SEASONAL EFFECTS ON THE FEEDING ECOLOGY AND HABITAT OF *CHERSINA ANGULATA* IN THE SOUTHWESTERN CAPE

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KEYWORDS

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Focal observations
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Reptile
Seed consumption
West Coast National Park

ABSTRACT

Nearly one-third of the world's tortoises live in South Africa, but little is known about their habitat requirements and feeding ecology. *Chersina angulata*, the angulate tortoise, is endemic to southern Africa, with a wide distribution along the western and southern coasts. Because this tortoise occupies a number of different habitat types, it has always been considered a generalist herbivore, although little is known about its diet and other needs. This study evaluates the habitat characteristics and feeding ecology of *C. angulata* at two study sites in the southwestern Cape, the West Coast National Park (WCNP) and Dassen Island (DI). The WCNP is a large conserved area in the Fynbos biome, along the southwestern coast of South Africa, whereas DI is a small offshore island with low floral and faunal diversity, just south of the WCNP. The efficacy of three methods used to study the feeding ecology of herbivores, focal observations, macroscopic faecal analysis and histological analysis of scats, was evaluated.

Plant cover, species diversity, and the variety of growth forms were substantially larger at the WCNP than on DI. In the WCNP, shrubs and grasses were the dominant growth forms but the vegetation also included herbs, succulents, restios, sedges and parasitic plants. A few perennial species such as the grass *Ehrharta villosa*, shrubs such as *Helichrysum niveum*, *Nylandtia spinosa* and *Rhus* spp., and succulents such as *Carpobrotus edulis* and *Ruschia* spp., provided most of the plant cover. DI had a depauperate flora, consisting of succulents and herbs, and ephemeral plants contributed more than perennials did to plant cover throughout the year. The succulents *Mesembryanthemum crystallinum* and *Tetragonia fruticosa* provided most of the cover on DI.

Angulate tortoises are herbivores and 72 diet plants in 32 plant families were identified to the species or genus level. Several diet species, however, could not be identified. In addition to angiosperms, the tortoises' diet included mosses, mushrooms, insects, snails and animal faeces. The most important growth forms in the diet were herbs and grasses. The diet of the WCNP tortoises was more diverse than the diet of DI tortoises, but the number of principal food items in the diet did not differ between the two sites. Over an annual cycle, WCNP tortoises had four principal food plants while DI tortoises had five principal food plants. At both sites, principal food plants changed with the season and few plants remained principal food items in more than one season.

Cynodon dactylon was a principal food item in three of the four seasons in the WCNP, whereas *Trachyandra divaricata* was a principal food plant each season on DI. Most principal food plants were grass or herb species but the sedge *Ficinia nigrescens*, and a succulent that could be identified only to the family level (Aizoaceae), featured strongly in the spring diets of DI and WCNP tortoises, respectively.

The three study methods did not provide the same type or quality of information about the feeding ecology of angulate tortoises. The small size and wary nature of angulate tortoises compromised focal studies because it was often not possible to see what the tortoises ate. This method, however, provided the interesting observation that rabbit faecal pellets contributed nearly 30% to summer and autumn diets on DI when food was scarce. Rabbit faeces may not only provide a source of nutrients but may also supplement the microflora, required to digest cellulose, in the tortoises' guts. Macroscopic evaluation of the tortoises' scats appeared to be an ineffective method to identify diet plants, and the bulk of the scat mass could not be identified. This indicates that angulate tortoises either selected food low in fibrous content or that the digestive system of the tortoises dealt efficiently with tough plant material. The macroscopic method was the only method that highlighted the large contribution of fruits / seeds to the diet of angulate tortoises. Since the tortoises digested many seeds only partially, or not at all, *C. angulata* is potentially an important agent of seed dispersal in the southwestern Cape. The macroscopic study showed that on DI, sand made up 28% of the scat mass in spring, whereas sand never made a substantial contribution to the scat composition of WCNP tortoises. Lithophagy may be an important strategy in a depauperate habitat, such as DI, because the abrasive action of sand may help with the digestion of tough plants, or the sand may provide the tortoises with important minerals that are deficient in their food plants.

The histological analysis of scats provided the most comprehensive diet list for *C. angulata*. Selection indices based on data from the histological analysis indicated that angulate tortoises were highly selective in their food choice. Most of the principal food items were selected out of proportion to their availability and the tortoises avoided the most abundant plants in their habitats. Several factors, such as palatability, accessibility and profitability, may have influenced their food choice. The proportional similarity indices for WCNP and DI tortoises, respectively, were 0.31 and 0.16, confirming that *C. angulata* is a food specialist and not a food generalist as was previously thought. This factor should be considered in the management of this species and in future conservation planning of its habitat.

DECLARATION

I declare that **Seasonal effects on the feeding ecology and habitat of *Chersina angulata* in the southwestern Cape** is my own work, that it has not been submitted for any degree or examination in any other university, and that all the sources I have used or quoted have been indicated and acknowledged by complete references.

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1 GENERAL INTRODUCTION

1.1 TORTOISES OF THE WORLD AND SOUTH AFRICA

Tortoises belong to the class Reptilia, and more specific, to the order Testudines (=Chelonia). Testudines includes not only tortoises, but also terrapins and turtles. The term Testudines is used when ancestral forms are included in the grouping, while Chelonia generally refers to the extant groups (Pough *et al.* 2001). Two suborders are distinguished, the side-necked chelonians, Pleurodira, and the hidden-necked chelonians, Cryptodira (Boycott & Bourquin 2000). The Pleurodira includes three families, the Chelidae, Pelomedusidae and Podocnemidae. The Cryptodira is more diverse and consist of 10 families, which include the family Testudinidae, to which tortoises belong (Ernst & Barbour 1989; Pough *et al.* 2001).

The latest report commissioned by the CITES Nomenclature Committee (Fritz & Havaš 2006) recognises 44 extant tortoise species, but this list excludes the newly described species *Homopus solus* from southern Namibia (Branch 2007). Thirteen tortoise species occur in South Africa, which gives South Africa the largest diversity of tortoise species in the world (Boycott & Bourquin 2000). The thirteen tortoise species in South Africa belong to five different genera and include *Stigmochelys pardalis* (previously known as *Geochelone pardalis*), *Kinixys belliana, Kinixys lobatsiana*, *Kinixys spekii*, *Kinixys natalensis*, *Homopus areolatus, Homopus femoralis*, *Homopus signatus*, *Homopus boulengeri*, *Psammobates geometricus*, *Psammobates oculifer* (previously *P. oculiferus*), *Psammobates tentorius* and *Chersina angulata* (names according to Fritz & Havaš 2006).

1.2 THE DISTRIBUTION AND BIOLOGY OF *CHERSINA ANGULATA*

The angulate tortoise, *Chersina angulata*, is of moderate size, with an elongated shell and convex carapace. The species can be distinguished from other South African tortoises by its large, undivided gular (Branch 1989). The colour pattern of the shell varies substantially but the shields are most often light brown in colour with dark edges and centres (Branch 1989; Boycott & Bourquin 2000). Males are larger than females and are easily identified by their long gulars and plastral concavities (Branch 1989; Mann *et al.* 2006). The gular is used by fighting males to overturn one another, and the plastral concavity aids copulation.

Chersina angulata is endemic to southern Africa and has a wide distribution along the western and southern coasts, from southern Namibia in the northwest to East London in the southeast (Fig. 1.1). Isolated populations are found in the interior and on several offshore islands (Greig & Burdett 1976; Branch 1991; Branch *et al.* 1995). Angulate tortoises occur in variable densities in several different vegetation types such as Fynbos/thicket mosaic, Karroid shrubland, Thicket, Renosterveld, and Succulent Karoo (Greig & Burdett 1976; Branch 1989, Baard 1994; Boycott & Bourquin 2000). The density of angulate tortoises can become particularly high in the southwestern Cape (Van Heezik *et al*. 1994) and in disturbed areas such as the partial clearance of thicket in the Eastern Cape (Branch 1984; Branch 1989).

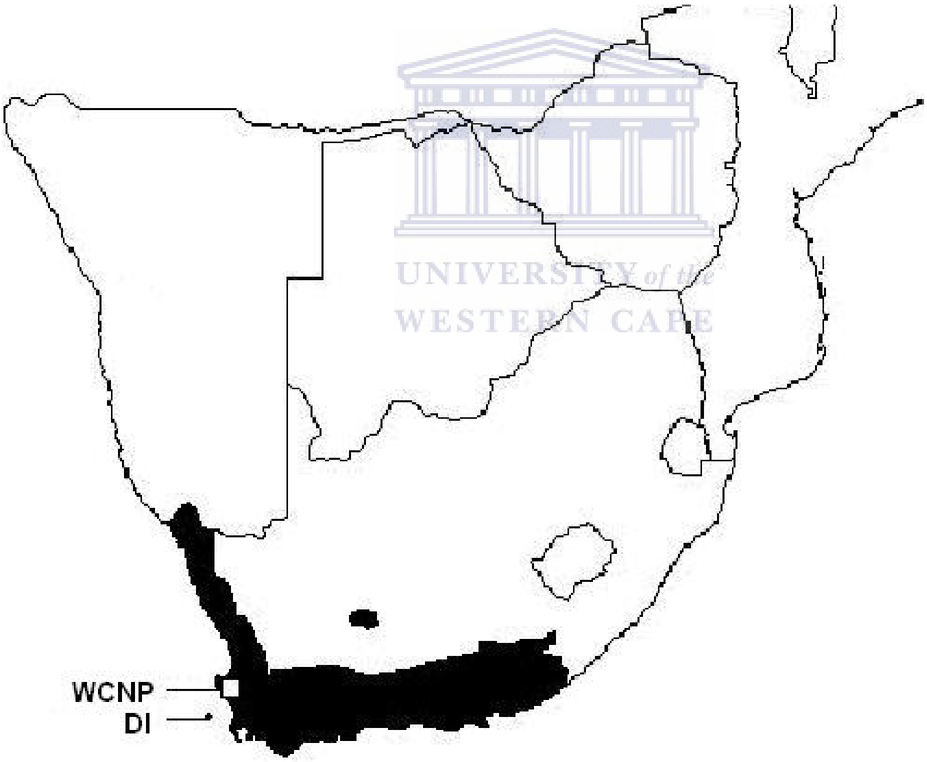

Figure 1.1 The distribution of *Chersina angulata* in southern Africa and the location of the study sites, the West Coast National Park (WCNP) and Dassen Island.

