Underground storage organs of plants as a food source for Pleistocene hunter-gatherers in the southern Cape

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Verklaring

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Abstract

The abundance and diversity of carbohydrate and protein resources in the southern Cape of South Africa may well have aided the survival of modern humans through the harsh climatic conditions of the late Pleistocene. Until now, the carbohydrate resources, in particular the underground storage organs (USOs) of some plant species have not been described from a forager's perspective. This is baffling when one considers that the Cape Floristic Region of South Africa harbors the highest diversity of geophyte (herbaceous plants which possess USOs) species in the world. I report on USO distribution and abundance in the southern Cape of South Africa and on the effort, nutritional return and energetic return rates of harvesting these USOs. To determine their distribution and abundance, I assessed identity and abundance in a hundred 25m^2 *plots. These data, along with biomass data of every species sampled, allowed me to quantify the variation of this potential food source over different habitat types in the southern Cape landscape. Furthermore, I observed the time it took for human subjects to gather a sample of six USO species in three different vegetation types and in two seasons. Proximal analyses of the nutritional content of each of these species provided data which, when combined with foraging time, enabled a basic quantification of the return rate of energy (in calories) per time unit. There is high variability in the distribution of edible USO abundance and biomass across the study area, with some sites having very high biomass. Such biomass hotspots are likely to have been targeted by foragers, returning biomass values comparable to other studies which have been conducted on extant hunter-gatherer communities. Due to considerable variation over the landscape, the hotspots of biomass did not correlate significantly with any abiotic variables we measured. This suggests that hotspots of high biomass may have been challenging to find, unless the cognitive skills required to locate such patches were sufficiently developed – certainly excellent knowledge of the landscape and botany would have been crucial if survival depended on locating these diet items. USO species belonging to the Iridaceae family had the highest overall and average biomass in the area, so it is not surprising that this family is best represented amongst USO plant remains found in the archaeological record. Little effort (time) was required to obtain the six species of USOs we observed, although the weights obtained were also low. The nutritional returns of the six test species were higher than in other studies. The return rates per simulated foraging event in this study therefore compare favorably to the anthropological observations of extant hunter-gatherer communities. The lines of evidence presented in this thesis therefore lend support to the hypothesis that the USO resources of the southern Cape would have provided a large component of the carbohydrate requirements for sustaining hunter-gatherer communities. The data set presented in this thesis can be considered a baseline for future studies.*

Keywords: biomass, energetic return rate, Iridaceae, carbohydrate, calories

Opsomming

Die digtheid en diversiteit van koolhidraat- en proteïenhulpbronne in die Suid-Kaap van Suid-Afrika mag die oorlewing van die moderne mens beïnvloed het tydens die ongunstige klimaatstoestande wat geheers het deur die laat Pleistoseen. Tot op hede is die koolhidraathulpbronne in die area nie beskryf vanuit 'n kosversamelaar se perspektief af nie, spesifiek nie die koolhidrate wat deur ondergrondse stoororgane (OSO's) van sommige plantspesies verskaf kan word nie. Dié feit is verstommend as mens in ag neem dat die Kaapse Floristiese Streek van Suid-Afrika die hoogste geofietspesies (kruidagtige plante met OSO's) diversiteit ter wêreld het. Ek rapporteer oor die verspreiding en digtheid van OSO's in die Suid-Kaap en op die inspanning, voedingswaarde en energie-opbrengskoerse verbonde aan die oes van dié OSO's. Verspreiding en digtheid is bepaal oor 'n honderd 25m^2 plotte. Dié data, saam met die biomassa-data van elke spesie wat geïdentifiseer was, is gebruik om potensiële voedselbronne te kwantifiseer in verskillende habitattipes in die Suid-Kaap. Ek het verder die tyd wat dit neem vir mense om die ses geïdentifiseerde OSO-spesies te oes in drie verskillende habitatte en twee seisoene waargeneem. Voedingswaarde-data, tesame met OSO-oestyd-data, is gebruik vir die basiese berekening van energie-opbrengskoerse van spesies deur middel van proksimale analises. Daar is hoë variasie in die verspreiding, digtheid en biomassa van eetbare OSO's gevind in die studie-area, met sommige plotte wat baie hoë biomassa bevat het. Hierdie areas van hoë biomassa sou heel waarskynlik deur kos-versamelaars geteiken gewees het, en gevolglik hoë opbrengste van biomassa bied, wat vergelykbaar is met die biomassa-waardes wat waargeneem word binne areas waar huidige jagter-versamelaar-gemeenskappe tans oorleef. As gevolg van die aansienlike variasie wat waargeneem is oor die landskap het die hoë-biomassa-areas nie beduidend gekorreleer met enige abiotiese veranderlikes wat gemeet is nie. Dit dui daarop dat hoë-biomassa-areas moeilik kan wees om te vind, tensy kognitiewe vermoëns wat noodsaaklik is om kolle van hoë biomassa te vind ontwikkel was. OSO-spesies wat aan die Iridaceae-familie behoort het die hoogste algehele en gemiddelde biomassa in die area gehad. Dit is dus nie verbasend dat dié familie die beste verteenwoordig word in die argeologiese rekord van OSO-plantoorskot nie. Min inspanning (tyd) was nodig om die OSO's van die ses geïdentifiseerde spesies te bekom, alhoewel die massa wat bekom is ook laag was. Die voedingswaarde-opbrengs (per eenheidsmassa) van die ses toetsspesies was hoër as in ander studies. Die energie-opbrengskoers per versamelingsgebeurtenis het gevolglik ook gunstig vergelyk met die antropologiese waarnemings wat van huidige jagter-versamelaars gemeenskappe gemaak is. Die resultate van hierdie studie ondersteun die hipotese dat die OSO-hulpbronne in die Suid-Kaap 'n groot komponent van die koolhidraat-vereistes van jagter-versamelaar-gemeenskappe sou gewees het. Die datastel wat in dié tesis aangebied word kan as 'n basisverwysing dien vir toekomstige studies.

Sleutelwoorde: biomassa, energie-opbrengskoers, Iridaceae, koolhidrate, kalorieë

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1. The southern Cape, a midden of information on our ancestors

1.1 Introduction

South Africa has one of the most complete sequences of archaeological evidence of the Middle (MSA 200ka-40ka) and Later Stone Age (LSA 40ka-30ka) (Brown et al., 2012; Lombard, 2012; McCall and Thomas, 2012) in Africa. In particular, there is a rich archaeological record of MSA and LSA coastal sites in South Africa with evidence of human habitation, although occupation of these sites was not always continuous (Avery, 1987; Deacon, 1995; Henshilwood and Marean, 2013; Henshilwood et al., 2001; Klein, 2001; Lombard, 2012; Marean, 2010a; Singer et al., 1982; Texier et al., 2010). Genetic data shows that our species went through multiple genetic bottlenecks during the Pleistocene (Ambrose, 1998; Manica et al., 2007; Ramachandran et al., 2005; Stoneking and Krause, 2011). This might have been due to the colder and drier conditions which persisted in Africa during glacial periods (Partridge and Demenocal, 1997). South Africa would have been cooler and drier during one glacial stage specifically: Marine Isotope Stage 6 (MIS-6: 195-123ka) (Partridge and Demenocal, 1997), a time which has a sparse archaeological record of humans across the world (Marean, 2010a). Where in Africa would humans have likely persisted through such a significant population bottleneck? One of the possible refugia suggested is the south coast of South Africa: the southern Cape (Marean, 2010a).

A multidisciplinary team led by Prof. Curtis Marean (Arizona State University) has been working for several years on an archaeological site at Pinnacle Point, near Mossel Bay, South Africa. This team is trying to decipher the behaviour and lives of hunter-gatherer people during the harsh climate of MIS-6 (195-123ka) (Marean, 2010b) from the archaeological evidence at this site. To this end, the concept of a Paleoscape was formulated to refer to the ancient landscape which would have existed in MIS-6 and other ice age periods similar to it through the middle to late Pleistocene. This Paleoscape would ultimately conceptualize the resources available to prehistoric humans and the abundance and distribution of these resources over the landscape of the southern Cape. The Paleoscape research team was formed and a host of interdisciplinary research employed in an attempt to recreate what the Paleoscape might have been like and how our ancestors might have lived in it.

A glacial period would certainly have had an impact on the environment and thus the natural resources available to humans existing in the Paleoscape. This in turn would have had a huge impact on their lives and survival strategies. The southern Cape has a very high diversity and abundance of marine invertebrates, especially molluscs (Branch and Branch, 1992), which could have offered a vast biomass of protein-rich food. It has been postulated that the essential fatty acids in marine protein sources such as shellfish might have sustained the brain development our ancestors underwent (Marean, 2010a; Parkington, 2010).

The botanical attributes of the south coast, however, are the topic of this thesis. The Cape Floristic Region (CFR) is a biodiversity hotspot situated in the south-western tip of South Africa and is home to the highest diversity and abundance of geophytes (herbaceous perennials with an underground storage organ) in the world (Procheş et al., 2005). There are 2098 species of geophyte in the CFR, which comprise 17% of the total plant species in this bioregion (Procheş et al., 2006). Many of these species are edible (Van Wyk and Gericke, 2000; Watt and Breyer-Brandwijk, 1932, 1962). Archaeologists refer to the underground parts of these plants as underground storage organs, or USOs, as a general term for bulbs, corms, tubers and rhizomes.

There is evidence of underground storage organ remains in some archaeological sites in South Africa (Deacon, 1984). Corm sheaths from the family Iridaceae (*Watsonia*, *Gladiolus)* are particularly prominent in the records (Deacon, 1970, 1972, 1993; Klein, 1974; Parkington, 1977); however, since the remains of most USO plants are unlikely to persist in the archaeological record, and there are no extant hunter-gatherer communities in the Cape, very little is known about the USOs as a resource for early humans in this region (most of the evidence is perishable) (Deacon, 1984; Klein, 2001; Parkington et al., 2009; Perry et al., 2007). People of Khoe-San origin were overwhelmed by European settlers starting in the mid-16th century; by the mid-1700s, they had lost their independence and were reduced to serving the needs of Europeans (Marks, 1972). Descendants of these peoples remain and are genetically distinct from other hunter-gatherer groups which still remain in southern Africa (pers. com. Dr. Sarah Schlebusch). However, due to the fact that their ancestral way of life has been subsumed by a western lifestyle, much of their knowledge of the natural food resources has been lost, as evidenced by the ethnobotanical research conducted in the area (De Vynck et al., 2013). Consequently, the research on USO resources available to early humans must rely on contemporary patterns, and research on foraging must rely on simulated studies (i.e. using field assistants to simulate foraging activities) and extrapolation from recorded Khoe-San foraging behaviour in other parts of southern Africa. Once these data have been collected, they will be used, along with a range of other data, to model the foraging activities of Pleistocene hunter-gatherers. The primary objective of my work was to explore the local abundance and biomass, cost of harvesting and nutritional status of USO species as a food source for hunter-gatherers in the southern Cape.

1.1.1 The role of USOs in modern human evolution

Recent genomic studies provide overwhelming evidence that the modern human lineage has an African origin (Blum and Jakobsson, 2011; Manica et al., 2007; Ramachandran et al., 2005; Ray et al., 2005; Schlebusch et al., 2012; Stoneking and Krause, 2011). Most evidence points to our lineage emerging around 195-160ka (Behar et al., 2008; Clark et al., 2003; Fagundes et al., 2007; Ingman et al., 2000; McDougall et al., 2005; Reed and Tishkoff, 2006; Tishkoff et al., 2007; White et al., 2003). The earliest archaeological evidence of anatomically modern humans is from sites in East Africa 190-150ka (McDougall et al., 2005; Tishkoff et al., 2007; White et al., 2003). It is not established whether these humans in East Africa might have given rise to the lineage leading to modern humans (Marean, 2010a), and it is still a case of debate as to where exactly in Africa the origin of modern humans occurred. Speculations derived from genetic, geographic, and archaeological data point to northwest or East Africa (Reed and Tishkoff, 2006; Stoneking and Krause, 2011), while some studies support the hypothesis that all modern humans originated from southern African hunter-gatherer communities (Henn et al. 2011). In fact, the deepest genetic divergence of contemporary humans is found between Khoe-San peoples of southern Africa and all other groups (Henn et al., 2011; Schlebusch et al., 2012; Stoneking and Krause, 2011).

One of the major genetic bottlenecks observed in our genome occurred 150ka, close to the origins of our species (Ambrose, 1998; Behar et al., 2008; Fagundes et al., 2007; Gonder et al., 2006; Lahr and Foley, 1994). This genetic bottle neck falls within MIS-6 (195-123ka), when the African climate was the coldest and driest in the Pleistocene (Partridge and Demenocal, 1997). As a consequence, hominins are likely to have experienced food scarcity (Marean, 2010a; Petit et al., 1999). This is why it is so crucial to determine if USO resources would have been able to help support hunter-gatherer people in the middle and later Pleistocene. USO species are adapted to seasonally harsh conditions due to their ability to store water and carbohydrates (Dominy et al., 2008; Vaughton and Ramsy, 2001), and are likely to have been less affected by harsh glacial environments than other plant groups. USOs typically have high yields of carbohydrates (Deacon, 1993; Dominy et al., 2008; Orthen, 2001; Parkington, 1977; von Willert et al., 1991) and high apparency to foragers owing to the temporal predictability in their phenology (De Vynck et al., 2013; Deacon, 1993; Parkington, 1977). Furthermore, humans face a relative lack of competitors to their exploitation compared to above-ground fruits, nuts and seeds (Conklin-Brittain et al., 2002; Laden and Wrangham, 2005; Marean, 2010a).

It is widely recognized that USOs were likely a prominent component of the hominin diet (Hatley and Kappelman, 1980; Ragir, 2000; Wrangham et al., 1999). It has been established that *Homo erectus* cooked USOs as a food item (Dominy et al., 2008) and that USOs were an important part of the diet of taxa from the hominid genera *Australopithecus* and *Paranthropu*s (Yeakel et al., 2007). Apart from the archaeological evidence of USO use by late Pleistocene people in southern Africa (Deacon, 1970, 1984; Parkington and Poggenpoel, 1971), observations of contemporary hunter-gatherer groups indicate widespread use of USOs as food source (Eder, 1978; Hladik et al., 1984; Hurtado and Hill, 1989a; Hurtado et al., 1985; Marlowe, 2005; O'Connell and Hawkes, 1984; Sato, 2001; Vincent, 1985).

In South Africa, historic literature of Khoe-San dependency on USOs is substantial (Bleek and Lloyd, 1911; Lee, 1969; Silberbaur, 1981; Tanaka, 1976). Unfortunately in many areas of South Africa, Khoe-San communities have either been displaced or westernized (Henn et al., 2011; Lee, 1973; Marks, 1972). Due to this westernization, most of the knowledge of possible USO food sources has been lost. As a consequence, I could not conduct observational studies as has been done elsewhere with existing hunter-gatherer communities.

The approach I took in this thesis was two-pronged. Firstly I conducted a spatial analysis of the distribution, abundance and biomass of USOs in the southern Cape of South Africa, as a way of assessing the potential resource base. In other anthropological studies, where gathering activities have been quantified, gatherers were followed and the density of edible plants determined in a patch chosen by a gatherer (invariably these patches had high density of the target species) (Sato, 2001; Vincent, 1985). Since this was not possible in my study area, I determined the distribution and density of USOs by sampling sites in the major vegetation units of the southern Cape landscape. Although the distribution, or area of these vegetation types would invariably have shifted and changed through the Pleistocene (Avery, 1987), the assumption was made that sampling a range of vegetative units would have captured the variation that might have occurred under much different climates. Importantly, the Cape Pleistocene climates were much more stable than those of many other parts of the world (Marean et al., In prep.), so plant communities may have been relatively stable. These spatial data on USO abundance are an important input for developing foraging models for the Paleoscape project.

Secondly, I employed experimental methods to simulate foraging characteristics of humans in the southern Cape. This is considered a valid way of gauging prehistoric behaviour (Peters et al., 1984; Smith et al., 1983). I based my experimental design on studies which observed foraging behaviour of hunter-gatherer communities like that of Vincent (1985). She tested the distribution and density of tuberous plants, the biomass of tubers, the amount of time required to obtain them and the nutritional return of these tubers (Vincent, 1985). With these baseline data I attempted to gauge the return rates possible from gathering certain USOs, and the carrying capacity of an area for human foraging. Most optimal foraging models assume that foragers will be selected to behave so as to maximize the net rate of return (of energy or nutrients) per unit foraging time (Grayson and Cannon, 1999; Smith et al., 1983). Smith et al. (1983), in particular, discuss the possibility of reconstructing and testing foraging habits of prehistoric people. The data presented in this thesis, together with the principles of foraging theory, have the potential to direct future research to develop a robust foraging model of hunter-gatherer people in the southern Cape.

