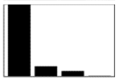


Figure 4. The estimated time necessary to obtain 2000 calories from USO foraging across a range of species and study systems. Foraging events are shown for the southern Cape whereas species averages are shown for the other systems. Data were obtained from the following study systems (all target species are tubers): Alyawara (O'Connel and Hawkes, 1981: p 123 – 125); Pintupi (Cane, 1989: p 105 – 110); Hadza (Vincent, 1985: p 135), Batak (Eder, 1978; p 62).

Tables

Table 1. General statistics regarding underground storage organs sampled from 100 plots (25 m^2) spanning six vegetation types found along the southern Cape coastal lowlands. Superscript letters denote significantly different values at p≤ 0.05 (one way ANOVA, followed by Kruskal-Wallis multiple comparison).

	Strandveld	Renosterveld	Riparian	Dune Cordon	Limestone Fynbos	Sand Fynbos
Plots	15	25	9	7	18	26
Plots with edible species (%)	14 (93)	24 (96)	7 (78)	7 (100)	17 (94)	18 (69)
Species	29	43	12	6	32	24
Edible	20	26	9	4	23	18
Poisonous	5	7	3	2	2	3
Unknown	4	10	0	0	7	3
Average Number of Species per plot	3.7±0.6 ^{x}	4±0.5 ^{x}	2±0.8 ^{y}	2±0.9 ^{y}	3.9±0.5 ^{x}	1.8±0.4 ^{y}
<u>Maximums</u>						
Sites for a single species	7 (46%)	8 (32%)	3 (33%)	4 (57%)	7 (38%)	6 (23%)
Species per site	11	12	6	4	9	6
Edible species per site	7	8	3	2	7	6
Poisonous species per site	3	4	3	2	2	2
Species of unknown status per site	2	3	0	0	2	1
Sites containing edible biomass	14/15	24/26	5/8	7/7	17/18	18/26
USO biomass per site (kg)	9.0	15.3	57.6	9.7	12.6	1.5

Edible USO biomass per site (kg)	4.3	7.5	1.2	6.6	12.5	1.5
Distribution of USO biomass [a]						
All						
Edible						

[a] The relative distribution of USO biomass across plots (25 m^2) in four categories: 0-0.5 kg, 0.5-1.0 kg, 1.0-1.5 kg, >1.5 kg (or 0-200 kg, 200-400 kg, 400-600 kg, >600 kg per ha).

Table 2. Nutritional analysis and caloric content of the six southern Cape USO species. Data are mean ± standard deviation values. n = number of replicates tests for each species. Also shown are data for species harvested by contemporary hunter-gatherers and the domestic potato.

Species	*Chasmanthe aethiopica*	*Cyanella lutea*	*Cyphia digitata*	*Ferraria crispa*	*Pelargonium lobatum*	*Watsonia meriana*	*Vigna frutescens* [a]	*Vatovaea pseudolablab* [a]	*Ipomoea* sp. [b]	*Cyperus* sp. [b]	Domestic potato [c]
N	6	6	15	9	6	3					
USO type	Corm	Corm	Tuber	Corm	Rhizome	Corm	Tuber	Tuber	Tuber	Corm	Tuber
% Protein	6.4±0.3	4.1±0.3	4.2±1.3	5.5±2.4	4.6±0.0	4.0±0.1	6.7	5.3	2±2	2±1	15.2
% Fibre	3.6±0.3	7.1±1.2	18.5±3.3	9.5±2.4	16.1±1.1	2.6±0.0	29.1	25.1	6±4	8±6	2.3
% Ash	4.2±0.6	1.8±0.2	6.6±1.2	7.8±1.9	11.5±1.3	2.9±0.1	7.9	12.9	2±2	2±1	7.6
% Fat	0.9±0.1	0.8±0.2	0.9±0.3	2.2±0.5	0.6±0.3	0.6±0.1	1.9	4.2	0.4±0.8	0.5±0.5	0.7
% Carb	50.5±6.2	43±1.3	5.4±1.3	38.7±13.1	19.7±4.2	39.0±0.9	54.37	52.4	22±12	38±23	74,2
Calories/100 g	228.3±26.6	191±8.1	40.7±11.1	189.9±63.5	97.6±19.5	172.8±1.3	76	79	97.6	162.9	367.175

Note: protein, fibre, ash and fat analyses were performed by the Department of Animal Sciences at Stellenbosch University, while the carbohydrate analyses were performed by Microchem Lab Services in Cape Town. Calorie estimates were calculated using conversion values reported by Vincent (1985): carbohydrates = 4.03 calories per 100 g of USO, protein = 2.78 cal/100 g, and fat = 8.37 cal/100 g.

[a] Data from Vincent (1985) USO gathered by Hadza,[b] Data from Brand-Miller and Holt (1998) USOs gathered by Aboriginal Australians,[c] Data from Wheeler et al. (1996).

PeerJ PrePrints | https://doi.org/10.7287/peerj.preprints.1573v1 | CC-BY 4.0 Open Access | rec: 8 Dec 2015, publ: 8 Dec 2015

Table 3. Biomass of USOs recorded in different parts of the world, in comparison to the biomass of USOs of the six species which had the highest biomass in this study. The number of plots (out of a hundred) in which each species was found is given in brackets.

Study	Sampling Strategy	Species	Min-Max (kg/ha)	Average (kg/ha)
This study	Random Stratified	*Chlorophytum crispum (1)*	0 – 841	8.4
		Chasmanthe aethiopica (8)	5 – 2664	46
		Cyphia digitata (11)	12 – 2351	26
		Pelargonium lobatum (3)	3.9 – 512	10.4
		Rhoicissus digitata (6)	12 – 1873	39.3
		Tritonia crocata (7)	3 – 506	15.6
Sato, 2001	Gatherer driven	*Dioscorea burkilliana*	3.1 – 13.6	7.8
		Dioscorea minutiflora	0.01 – 0.9	0.5
		Dioscorea praehensilis	0.3 – 1.1	0.7
		Dioscorea smilacifolia	0.1 – 0.4	0.2
		Dioscoreophyllum cumminsii	0.2 – 6.6	3.1
Vincent, 1985	Gatherer driven	*Vigna frutesens* var. *frutescens*	0 – 1800	300
		Vatovaea pseudolablab	2400 – 59,700	21,600
Youngblood, 2004	Observer driven	*Cyperus usistatus*	1100 – 18,000	7800
		Talinum caffrum	600 – 32,500	20,000
		Albuca canadensis	1600 – 44,000	28,000
		Pelargonium sidoides	900 – 102,000	60,000