Chersina angulata is a relatively common tortoise and more information exists on its biology than that of any other tortoise species in South Africa. Female angulate tortoises have an unusual reproductive pattern, producing and laying one egg at a time, up to six eggs per year (Hofmeyr 2004). The tortoises are active throughout the year and shift their activity pattern from bimodal in summer to unimodal in winter (Ramsay *et al*. 2001). Their activity pattern is strongly linked to prevailing weather conditions, particularly ambient temperature (Ramsay *et al.* 2001). Angulate tortoises can bask for several hours per day (Keswick *et al*. 2006), and appear to have some physiological control over their heat exchange rates (Perrin & Campbell 1980; Els *et al.* 1988). They spend most of their time in the cover of vegetation, but males appear to be active for longer periods and to spend more time feeding than females do (Keswick *et al*. 2006). Angulate tortoises survive well in captivity (Boycott & Bourquin 2000), but information about this herbivore's natural diet is limited to a list of plants that they eat in Sardinia Downs, Eastern Cape (Els 1989).

Food availability affects fecundity and survivorship (Caughley & Sinclair 1994), so knowledge of the foraging ecology of tortoises is important for their management and conservation. *Chersina angulata* occurs in several conserved areas (Branch 1989) and is not rated nationally or internationally, but is listed as a CITES Appendix II species (Boycott & Bourquin 2000). Nevertheless, habitat destruction over their range, particularly along the coastline and in the fertile valleys of the southwestern Cape, gives reason for concern. Habitat transformation has reduced Strandveld (a vegetation type with high densities of angulate tortoises) to less than 40% of its original area (Knight 1991). Additionally, population densities near urbanised areas have declined dramatically (Branch 1989). The ongoing negative impact of man on the environment makes it essential to better understand the feeding ecology and habitat requirements of angulate tortoises.

1.3 FEEDING ECOLOGY AND METHODOLOGIES

To determine food preferences and the significance of food items on the ecology of angulate tortoises, we need more information than just diet lists (Rall & Fairall 1993), or the quantitative composition of the diet. A better understanding of the feeding ecology of tortoises requires that food intake be considered in relation to food availability (Mason *et al*. 1999), and that seasonal changes in food availability and diet are assessed (Lagarde *et al*. 2003).

The vegetation composition of tortoises' habitats can be determined by several different methods. To estimate the relative availability of plant species in Valley Bushveld for leopard tortoises, Mason *et al*. (1999) used the canopy line-intercept method and identified all plants at 10 mm intervals at ground level. Rall & Fairall (1993) counted all plant species in a 1 m^2 frame quadrat, which they centred over food plants of leopard tortoises and Kalahari tent tortoises, whenever they observed the tortoises feeding. Lagarde *et al*. (2003) spaced 27 frame quadrats (1 m^2) randomly in the habitat of the steppe tortoise to estimate plant cover in their habitat. The size and number of sampling units are important considerations in quadrat sampling, and the choice between a few large sampling units or a large number of small units is determined by the requirements of the study (Greenwood 1996).

Methods used to determine the diets of foraging animals include direct observation of feeding animals, stomach content analysis, scat analysis, and fistula techniques (Stewart 1967; Saunders *et al*. 1980; Holechek *et al.* 1982). Direct observation is generally considered an effective method to record diet composition, but this method is subject to observer error, and is often confounded when the animals eat the whole plant (Smith & Shandruk 1979; McInnis *et al*. 1983). Two intrusive methods include oesophageal fistulation, which requires surgery (McInnis *et al.* 1983), and the analysis of stomach content, which can be accomplished by stomach flushing (Legler 1977) or killing the animal (McInnis *et al*. 1983). Scat analysis is non-intrusive and is the preferred method to study the diet of endangered or secretive animals (McInnis *et al*. 1983). Microhistological identification of plant epidermi in a herbivore's scats provides a detailed list of plants eaten, but this method may overestimate the importance of some diet items, such as grasses, and underestimate the importance of others, such as herbs (Vavra *et al*. 1978; Smith & Shandruk 1979; McInnis *et al*. 1983). Nevertheless, Vavra et al. (1978) found that the ranking of diet species, as determined through faecal analysis and oesophageal fistulation, was similar.

When data exist for availability and consumption of a particular diet item, it is possible to calculate if the animal consumes the food item out of proportion to availability. Plant species consumed in excess of their availability are preferred species, and are species that generally enhance the diet nutritionally (Stuth 1991). Abundant plants are often consumed in similar proportions to their availability, and these plants generally have lower nutritional value than the preferred plants (Stuth 1991). Some plant species are consumed in lower proportions than what are available because the plants may be toxic or unpalatable (Stuth 1991). When animals use food resources in proportion to their availability, the animals are generalist feeders, in contrast to specialist feeders, who are highly selective (Feinsinger *et al.* 1981). Knowledge about the foraging niche breadth of tortoises should facilitate their management and conservation.

1.4 RESEARCH OBJECTIVES AND THESIS ORGANISATION

The ultimate aim of this study was to understand the feeding ecology and habitat requirements of *C. angulata* in the southwestern Cape. To achieve this aim, I asked the following questions:

a) Which plants and other items do angulate tortoises eat?
b) Are all growth forms (e.g., herbs, shrubs and grasses) of equal importance in their diet?
c) Does their diet change with season?
d) Are angulate tortoises generalist or specialist feeders?
e) Which of focal observation, macroscopic-, or histological scat evaluation is the most effective method to elucidate the food requirements of angulate tortoises?
f) How are the habitats of angulate tortoises characterised with respect to plant cover, plant species, and growth forms?
g) Do plant cover and composition change with season?
h) Does habitat quality influence the feeding ecology of angulate tortoises?

To answer these questions, I evaluated vegetation composition and cover of two disparate angulate tortoise habitats over five successive seasons. Over the same periods, I studied the feeding activity of angulate tortoises at these sites through focal observations, and collected tortoise scats for subsequent macroscopic and histological evaluation. The fieldwork was done at the West Coast National Park (WCNP) and Dassen Island (DI), two conserved areas in close proximity, but with substantial differences in size, weather conditions, vegetation composition and plant diversity. The information gained through this study can be used to (a) facilitate conservation and management of angulate tortoises and their habitats, and (b) to broaden understanding of the way tortoises and other herbivores may respond to changes in their natural habitat.

Apart from the general introduction (Chapter 1), the thesis is comprised of six research chapters. Chapter 2 evaluates seasonal changes in plant cover, species diversity and major growth forms at the two study sites, the WCNP and DI. Chapter 3 considers the activity patterns of angulate tortoises at the study sites, and the foraging behaviour and diet of the tortoises. The results of the macroscopic scat analysis are presented and discussed in Chapter 4, while results of the histological evaluation of scats, collected over four seasons, are presented and interpreted in Chapter 5. Data from the previous chapters are combined in Chapter 6 to evaluate the feeding strategies of angulate tortoises and to calculate preference indices. In Chapter 7, the epidermal characters of plants identified at the study sites are presented and the data are used to construct identification keys for 18 monocotyledonous and 63 dicotyledonous plant taxa at the study sites.

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2 HABITAT EVALUATION

A revised version of Chapter 2 was published in the South African Journal of Science.

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2.1 ABSTRACT

Understanding variation in vegetation communities is integral to characterising resource requirements of herbivores over their range. Here I evaluate seasonal environmental effects upon the plant composition of two contrasting angulate tortoise habitats in the southwestern Cape. Plant cover, species diversity and the variety of growth forms were substantially larger at the West Coast National Park (WCNP) than on Dassen Island (DI). Although shrubs and grasses were dominant growth forms at the WCNP, herbs, succulents, restios, sedges and parasitic plants contributed 30% of the cover. Most species had low relative cover indices, and a few perennial species provided most of the cover. On DI, succulents and herbs were the only growth forms and ephemeral plants contributed more than perennials did to plant cover throughout the year. Seasonal fluctuations in plant cover, species richness and diversity on DI were larger than in the WCNP, despite DI having higher annual rainfall and milder temperatures. The perennial flora in the WCNP provided greater stability with smaller responses to high summer aridity and large temperature fluctuations. Although the WCNP supports a greater variety of herbivores, DI has a higher density of angulate tortoises, showing this species' resilience and adaptability to a depauperate flora.

2.2 INTRODUCTION

Climatic and landscape diversity are major determinants of vegetation distribution, structure and composition (Partridge 1997; Schulze 1997). Climatic parameters, such as the proportional contribution of winter rainfall, summer aridity (Rutherford & Westfall 1986), and moisture availability (Ellery *et al.* 1991), have been used successfully to differentiate southern African biomes. The Fynbos biome is characterised by a high proportion of winter rainfall and a moderate to low summer aridity index (Cowling *et al.* 1997). However, regional gradients in climate, physiography and soils are reflected in compositional changes of plant communities. The decreasing coast-to-interior rainfall is associated with asteraceous and restioid fynbos replacing proteoid and ericaceous elements, while an increasing abundance of grasses from west to east is associated with decreasing summer aridity (Campbell 1983; Cowling *et al.* 1997).

The composition of vegetation communities can change seasonally in response to environmental fluctuations. The magnitude of change is more pronounced in communities with a strong annual component. When perennials are present, inter- and intra-specific competition determines spacing among perennial plants, which influences the abundance of annuals (Cunliffe *et al.* 1990; Milton *et al.* 1997). Prolonged drought (Milton *et al.* 1995), grazing (Van Rooyen 1999), and other disturbance (Milton 1995) can also change the composition of plant communities; perennial shrubs decrease while annuals and succulents can increase in abundance. Seasonal and long-term changes in vegetation composition and quality will influence the fauna, particularly herbivores, associated with the community.