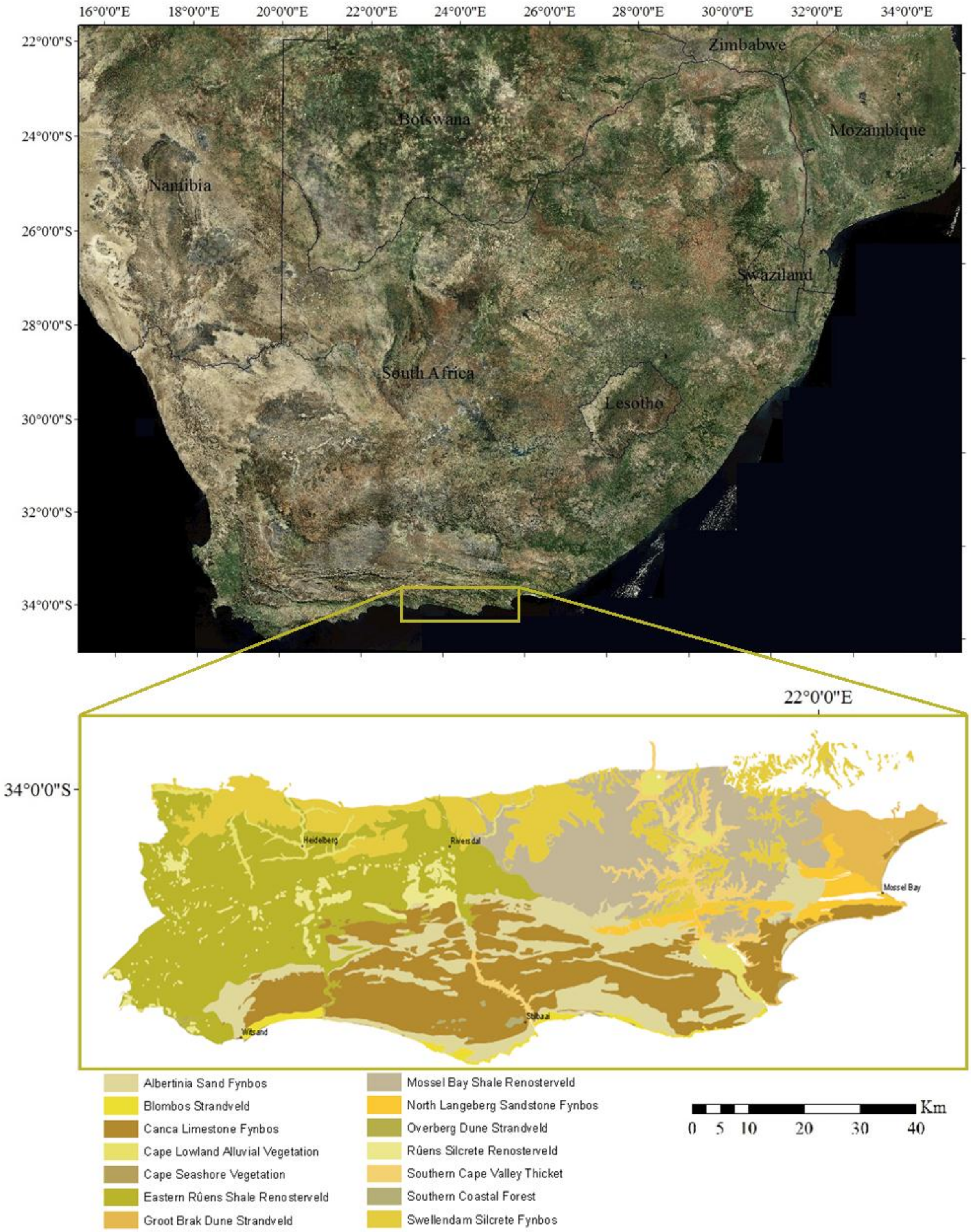

Figure 1.1 A map of the study area in the southern Cape of South Africa, and the main vegetation types found within it. Vegetation units sourced from Mucina and Rutherford (2006).

1.1.2 Study Area

The study area is in the Western Cape of South Africa, stretching from Mossel Bay in the east, to the mouth of the Breede River in the west, and from the Indian Ocean in the south to the foot of the Langeberg range in the north. The landscape consists of undulating coastal plain incised by four major rivers: Gourits, Goukou, Duiwenhoks and the Breede. The area ranges in altitude from sea level to 431 m. The area receives relatively low rainfall (350 – 450 mm annually) which is considered to have a sub-Mediterranean climate (dry summers but heavy rain can occur anytime of the year); mild temperatures (no frost) (Schulze, 1965).

The study area falls within the Cape Floristic Region (CFR) and contains 14 distinct vegetation types (Mucina and Rutherford, 2006) (figure 1.1). These vegetation types belong to six unique, broader vegetation units namely: Renosterveld, Limestone Fynbos, Sand Fynbos, Riparian vegetation, Strandveld and Dune Cordon vegetation.

The major determinants of vegetation distribution are edaphic. Renosterveld occurs on relatively fertile, clay-rich soils derived from shale and mudstone (Mucina and Rutherford, 2006). Renosterveld 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 the Riviersonderend mountains) is considered a distinct type of Renosterveld, which has a high grassy element and between 50 and 70% plant cover (Mucina and Rutherford, 2006).

Fynbos, the most widespread vegetation of the CFR, is – like Renosterveld – a fire-prone evergreen shrubland. Fynbos 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 are highly distinct floristically.

Strandveld is a mosaic of subtropical thicket, with bush clumps and Fynbos elements associated with ancient (late Cenozoic) dune sands (Mucina and Rutherford, 2006). While Restionaceae (*Thamnochortus* spp.) are common, species richness of Proteaceae and Ericaceae is low. (Mucina and Rutherford, 2006). Owing to the low flammability of the thicket, and low cover of other shrubs, Strandveld is less prone to fire than surrounding pure Fynbos vegetation types (Mucina and Rutherford, 2006).

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).

Riparian vegetation is an azonal type associated with alluvial soils of the major rivers in the region. Riparian vegetation comprises a tree or tall shrub component dominated by the winter-deciduous *Acacia karoo*. Alluvial soils are fertile loams.

1.1.3 Research context

This MSc in Conservation Ecology might appear off-topic for a conservation related degree. Conservation is, however, an eclectic, multidisciplinary subject. The connection to conservation comes in various guises. Firstly, there is a strong push to declare the southern Cape coastline as a heritage coastline – with obvious positive benefits to biodiversity conservation. Doing so opens up possibilities to link the past with the future, so that the lessons learned can assist with future challenges of food security, water and energy. In April 2013, Pinnacle Point, a group of caves on the southern Cape coast near Mossel Bay, were declared as a provincial heritage site, bringing the attention of policy makers and the general public to the archaeological and biodiversity significance of this region. A key message in this thesis is that floral biodiversity may well have played an important role in the evolution of our own species – a very powerful conservation message.

1.2 Thesis outline

Chapter 1 - The southern Cape, a midden of information on our ancestors

This chapter serves as a general background to the study and outlines the study rationale.

The two data chapters (Chapters 2 and 3) are written in an article format following the guidelines of the Journal of Anthropological Archaeology, and some duplication between the article chapters is unavoidable.

Chapter 4 outlines the key findings of the data chapters and serves as the synthesis of the thesis. It includes some recommendations for amendments to my study design, and pointers for further research.

Chapter 2 - The distribution, abundance and biomass of USOs in the southern Cape, South Africa (from a foraging perspective)

In this chapter I report on USO distribution and abundance in the southern Cape of South Africa. Standard botanical methods and stratified random sampling were employed to collect data. These data provide information on USO resources potentially available to gatherers in different vegetation types across the landscape, what the USO species characteristics are and, specifically, the abundance of edible USOs. The breadth of diet (USO species which would have been included in a gatherer's diet) is informed by the different species of edible USOs and their attributes, which might make them more or less attractive to a forager. The key questions of this chapter are:

> How does the richness and biomass of edible USOs vary across a vegetationally complex environment?
>
> How does the biomass of edible USOs compare to other areas of the world, where hunter-gatherer communities were/are present?
>
> Can the edible biomass of USOs using abiotic variables be predicted?

Are edible USOs overrepresented among particular taxa, USO growth forms (corms, bulbs, rhizomes and tubers) or depth of the storage organ?

Chapter 3 - Costs of harvesting, nutritional value and energetic return rate of underground storage organs in the southern Cape, South Africa

In this chapter I analyse the foraging effort (using Khoe-San foraging methods) and nutritional return rate of foraging for six edible USO species, in different vegetation types and different seasons, in the southern Cape of South Africa. The energy required by a gatherer to obtain underground storage organs (USOs), and their nutritional return, influence which species gatherers might have included in their diet. Due to the fact that there are no more hunter-gatherer people remaining in the southern Cape, I employed local, Khoe-San descendants as field assistants, and observed them doing focused foraging. To this end, I selected USO species common in the archaeological, historical and ethnobotanical literature. I determined the energy inputs and returns from gathering these species in different habitats, in different seasons. These data provide information on the return rates of energy in relation to foraging time. The key questions of this chapter are:

How long does it take to gather these USO species in the southern Cape?

What are the nutritional returns of such USOs?

What is the accumulated return rate of individual simulated foraging events (a certain species, in a vegetation type and season)?

How do the return rates of foraging of selected USO species compare to other USO species gathered elsewhere in the world?

Chapter 4 - USOs in the context of hunter-gatherer diets in the southern Cape

Combining the insights gained from Chapters 2 and 3, I speculate on the role that USOs might have had on hunter-gatherer diets of the Pleistocene. Despite the limitations of this study, one can still make useful inferences about hunter-gatherer foraging for USOs. Furthermore, the study raises a host of questions requiring further research. I consider the influence a stable carbohydrate resource could have had on the cognitive development observed in our species and also discuss how the outputs my dissertation might contribute to research for the greater Paleoscape project.

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2. The distribution, abundance and biomass of USOs in the southern Cape, South Africa (from a foraging perspective)

2.1 Abstract

Underground storage organs (USOs) serve as a staple source of carbohydrates to most hunter-gatherer communities. While the way of life of hunter-gatherer societies which occupied the southern Cape is no longer in existence, evidence of Pleistocene hunter-gatherers' use of such plants in the Cape archaeological record is extensive. To date, no quantification of the USO resources of the southern Cape has been conducted. I endeavoured to identify how edible USO biomass: varies across a vegetationally complex area, compares to the edible USO biomass observed in extant hunter-gatherer communities, if it can be predicted using abiotic variables and if this biomass is associated with particular taxa, USO types and USO depth. I sampled a hundred plots in the southern Cape and recorded the USO species' abundance and weight. With these data I was able to determine the biomass of edible USOs across the landscape. USO biomass varies markedly, but certain sites have USO biomass upwards of 2400kg/ha. Although the biomass observed in this study is lower than that reported from some African savanna habitats, the results fall within the range of biomass values that still support hunter-gatherer communities. None of the abiotic variables we recorded were useful for predicting USO biomass. Toxic species had large USOs growing near the soil surface, while the USOs of edible species were significantly smaller and located deeper in the soil. The Iridaceae family contained the most edible species and had the highest edible biomass. While there are patches in the vegetationally complex area which have high USO biomass, finding them might have proven a challenging endeavour. I speculate that locating resource-rich patches in space and time would have required considerable cognitive development among Pleistocene hominins and could have been a trigger for the emergence of our species.

Keywords: hunter-gatherer, homonins, Iridaceae, biomass hotspots

2.2 Introduction

Hunter-gatherer and nomadic people depend on plants harvested in their natural habitat for their carbohydrate intake. Chief among these are plants with underground storage organs (USOs) (Eder, 1978; Hurtado et al., 1985; Laden and Wrangham, 2005; Lee, 1973; O'Connell and Hawkes, 1984; Sato, 2001; Vincent, 1985; Wrangham et al., 2009).

It has been hypothesised by Marean (2010b) that the juxtaposition of a rich and abundant marine invertebrate fauna and a similarly diverse underground storage organ (USO) flora, enabled the persistence of humans on the Cape south coast, despite the relatively arid and cool climates of MIS-6 (195-123ka). To date, no research has been conducted on Cape USOs as a resource for hunter-gatherers, despite archaeological (Deacon, 1995, 1984; Hatley and Kappelman, 1980; Henshilwood and Marean, 2013; Laden and Wrangham, 2005; McCall and Thomas, 2012; Parkington, 1972; Rector and Verrelli, 2010), ethnographical (Lee, 1969; Van Vuuren, 2013; Van Wyk and Gericke, 2000) and historical (Bleek and Lloyd, 1911) evidence of their importance in the diet of San and Khoe people.

In this chapter, I address the gap by quantifying the abundance of USOs across six major vegetation types in the Cape south coast. Since the Khoe-San descendants in the area have been influenced by agrarian technology for almost 200 years, there is no longer a tradition of harvesting USOs (Marks, 1972). Therefore I could not use foragers to identify patches of habitats, suitable for foraging, as in other studies (Eder, 1978; Hurtado and Hill, 1987; O'Connel and Hawkes, 1981; Sato, 2001; Vincent, 1985). Instead, I conducted stratified random sampling of the natural remaining area, in order to assess the characteristics of the USO flora.

In particular, I asked the following questions:

> How does richness and biomass of edible USOs vary across a vegetationally complex environment?
>
> How does the biomass of edible USOs compare to other areas of the world, where hunter-gatherer communities were/are present?
>
> Can edible biomass of USOs using abiotic variables be predicted?
>
> Are edible USOs overrepresented among particular taxa, USO growth forms (corms, bulbs, rhizomes and tubers) or depth of the storage organ?

Understanding the spatial variability and predicting where in the landscape high biomass of USOs can be found is a first step in quantifying the opportunities and constraints of foraging for USOs in the southern Cape. I hypothesise that the abundant source of complex carbohydrates, in the form of USOs, from a variety of taxa across the southern Cape region could have been an important food source for hunter-gatherer people living in the region.

2.3 Methods

2.3.1 Study Area

The focus of this chapter is a ca. 600 000 hectare area located in the southern Cape of South Africa, from Mossel Bay in the east to the Breede River in the west, and from the coastline to the foot of the Langeberg-Outeniqua mountains (figure 2.1). The area is exceptionally diverse in many aspects. Mucina and Rutherford (2006) describe 14 vegetation types in the area (spatial distribution of vegetation types in figure 2.1), while Vlok and de Villiers (2007) describe 71 terrestrial vegetation units within four different biomes. USO species are abundant and/or species rich in 33 of the 71 vegetation units (Vlok and De Villiers, 2007).

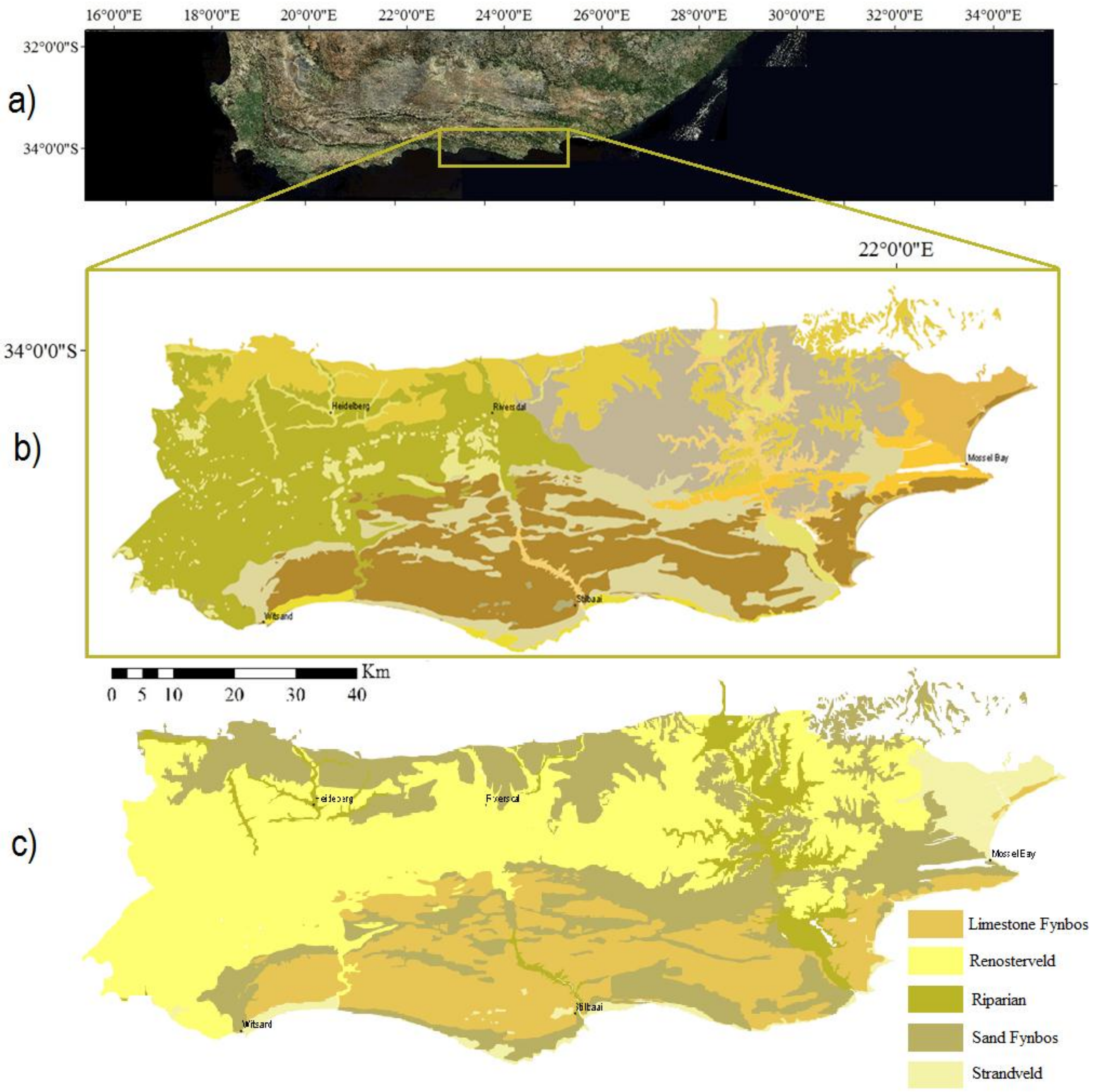

Figure 2.1 a) The study area's location in the southern Cape of South Africa. b) The distribution of the 14 vegetation types which occur in the study area, as described by Mucina and Rutherford (2006). c) The 14 vegetation types described by Mucina and Rutherford (2006) were consolidated into six main vegetation types. Strandveld and Dune Cordon vegetation are grouped together in this map.