Angulate tortoises have a broad coastal distribution along the southern and western coasts of South Africa, corresponding roughly to the boundaries of the Fynbos and Succulent Karoo biomes. These tortoises reach particularly high densities in the southwestern Cape and on nearby islands. Dassen Island is a continental island that was separated from the mainland *ca*. 14 000 years ago after the glacial maximum (Tankard 1976). In contrast to the rich biodiversity on the mainland, Dassen Island has a depauperate strandveld flora (Hurford 1996) and fauna (Brooke & Crowe 1982). Resources available to herbivores and the climatic regime may differ widely between Dassen Island and fynbos/thicket mosaic habitats on the mainland. Comparing vegetation composition and dynamics of the two sites might elucidate the factors that influence the distribution of angulate tortoises. I thus studied the resource utilisation of angulate tortoise populations at Dassen Island and the nearby mainland, while evaluating vegetation at the two sites. Here I report differences between the vegetation composition of the sites, and evaluate seasonal changes in vegetation cover, species richness and heterogeneity.

2.3 MATERIALS AND METHODS

2.3.1 Study sites

The West Coast National Park (WCNP, 30 000 ha) is a conserved area along the southwestern coast of South Africa. The study site at Abrahamskraal (33°13’S, 18°09’E) falls in the habitat unit, Langebaan fynbos/thicket mosaic (Cowling & Heijnis 2001), found on calcareous coastal sands. Fynbos/thicket mosaic consists of asteraceous or restioid fynbos intermingled with largely evergreen thicket species. Asteraceous fynbos occurs in the driest fynbos sites, whereas restioid fynbos occurs in more mesic areas where conditions are limiting for shrub growth (Cowling *et al.* 1997). Dassen Island (DI, 222 ha, 33°25’S, 18°06’E) is 9 km from the West Coast, just south of the WCNP. The vegetation consists of a depauperate flora with low-growing, salt-loving species, including several aliens (Hurford 1996).

Both the WCNP and DI have a Mediterranean climate. Summer and autumn months are hot and dry, but drought conditions are alleviated by periodic mist that provides valuable moisture to flora and fauna (Schaefer & Schaefer 1993). Winter and spring conditions are mild and rainfall occurs mainly between April and October. To evaluate climate differences between sites, I obtained monthly rainfall and temperature data for the WCNP (Geelbek) and DI from the South African Weather Bureau.

2.3.2 Vegetation surveys

The sampling design represents a compromise to allow comparisons between tortoise and vegetation surveys. It is not feasible to survey for tortoises on small plots spread through the habitat, so I established two large quadrats, representative of the local vegetation and separated by approximately 500 m, at each site. Each quadrat measured 120 x 80 m (0.96 ha, 9 600 m^2), and was divided by bamboo canes into a grid of 5 x 5 m cells (384 cells of 25 m^2). The surveys commenced on DI in January 1999. Subsequent surveys were first completed on DI, followed by WCNP surveys within the ensuing 2-4 weeks: March/April 1999 (only one quadrat at WCNP), July/August 1999, September/October 1999 and January/February 2000. The final WCNP survey was done in April 2000. I assessed cells individually and estimated percent plant cover (in 10% gradations) as the area covered by live or dead plant material rooted to the ground. Debris represented dead plant material not attached to the ground, and was not considered in the percent cover. When surveying vegetation (alive or dead) in each cell, I scored the vegetation's appearance from one to five to establish a condition index. A score of one represented sparse and dry vegetation while a score of five represented dense and green vegetation. For each plant species in a cell, I noted the condition and assigned a dominance rank. Dominance ranking was based on the total cover provided by the species and included live and dead plant material. The first, second and third most abundant species were given scores of four, three and two, respectively. Other species present received a score of one. Unidentified dead plants (rooted), grass and seedlings were also considered in the ranking, and for Dassen Island, mosses were included in the seedling category.

I used morphological characteristics and phenological stages to identify most plants to the genus or species level. In the WCNP, I combined all grass species, except *Ehrharta villosa*, in one category. Since *Carpobrotus quadrifidus* (rare) was misidentified as *C. edulis* (abundant) in the non-flowering seasons, I combined it with *C. edulis* in the analysis. On DI, it was often difficult to distinguish the rare *Tetragonia decumbens* from the abundant *T. fruticosa* and I consequently combined the two species in the analyses.

2.3.3 Relative cover index (RCI), species diversity and equitability

The RCI for each plant species or category in a cell was calculated as the product of the dominance score (4 to 1) and the fractional plant cover in that cell. Subsequently, I calculated the mean seasonal RCI for each species or plant category in a quadrat (N = 384) and for the two quadrats combined at each site (N = 768). The mean total RCI for each item over the last four seasons was calculated for each study site and used to rank the item in order of importance in the landscape. In addition to species RCI, I calculated RCI for two combinations of plant categories: (a) succulents, non-succulent herbs, non-succulent shrubs, parasitic plants, grasses, and restios (including sedges), and (b) annuals and perennials.

I compared species diversity between quadrats, sites and seasons using the (a) Shannon-Wiener index of diversity ($H' = -\Sigma\, p_i \log p_i$, where p_i is number of quadrat cells with species i / sum of the number of quadrat cells containing species i to species j), and (b) Simpson's index of diversity ($D' = 1 - D$, where $D = \Sigma\, p_i^2$). The Shannon-

Wiener index is sensitive to changes in the abundance of rare species, while Simpson's index is sensitive to changes in the abundant species (Waite 2000). I also compared equitability of abundance, using the Shannon-Wiener index of evenness, $J' = H' / H_{max}$, where H_{max} is the logarithm of the total number of species (Waite 2000). Equitabilities near one indicate more even or homogeneous species distributions than do equitabilities near zero; equitabilities near zero indicate strong species dominance.

2.3.4 Statistical analysis

The data rarely satisfied assumptions of normality and homoscedasticity, preventing simultaneous evaluation of site, season and quadrat effects through parametric analysis of variance (ANOVA). Instead, I evaluated effects separately either through non-parametric one-way ANOVA or by testing for differences between two sample medians (Mann-Whitney Rank Sum Tests, T statistic) or means (Student's t-tests, t statistic).

The same quadrats were surveyed each season, so I used Friedman's repeated measures ANOVA (FRMA, χ^2 tests) to evaluate separately the effects of season upon quadrat means, and upon site means, for percent cover, condition, and RCI. When testing the effect of season upon site means (N = 768), I report effects over five seasons for DI and over four seasons for WCNP, unless stated otherwise. I also used FRMA to make within-season comparisons among the mean RCI for the different species, and among the different plant growth forms within a site. Post hoc analyses following ANOVA were completed using the Student-Newman-Keul's method. When comparing matched pairs within a season (e.g., mean RCI of annuals versus mean RCI of perennials), I used a Wilcoxon signed-ranks test ($T-$ or $T+$ statistics), or paired t-tests (t statistic) when data were parametric.

Statistical comparisons were completed using SigmaStat 2.0 or Statistica '99, except t-tests for Shannon-Wiener diversity indices were calculated according to Zar (1999). I used a minimal significance criterion of $P < 0.05$ for all tests, including post-hoc analyses. To simplify data summaries and to facilitate interpretation and future comparisons, I summarised data as means rather than presenting non-parametric summaries.

2.4 RESULTS

2.4.1 Temperature and rainfall

Ambient temperatures varied more in the WCNP than on DI (Fig. 2.1a). From January 1998 to December 2000, the WCNP experienced higher maximum and lower minimum temperatures than DI experienced (all $P < 10^{-5}$). At both study sites, rain fell mainly from April to September (Fig. 2.1b), but from January 1998 to December 2000, monthly rainfall was significantly higher at DI than in the WCNP ($P = 0.004$).

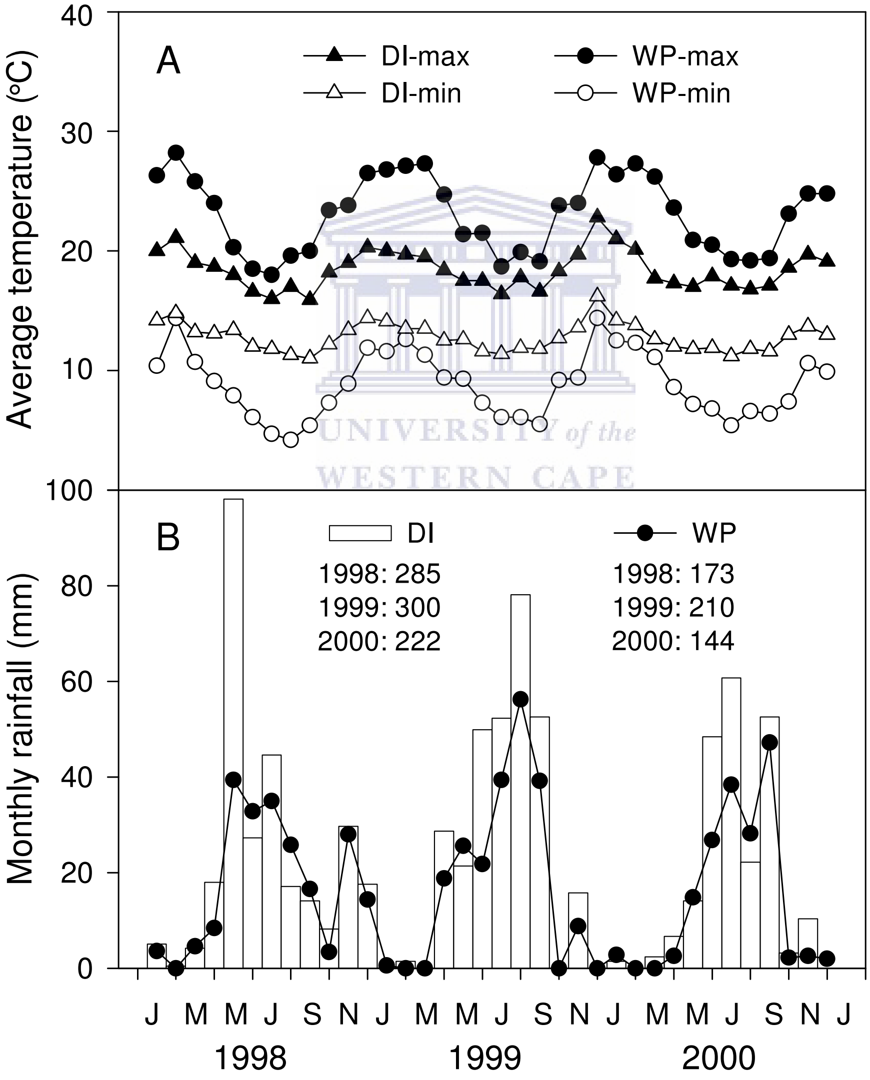

Figure 2.1 Average monthly temperatures (A) and rainfall (B) for the West Coast National Park (WP) and Dassen Island (DI) from 1998 to 2000. Annual rainfall (mm) is indicated below the legend.