Sampling occurred over a period of three months in the spring of 2011 (August through October), a time of maximum apparency of USO species in the study area (de Vynck et al., in prep) and elsewhere in the CFR (Johnson, 1993), in six main vegetation types. The 14 southern Cape vegetation types (Mucina and Rutherford, 2006) were consolidated into six main vegetation types: Renosterveld, Limestone Fynbos, Sand Fynbos, Strandveld, Dune Cordon and Riparian vegetation (figure 2.1). They have very different edaphic and floristic characteristics.

The major determinants of vegetation distribution are edaphic. Renosterveld occurs on relatively fertile, clay-rich soils derived from shale and mudstone (Mucina and Rutherford, 2006). Renosterveld 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 of Renosterveld, which has a high grassy element and between 50 – 70% plant cover (Mucina and Rutherford, 2006).

Fynbos, the most widespread vegetation of the CFR, is – like Renosterveld – a fire-prone evergreen shrubland. Fynbos 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 are highly distinct floristically.

Strandveld is a mosaic of subtropical thicket bush clumps and Fynbos elements associated with ancient (late Cenozoic) dune sands (Mucina and Rutherford, 2006). While Restionaceae (*Thamnochortus* spp.) are common, species richness of Proteaceae and Ericaceae is low (Mucina and Rutherford, 2006). Owing to the low flammability of the thicket, and low cover of other shrubs, Strandveld is less prone to fire than surrounding pure Fynbos vegetation types (Mucina and Rutherford, 2006).

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).

Riparian vegetation is an azonal vegetation type associated with alluvial soils of the major rivers in the region. Riparian vegetation comprises a tree or tall shrub component dominated by the winter-deciduous *Acacia karoo*. Alluvial soils are fertile loams.

In total, one hundred plots of 25m^2 were sampled, with the percentage of plots in each vegetation type proportional to the area in which the vegetation types occurs in the southern Cape. This produced seven plots in Dune Cordon, 18 in Limestone Fynbos, nine in Riparian vegetation, 25 in Renosterveld, 26 in Sand Fynbos and 15 in Strandveld vegetation. Since the Renosterveld of the southern Cape is significantly transformed by agriculture, in particular deeper soils on gentle terrain, the sites in this vegetation type were biased in favour of the steeper slopes. This is a common problem in studies conducted on Renosterveld, of which only 3 – 9% natural vegetation remains (Newton & Knight 2005).

The following variables were recorded in each of the 100 plots: GPS coordinates, percentage plant cover, aspect, elevation, percentage rock cover (bedrock, boulder and pebble), soil depth and vegetation type. The diversity and abundance of visible USO species were then measured by counting the number of plants per USO species in each plot. Voucher specimens of each species were collected and housed in the herbarium at Nelson Mandela Metropolitan University (Ria Olivier Herbarium). All specimens were identified to species level.

Between 10 and 15 specimens of each USO species encountered were collected and the depth to the storage organ, length of the storage organ and its weight were recorded. Using these data, I quantified the mean biomass of USOs per species, per unit area and per vegetation type.

A category of edibility (edible, poisonous and unknown) was assigned to each species using the ethnobotanical literature (Van Wyk and Gericke, 2000; Van Wyk et al., 2002; Watt and Breyer-Brandwijk, 1932, 1962). Because of their impact on agriculture and the medical wellbeing of people, most poisonous species have been well described, but there is much less information available on edible USOs. In some cases I assigned as edible any species of a genus well documented for this trait (e.g. *Babiana*, *Watsonia*, *Gladiolus*); in other cases (e.g. *Moraea*), species with no documentation regarding use were allocated to the "unknown" category. I also relied on De Vynck's (in prep) ethnobotanical research from the study area for additional information.

2.3.2 Data analysis:

All data were analysed using Statistica® 8, unless indicated otherwise. I performed Kruskal-Wallis test and one way ANOVAs to test for significant differences among variables observed in each plot (species richness, soil depth, percentage rock cover, soil pH of plot soil) and vegetation type.

USO biomass per plot was calculated by multiplying the mean weight of each species encountered by its respective population size, and summing across all species. This was done separately for each of the edibility categories. Since the data had a Poisson structure, log transformation was used to normalize the distribution. A one way ANOVA for unbalanced design was performed to test for significant differences of biomass in the different vegetation types using the R 3.0.1 Statistical Software®.

Multiple correspondence analysis (MCA) was used to assess the relationships between abiotic factors and edible USO biomass per plot. I converted the continuous variables measured, into categorical variables using a range of thresholds in R 3.0.1 Statistical Software®.

I performed a principal component analysis (PCA) to determine the relationships between USO depth and weight and edibility categories. This PCA captures the majority of the variability observed in the data by grouping together variables on the two axes in a combination which explains the most variation. To determine the relationship between the weight, depth and size of USO in relation to their USO type and edibility classes I performed Kruskal-Wallis tests and one way ANOVAs.

Preceding each Kruskal-Wallis test, I determined if the data were distributed normally, followed by a Levene's test for homogeneity of variances and lastly a least significant difference test.

2.4. Results

During the three months of sampling, 83 USO species, comprising 50 genera in 17 families were collected. Iridaceae (35 species, 42%) and Hyacinthaceae (14 species, 17%) were the most common and abundant families (See Appendix A for a full list of species). 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%).

Spatial distribution of species richness varied markedly in the region with some plots containing up to 13 USO species (figure 2.2). Species richness varied between habitats; Renosterveld, Strandveld and Limestone Fynbos had significantly higher species richness than the other vegetation types (see figure 2.4 and table 2.1).

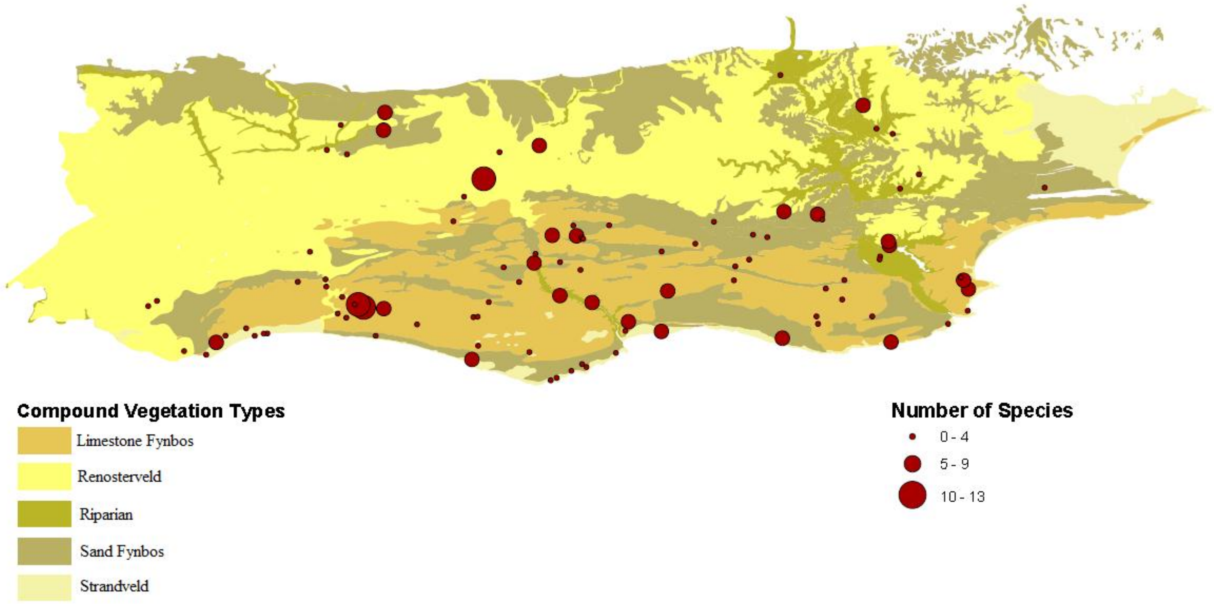

Figure 2.2 The number of USO species encountered in each 25 m^2 plot. The size of the circle is relative to the number of species collected in the plot.

Table 2.1 Average and standard deviation of: species richness, edible biomass, percentage vegetation cover, soil depth, percentage rock cover and pH of soil of different vegetation types. n = is the number of plots sampled for each vegetation type. Superscript letters in a column denote significantly different values at p≤ 0.05 (one way ANOVA, followed by Kruskal-Wallis multiple comparison).

Vegetation type	n	Species Richness	Edible USO Biomass (kg/ha)	Vegetation Cover (%)	Soil Depth (m)	Rock Cover (%)	pH
Dune Cordon	7	2.00±0.87 ^{b}	132.68±139.54 ^{ab}	86.57±8.87 ^{a}	>1.0±0.00 ^{a}	0.00±0.00 ^{b}	7.21±0.82 ^{a}
Limestone Fynbos	18	3.89±0.54 ^{a}	80.77±98.33 ^{ab}	66.00±15.94 ^{bc}	0.54±0.36 ^{c}	17.56±19.45 ^{a}	7.19±0.39 ^{a}
Riparian vegetation	9	2.00±0.77 ^{b}	127.09±139.5 ^{a}	87.56±17.64 ^{a}	>1.0±0.00 ^{a}	9.22±24.73 ^{ab}	6.34±0.94 ^{b}
Renosterveld	25	4.00±0.46 ^{a}	160.51±159.74 ^{a}	68.92±13.95 ^{b}	0.72±0.34 ^{b}	15.40±18.59 ^{a}	5.28±0.73 ^{c}
Sand Fynbos	26	1.85±0.45 ^{b}	52.22±77.67 ^{b}	60.62±15.97 ^{c}	0.87±0.27 ^{a}	6.35±12.66 ^{b}	5.33±0.86 ^{c}
Strandveld	15	3.73±0.60 ^{a}	112.20±145.26 ^{ab}	69.53±11.15 ^{bc}	>1.0±0.00 ^{a}	0.00±0.00 ^{b}	6.46±1.02 ^{b}
p		<0.01	0.14	<0.01	<0.01	<0.01	<0.01
F		3.65	1.69	6.79	7.57	3.41	20.33

○

The edible biomass available over the landscape varied within and among vegetation types (figure 2.3, table 2.1). In all vegetation types, most plots have very low edible biomass; however in Strandveld and Renosterveld a few plots have high biomass.

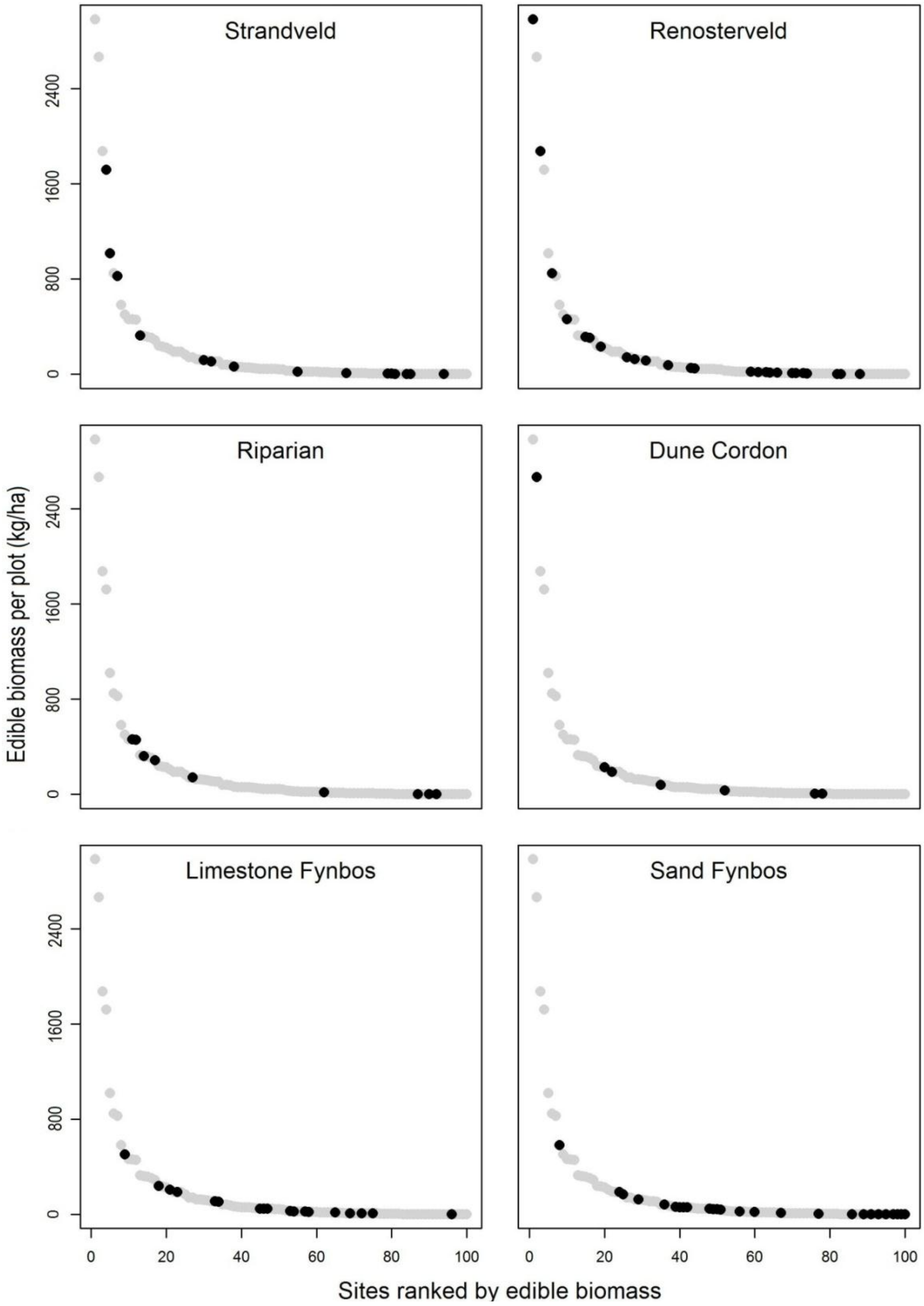

Figure 2.3 Edible biomass of USOs (ranked) in every plot (kg/ha), for different vegetation types. Black dots represent the position of plots in the particular vegetation type and the grey dots are all of the 100 plots.

There is a weak positive, but significant, relationship between USO biomass and species richness for Limestone Fynbos, Renosterveld and Riparian vegetation. The overall relationship however is weak; thus one cannot generalize that higher species richness leads to higher edible biomass. There was no correlation between overall USO biomass and species richness (figure 2.4).