2.4.2 Plant cover and condition

Percent plant cover was significantly higher in the WCNP than on DI during each of the four comparable seasons (all $P < 10^{-5}$). Condition on DI was not assessed in summer and autumn 1999, but WCNP plants had a higher condition index than DI plants had (all $P < 10^{-5}$) during winter 1999 (3.14 *vs*. 2.52), spring 1999 (3.79 *vs*. 2.92) and summer 2000 (3.39 *vs*. 2.61). Both sites showed strong seasonal changes in plant cover (all $P < 10^{-5}$) and condition (all $P < 10^{-5}$). The variation in percent cover suggests that cover varied more among seasons on DI than at the WCNP (ca. 60% and 18%, respectively between autumn and spring 1999). Percent cover increased after the first rains in autumn and reached maximum values in spring. At both sites, spring values for plant condition also exceeded values for all other seasons.

Quadrats were selected to robustly characterise plant availability at each site. Consequently, there were many quadrat differences in plant cover (Fig. 2.2) and condition. At the WCNP, quadrat two had a higher plant cover than quadrat one during spring and summer (all $P < 0.004$), while cover was similar in autumn and winter. Condition in quadrat two was higher than in quadrat one in winter, spring and autumn (all $P < 0.002$), but not in summer. At DI, plant cover differed significantly between quadrats in each season (all $P < 10^{-5}$) with greater fluctuations in quadrat one than in quadrat two. Quadrat one had lower plant cover than quadrat two in the first two seasons, but in subsequent seasons, quadrat one had higher plant cover than did quadrat two. Although quadrat one had a higher condition than did quadrat two in winter, this value decreased below the condition index of quadrat two during the subsequent spring and summer (all $P < 10^{-5}$).

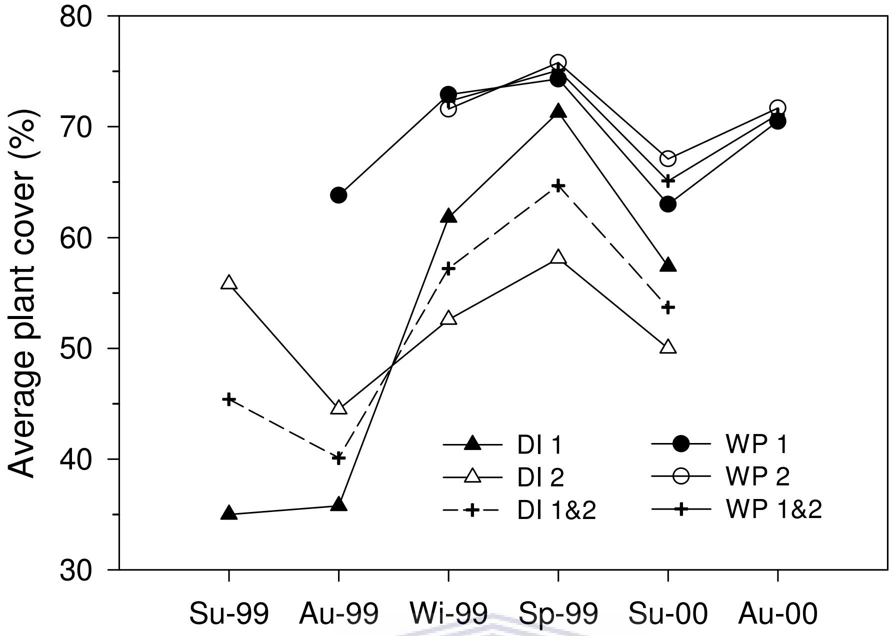

Figure 2.2 Seasonal changes in plant cover of quadrats (1, 2 and combined) at the West Coast National Park (WP) and Dassen Island (DI), South Africa. West Coast National Park quadrat two (WP 2) was not sampled in autumn 1999.

2.4.3 Relative cover index

Plant species richness at WCNP exceeded that at DI (Table 2.1), with 45 and eight identifiable species, respectively. All subsequent evaluation of species richness excludes *Tetragonia decumbens* on DI, and *Carpobrotus quadrifidus* in WCNP. The relative cover indices (RCI) of WCNP plants varied by more than three orders of magnitude (0.0005 to 0.98). This was in part because some species were abundant in each season (e.g., *Ehrharta villosa*), while others were scarcely seen in one season (e.g., *Pelargonium* sp.). The 10 plant items with the highest RCI at WCNP contributed approximately 80% to annual cover and had minor seasonal variation in RCI. Nine of the top 10 items were perennials, the exception being *Senecio elegans*, an annual herb. The presence of *S. elegans* in the top 10 RCI was due to *S. elegans* persisting intact after it died. Twenty-four plant families were present in the WCNP quadrats.

Asteraceae was the most speciose (eight species) and 15 families were represented by a single species. Nearly two-thirds of the WCNP species were scarce, with annual RCI less than 0.08 and not differing from zero or each other.

In contrast, only seven plant species (excluding *T. decumbens*) were identified in DI quadrats and five of these were annuals (Table 2.1). Total RCI at DI varied by more than 200 fold; high RCI were associated with an annual (*Mesembryanthemum crystallinum*, which included dead plant material in autumn and winter) and a perennial (*Tetragonia fruticosa*), which were present in each season. These two species contributed 64% of the total RCI. Six plant families were represented at DI with Aizoaceae containing three species (including *T. decumbens*). Only two species were detected at both sites, *S. elegans* and *Cysticapnos vesicaria*. These two species were rare in DI quadrats, where their total RCI did not differ from zero. When *S. elegans* was found at both sites (spring 1999), the WCNP RCI greatly exceeded that of DI ($P < 10^{-5}$). The annual herb *C. vesicaria* was available at both sites, but only during spring 1999, and the RCI were similar between sites.

Season affected RCI for all annual species at DI (all $P < 10^{-5}$) and the WCNP (all $P < 10^{-5}$), except for *Pelargonium* sp. at WCNP, which had a very low abundance and was present only in spring. I also detected strong seasonal effects upon the two perennial plant species on DI (all $P < 10^{-5}$) and upon the more abundant perennials in the WCNP. The RCI of some perennial plants (e.g., *Thamnochortus spicigerus, Afrolimon purpuratum* and *Cliffortia filifolia*) with a relatively high total cover did not change seasonally, although some perennial plants with lower total cover (*Asparagus rubicundus* and *Conicosa pugioniformis*) differed across seasons. The RCI of seedlings at WCNP ($P < 10^{-5}$) and seedlings and mosses at DI ($P < 10^{-5}$) changed considerably among seasons, being present mainly in winter and spring.

Table 2.1 Contribution of plant species and major plant forms to cover at Dassen Island and the West Coast National Park. Plant type distinguishes annual (A) and perennial (P) plant species. Seedlings, mosses and dead plant material were categorised as other (O). Growth form distinguishes succulents (Su) from non-succulents. Non-succulents were categorised as shrub (S), herb (H), grass (G), restio (R), cyperid (C) or parasite (Pa). Total relative cover index (RCI) represents one-year averages taken for the last four seasons at each site. Seasonal values indicate means for two quadrats (*N* = 768), except for West Coast National Park in autumn 1999 (*N* = 384). Species or category rows with hashes were not significantly influenced by season. Letter superscripts in the Total RCI column indicate which species or categories were similar in post hoc analyses (non-parametric). *Tetragonia fruticosa* includes *T. decumbens* and *Carpobrotus edulis* includes *C. quadrifidus*.

Family	Plant species	Plant type	Growth form	Su 1999	Au 1999	Wi 1999	Sp 1999	Su 2000	Au 2000	Total RCI
Dassen Island										
Aizoaceae	*Mesembryanthemum crystallinum*	A	Su	1.700	1.479	1.092	1.329	1.685		1.396
Aizoaceae	*Tetragonia fruticosa*	P	Su	1.243	0.866	0.785	1.141	1.287		1.020
Urticaceae	*Urtica urens*	A	H	0.000	0.000	1.038	1.592	0.000		0.657
–	Seedlings and mosses	O	O	0.000	0.000	0.647	0.933	0.075		0.414
Primulaceae	*Anagallis arvensis*	A	H	0.000	0.000	0.687	0.000	0.000		0.172
Asphodelaceae	*Trachyandra divaricata*	P	H	0.033	0.000	0.076	0.102	0.134		0.078
Asteraceae	*Senecio elegans*	A	H	0.023	0.000	0.000	0.073	0.000		0.018^a
Fumariceae	*Cysticapnos vesicaria*	A	H	0.000	0.000	0.000	0.029	0.000		0.007^a
–	Dead plant material	O	O	0.000	0.000	0.000	0.000	0.005		0.001^a
West Coast National Park										
Poaceae	*Ehrharta villosa*	P	G		1.389	1.308	0.923	0.793	0.887	0.978
Aizoaceae	*Carpobrotus edulis*	P	Su		0.632	0.640	0.547	0.579	0.673	0.610
Poaceae	Grass (e.g., *Cynodon dactylon*)	P	G		1.294	0.484	0.865	0.451	0.543	0.586
Asteraceae	*Helichrysum niveum*	P	S		0.595	0.350	0.550	0.617	0.592	0.527
Polygalacea	*Nylandtia spinosa*	P	S		0.166	0.415	0.423	0.412	0.466	0.429
Anacardiaceae	*Rhus laevigata*	P	S		0.131	0.274	0.304	0.419	0.441	0.360
Anacardiaceae	*Rhus lucida*	P	S		0.037	0.246	0.280	0.368	0.387	0.320
Aizoaceae	*Ruschia* sp.	P	Su		0.425	0.241	0.237	0.227	0.255	0.240^b
Aizoaceae	*Ruschia macowanii*	P	Su		0.228	0.230	0.253	0.231	0.244	0.240^b
Asteraceae	*Senecio elegans*	A	H		0.009	0.191	0.447	0.091	0.056	0.196^b
–	Dead plant material	O	O		0.000	0.195	0.223	0.095	0.155	0.167
–	Seedlings	O	O		0.000	0.541	0.011	0.000	0.000	0.138
Fabaceae	*Psoralea repens*	P	S		0.000	0.068	0.195	0.141	0.113	0.129
Asteraceae	*Felicia hyssopifolia*	P	S		0.000	0.129	0.126	0.104	0.101	0.115
Restionaceae	*Thamnochortus spicigerus*$^{\#}$	P	R		0.009	0.111	0.117	0.113	0.117	0.114