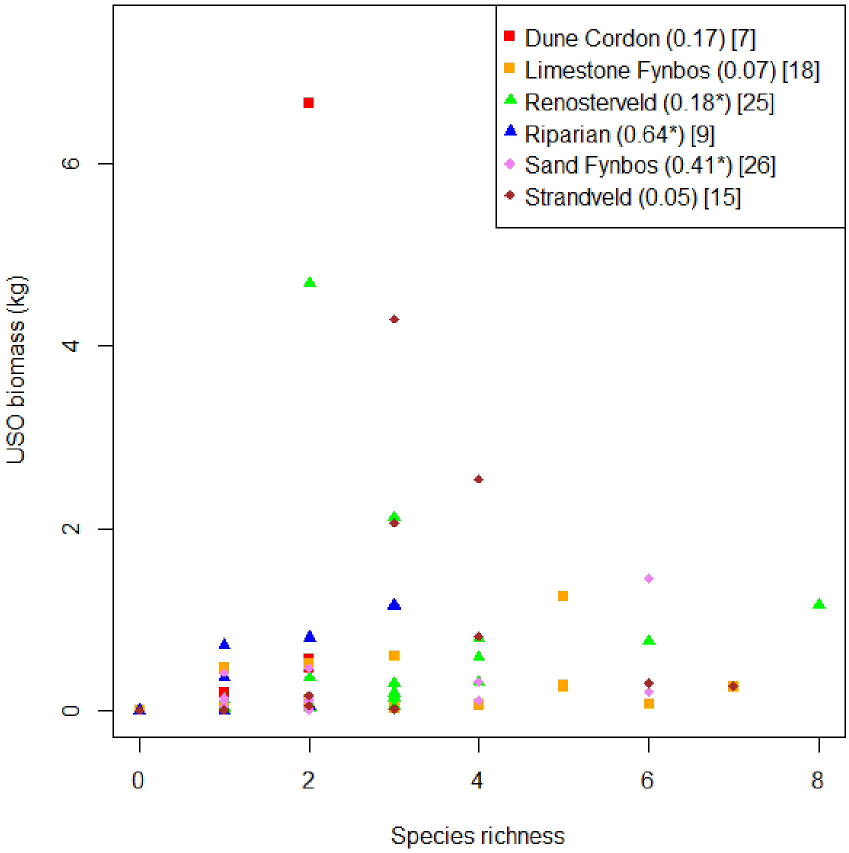

Figure 2.4 Species richness versus biomass of edible species. $r^2 = 0.08$, $p<0.001$. r^2 values are in round brackets, the number of plots sampled for each vegetation type in square brackets.

Considering only the species with the highest biomass, their abundance and distribution is very variable. *Chlorophytum crispum* occurred in only one plot and that biomass was so high that it is still one of the six species with the highest mean edible biomass recorded (figure 2.5, table 2.2). Other species like *Chasmanthe aethiopica* and *Cyphia digitata* occurred widely and still had instances of very high biomass (2663.8kg/ha and 2350.9kg/ha respectively) (figure 2.5, table 2.2).

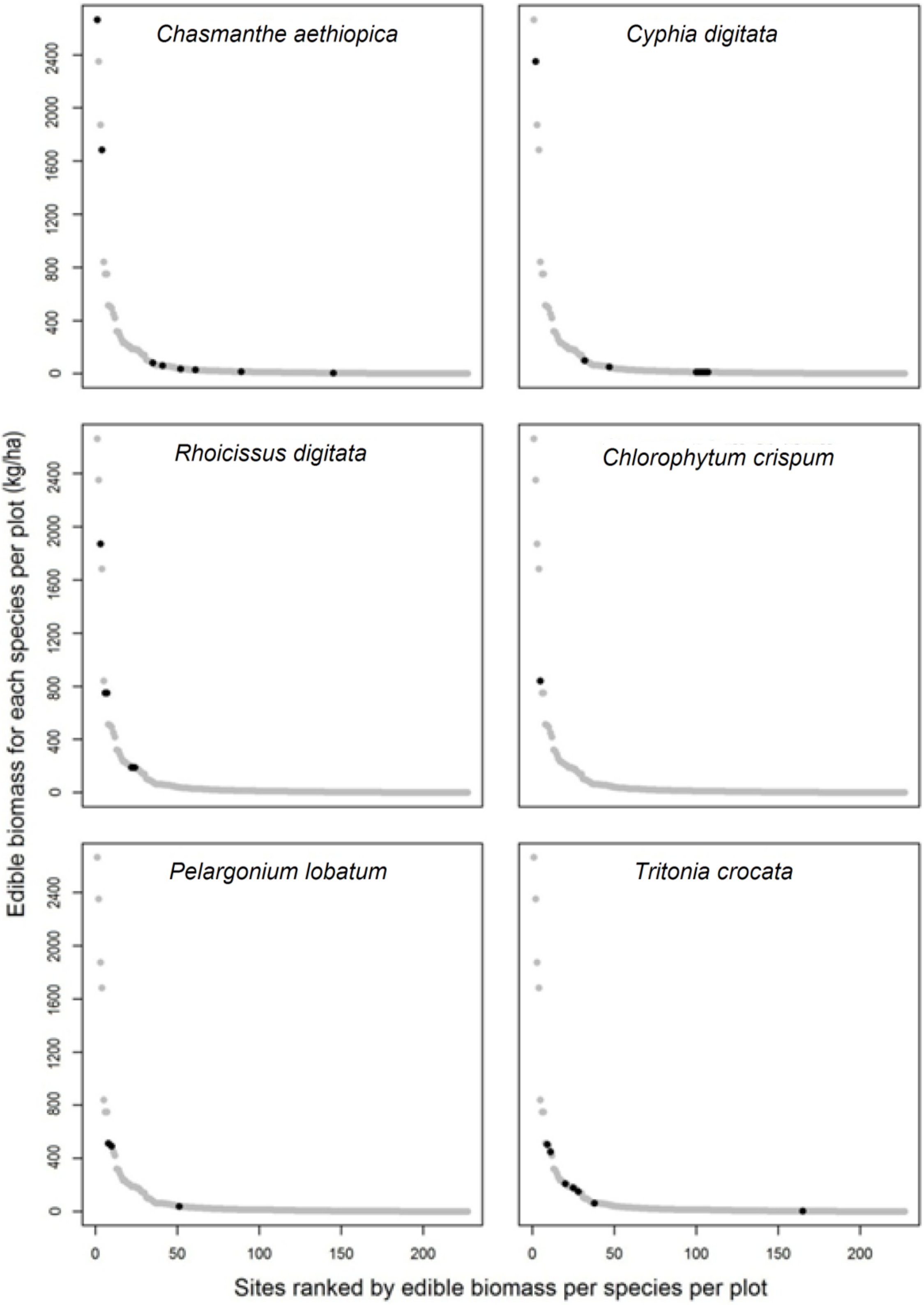

Figure 2.5 The six edible species with the highest biomass in the 100 plots measured. The grey dots are the biomass recordings for all species over all plots, while the black dots are the biomass of the particular species in different plots.

The six species which had the highest biomass in our study compare favourably with other studies which recorded biomass of USO species, if the patches with the highest biomass were to be targeted. Comparisons are hard to draw however, because sampling strategies differ so widely in the literature (table 2.2). Anthropological studies focus sampling on patches of high abundance (gatherer driven), whereas in this study stratified sampling was used in order to extrapolate the data to a larger area. In Youngblood (2004), the foraging was driven by the researcher herself (observer driven), using the same methods as in other anthropological studies.

Table 2.2 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. Round brackets = the number of plots out of a hundred, in which USOs of the particular species were recorded in.

Study	Sampling Strategy	Species	Min-Max (kg/ha)	Average (kg/ha)
This study	Stratified sampling	*Chlorophytum crispum (1)*	0 – 841.0	8.4
		Chasmanthe aethiopica (8)	4.7 – 2663.8	45.7
		Cyphia digitata (11)	12.4 – 2350.9	26.0
		Pelargonium lobatum (3)	39.4 – 512.4	10.4
		Rhoicissus digitata (6)	12.4 – 1873.1	39.3
		Tritonia crocata (7)	3 – 505.6	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 – 59700	21600
Youngblood, 2004	Observer driven	*Cyperus usistatus*	1100 – 18000	7800
		Talinum caffrum	600 – 32500	20000
		Albuca canadensis	1600 – 44000	28000
		Pelargonium sidoides	900 – 102000	60000

There is no clear relationship between biomass and any variables investigated in the multiple correspondence analysis (MCA) (figure 2.6), since no clear separation between the ellipses of biomass categories occurred in the MCA; this would indicate the environmental predictors recorded are not driving the variation observed in biomass. Only Limestone Fynbos and Renosterveld are clearly delimited (far right, third row of figure 2.6), and correspond to the separation of ellipses observed for the geology. This simply indicates that the edaphic environment drives the vegetation type (Principle of Fynbos Ecology (Goldblatt, 1997)). There is a lot of overlap between the other ellipses for vegetation types, suggesting they share similar environmental parameters. In fact, the distinguishing factor is the floral assemblage, which is not captured by the MCA.

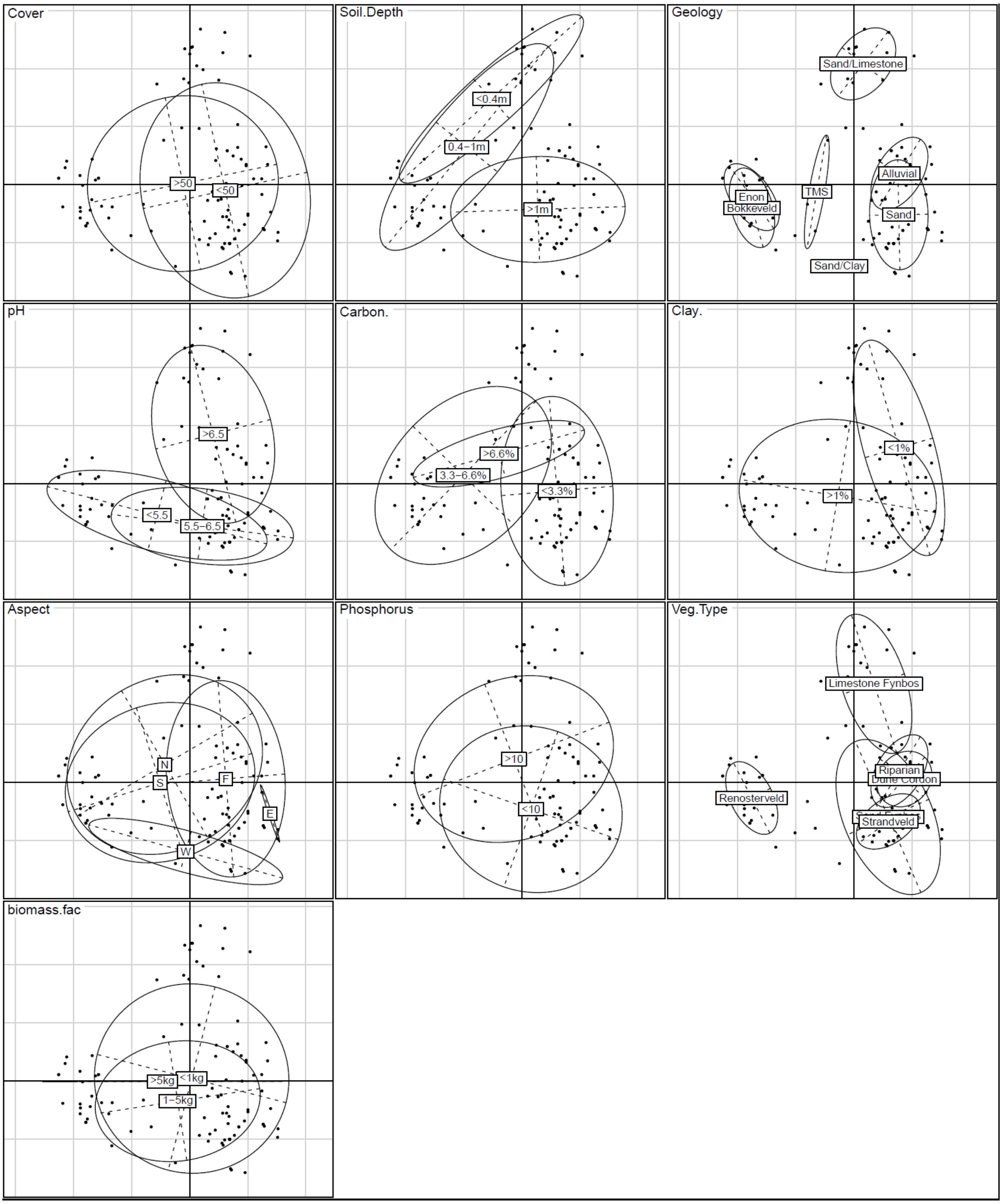

Figure 2.6 Multiple correspondence analysis (MCA) of abiotic variables' relationship to USO biomass. Each matrix represents the distribution of data for the 100 plots recorded for each variable, from top left to right: percentage plant cover, soil depth, geology, pH of soil, carbon content of soil, clay content of soil, aspect, phosphorous content of soil, vegetation type and edible biomass.

USO length and weight are correlated (figure 2.7). Poisonous species tend to have larger and heavier USOs (blue points in figure 2.7, table 2.3), as the points are drawn towards USO length and weight. Poisonous species' USOs also occur significantly shallower in the soil (table 2.3). Thus poisonous species have shallower, bigger and heavier USOs than other species. The few poisonous points which are not drawn toward USO length and weight in figure 2.7 are species mostly belonging to the Iridaceae family, in which a few *Moraea* species are known to be very toxic. Edible species had a wide range of USO weights and depths (red data points). Species for which the palatability was not known were not associated with any variable in particular.

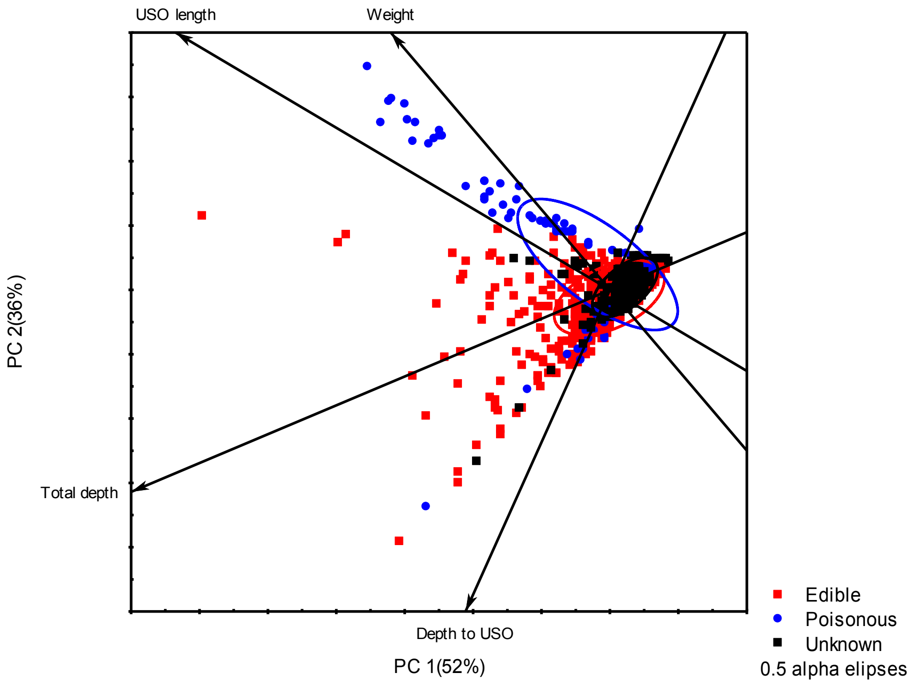

Figure 2.7 Principal Component Analysis of USO length, weight and depth of different edibility classes. The axes capture 88% of variation in the data set.

Two families had significantly higher biomass than all the other families and also differed significantly from one another (Iridaceae and Hyacinthaceae), whereas all the other families did not significantly differ in average biomass, with biomass between 0.4-0.7 kg/ha. Iridaceae had the highest species richness, frequency of encounters and average biomass of any family. One could expect to find 6 kg/ha of Iridaceae USOs in this landscape on average, while some plots had far greater biomass.

Table 2.3 Depth and weight of different USO categories, frequency encountered and average plot biomass of the two most abundant families (means ± standard deviations). Superscript letters in a column denote significantly different values at p≤ 0.05 (one way ANOVA, followed by Kruskal-Wallis multiple comparison). n = the number of plant individuals sampled, except for families, where it denotes the number of plots.

	n	Depth to USO (mm)	Weight (g)
Edible	690	47.81 ± 36.60^{a}	18.98 ± 75.95^{b}
Poisonous	192	27.74 ± 32.16^{b}	247.58 ± 580.79^{a}
Unknown	192	50.45 ± 116.64^{c}	4.29 ± 6.04^{b}
p		<0.01	<0.01
F		9.83	66.57
Bulb	213	23.00 ± 19.21^{c}	226.76 ± 554.83^{a}
Corm	560	50.85 ± 38.29^{ab}	3.11 ± 6.81^{c}
Tuber	159	55.17 ± 129.21^{a}	11.29 ± 14.95^{bc}
Rhizome	142	41.27 ± 28.07^{b}	67.73 ± 157.06^{b}
p		<0.01	<0.01
F		13.74	42.06
Family		Frequency encountered	Average biomass (kg/ha)
Iridaceae	100	279	5.72 ± 4.18^{a}
Hyacinthaceae	100	189	1.83 ± 4.49^{b}
p			<0.001
F			23.144

2.5 Discussion

The southern Cape has very high USO species diversity, with 83 species recorded, and with Limestone Fynbos, Renosterveld and Strandveld being the richest habitats. This is in accordance with the diversity of geophyte species (herbaceous plants with USOs) in the Cape Floristic Region, which is the highest in the world (Procheş et al., 2006, 2005). The question remains: could these USOs have been an important food source for hunter-gatherer people in the region?

2.5.1 How does richness and biomass of edible USOs vary across a vegetationally complex environment?

When the average USO biomass in different vegetation types is considered, Sand Fynbos had lower USO biomass than other vegetation types, while Dune Cordon, Riparian vegetation and Renosterveld had the highest biomass. The high variability in abundance and species composition of USOs causes the variation to be so high that almost no significant difference is observable in the edible biomass of USOs between vegetation types. Thus at first glance, there seems to be very low predictability in the edible biomass of USOs of the southern Cape. This however is not a true presentation of the edible biomass of USOs available to hunter-gatherers. In most foraging theory research, hunter-gatherer foraging is observed and the areas they choose to gather in are the habitat (patches) with the highest biomass (Sato, 2001; Vincent, 1985). These somewhat biased data have been used to extrapolate to the biomass of an area. In this study I applied ecological survey methods to the area, thus obtaining representative data of the biomass which might have been available to hunter-gatherers across the southern Cape region. The aim was to see if spatial occurrence of edible biomass in this very heterogeneous region could be predicted.

When the patches of high biomass encountered are considered, it is clear that certain habitat types are better than others, specifically sites associated with Renosterveld and Strandveld.

The question remains, would more species of USOs lead to higher biomass of USOs in an area? I could find no discernible pattern one way or the other.

2.5.2 How does the biomass of edible USOs compare to other areas of the world where hunter-gatherer communities were/are present?

The average USO biomass we observed in the southern Cape is lower than in Savanna habitats, but higher than in Forest habitats. Our results are, however, hard to compare to anthropological studies, because of widely divergent sampling strategies. When one examines the plots which had the highest biomass (plots that a gatherer might have decided to gather in), it is clear that there is considerable edible USO biomass available to gatherers (from 800 to over 2600kg/ha for certain plots).

The same observation is clear when we consider the six species which had the highest biomass in this study; the maximum biomass observed in some plots was very high, over 2600kg/ha. Assuming that the energy inputs into obtaining these USOs and the nutritional returns from consuming them are similar to sites where hunter-gatherers still occur (the focus of Chapter 3), the southern Cape would certainly have supported human foragers. The biomass represented in this area is within the range of biomass values reported for other areas where hunter-gatherer communities still persist (Hladik et al., 1984; Sato, 2001; Vincent, 1985).

2.5.3 Can edible biomass of USOs using abiotic variables be predicted?

Of all of the variables measured, none had a clear significant correlation to USO biomass. This might be because the factors determining USO species abundance are so complex and drivers differ for every single vegetation unit, of which there are 74 (Vlok and De Villiers, 2007). USO biomass is not evenly distributed within or between vegetation types. For the majority of sites within each vegetation type, the biomass is low.

There are, however, hotspots with high biomass and gatherers would have focused on these. The predictability of finding these hotspots seems low, if the variables we measured are considered. This would influence the amount of energy that would have to be invested by gatherers to find such hotspots.

2.5.4 Are edible USOs overrepresented among particular taxa, USO growth forms (corms, bulbs, rhizomes and tubers) or depth of the storage organ?

The respective vegetation types have specific communities of plant species, of which USOs comprise a big part. The USO species composition will inevitably have a large effect on not only the inputs required to get USOs out of the soil, but also the nutritional returns. This is why I investigated the attributes which make the different taxa more or less attractive or rewarding to any prospective gatherers.

The USO species are representative of 17 different families. This is an appropriate level of classification to compare the USO species, as the attributes which influence their accessibility (average depth below ground, average size of USO) and edibility can be more easily examined. Some families are known to have toxic compounds in them. These compounds (secondary metabolites such as alkaloids) are usually a survival mechanism to deter herbivory and therefore to protect the USO (Van Wyk and Gericke, 2000; Van Wyk et al., 2002; Watt and Breyer-Brandwijk, 1932). Such families include Amarylidaceae, Hyacinthaceae and Colchicaceae, and are well known to be responsible for significant stock loss annually (Van Wyk and Gericke, 2000; Van Wyk et al., 2002; Watt and Breyer-Brandwijk, 1932). A few species in the Iridaceae are also toxic and contain secondary metabolites in lethal concentrations, especially in the genus *Moraea* (Norwood Young and Fox, 1982). This however does not describe Iridaceae. Many edible species in this family have been documented through archaeological and ethnobotanical evidence (*Watsonia, Gladiolus, Ferraria, Freesia, Babiana*) (Deacon, 1993; Texier et al., 2010). Out of the 83 USO species found, only 15 are known to be poisonous (Appendix A). Poisonous species, and species which possess bulbs, had significantly shallower and heavier USOs, this could be due to the fact that these species are protected against herbivory and do not need to grow deep to protect their USOs. Iridaceae comprised the majority weight of all the USO biomass recorded (even with poisonous biomass included) and had significantly higher average weight in all plots in comparison to all the other families. All Iridaceae possess corms, which are high in carbohydrate content and low in fibre content (Dominy et al., 2008; Orthen, 2001). Dominy et al. (2008) indicate that the fracture strength of bulbs and corms are the lowest (this is due to the low fibre content) and this means they could have been easily masticated and digested by hominins. Corms had the lowest average USO weight, and tubers and corms occurred deep in the soil. One has to now consider how the spatial abundance of these species could influence their suitability as a food source for humans.

Even though corms were small on average, they grew in great abundance and had a significantly higher biomass than the other USO types. In contrast, tubers had a significantly lower biomass than any other USO type. This indicates that the majority of edible USO biomass is of high quality and could provide a vast amount of energy (the focus of the next chapter).

2.6 Conclusion

All of these factors considered, it seems that the average edible biomass of the southern Cape region is very variable, but high in selected areas. It has been observed that behaviour of coastal hunter-gatherer communities is atypical in comparison with inland communities (Perlman, 1980). This is due to the sporadic nature of terrestrial resources, and predictable aquatic resources. Some cognitive ability is needed to develop an understanding of the heterogeneous environment to predict which areas could have the highest biomass of high quality food, accompanied by a good botanical knowledge of what is edible. The hypothesis that a vegetationally complex environment would have been a selective pressure on cognitive ability has been postulated by different authors (Deacon, 1993; Parkington et al., 2009). This hurdle of navigating in a vegetationally complex environment could have possibly been overcome by Pleistocene people who could have enjoyed a diet rich in fatty acids, essential for brain development and evolution (Marean, 2010b; Mathias et al., 2012; Parkington, 2010). The high edible biomass of carbohydrates in Strandveld and Dune Cordon could be pared with the high abundance of sessile protein in shellfish, within walking distance of these vegetation types. What remains to be seen is exactly what inputs these peoples could have endured when foraging for southern Cape USOs and exactly what nutritional returns they could have received – this is the subject of the next chapter.

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3. Costs of harvesting, nutritional value and energetic return rate of underground storage organs in the southern Cape, South Africa

3.1 Abstract

The quantification of foraging for underground storage organs (USOs) of different hunter-gatherer communities has been studied across the world, where such people still maintain their way of life. Using similar methods, the cost of harvesting USOs, their nutritional content and energetic return rate can be quantified for areas were hunter-gatherer people have gone extinct. The characteristics of the USO resources in the southern Cape have not been quantified, despite the extensive ethnobotanical, historical and archaeological record of hunter-gatherer communities' dependency on USOs. The aim of this study was to establish a baseline data set on the foraging by humans of the USO resources of the southern Cape by observing the time it takes to harvest six target test species, in three different vegetation types, in two different seasons. The nutritional returns and energetic return rates of the species were also quantified. We found that the time it takes to obtain the USOs of our test species is shorter than in other studies, but that the weight obtained is proportionally lower than in other studies. The calories contained within these test species differed greatly, with cormous species yielding very high caloric contents. Different simulated foraging events yielded very different return rates: species, vegetation type and seasonality all influenced the yield. Many of the simulated foraging events could have satisfied an adult's estimated daily caloric requirements in well under five hours of activity, and if the optimum combination of scenarios is pursued (species, vegetation type, season), these requirements could be satisfied within an hour. The simulated foraging events with the highest return rates compare well with the literature of return rates from other systems. Thus the six test species have sufficient return rates to support a hunter-gatherer community, similar to those seen in extant hunter-gatherer societies. If all edible species in each vegetation type were included in such a study, the returns would likely be even higher.

Keywords: hunter-gatherer, caloric content, USO weight, handling time

3.2 Introduction

Recent archaeological and genetic research suggests the southern Cape coast of South Africa as a locality where modern humans persisted during late Pleistocene glacials, when most of Africa was colder and drier (Brown et al., 2012; Marean, 2010a). The southern Cape forms part of the Cape Floristic Region (CFR), home to the highest diversity of geophyte species (herbaceous plants which possess underground storage organs) in the world (Procheş et al., 2005). Geophytes comprise 2098 species or 17% of the total plant diversity in the CFR (Procheş et al., 2005, 2006). Research on hunter-gatherer communities indicates widespread dependency on underground storage organs (USOs) as the staple source of carbohydrate (Deacon, 1993; Hurtado and Hill, 1989b; Lee, 1973, 1968; Parkington, 2010, 1977; Vincent, 1985; Wrangham et al., 2009).

In the late Pleistocene it is likely that the Cape south Coast was inhabited and foraged by people similar in stature and habit to the Khoe-San people (Pfeiffer and Sealy, 2006). The knowledge regarding hundreds of USO species that are palatable or even edible has been lost, as the native Khoe-San peoples' way of life is extinct in many parts of South Africa, and Khoe-San descendants are almost entirely dependent on cereal-based carbohydrates (Henn et al., 2011; Lee, 1973). Ethnobotanical research on people of the area reveal that less than five USO species are still known as edible by local community members with the greatest botanical knowledge (De Vynck et al., 2013). The effort related to collecting USOs has therefore not been determined for this environment; neither has the nutritional returns one could expect to receive when consuming these USOs. Since no subsistence hunter-gatherer people remain in the study area (Henn et al., 2011), I observed local woman of Khoe-San origin, simulating foraging for test species of USOs. Experimental tests like these are considered a valid proxy for post-dicting prehistoric behaviour or hypothetical gathering behaviour (Peters et al., 1984; Smith et al., 1983).

In order to establish a baseline, simulated data on the foraging of the USO resources in the study area, I focused on specific USO species (in order to ensure a short learning curve for the field assistants to optimally seek and find a specific species) in three vegetation types and two different foraging seasons. The resultant data could then be used to compare nutritional return rates recorded in the literature on extant gatherer communities, with the caveat that the simulated approach and the low number of target species are likely to underestimate returns, especially given the high diversity of edible USOs in the study area. My main objective was to: a) determine nutritional return rates and assess the effects of species, vegetation type and season on them, and b) assess the extent to which simulated foraging events fulfilled human nutritional requirements. I determined the effort (time) required to obtain certain edible USOs, the nutritional returns of these USOs and the energetic return rates of different foraging attempts.

The southern Cape is located in a transitional zone between winter and summer rainfall regions. While rain falls in winter, there is also some summer rain (Schulze, 1965), unlike much of the CFR, which experiences cold wet winters (Nicholson, 2000). This influences plant phenology and therefore visibility of potential food items (Deacon, 1984). Seasonality also influences the nutritional value of USOs, which declines when new growth and flowers use stored carbohydrates and other nutrients in the USO (Johnson, 1993; Ruiters and McKenzie, 1994). Autumn (especially March and April) is the driest time of the year and is predicted to be the most challenging time to procure nourishment from the resources that would have been available to hunter-gatherers. There are however a few species of USOs which flower during these driest times of the year; such species separate their vegetative growth (leaving time) and reproductive growth (flowers) (Johnson, 1993). This is crucial since USOs have been considered fall-back foods, and are potentially available when favoured items are not due to seasonality (Wrangham et al., 2009).

I hypothesise that in autumn, because the above ground parts of some USOs are not visible, the opportunity for harvesting an abundance of USOs would be lower, and that due to dry soil, the inputs to obtain these USOs should also be higher. Based on previous research of USO type properties (Dominy et al., 2008; Orthen, 2001), I predict that corms should have higher nutritional return than any other USO type.

Furthermore, I predict that owing to the high abundance and biomass of USOs in the study area (Chapter 2), there would be a positive net return of energy for hunter-gatherer foraging for USOs in the southern Cape, and hunter-gatherers could have met the daily requirement of diet in part by harvesting USOs of the southern Cape.

3.3 Methods

3.3.1 Study area and study species

The study was conducted in the southern Cape coastal lowlands of the Western Cape, South Africa (figure 1.1). The area is exceptionally diverse in many aspects. Mucina and Rutherford (2006) describe 14 vegetation types in the area while Vlok and de Villiers (2007) describe 71 terrestrial vegetation units within four different biomes. USOs are abundant and/or species rich in 33 of the 71 vegetation units (Vlok and De Villiers, 2007). From this exceptional diversity I selected three vegetation types which are the most widespread in the southern Cape coastal lowlands, namely Renosterveld, Limestone Fynbos and Strandveld (see row 1 of figure 3.1 below).

Renosterveld occurs on relatively fertile, clay-rich soils derived from shale and mudstone (Mucina and Rutherford, 2006). Renosterveld 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 of Renosterveld, which has a high grassy element and between 50 – 70% plant cover (Mucina and Rutherford, 2006). Fynbos, the most widespread vegetation of the CFR, is – like Renosterveld – a fire-prone evergreen shrubland. Fynbos is associated with nutrient-poor, sandy soils. (Mucina and Rutherford, 2006). Limestone Fynbos grows on shallow, alkaline sands derived from late Cenozoic limestones. Strandveld is a mosaic of subtropical thicket bush clumps and Fynbos elements associated with ancient (late Cenozoic) dune sands (Mucina and Rutherford, 2006). While Restionaceae (*Thamnochortus* spp.) are common, species richness of Proteaceae and Ericaceae is low (Mucina and Rutherford, 2006). Owing to the low flammability of the thicket, and low cover of other shrubs, Strandveld is less prone to fire than surrounding pure Fynbos vegetation types (Mucina and Rutherford, 2006).

Each vegetation type has its own species composition and suite of edible USO species (Chapter 2). Focal species were selected on the basis of a few crucial factors: ethnobotanical research of edible USO species in the region conducted by De Vynck (in prep.) (see table 3.1) helped advise which species to include based on their edibility and abundance in the study area. Owing to high beta diversity, no one species occurred in all vegetation types. *Cyphia digitata, Watsonia meriana* and *Cyanella lutea* were sampled in Renosterveld, situated in Werner Frehse Nature Reserve (-34.119923ºE, 21.25013ºN). Limestone Fynbos species *C. digitata, P. lobatum, C. lutea, F. crispa* and *C. aethiopica* were sampled in Pauline Bohnen Nature Reserve (-34.360903ºE, 21.4302ºN), while the Strandveld species, *Chasmanthe aethiopica* and *Ferraria crispa* were sampled in Gouritzmond Nature Reserve (-34.350611ºE, 21.875795ºN) and Skulpiesbaai Nature Reserve (-34.389735ºE, 21.4199ºN).

Figure 3.1
Row 1: a) Limestone Fynbos b) Strandveld vegetation c) Renosterveld vegetation.
Row 2: a) Field assistant (novice gatherer) searching for USOs in a Renosterveld patch, recorded as searching time. b) When an individual of one of the test species is found, it is dug out and the time it takes is recorded: digging time. c) The result is a cleaned tuber of *Cyphia digitata* ready to be weighed: total handling time.
Row 3: a) *Ferraria crispa* exhibiting vegetative reproduction, which often resulted in the search and/or digging time of such specimens to be 0. b) USO of *Watsonia meriana*, after the extensive corm sheath had been removed. c) *Chasmanthe aethiopica* (sword-shaped leaves) growing in high abundance in a patch of Strandveld, most of the plants are clones.

Table 3.1 List of test species and their attributes. These attributes differ between vegetation types or different micro-climates. * = The months within which green or dried leaves are visible to a gatherer.