Table 2.1 continued

Family	Plant species	Plant type	Growth form	Su 1999	Au 1999	Wi 1999	Sp 1999	Su 2000	Au 2000	Total RCI
Asteraceae	*Trichogyne verticillata*	A	H		0.215	0.000	0.198	0.100	0.104	0.100
Plumbaginaceae	*Afrolimon purpuratum*[#]	P	S		0.078	0.074	0.087	0.085	0.078	0.081
Rosaceae	*Cliffortia filifolia*[#]	P	S		0.000	0.065	0.070	0.073	0.071	0.070[c]
Asteraceae	*Stoebe* sp.	P	S		0.000	0.000	0.067	0.086	0.109	0.066[c]
Asteraceae	*Oncosiphon suffruticosum*	A	H		0.035	0.000	0.114	0.077	0.068	0.065[c]
Solanaceae	*Lycium tetrandrum*[#]	P	S		0.015	0.053	0.041	0.039	0.029	0.041[c]
Thymelaeaceae	*Passerina corymbosa*[#]	P	S		0.008	0.035	0.037	0.040	0.032	0.036[c]
Geraniaceae	*Geranium incanum*[#]	P	H		0.091	0.022	0.030	0.048	0.038	0.034[c]
Celastraceae	*Gymnosporia buxifolia*[#]	P	S		0.000	0.020	0.024	0.028	0.024	0.024[c]
Cyperaceae	*Ficinia nigrescens*[#]	P	C		0.013	0.023	0.022	0.025	0.024	0.024[c]
Asteraceae	*Chrysanthemoides monilifera*[#]	P	S		0.013	0.018	0.020	0.016	0.018	0.018[c]
Apiaceae	*Stoibrax capense*	A	H		0.000	0.000	0.054	0.000	0.000	0.013[c]
Asteraceae	*Senecio burchellii*	P	S		0.000	0.021	0.019	0.006	0.000	0.011[c]
Solanaceae	*Lycium* sp. 1	P	S		0.000	0.043	0.000	0.000	0.000	0.011[c]
Asparagaceae	*Asparagus rubicundus*	P	S		0.000	0.017	0.011	0.000	0.005	0.008[c]
Lamiaceae	*Ballota africana*[#]	P	H		0.000	0.012	0.007	0.005	0.005	0.007[c]
Fumariceae	*Cysticapnos vesicaria*	A	H		0.000	0.000	0.023	0.000	0.000	0.006[c]
Aizoaceae	*Conicosia pugioniformis*	P	Su		0.000	0.006	0.015	0.000	0.000	0.005[c]
Santalaceae	*Osyris compressa*[#]	P	Pa		0.000	0.004	0.004	0.006	0.005	0.005[c]
Zygophyllaceae	*Zygophyllum flexuosum*[#]	P	S		0.000	0.002	0.007	0.006	0.002	0.004[c]
Rhamnaceae	*Phylica thunbergiana*[#]	P	S		0.004	0.002	0.003	0.003	0.002	0.002[c]
Gentianaceae	*Chironia baccifera*[#]	P	S		0.001	0.005	0.000	0.002	0.000	0.002[c]
Chenopodiaceae	*Manochlamys albicans*[#]	P	S		0.004	0.000	0.004	0.000	0.000	0.001[c]
Santalaceae	*Thesidium* sp.[#]	P	Pa		0.000	0.002	0.000	0.002	0.000	0.001[c]
Geraniaceae	*Pelargonium* sp.[#]	A	H		0.000	0.000	0.003	0.000	0.000	0.001[c]
Loranthaceae	*Septulina glauca*[#]	P	Pa		0.000	0.003	0.000	0.000	0.000	0.001[c]
Fabaceae	*Trifolium burchellianum*[#]	P	H		0.000	0.000	0.002	0.000	0.000	0.001[c]
Santalaceae	*Osyris* sp.[#]	P	Pa		0.000	0.000	0.000	0.000	0.002	0.000[c]
Solanaceae	*Lycium* sp. 2[#]	P	S		0.016	0.000	0.000	0.000	0.000	0.000[c]
Asparagaceae	*Asparagus lignosus*[#]	P	S		0.006	0.000	0.000	0.000	0.000	0.000[c]
Anacardiaceae	*Rhus glauca*[#]	P	S		0.002	0.000	0.000	0.000	0.000	0.000[c]

2.4.4 Species diversity

In the WCNP, species richness in combined quadrats increased 20% from 30 species in autumn to 36 species in spring, with quadrat two consistently having a higher richness than quadrat one. Although DI had few species, richness increased from two species in autumn to six species in spring (200% increase), with minor differences occurring between quadrats (Fig. 2.3a).

Species diversities at both sites varied considerably among seasons (Fig. 2.3b). In the WCNP, the Shannon-Wiener index varied more than the Simpson's index, indicating season affected rare species more than it affected common species. Species diversity differed among seasons ($P < 0.001$), except between summer and autumn 2000. The highest diversity was recorded in spring (H' and D'), corresponding with high species richness in this season. Diversities in quadrat two were higher than diversities in quadrat one in every season ($P << 0.001$). Dassen Island had significantly lower diversity indices than the WCNP had (P << 0.001), and seasonal fluctuations were greater than in the WCNP (Fig. 3b). In DI, species diversity differed among all seasons ($P << 0.001$) and was highest in winter. The diversity index was low in autumn when I recorded only two species. Both quadrats on DI contained few plant species, but the diversity indices for the quadrats differed in four of the five seasons ($P < 0.05$); in spring 1999, the quadrats had similar diversities.

Species evenness in the WCNP showed smaller changes among seasons compared to wide fluctuations in evenness on DI (Fig. 2.3c). Evenness in the WCNP remained high in summer and autumn 2000, although richness and diversity decreased after spring. On DI, evenness increased sharply from summer to autumn 1999. This high value in autumn corresponded with the lowest richness and diversities for DI.

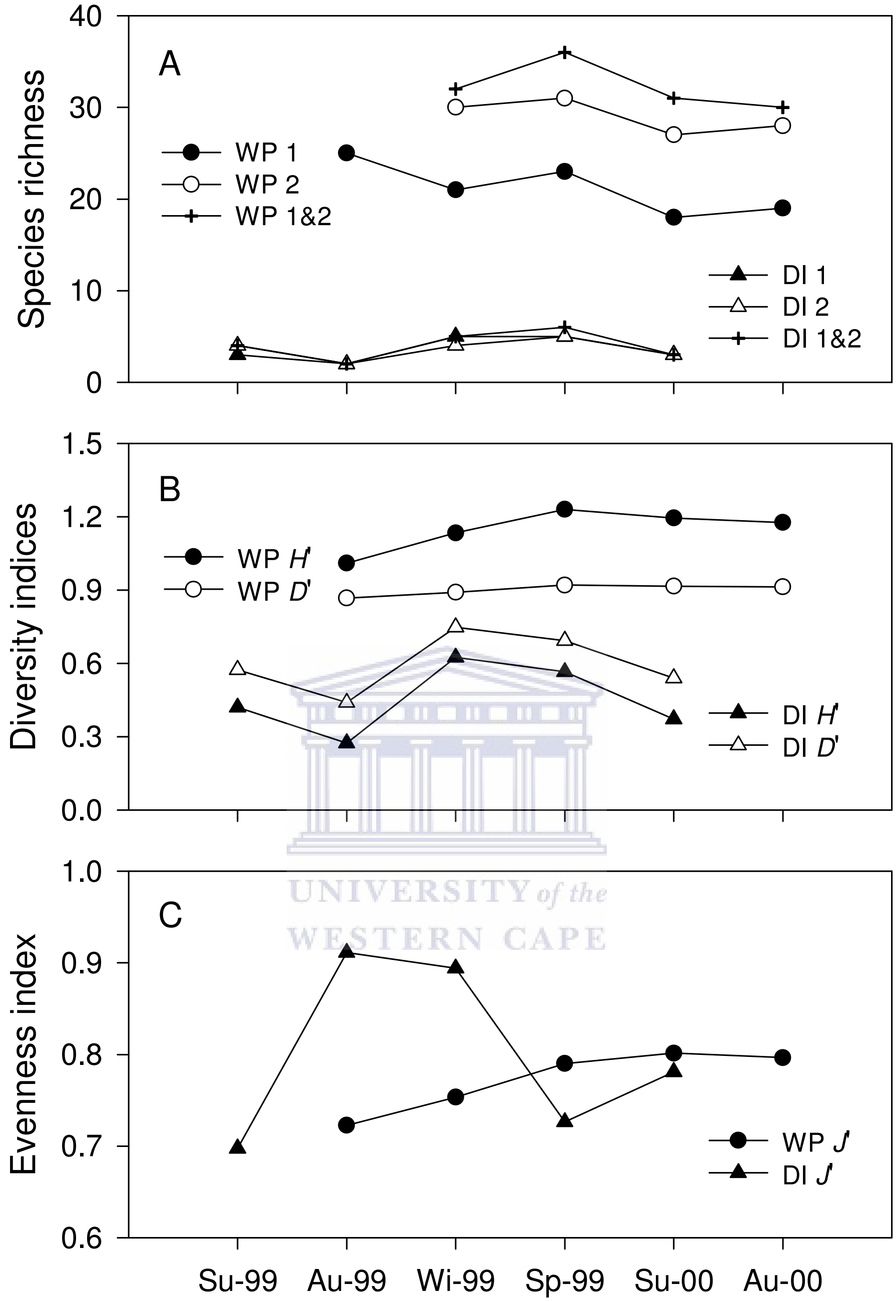

Figure 2.3 (A) Seasonal changes in species richness of quadrats (1, 2 and combined) at the West Coast National Park (WP) and Dassen Island (DI). (B) The Shannon-Wiener (*H'*) and Simpson's (*D'*) diversity indices, and (C) the Shannon-Wiener evenness index (*J'*) were calculated for combined quadrats (*N* = 768), except for WP in autumn 1999 (*N* = 384).

2.4.5 Major growth forms

Succulents and herbs were present at both sites (Fig. 2.4, Table 2.1), but their total RCI over an annual cycle were higher on DI than in the WCNP (all $P < 10^{-5}$). Succulents were the dominant growth form on DI ($P < 10^{-5}$) but herb RCI were elevated in winter and spring ($P < 10^{-5}$). Although succulents had a higher RCI in quadrat two ($P < 0.01$), herb cover did not differ between the quadrats. Non-succulent shrubs, restios and grasses were not available on DI quadrats, although I observed small amounts of grasses outside the quadrats.

A variety of growth forms was present at the WCNP (Fig. 2.4, Table 2.1). Over an annual cycle, shrubs had the highest RCI, followed by grasses, succulents, herbs, restios and parasitic plants ($P < 10^{-5}$, all SNK post hoc results $P < 0.05$). Seasonal changes in RCI were prominent for herbs, grasses, shrubs and succulents (all $P < 10^{-5}$), but the RCI for restios and parasitic plants did not change seasonally. The RCI for herbs increased in spring, while succulent RCI was highest in autumn. The shift in importance of shrubs and grasses between autumn 1999 and autumn 2000 can be explained in part by the higher grass and lower shrub composition of quadrat one compared to quadrat two (both $P < 10^{-5}$); quadrat one was the only quadrat surveyed in autumn 1999. Nevertheless, grass RCI decreased over time in quadrats one (five seasons) and two (four seasons), while the RCI for shrubs increased in both quadrats. It thus appears if the overall importance of shrubs increased in the landscape, while the importance of grasses decreased. Quadrats in the WCNP also differed in levels of succulents ($P < 10^{-5}$, higher in quadrat one) and restios ($P < 10^{-5}$, higher in quadrat two), but not for herbs or parasitic plants.

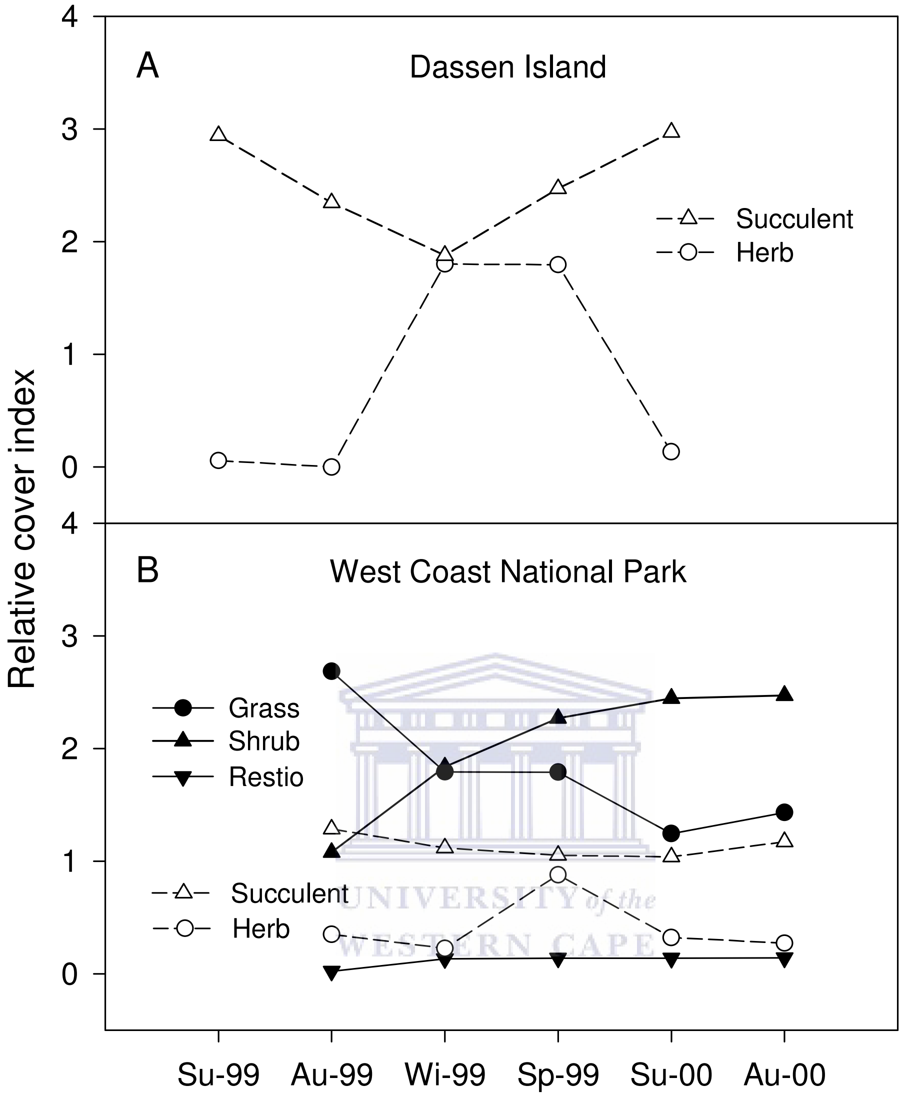

Figure 2.4 Seasonal changes in the relative cover indices (RCI) of major growth forms at Dassen Island (A) and the West Coast National Park (B). Seasonal values are for two quadrats (*N* = 768), except for autumn 1999 (*N* = 384) at the West Coast National Park. The restio RCI include the sedge RCI. Mean RCI for parasitic plants at the West Coast National Park is not indicated.

Dassen Island and the WCNP contrasted dramatically in their levels of annuals and perennials. Dassen Island had a higher RCI for annuals and a lower RCI for perennials than the WCNP had (both $P < 10^{-5}$; Fig. 2.5). On DI, annuals made a larger contribution to total cover than perennials ($P < 10^{-5}$), but quadrats also differed in composition. Compared to quadrat two, quadrat one had a higher RCI for annuals and a lower RCI for perennials (both $P < 10^{-5}$). Season affected annuals and perennials (both $P < 10^{-5}$) on DI, with high spring and winter values for annuals, and high summer values for perennials.

Perennials were the dominant plant type in the WCNP ($P < 10^{-5}$), with a higher RCI for quadrat two than for quadrat one ($P < 10^{-5}$). The RCI for annuals did not differ between the quadrats. At the WCNP, I detected seasonal changes in RCI for perennials and annuals (both $P < 10^{-5}$). The RCI for perennials was high in spring (mainly quadrat one) and autumn (mainly quadrat two), while summer had the lowest RCI. Annual RCI was highest in spring for both quadrats, but were lowest in winter for quadrat one, and in autumn for quadrat two.

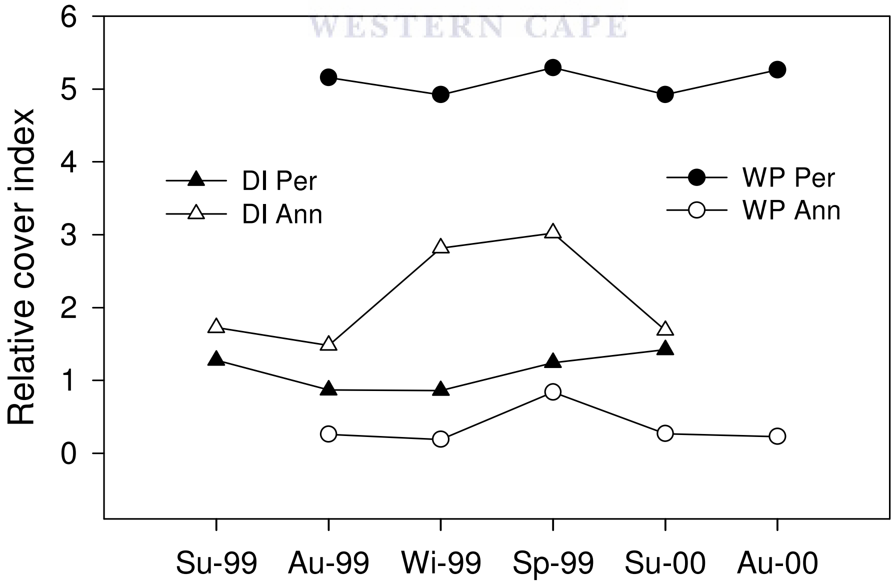

Figure 2.5 Seasonal changes in mean relative cover index for annual (Ann) and perennial (Per) plants at Dassen Island (DI) and the West Coast National Park (WP). Seasonal values are for two quadrats (N = 768), except for West Coast National Park in autumn 1999 (N = 384).