Species	Family	USO type	Flowering Period	Apparency above ground*
Chasmanthe aethiopica	Iridaceae	Corm	April – July	April – Feb
Cyanella lutea	Tecophilaeaceae	Corm	Sept – Oct	June – Jan
Cyphia digitata	Campunulaceae	Tuber	July – Nov	July – Dec/All year
Ferraria crispa	Iridaceae	Corm	July – Oct	March – Feb
Pelargonium lobatum	Geraniaceae	Rhizome	Aug – Nov	June – Dec
Watsonia meriana	Iridaceae	Corm	July – Oct	All year

3.3.2 Foraging effort

I compiled a quick guide of my test species, which I gave to local women employed as novice gatherers, to study before I measured the handling time of gathering the selected test species over two seasons and within the three vegetation types. The time it took to find a particular specimen of one of the test species (search time), and how long it took to dig out the USO of that specimen (digging time) was recorded. The total time to obtain the USO of a specimen is the handling time (sum of the search time and digging time). The field assistant (novice gatherer) used a digging stick, with a traditional digging stone, as the only tool to aid gathering (see figure 3.1). This method of harvesting USOs is a prominent feature of cave paintings in southern Africa (Lewis-Williams, 1987). The digging stone is an archaeological find (found in the Stillbay area), supplied to me by Jan de Vynck. I made the digging stick from a branch of a wild olive tree (which was slightly thinner than the hole in the digging stone) and shaped the tip like a chisel and hardened it in a fire. The digging stone weighed 1.84kg, while the digging stick was 111.2cm long and weighed 0.41kg. I assumed that the effort to excavate USOs would be comparable to prehistoric people living in this landscape, as this technology existed during the late Pleistocene (Parkington and Poggenpoel, 1971).

In each vegetation type, the field assistant started searching for one of the test species (search time was recorded), from a predetermined point in the field (which the field assistant picked). Once located, the time taken to excavate the USO of the specimen was recorded (digging time). The USO was immediately cleaned, weighed and numbered. If another specimen of that species was spotted in proximity to the excavated specimen it was also harvested. For such specimens the search time was 0, and the digging time was measured. If more than one plant was dug out in the same event, the digging time was shared for those two plants. When analyzing the data, the plants which shared search time or digging time were grouped together. Thus the sample size is often indicative not of how many plants were excavated, but how many search times or digging times there were.

3.3.3 Nutritional returns

The USOs that had been removed were stored in paper bags and transported to Stellenbosch University for analysis at the Department of Animal Sciences and Microchem laboratory (Cape Town) where the moisture, ash, protein, carbohydrate, fat and fibre content were determined according to analytical procedures 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). In other studies on USO nutritional content (Eder, 1978; Hurtado and Hill, 1990; Vincent, 1985; Youngblood, 2004), carbohydrate content is determined by quantifying the net weight of all the other substances that make up the weight of the test matter and subtracting that from the total weight of the USO (Murray et al., 2001). However, this method is not appropriate for determining the carbohydrate content of plants. Thus we used the amyloglucosidase/α-amylase method (996.11, AOAC) (Megazyme, 2011).

I converted the percentage content of the nutritional content data by the values used in Vincent, (1985), so caloric results would be comparable: Carbohydrates have a value of 4.03 calories per 100g of USO, protein 2.78 cal/100g, and fat 8.37 cal/100g. Following Murray et al. (2001) and Vincent (1985), fibre content was not included in the caloric returns of USOs. Based on current analyses of hunter-gatherer communities and theoretical studies of prehistoric people, it is reasonable to assume that a diet of 1900-2000 calories is sufficient to support hunter-gatherer people of small stature and high physical activity (Hurtado and Hill, 1989b; Lee, 1968; Speth and Spielmann, 1983). I used this 2000 calorie threshold (hereafter Estimated Daily Caloric Requirement: EDCR) as the baseline caloric intake necessary to sustain hunter-gatherer people in the southern Cape.

3.3.4 Data Analysis

Owing to the fact that gathering sites in different vegetation types and seasons included a highly uneven representation of the focal species, it was not possible to model the effects of these two variables comprehensively for each combination of vegetation type and season. When I refer to a group, I am referring to the experimental unit, where search time and digging time was shared for different plants harvested and therefore treated as a unit. When I refer to a simulated foraging event, I refer to the cumulative gathering time and calories for sequential harvesting of specimens belonging to one species.

I used Kruskal-Wallis one-way ANOVA to test for significant differences in the search, digging, handling time and weight of the six species. The respective data sets fulfilled a Levene’s test for homogeneity of variance. I used Least Significant Difference (LSD) tests as a post hoc test to compare the significant differences among the means.

The experimental design precluded the possibility of testing the effects of seasonality and season on species' nutritional content. I tested the means by a LSD test for different species to determine if they differed significantly. These results should be interpreted as a gross under-representation of every vegetation types' ability to provide sufficient nutrition for hunter-gatherers, as many more species are edible in each of the vegetation types.

To compare the return rates of foraging for different species in different vegetation types in different seasons, I combined the nutritional values of each foraging scenario (species, in certain vegetation types and season) to the equivalent weight which was collected, and divided that by the amount of time it took to obtain that weight of USO. The same equation was applied to the subsequent USO specimens collected during the same simulated foraging event, and the cumulative calories gained per time unit for simulated foraging events resulted in slopes. In this way every simulated foraging event was modelled using a linear regression. The resulting slope was then used to extrapolate the linear regressions of the calories gained per time unit to reach the Estimated Daily Caloric Requirement (EDCR) of 2000 calories in this way the different species in different environments were compared.

3.4 Results

The handling time for all target species was very low (2.4 – 10.6 minutes). Although there was an overall significant difference in handling time among all species – driven largely by differences in digging time, overall species were remarkably similar. *Cyphia digitata* and *Watsonia meriana* had a significantly higher handling time than almost all the other species.

Table 3.2 Search time, digging time and handling time of test species. n = number of groups per species. Superscript letters in a column denote significantly different values at p≤ 0.05 (one way ANOVA, followed by Kruskal-Wallis multiple comparison).

Test Species	Growth form	n	Search time (min)	Digging time (min)	Handling time (min)
Chasmanthe aethiopica	Corm	19	3.0±3.8^{b}	0.6± 0.2^{a}	3.6±3.8^{ac}
Cyanella lutea	Corm	12	1.3±1.4^{ab}	1.4±0.9^{a}	2.7±1.7^{a}
Cyphia digitata	Tuber	37	3.0±4.2^{b}	7.6±6.4^{c}	10.6±7.9^{bc}
Ferraria crispa	Corm	30	1.2±1.2^{a}	1.3±1.1^{a}	2.4±1.7^{a}
Pelargonium lobatum	Rhizome	17	1.5± 2.0^{ab}	0.9±0.7^{a}	2.4±2.1^{a}
Watsonia meriana	Corm	9	2.5±3.8^{ab}	4.8±4.4^{b}	7.3±4.7^{c}
p			0.08	0.01	0.01

F	1.79	15.54	13.17

In general, species which possessed corms had the lowest weight (2.4 – 18.3g) (table 3.3), although not enough species were sampled to compare USO types. *Cyphia digitata* and *Pelargonium lobatum* had the highest weight; the other species were not significantly different from one another. Per species the return rates (kg/hour) one could harvest from every species are not high. These values are for each species in every vegetation type and for both seasons (excluding *Cyanella lutea*, which is only visible in spring).

Table 3.3 Weight and weight collected of different USO species per hour, n = number of groups sampled per species. Superscript letters in a column denote significantly different values at p≤ 0.05 (one way ANOVA, followed by Kruskal-Wallis multiple comparison).

Test species	USO type	n	Average weight of USO	Kg/h
Chasmanthe aethiopica	Corm	19	9.3±5.9 ^{a}	0.2±0.1 ^{ab}
Cyanella lutea	Corm	12	2.4±1.1 ^{a}	0.1±0.0 ^{c}
Cyphia digitata	Tuber	37	58.6±31.1 ^{c}	0.3±0.2 ^{b}
Ferraria crispa	Corm	30	15.9±16.1 ^{a}	0.4±0.6 ^{b}
Pelargonium lobatum	Rhizome	17	31.1±23.6 ^{b}	0.8±0.7 ^{a}
Watsonia meriana	Corm	9	18.3±4.4 ^{ab}	0.2±0.1 ^{b}
p			<0.01	<0.01
F			24.73	10.74

The proximal analysis of the nutrients (table 3.4) contained in different USO species, and the resulting caloric content, was interesting. *Chasmanthe aethiopica* had the highest caloric content (228 calories in hundred grams) whereas *Cyphia digitata* had the lowest caloric content. Due to the low replicates of nutrient analysis, tests for significant differences are pointless. The information serves as a comparison between proximal analyses in the literature, where calories/100g was observed of similar or lower values.

Table 3.4 Average values of the proximal nutrient analysis of the different USO species, and the caloric content the USOs offer (protein, fibre, ash and fat analyses were done by the Department of Animal Sciences at Stellenbosch University, while the carbohydrate analysis was done by Microchem Lab Services in Cape Town). n = number of replicates tests for each species.

Species	n	% Protein	% Fibre	% Ash	% Fat	% Carbohydrate	Calories/100g
Chasmanthe aethiopica	6	6.37±0.25	3.64±0.32	4.16±0.61	0.85±0.13	50.49±6.16	228.30±26.61
Cyanella lutea	6	4.07±0.27	7.05±1.16	1.81±0.21	0.79±0.24	42.95±1.32	191.02±8.08
Cyphia digitata	15	4.23±1.34	18.46±3.25	6.63±1.24	0.86±0.25	5.40±1.31	40.72±11.09
Ferraria crispa	9	5.49±2.42	9.45±2.44	7.78±1.93	2.24±0.46	38.68±13.13	189.89±63.49
Pelargonium lobatum	6	4.58±0.04	16.09±1.06	11.49±1.30	0.64±0.31	19.74±4.16	97.64±19.47
Watsonia meriana	3	4.01±0.08	2.64±0.03	2.88±0.08	0.56±0.08	38.95±0.90	172.80±1.25

When the energy gained in a simulated foraging event was considered (harvesting one species, in one vegetation type, in a season), the resulting calories gained from time invested is very variable depending on the species, vegetation type and season. Some foraging alternatives could give a gatherer high energy returns (reaching up to 1686.2 calories in 21.3 minutes for *Ferraria crispa* in Strandveld, in spring), whereas other simulated foraging events yielded poor returns (177.9 calories in 121.4 minutes for *Cyphia digitata*, in Renosterveld, in autumn). However, these slopes are difficult to interpret making it challenging to distinguish the effects of vegetation type and seasonality on gathering return rates.

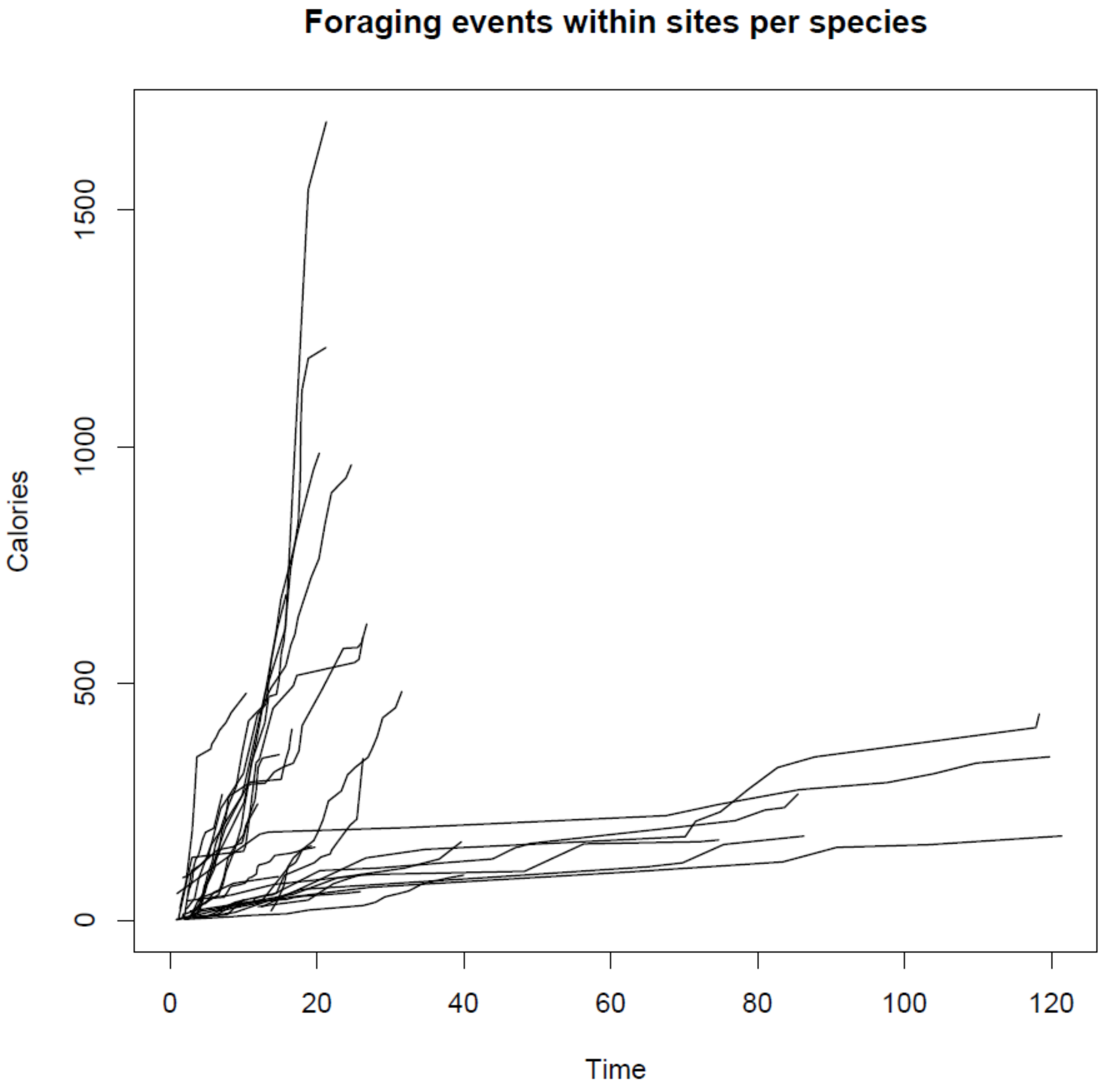

Figure 3.2 Gained calories for time invested in foraging for each simulated foraging event (per species, per vegetation types, per season).

In order to better compare different foraging scenarios (different species, vegetation type and season) from figure 3.2, we performed a linear regression of each simulated foraging event. The resulting slope was used to calculate the time it would take to reach the EDCR (table 3.5). We can see that many simulated foraging events would satisfy one adult's caloric requirements under four hours. *Cyphia digitata* and *Cyanella lutea* were the only two species which had EDCR longer than five hours.

Per species, it appears that a hunter-gatherer dietary requirement could be obtained for most species within two hours, excluding *Cyphia digitata* and *Cyanella lutea*, which could take up to 21.2 hours and 17.6 hours respectively.

Table 3.5 The time it would take to reach the daily dietary requirement of 2000 calories (EDCR) (if each simulated foraging event, which consisted of more than eight specimens harvested, was continued to this threshold amount of calories). Out of these 26 simulated foraging events, 16 had an EDCR lower than five hours (highlighted). n = number plants collected during simulated foraging event.

n	Test species	Vegetation type	Season	EDCR	Time (min)	Calories	r^2
15	*Chasmanthe aethiopica*	Strandveld	Spring	0.6	10.4	479.4	0.84
12	*Ferraria crispa*	Strandveld	Spring	0.6	21.3	1686.2	0.76
23	*Chasmanthe aethiopica*	Strandveld	Spring	0.8	21.2	1209.3	0.73
14	*Pelargonium lobatum*	Limestone Fynbos	Spring	0.8	20.3	986	0.9
11	*Ferraria crispa*	Strandveld	Spring	0.9	15.8	688	0.93
24	*Watsonia meriana*	Renosterveld	Spring	0.9	24.7	961.7	0.96
12	*Ferraria crispa*	Limestone Fynbos	Autumn	1	7.1	265.6	0.9
16	*Pelargonium lobatum*	Limestone Fynbos	Spring	1.4	26.2	596.5	0.85
22	*Chasmanthe aethiopica*	Limestone Fynbos	Spring	1.5	16.6	403.4	0.88
16	*Pelargonium lobatum*	Limestone Fynbos	Autumn	1.5	14.9	349.7	0.85
20	*Watsonia meriana*	Renosterveld	Spring	1.5	26.8	625.5	0.97
9	*Ferraria crispa*	Limestone Fynbos	Spring	1.9	11.9	245.7	0.83
19	*Watsonia meriana*	Renosterveld	Spring	2.8	31.6	482.9	0.71
27	*Cyanella lutea*	Limestone Fynbos	Spring	3.9	19.7	154	0.97
19	*Ferraria crispa*	Limestone Fynbos	Spring	4.4	26.3	341.5	0.79
11	*Pelargonium lobatum*	Limestone Fynbos	Autumn	4.9	19.2	156.9	0.84
18	*Cyanella lutea*	Renosterveld	Spring	8.7	10.6	43.5	0.96
8	*Cyphia digitata*	Limestone Fynbos	Autumn	8.9	39.7	165.6	0.96
12	*Cyphia digitata*	Limestone Fynbos	Autumn	9.6	118.3	435.6	0.92
11	*Cyphia digitata*	Limestone Fynbos	Spring	10.6	119.7	345.1	0.22

13	*Cyphia digitata*	Renosterveld	Spring	11	85.5	266.4	0.94
14	*Cyanella lutea*	Limestone Fynbos	Spring	12.8	25.9	60.2	0.91
8	*Cyphia digitata*	Renosterveld	Autumn	13.6	74.7	169.5	0.88
8	*Cyphia digitata*	Renosterveld	Autumn	16.9	86.3	177.7	0.94
13	*Cyanella lutea*	Renosterveld	Spring	17.6	40	95.1	0.83
8	*Cyphia digitata*	Renosterveld	Autumn	21.2	121.4	177.9	0.91

I focused on the highlighted simulated foraging events from table 3.5 (simulated foraging events which have an EDCR lower than five hours), and compared them to the calories gained per unit time in different studies conducted on extant hunter-gatherer communities gathering underground storage organs. It is clear that all of these simulated foraging events fall within the range of caloric returns which are observed in hunter-gatherer communities.