2.5 DISCUSSION

2.5.1 Vegetation types

The WCNP has strong winter rainfall and is located in fynbos/thicket mosaic habitat (Cowling & Heijnis 2001), previously categorised as strandveld or dune thicket. The WCNP site contained open to dense scrub vegetation, interspersed with dense patches of the restioid, *Thamnochortus spicigerus*. Non-succulent shrubs (41% of total RCI) and grasses (29%) formed the dominant vegetation throughout the year. Asteraceous fynbos elements (Cowling *et al.* 1997) were conspicuous in the landscape (e.g., *Felicia hyssopifolia, Cliffortia filifolia*, *Passerina corymbosa*), but thicket obligate resprouters (e.g., Anacardiaceae and Celastraceae) contributed 13% to the cover. The most speciose families, Asteraceae and Aizoaceae, each contributed 20% to annual RCI. Fynbos elements at the site best fit the asteraceous fynbos community, which is differentiated by a high cover of non-ericaceous ericoids, may have a high grass cover, and occupies the driest fynbos sites (Cowling *et al.* 1997). Boucher & Jarman (1977) described 20 terrestrial plant communities near the Langebaan Lagoon. Although the quadrats contained elements of dune sands communities (*Thamnochortus spicigerus* restioid herbland, *Didelta-Psoralea* open grassland, *Hermannia pinnata* dwarf succulent shrubland), the study site did not fit the description of any particular community. The quadrats were larger than, but not as numerous and widespread as, those of Boucher & Jarman (1977).

In certain regions of strandveld, succulents are more prevalent and strandveld blends into the Succulent karoo (Acocks 1988). However, disturbance and drier soils can also increase the prevalence of succulent vegetation. The degradation of West Coast Strandveld results in a change of scrub dominance to succulents, perennial herbs, and finally a dominance by annuals (Boucher 1981). Before the WCNP was proclaimed in 1985, Abrahamskraal was used mainly for hunting and grazing (Schaefer & Schaefer 1993) and remained relatively undisturbed. However, between 1989 and 1991 an artificial vlei was constructed near quadrat one (S. Yssel, SANP, pers. comm.), disturbing surrounding vegetation. Succulents contributed 20% to plant cover at Abrahamskraal but were more prevalent in quadrat one than quadrat two. Additionally, quadrat one had a lower cover for non-succulent shrubs and perennials, and lower species richness and diversity than that of quadrat two. Although differences between quadrats may represent natural landscape heterogeneity, it appears if recent anthropogenic disturbance contributed to these differences.

The vegetation at DI showed little similarity to the fynbos/thicket mosaic vegetation of the WCNP. Only two species occurred at both sites and DI had lower species richness and diversity than did the WCNP. When DI became separated from the mainland, increased salt levels, colonisation by seabirds, and isolation from the mainland would have changed the flora and fauna (Brooke & Crowe 1982). Human exploitation exacerbated these changes, and the present ecological state of the island is probably of recent formation (Brooke & Crowe 1982). Continental islands have different species compositions from that of adjacent mainlands, and the diversity on islands increases with increasing island size (Gilbert 1980). Distance from the coast had no effect on the species richness of 15 continental islands, including DI, off the southwestern coast of South Africa (Brooke & Crowe 1982). However, species richness increased significantly with the size of the island; DI, the largest island, had more species, including plant species, than the smaller islands. The results show that species richness and diversity on DI were significantly lower than that on the adjacent mainland and that vegetation composition differed between DI and the WCNP. Due to the sampling method, species richness for both sites was underestimated. However, since both sites were sampled in a similar manner, comparisons between sites are valid.

Hurford (1996) identified three perennial and 29 ephemeral plant species at DI and found that 59% of the species are plants that thrive in disturbed areas. The high proportion of ephemeral plants, low species richness, and few growth forms relative to the mainland, indicate the strong effect of disturbance on DI vegetation. A dense perennial cover excludes annual species, but annual plants become established when disturbance prevents the formation of a dense perennial cover (Yeaton *et al.* 1993). Burrowing activity of animals reduces perennial cover and advances the establishment of annuals (Dean & Milton 1991). On DI, African penguins (*Spheniscus demersus*) often dig nests underneath the most abundant perennial species, *Tetragonia fruticosa* (pers. obs.). Additionally, the introduced European rabbit (*Oryctolagus cuniculus*) reached high densities on DI and their digging for food and shelter disturbs the environment (Hurford 1996). The activities of these species probably contribute to the high incidence of annuals on DI. The combined effects of island biogeography and the high level of past and present disturbance on DI probably account for the depauperate flora and prevalence of annual plants in this community.

2.5.2 Seasonal effects

Strong winter rainfall and summer aridity characterise the Mediterranean climate of DI and the WCNP. The DI climate is milder, with higher annual rainfall and less extreme seasonal fluctuations in temperature than the WCNP climate. Both sites showed pronounced seasonal effects on plant cover, condition, species richness and diversity. A general trend was that the first rains in autumn stimulated plant growth, and sustained rain through winter and spring culminated in the highest species richness and total plant cover in spring. There were, however, subtle differences between the timing of events at the sites. These differences could be ascribed to different climate regimes.

At DI, species diversity and the RCI for herbs and annuals were high in winter, while these parameters peaked during spring in the WCNP. Although autumn rains commenced at the same time at the two sites, maximum temperatures in the WCNP were on average 4–8℃ higher than on DI during autumn and early winter. Higher temperatures would increase evaporation potential and reduce the amount of water available to plants. The different thermal regimes might thus explain why plants at DI responded quicker to rainfall and showed earlier RCI peaks than in the WCNP. However, species-specific phenologies might have also contributed to different timings recorded at the sites.

Total plant cover and perennial plant cover in the WCNP were highest in spring and decreased substantially in summer. In contrast, perennial cover at DI increased from winter through spring to reach maximum values in summer. Additionally, total plant cover on DI remained relatively high in summer, although summer cover was lower than values in spring and the preceding winter. Rainfall at both sites was low in late spring and summer. However, lower temperatures at DI compared to the WCNP, would have caused a lower evaporation potential, which may have allowed plants to extend cover and condition over a longer period than possible in the WCNP. These results should be interpreted cautiously since the two sites did not have a similar species composition. The perennial contributing most to summer cover at DI was a succulent (*Tetragonia fruticosa*). Succulent cover in the WCNP showed minor seasonal fluctuations (although statistically significant), with the highest RCI in autumn, at the end of the dry season.

Despite the milder climate of DI, plant cover was always lower than at the WCNP; large areas on DI resembled a barren landscape towards the end of the dry season. Seasonal fluctuations for most plant categories were larger on DI relative to fluctuations at the WCNP. I ascribe these differences to the different plant composition of the sites – the highly ephemeral composition of DI versus the predominantly perennial composition in the WCNP. The perennial component at the WCNP was more resilient to large environmental fluctuations and provided greater stability to the plant community. The more stable community in the WCNP supports a great variety of herbivores, from small reptiles to large mammals and birds.

2.5.3 Angulate tortoises

It seems an anomaly that the depauperate and highly unstable ecosystem at DI supports a higher angulate tortoise density than the WCNP (M.D. Hofmeyr, unpubl. data). Important considerations include apparently lower predation pressure on DI than in the WCNP (pers. obs.), and that competition with the diverse herbivore fauna in the WCNP might limit the density of angulate tortoises.

Apart from angulate tortoises, European rabbits are the only significant herbivore on DI. Their high endothermic metabolic demands require the availability of food throughout the year. Consequently, the rabbit population on DI regularly experiences high mortality in late summer and autumn (pers. obs.). Being ectotherms, tortoises have low metabolic requirements. During unfavourable periods, angulate tortoises seek shelter and can remain inactive for extended periods (Ramsay *et al.* 2002), probably sustaining their low metabolic needs with stored resources (Henen 1997). Mild temperature maxima and minima at DI provide a favourable climate for tortoise activity (Ramsay *et al.* 2002) and probably contribute to high tortoise densities on DI. Less extreme temperatures at DI also allow angulate tortoises to tolerate lower plant cover; WCNP tortoises would need greater cover to escape the higher temperature maxima of the WCNP. Herbs and annuals are preferred food of angulate tortoises (see Chapters 3, 4 and 5) and these items are available for longer periods on DI than in the WCNP. I thus ascribe the high density of angulate tortoises on DI to the favourable temperature regime, the availability of annuals and herbs over several seasons and the low level of predation on the island. Despite the low plant diversity on DI, the island apparently offers the critical resources that angulate tortoises require.

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3 ACTIVITY PATTERNS AND FEEDING OBSERVATIONS

3.1 ABSTRACT

Angulate tortoises have a wide distribution along the southern and western coasts of South Africa, but little information exists on the food requirements of the species over its range. I used focal observations to study the diet of angulate tortoises over four seasons at two sites in the southwestern Cape, the West Coast National Park (WCNP) and Dassen Island (DI). Seasonal fluctuations in temperature, rainfall and the availability of food plants influenced the activity pattern and feeding activity of angulate tortoises. Activity levels were higher during the wet season, winter and spring, than during the dry season, summer and autumn. The composition of the diet differed between the study sites and among seasons. Tortoises in the WCNP had a diverse diet, which included grasses, shrubs, herbs and succulents, whereas herbaceous plants formed the bulk of the tortoises' diet on DI. At both sites, herbs and seedlings were important diet components during the wet season, whereas the dry season's diet consisted largely of dry plant material. Angulate tortoises on DI supplemented their intake of dry plant material with rabbit faecal pellets, which contributed more than 27% to the composition of their diet in summer and autumn.

3.2 INTRODUCTION

Food is a primary resource of animals, and food availability affects fecundity and survivorship (Caughley & Sinclair 1994). Understanding the food requirements of organisms is thus of critical importance in wildlife management (Litvaitis 2000). The quality and availability of plant species change seasonally, and the food requirement of herbivores may change across seasons (Gibson & Hamilton 1983; Caughley & Sinclair 1994). Two methods that are often used to study food habits of animals include direct observations of individuals, and the identification of food remnants in the animals' faeces.

Direct observation is a simple non-invasive procedure for determining an animal's diet (Holechek *et al*. 1982). Through direct observation, individual animals or groups are observed as they forage during their normal daily activities. It is critical, however, that the presence of the observer does not influence the animals' natural activities. The accuracy of the feeding records increases with the degree to how tame the animal is (Holechek *et al*. 1982). In general, tortoises are shy animals that are easily disturbed when being approached. The endangered geometric tortoise (*Psammobates geometricus*) is an example of a cryptic, easily startled tortoise, which is why little information is available on the diet of these animals (Balsamo *et al*. 2004). Directly observing shy animals can be difficult, but not impossible. The speckled padloper (*Homopus signatus signatus*) is one of the world's smallest tortoises and in the past very little was known about its dietary requirements. By directly observing feeding tortoises, Loehr (2002) reported that speckled padlopers consume a variety of herbs, shrubs, succulent plants and grasses.