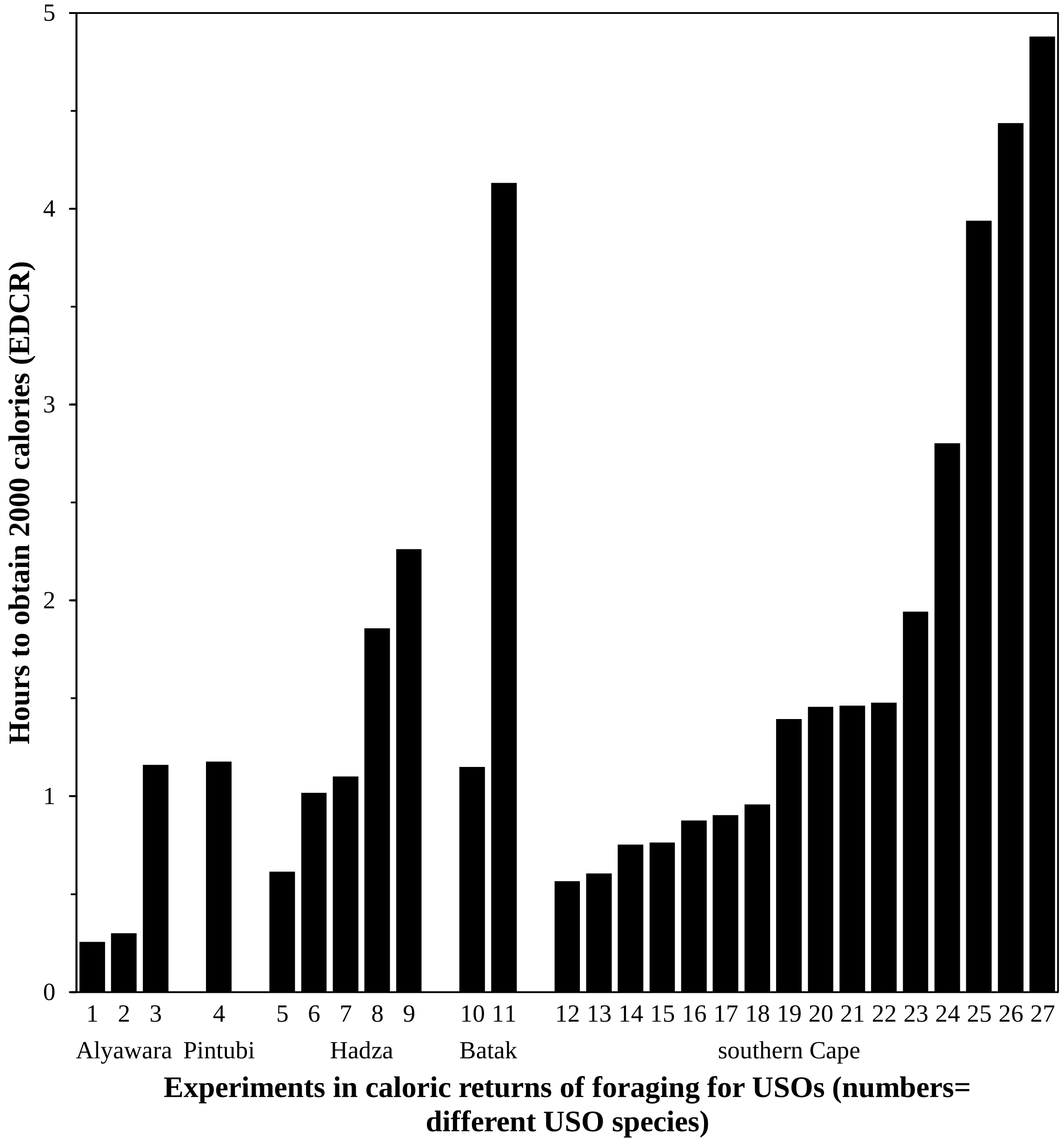

Figure 3.3 Histogram of caloric returns observed during simulated foraging events for different USO species across the world, and the caloric return for the simulated foraging event of this study which would take under 5 hours to satisfy one hunter-gatherer adult. From left to right, the Alyawara gathering different tuberous species, 1 – 3 (Wright, 1994 from O'Connel and Hawkes, 1981: 123 – 125), the Pintubi gathering a tuberous species, 4 (Wright, 1994 from Cane, 1989: 105 – 110), the Hadza gathering different tuberous species, 5 – 9 (Vincent, 1985: 135), the Batak gathering different yam species, 10 – 11 (Eder, 1978; 62) and finally, simulated foraging events for different USO species observed in the southern Cape during this study, 12 – 27. (unit = hours to obtain 2000 calories).

All six test species of this study give a high energy return for foraging. One adult could satisfy their energetic needs within less than two hours if the optimum species is pursued. If the optimum combinations of edible species are included in a diet and the habitats gathered within (in which different edible species occur in different densities), it is possible to yield even higher returns than reported in these results.

3.5 Discussion

Food that is consumed by humans has to cover the basal metabolic rate, metabolic response to food, energy cost of physical activities and accretion of new tissue during growth and pregnancy (FAO, 2003). It is reasonable to estimate that a diet of 1900 – 2000 calories is sufficient to support hunter-gatherer people of small stature and high physical activity (Hurtado and Hill, 1989b; Lee, 1968; Speth and Spielmann, 1983).

This excludes the protein necessary for a balanced diet and normal metabolic functioning (Hurtado and Hill, 1989b; Lee, 1968). The main objective of this thesis is to determine whether USOs comprised a nutritious component of the overall diet, and could have helped sustain hunter-gatherer communities of the Pleistocene in the southern Cape. This study suggests they could have.

With palaeo-anthropological studies on human foraging, simulated experimental work is often the only route to take in order to shed some light on foraging behaviour of prehistoric humans (Grayson and Cannon, 1999; Peters et al., 1984). Humans consume only the highest quality plant and animal food in their environment, never mind if these sources are less accessible or require energy to make them edible (Kaplan et al., 2000). From the six edible species' return rates studied here, it is clear that their potential as food sources differ in many respects. If all the 53 edible species found in Chapter 2 were included, a more accurate picture of the USO resources available to hunter-gatherers could have been assessed.

The first important consideration of foraging in a certain area is the energetic inputs required to obtain USOs. The inputs to harvest different USOs differed, but were in general magnitudes lower than found in other studies, where handling time is usually 5 – 15 times longer (Eder, 1978; Sato, 2001; Vincent, 1985). Comparisons of inputs required to harvest USOs with other studies are difficult however, because many women dig at the same time for each USO, and the search time in other studies only indicates the time it takes to find a specimen within a patch of high abundance of a test species.

The weight one can obtain per hour for different species is low in general (0.1 – 0.8kg/h) in comparison to other studies (1.7 – 4.7kg/h). This is largely due to the bigger USO sizes of test species in other studies (Eder, 1978; Hurtado and Hill, 1987; Vincent, 1985), where one USO can weigh up to 3kg. However these tuber or rhizomes are often fibre and water dense, which of course would lower their net return rates. We report fibre content lower than 10% (2.6% – 9.5%) for cormous species.

Fibre is often associated with a low-quality diet (Milton, 1999). Humans exhibit an impaired ability to digest fibre, due to their small cecum which is important for the fermentation of fibre (Carmody and Wrangham, 2009; Lambert, 1998). The fracture strength of fibre dense USOs is higher, which follows that mastication of fibre dense USOs is more cumbersome (Dominy et al., 2008). Furthermore the human gut has a finite capacity for food; filling it up with useless material would hinder one from consuming and digesting carbohydrate dense plant foods (Milton, 1999, 2000a). Fibre was unlikely to have been an attractive prospect for hunter-gatherer communities, who were fighting to survive, and likely seeking the highest return rates of energy for any food resource they decided to pursue and consume. *Cyphia digitata*, although the largest species (weighing 58.6g on average), is high in water and fibre content (70% water, 18.5% fibre). It offers relatively low net returns for gathering (40.7 calories/100g).

From my results, *Cyphia digitata* and *Perlargonium lobatum* have high fibre content (18.5%, 16.1% respectively). However, unlike *C. digitata*, *P. lobatum* had medium levels of carbohydrates (19.7%). Due to the ease of digging out these rhizomes and their relatively large size, they give very high net returns to a gatherer, higher even than the energy laden, virtually fibreless, small cormous species (*P. lobatum* = 748ca/h, cormous species = 101 – 728ca/h).

The time and effort to make a USO edible (processing) has not been taken into account in this study. All species but *P. lobatum* require limited processing according to ethnographical data. *P. lobatum* requires a lot of processing to render it palatable. This is not uncommon as nonsomatic digestion (making food more digestible before ingestion) is a characteristic of human behaviour (Carmody and Wrangham, 2009; Milton, 2000b, 1999; Wrangham and Carmody, 2010) and could have had a great influence on the digestibility of such rhizomes. Corms, in contrast, are housed in neat corm sheaths, which are easily pried apart to present a clean, energy laden, low fibre parcel that may be eaten raw (see figure 3.1, row 3). Such corm and bulb sheaths are often found in various archaeological sites in southern Africa and are the most common USO remains found in archaeological sites. Iridaceae are specifically mentioned as very important to hunter-gatherers by Deacon (1993) and Parkington (Deacon, 1993; Parkington, 2010, 1977).

Plant use changes with seasonality (Tanaka, 1976); this is due to many factors, but the archaeological evidence suggests that the apparency of USO species plays a big role (Deacon, 1984). Deacon and Parkington both argue that the emergence or apparency of Iridaceae species was augmentable by using fire (Deacon, 1993; Parkington, 1977; Parkington et al., 2009). USOs above ground parts are more obvious after a veldfire (Deacon, 1984). In other words, no matter when the leafing or flowering period of a plant is, the above ground parts which assist humans in finding the specimen, could be adjusted with the use of fire, which stimulates plants to emerge. This is an important fact when one considers that Iridaceae species have a short emergence time during spring, and if one can control when they emerge the time span they can support you through the year widens. Such characteristics of taxa could improve their ability to support hunter-gatherer communities even further.

When I considered the calories gained per simulated foraging event, great differences between the simulated foraging events were evident. If each different alternative of foraging (different species, vegetation types and seasons) is considered, it is possible that if the optimum species, and vegetation type were pursued, a hunter-gatherer's dietary requirements could be filled within an hour. If we compare the EDCR of each simulated foraging event to other studies, we see that the EDCR of 16 simulated foraging events fall within the bounds of EDCRs found in other studies based on the foraging behaviour of existing hunter-gatherer communities (Eder, 1978; Hurtado and Hill, 1990, 1987; Lee, 1969; Sato, 2001; Vincent, 1985). The different sampling strategies in these studies once again mean that comparisons are hard to make (other studies only gather in high abundance patches, with more than one gatherer digging, and most studies consider the processing time, although it is marginal in the studies chosen for comparison in this study).

3.6 Conclusion

A hunter-gatherer diet in the southern Cape may have included many species, if all the edible species observed in Chapter 2 were analysed, although the carbohydrate needs of most hunter-gatherer societies are met with only a few plant species (Hurtado et al., 1985; Lee, 1973; Milton, 2000b). Cormous species are noted in the historic literature as one of the most important parts of the San diet (Bleek and Lloyd, 1911; Van Vuuren, 2013). I believe species with corms would have been ranked highest in preference when available, despite the smaller size of their USOs. It has even been suggested that in southern Africa the available food sources in the Pleistocene might have comprised of smaller package size (Deacon and Lancaster, 1988; Pfeiffer and Sealy, 2006).

Rhizomes and tubers could have been fall-back foods, which would have been harvested during the driest, food-scarce time of the year, namely autumn. During this time very few of the 53 edible USO species would be visible. Both rhizomes and tubers collected as test species in this study are in fact visible in the driest autumn months, when many possibly higher ranked Iridaceae are not available, although augmentation of the emergence of Iridaceae is possible by fire.

Although the issue of diet breadth remains up for debate, there can be no doubt that the southern Cape could have met a number of hunter-gatherer people’s dietary needs, as the USO return rate of harvesting is similar to that of extant hunter-gatherer populations. If we consider that only six species were measured in this instance, and that in any habitat the EDCR would have been delivered within an hour or two of foraging, the net return would have been significantly higher if all edible species were included in such a study.

These results could be considered a baseline for future research. The number of test species I included and the number of replicates of nutritional analyses should be broadened to provide a more comprehensive view of foraging in the southern Cape.

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4. USOs in the context of hunter-gatherer diets in the southern Cape (Synthesis).

"These findings are sufficient to broadly model prehistoric plant use in an area where direct ethnographic observation of foraging groups is not available" (Youngblood, 2004).

This statement was made about results similar to this study, based on experimental determination of the USO biomass and nutritional content of four USO species. However, despite the preliminary evidence presented in this thesis, there is still a wide gap in the information needed to understand ancient hunter-gatherer diets, to model prehistoric plant use and therefore to understand the Paleoscape at the time our lineage likely came into being. The data presented in this thesis does not describe all of the variables which might influence the availability of USOs in the southern Cape as a food source for humans. In an attempt to further understand the Pleistocene diet of hunter-gatherer people and to integrate the findings presented in this thesis, I look to the principals of optimal foraging theory.

According to foraging theory, foragers will behave so as to maximize the net rate of return (of energy or nutrients) per unit of foraging time (Grayson and Cannon, 1999; Smith et al., 1983). Major decision categories of optimal foraging theory include: diet breadth (which and how many resource types to harvest), patch choice (which habitats are best for foraging and returns), time (energy) allocation (time spent foraging in different habitats or patches), foraging-group size and settlement location (Smith et al., 1983).

4.1 Foraging theory

Diet breadth

When a hunter-gatherer (in this case a gatherer) encounters a potential item of food, they have one of two options: to handle it (dig it out) or to search for another item of food (Hawkes and O'Connell, 1992; Smith et al., 1983). Due to the different attributes of each edible USO species, "prey type" (species) can be ranked by the nutritional returns and the predictability of the energy necessary to obtain USOs (Hawkes and O'Connell, 1992; Smith et al., 1983).

The breadth of species available to include in a gatherer's diet would influence many aspects of the foraging activity. This is especially relevant when there are so many edible species, as described in Chapter 2. These species represent a range of USO types (corms, bulbs, rhizomes and tubers); the nutritional returns are highly variable and are distributed patchily across many different habitats over the landscape (Deacon, 1984; Parkington, 2010).

To rank the importance of a species in the diet of a gatherer, it is important to know not how commonly it will occur in a gatherer's diet, but only whether it will be taken when encountered; thus a rare, highly ranked species might appear unimportant, because it seldom occurs in the diet. This phenomenon would be seen for species which have a narrow apparency, but are still a coveted food item. If I could draw an example from everyday life (of non-vegetarians) to explain my point: we would rather eat a tender fillet steak than a piece of bread. Fillet would be a higher ranked food source, even though the opportunity to eat a fillet does not present itself often and most of the time our staple is bread (bread would be a low ranked food source). Similar to my example, low- ranked species might be abundant and could be a staple due to the fact that the encounter rates are high (like *Cyphia digitata* and *Pelargonium* species which are apparent in autumn, when few cormous species are visible). Such low-ranked species seem to have lower energetic return rates due to their poorer nutritional content. The nutritional returns of each species have bearing on the ranking thereof in the diet breadth (Smith et al., 1983), because a more nutritious, tastier option will also be ranked higher within the diet breadth. However, humans are adapted for nonsomatic digestion (Milton, 1999), often by cooking (Carmody and Wrangham, 2009; Lambert, 1998); this could have greatly improved the nutritional absorption of species, such as those belonging to the genus *Pelargonium*. Furthermore, if more prey items (in this case, USO species) are added to the diet, the search time is less because the chance of encountering one of the species is higher (Smith et al., 1983). This adds another incentive for foragers to include an array of USO species in their diet.

Diet breadth is therefore clearly a very complex aspect of foraging to predict. This is confounded by the fact that there are no experienced gatherers to discern which of the edible USO species would have a high net return of energy or what their rank might be within diet breadth. To determine the rank of USO species within diet breadth, I would have had to conduct similar research as presented in Chapter 3 on a wider range of species to capture the potential of each species as a prey item in order to obtain their rank within the potential breadth of a palaeo-diet. This is an impossible task, as sampling is destructive and time consuming; beyond the scope of this study. This type of intense study sometimes results in “misplaced specificity” (Grayson and Cannon, 1999), and leads to weak description of diet breadth. Simms and Steven (1987) suggested that one should rather categorise species according to ordinal level return-rate estimates. In this study it seems appropriate to rank the species according to the vegetation type within which they occur, their growth habits, growth form and phenology.

What is, however, clear from my two data chapters is the importance of cormous species belonging to the family Iridaceae. This is backed up by evidence from the ethnographic, historical and archaeological records (Bleek and Lloyd, 1911; Deacon, 1984, 1993, Norwood Young and Fox, 1982; Parkington, 1977; Van Vuuren, 2013; Van Wyk and Gericke, 2000).

Parkington (1977) suggests an interesting pattern of gathering for hunter-gatherers due to the growth habits which Iridaceae exhibit in different vegetation types. He suggests that due to the fact that genera like *Chasmanthe* and *Watsonia* grow in high abundance, are virtually evergreen and occur in micro habitats in rocky environments (found in Mountain Fynbos and Renosterveld), that they would have been common in the palaeo-diet and perhaps served as a staple. While species from *Gladiolus* and *Moraea* grow in other vegetation types in lower abundance, their appearance could have been augmented with fire, and thus be gathered in other times (Parkington, 1977). Using fire-stick farming (Deacon, 2001, 1993), Iridaceae could have comprised all the carbohydrate requirements of hunter-gatherers.

Due to all of these lines of evidence I would rank the USO species we encountered in the southern Cape in the following order based on their USO type:

Iridaceae ranked highest. Species which grow in high abundance might have been a staple, while other species frequency in the diet would be determined by seasonality/fire-stick farming. USO species which possess tubers and rhizomes might still have been important in the diet as a fallback food during autumn and due to their lower nutrient content and higher processing time might have been lower ranked. Bulbous species have high water content and could have served as thirst quenchers, (*Albuca canadensis* = 77% water (Youngblood, 2004)), but due to the lack of starch would not have been a true contributing factor to a palaeolithic diet.

Patch choice

When a forager is faced with a heterogeneous environment like the southern Cape, knowledge of the area and the species (resources) it contains is essential. "The optimal solution is to add patch types to the itinerary until total foraging time (within-patch as well as between patches) per unit harvest is minimized" (Smith et al., 1983).

It was clear that resources harvested from Renosterveld had longer handling times, due to the hard, clayey soil, despite high USO abundance. In hard soils, geophytes which grow deep in the soil and which are sparsely distributed, would have the highest inputs (regardless of their nutritional returns), although some species like *Watsonia meriana*, which are very specific in their growth habits, grow in hard soils but in high abundance and have very high returns due to the low search time, low digging time and high nutritional returns.

Another important consideration in patch choice are the protein resources available in it: supplement protein from territorial antelope that were caught in the patches of high abundance of *Watsonia* spp. has been observed in Later Stone Age archaeological sites (Deacon, 1993; Klein, 1981). Of course, coastal vegetation, which did offer very high net returns for foraging in this study, would have the protein rich, shellfish sources approximate to it (Parkington, 2010). It is logical that if one patch could satisfy all the dietary needs of a community for a while, most of the needed resources would be taken from this area to minimize inputs required to meet the dietary requirements. Such patches, with the unique juxtaposition of a rich variety of resources would have made a balanced diet easy to maintain.

The biomass of USOs observed can provide an indication of the carrying capacity of a habitat, and could therefore indicate how long a patch could sustain a hunter-gatherer community of a determined size. Thus even if the biomass is lower than in other studies, it would only reflect that humans would have had to move camp when the biomass resources close to it were exhausted. This pattern of moving to richer carbohydrate sources of USOs is not uncommon in extant hunter-gatherers. For example, the Cuiwa of Venezuela will move closer to abundant patches of rhizomes during the dry season, as soon as they have exhausted nearby patches (Hurtado and Hill, 1987). Once they learnt to locate resource-rich patches, great rewards of easily accessible, carbohydrate rich USO biomass awaited them.

It must also be mentioned that besides the importance of USOs there are many other desirable source of carbohydrates in the study area. There are numerous above ground fruits, nuts and berries, which are all specific to certain habitat types. The importance of fruits and nuts has been highlighted in a few hunter-gatherer studies, were almost half of the dietary needs of !Kung San are met by one nut-species (Lee, 1973). These sources of calories would have made the time it took to reach the daily caloric requirements of individuals even lower.

It is clear from the results in Chapter 2 and 3 that the southern Cape is a very heterogeneous environment with abundant resources in some areas, but a virtual dietary desert in others (in respects to USOs). Due to this variability it seems that patch choice might have been an important factor in accomplishing high efficiency gathering of USOs. Did hunter-gatherer people focus on a few species with high habitat predictability or high nutritional return, thus focusing patch choice on these habitats? Or did they rather gather generally through all the habitat types and opportunistically harvest any edible species they came across? These questions relating to specific scenarios of patch choice that could have been exhibited in the southern Cape are hard to answer based on empirical evidence and experiment methods presented in this thesis.

4.2 Carbohydrates and cognition

The development of modern human behaviour is attributed to various factors, and evidence suggests that humans in the late Pleistocene had high levels of cognitive ability (Lombard, 2012). Some authors even describe them as exhibiting modern behaviour (McCall and Thomas, 2012). The importance of protein in the diet cannot be underestimated in this respect. Poly-unsaturated fatty acids (PUFA) are crucial for brain development (Carmody and Wrangham, 2009; Speth and Spielmann, 1983; Tanaka et al., 2009). PUFA can almost exclusively be obtained from non-lean, animal protein. Shellfish would have been an excellent source of PUFA and is readily available in large quantities on the southern Cape Coast (Marean, 2010b; Parkington, 2010). This resource is not influenced by the seasonality of the terrestrial environment, and thus would have been immune to the emaciation that terrestrial protein resources would have suffered during the dry season. Evidence of exploitation of shellfish is very well documented in the southern Cape, up to the late Pleistocene (Deacon, 1993; Klein, 1974; Marean, 2010b; Parkington, 2010; Parkington et al., 2009)

However important protein might be, it seems that we have evolved to consume both protein and carbohydrates (Milton, 1999). This is illustrated best by the starvation observed in hunter-gatherer communities which depend on lean meat in the dry season, when no plant foods are available (Speth and Spielmann, 1983). The specific dynamic action of carbohydrates is the lowest of any macro-nutrient, while the protein sparing abilities (indication of a food’s ability to spare protein for it’s true purpose of tissue building and not an energy source) are the highest (Speth and Spielmann, 1983). In short, this means that with carbohydrates included in a diet, there is more energy available for vital organs and brain development, and more protein available for normal growth and healing. Most human organs, specifically the brain, require glucose (Speth and Spielmann, 1983). Glucose rich carbohydrates would have been vitally important for brain development of early hominids (Milton, 2000).

Enhanced cognitive ability could have been a great advantage when foraging in an environment that has resources distributed unevenly, where a big component of successful foraging in the southern Cape could have been decision making ability. Due to the seemingly low predictability of USO biomass, ambiguous decisions based on very little information (comparison process) would have to be made, with decision outcomes based on chance. Means, variances and need levels are important for human foraging decision-making under uncertainty or ambiguity, and the importance of experience cannot be overstated (Rode et al., 1999). The learning curve observed in human foraging is evident in many studies, where a forager's foraging productivity and efficiency is maximized in midlife (Gurven and Hill, 2009; Kaplan et al., 2000). This important aspect of gathering was not considered in this thesis due to the constraints caused by simulating gathering, as opposed to observing the gathering of experience gatherers.

The methods of harvesting might also have been improved by cognitive ability and made gathering far more efficient. Due to the fact that traditional gathering practices do not occur in the study area any longer, prehistoric foraging was simulated by the use of a reproduced, weighted digging stick. It is commonly accepted that digging stones were used during gathering activity by women as depicted in rock art (Lewis-Williams, 1987; Ouzman, 1997) and in a few ethnographic studies (Bleek and Lloyd, 1911; Dunn, 1879; Sparrman and Forster, 1785). However, the use of the digging stone might vary between differing habitats and soil conditions (Mazel and Parkington, 1981). Knowledge of where the use of a weighted digging stick might have been most profitable is, seemingly, lost. The experienced gatherer probably knew exactly where it would be profitable to use a weighted digging stick and where it would not be favourable. In the future this aspect of gathering will also be investigated, by experimental studies of the mechanical properties of gathering USOs with a weighted digging stick.

4.3 Thesis Context

From the results of this thesis it is safe to deduce that USOs would invariably have played an important role in the diet of hunter-gatherer people during the late Pleistocene, where rich shellfish resources would have likely been utilised in conjunction with USO use. The exact dimensions of such a diet breadth are almost impossible to gauge and further research is required. It is clear that the contemporary USO resources in the southern Cape would have been sufficient to support an undetermined group size of hunter-gatherer people. Where before the importance of different taxa within a palaeo-diet were hypothesised, we can now say with a degree of certainty that some taxa are important and could have had a high rank within the diet breadth.

While these results shed light on the characteristics of USO resources in the area, it is by no means a comprehensive view of foraging in the southern Cape. To formulate a foraging model much more detailed data are needed on the energetics of harvesting, where the exact caloric cost of harvesting is calculated and all variables of foraging are considered. For instance, I did not test processing time, group size, or camp location. Traditionally such models are based on data collected from observing experienced foragers harvesting a certain resource. This approach is not possible in the southern Cape, and the challenges associated with this research problem are highlighted by this thesis. This is evidenced by the fact that I had to employ botanical methods to determine biomass abundance and distribution over the landscape. In other studies, anthropological methods of observing foragers have been employed; this means that comparisons to the anthropological literature are cumbersome and have to be approached with care.

Furthermore the effort of harvesting I report on in this thesis is a very limited view of the gathering inputs of the area, and could be a great under- or over-estimate. Food sharing (kin ship) (Kaplan et al., 2000) would need to be considered and in future studies larger gathering groups will need to be used, more species ranked in categories, more patches sampled and processing time also calculated to be able to develop a more accurate foraging model for the southern Cape. The biomass of USOs in other areas where the archaeological record is rich has also not been described. Areas to the east of the current study site, and the West Coast, will be studied in future research. Specific taxa which exhibit characteristics which make them attractive to a human gatherer, will also be investigated further. Such characteristics include: vegetative reproduction, corm/bulb sheaths, USO depth below ground, phenology and starch content of USOs.

My hope is that this future research will help us to understand the USO resources available over the wide range of rainfall regimes that occur across the Cape Floristic Region, as well as an understanding of the specific characteristics of these USO species, where possible co-evolution between hominins and such USO species could have occurred.

4.4 References

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Appendix A: Species observed during data collection of Chapter 2

Species	Growth form	Family	Edibility	Frequency encountered
Albuca flaccidum	Bulb	Hyacinthaceae	Edible	12
Albuca fragrans	Bulb	Hyacinthaceae	Edible	5
Albuca maxima	Bulb	Hyacinthaceae	Edible	7
Androcymbium eucomoides	Corm	Colchicaceae	Poisonous	4
Babiana patula	Corm	Iridaceae	Edible	13
Babiana ringens	Corm	Iridaceae	Edible	1
Babiana tubulosa	Corm	Iridaceae	Edible	4
Bonatea speciousa	Tuber	Orchidaceae	Unknown	1
Brunsvigia orientalis	Bulb	Amaryllidaceae	Poisonous	2
Bulbinella caudafelis	Rhizome	Asphodelaceae	Unknown	2
Chasmanthe aethiopica	Corm	Iridaceae	Edible	8
Chlorophytum crispum	Rhizome	Anthericaceae	Edible	1
Chlorophytum undulatum	Rhizome	Anthericaceae	Edible	3
Crossyne guttata	Bulb	Amaryllidaceae	Poisonous	1
Cyanella lutea	Corm	Tecophilaeaceae	Edible	11
Cyperus esculentus	Corm	Cyperaceae	Edible	1
Cyphia digitata	Tuber	Campulaceae	Edible	11
Cyphia phyteuma	Tuber	Campulaceae	Edible	1
Dipcadi viride	Bulb	Hyacinthaceae	Poisonous	2
Drimia fosteri	Bulb	Hyacinthaceae	Poisonous	7
Empodium gloriosum	Corm	Hypoxidaceae	Unknown	3
Eriospermum cordiforme	Tuber	Convallariaceae	Poisonous	1
Eriospermum lancifolium	Tuber	Convallariaceae	Poisonous	2
Eriospermum pubescens	Tuber	Convallariaceae	Poisonous	2
Ferraria crispa	Corm	Iridaceae	Edible	2
Freesia alba	Corm	Iridaceae	Edible	6
Freesia caryophyllacea	Corm	Iridaceae	Edible	1
Freesia leichtlinii	Corm	Iridaceae	Edible	7
Geissorhiza aspera	Corm	Iridaceae	Edible	2
Gladiolus cunonius	Corm	Iridaceae	Edible	13
Gladiolus floribundus	Corm	Iridaceae	Edible	5

Gladiolus involutus	Corm	Iridaceae	Edible	1
Gladiolus rogersii	Corm	Iridaceae	Edible	2
Gladiolus sp 1	Corm	Iridaceae	Edible	1
Gladiolus stellatus	Corm	Iridaceae	Edible	3
Haemanthus coccineus	Bulb	Amaryllidaceae	Poisonous	3
Hesperantha juncea	Corm	Iridaceae	Edible	8
Holothrix burchellii	Tuber	Orchidaceae	Unknown	2
Holothrix mundii	Tuber	Orchidaceae	Unknown	2
Ixia flexuosa	Corm	Iridaceae	Edible	3
Ixia micandra	Corm	Iridaceae	Edible	8
Lachenalia bulbifera	Bulb	Hyacinthaceae	Unknown	2
Lachenalia pustulata	Bulb	Hyacinthaceae	Unknown	6
Lachenalia rubida	Bulb	Hyacinthaceae	Unknown	1
Lachenalia sp 2	Bulb	Hyacinthaceae	Unknown	1
Lachenalia sp 4	Bulb	Hyacinthaceae	Unknown	1
Lapeirousia pyramidalis	Corm	Iridaceae	Poisonous	1
Ledebouria revoluta	Bulb	Hyacinthaceae	Poisonous	1
Ledebouria valifolia	Bulb	Hyacinthaceae	Poisonous	2
Massonia echinata	Bulb	Hyacinthaceae	Unknown	3
Moraea flaccida	Corm	Iridaceae	Poisonous	3
Moraea fugax	Corm	Iridaceae	Edible	3
Moraea inconspicua	Corm	Iridaceae	Unknown	1
Moraea pollyanthos	Corm	Iridaceae	Poisonous	8
Moraea setifolia	Corm	Iridaceae	Edible	1
Moraea tripetala	Corm	Iridaceae	Unknown	5
Oxalis obtusa	Corm	Oxalidaceae	Edible	1
Oxalis pes-caprae	Corm	Oxalidaceae	Edible	4
Oxalis polyphylla	Corm	Oxalidaceae	Edible	1
Pelargonium lobatum	Rhizome	Geraniaceae	Edible	3
Pelargonium repaceum	Rhizome	Geraniaceae	Edible	1
Pelargonium triste	Rhizome	Geraniaceae	Edible	5
Rhoicissus digitata	Rhizome	Vitaceae	Edible	6
Romulea rosea	Corm	Iridaceae	Edible	2
Satyrium carneum	Tuber	Orchidaceae	Edible	3
Satyrium corrifolium	Tuber	Orchidaceae	Edible	1

Satyrium longicolle	Tuber	Orchidaceae	Edible	2
Satyrium stenopetalum	Tuber	Orchidaceae	Edible	1
Spiloxene flaccida	Corm	Hypoxidaceae	Unknown	1
Trachyandra cilliata	Rhizome	Asphodelaceae	Edible	16
Trachyandra falcata	Rhizome	Asphodelaceae	Edible	1
Trachyandra revoluta	Rhizome	Asphodelaceae	Edible	7
Tritonia crocata	Corm	Iridaceae	Edible	7
Tritonia squalida	Corm	Iridaceae	Edible	7
Tulbaghia alliacea	Bulb	Alliaceae	Unknown	4
Wachendorfia paniculata	Rhizome	Haemodoraceae	Unknown	6
Watsonia alletroides	Corm	Iridaceae	Edible	5
Watsonia coccinea	Corm	Iridaceae	Edible	1
Watsonia fergusoniae	Corm	Iridaceae	Edible	2
Watsonia fourcadei	Corm	Iridaceae	Edible	5
Watsonia laccata	Corm	Iridaceae	Edible	1
Watsonia meriana	Corm	Iridaceae	Edible	1
Wurmbea marginata	Corm	Colchicaceae	Poisonous	1