To further increase the reliability of feeding observations, scientists have evaluated the vegetation in the animals' habitat before they do feeding observations. Scientists studying the feeding ecology of the giant tortoises on the Aldabra Atoll recorded the plants that tortoises consume only in transects where, prior to the study, the vegetation had been surveyed extensively for over a year (Gibson & Hamilton 1983). This reduced the chances of misidentifying plants consumed by tortoises. Giant tortoises on the Aldabra Atoll were thus identified as being selective feeders, preferring to consume tortoise turf, herbs, and long grasses (Gibson & Hamilton 1983).

The angulate tortoise, *Chersina angulata*, is found in southern and western South Africa and on several continental islands off the southwestern coast (Branch 1989;

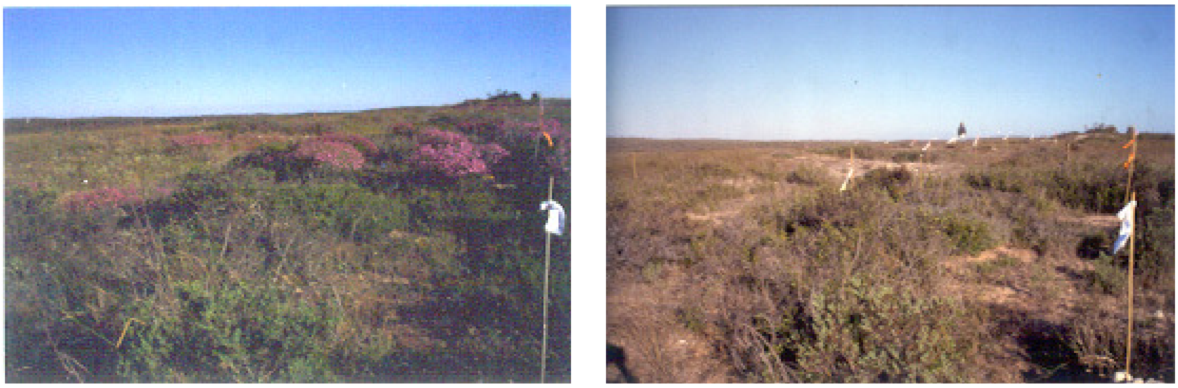
Boycott & Bourquin 2000). Angulate tortoises can reach high densities in West Coast Strandveld while partial clearance of Thicket vegetation in the Eastern Cape dramatically increases angulate tortoise densities (Branch 1989). The density of angulate tortoises is low in Coastal Fynbos, Renosterveld, the Succulent Karoo and Nama Karoo (Branch 1989; Baard 1994; Boycott & Bourquin 2000), but it is not clear which factors influence the density of *C. angulata* over its range.

The distribution of *C. angulata* spans several vegetation types in the Fynbos and Succulent Karoo biomes, indicating that this species may not require a specialised diet (Boycott & Bourquin 2000). In the Eastern Cape, grasses and annuals are important in the diet of *C. angulata* (Els 1989), but no information exists on the feeding ecology of *C. angulata* in the vegetation types of the Western Cape. This chapter evaluates seasonal changes in the diet of *C. angulata* at two study sites, with different vegetation communities, in the southwestern Cape. The results reported here were obtained through direct focal observations.

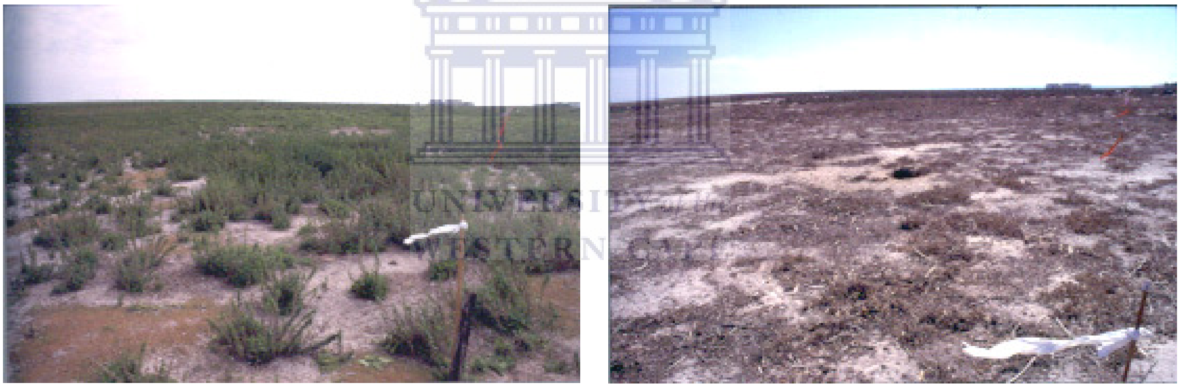
3.3 MATERIALS AND METHODS

3.3.1 Study sites

I studied the feeding ecology of *C. angulata* at Abrahamskraal in the West Coast National Park (WCNP, 30 000 ha, 33°13’S, 18°09’E) and at Dassen Island (DI, 222 ha, 33°25’S, 18°06’E) from March 1999 to February 2000. Both sites have a Mediterranean climate with hot, dry summers and cool, wet winters, but temperature fluctuations on DI are less extreme and DI rainfall is higher than in the WCNP (Joshua *et al*. 2005; see Fig. 2.1 in Chapter 2). Shrubs and grasses dominate the diverse vegetation of the WCNP, whereas the depauperate vegetation of DI is highly ephemeral (Joshua *et al*. 2005; see Chapter 2). The ephemeral vegetation of DI caused larger changes in plant cover on DI relative to that in the WCNP (Fig. 3.1), which has less ephemeral vegetation (Chapter 2). Nevertheless, angulate tortoise density on DI is approximately five to eight times higher than in the WCNP (M.D. Hofmeyr, unpubl. data).



WCNP – Wet season WCNP – Dry season



DI – Wet season DI – Dry season

Figure 3.1 The condition of the vegetation in the study quadrats during the wet and dry seasons, respectively, in the West Coast National Park (WCNP) and on Dassen Island (DI). The vegetation in the WCNP was predominantly perennial, with high plant cover throughout the year, whereas the vegetation on DI was predominantly ephemeral, and the plant cover fluctuated widely between the wet and dry seasons.

3.3.2 Feeding observations

I used two methods to record the feeding activity of *C. angulata* in the WCNP and at DI over four consecutive seasons (Table 3.1).

(a) Quadrat scans

Each season, two to four observers thoroughly searched the study quadrats (total area = 2 ha per site; see Chapter 2) for tortoises and recorded the behaviour of each tortoise encountered. A tortoise was categorised as “Inactive” when the tortoise was in a refuge under vegetation, with the head and appendages withdrawn into the shell. All tortoises that were stationary but not withdrawn into their shells were considered active, and categorised as “Immobile”. This category could include tortoises that were resting after activity, tortoises that froze their activity after they became aware of an observer, and tortoises that were basking. These tortoises could be in the open or in partial cover. Angulate tortoises often bask while in the cover of vegetation (Keswick *et al.* 2006; pers. obs.) and it was not always possible to distinguish basking from other stationary conditions. The other four categories described the active behaviours: “Walking”, “Feeding”, “Drinking” and “Socialising” (courtship and fighting behaviours).

(b) Focal observations

During each season (Table 3.1), I searched in and around the study quadrats for active tortoises and used binoculars to observe their behaviour from a distance of approximately 10 to 20 m. When a tortoise was feeding, I first tried to identify the food item through the binoculars, but if this was not possible, I approached the tortoise and collected the food item for later identification. I noted what items the tortoises ate, but could not accurately and consistently count the number of bites or the relative size of bites (small, medium or large) during most feeding observations. Consequently, bite counts were variable and unreliable, and not used in the calculations. The high tortoise density at DI made it relatively easy to find active tortoises, but random searching was not effective in the WCNP. Consequently, I marked the resting position of approximately four to eight tortoises per day, at sunrise or sunset, for subsequent observation.

Table 3.1 Dates and duration of quadrat scans and focal observations at Dassen Island (DI) and the West Coast National Park (WCNP).

	Autumn	**Winter**	**Spring**	**Summer**
DI				
Month	Mar-1999	Jul-1999	Sep-1999	Jan-2000
Scans (days)	3	4	4	3
Scans (man-hours)	50.94	37.26	49.54	40.76
Focals (days)	5	7	4	6
Focals (man-hours)	17.75	44.25	24.73	59.25
WCNP				
Month	Apr-1999	Aug-1999	Oct-1999	Feb-2000
Scans (days)	2	4	3	2
Scans (man-hours)	27.40	38.60	25.93	24.50
Focals (days)	9	3	4	5
Focals (man-hours)	48.67	20.73	24.53	41.58

3.3.3 Data analyses

3.3.3.1 Feeding observations

Where possible, food plants were identified to the species level for fresh and dry plant material. In many instances, it was not possible to identify individual grass species, particularly small annual grasses, thus I treated grass as one taxonomic category. I could not identify the seedlings that the tortoises consumed and treated seedlings as a specific category. On DI, the tortoises ate moss species, which often grew among the seedlings, and the few feeding records for moss were grouped in the seedlings category. Because plant debris may form an important component of the diet in some seasons, I divided unidentified (UI) plant material into fresh and dry plant material.

To compare the results of the focal studies with results obtained through faecal analyses (see Chapters 4 and 5), I analysed feeding records on a presence-absence basis (MacDonald & Mushinsky 1988). One feeding record consisted of an observation of an individual consuming a particular food species, irrespective of how many bites were taken or how long the tortoise fed on that plant. If the tortoise took bites from different plants of the same species, it was still counted as a single feeding record. Two feeding records for the same individual thus meant that the tortoise consumed material from two different plant species.

I used the feeding records to calculate (a) the percent frequency with which tortoises selected various plant species or food categories (percent occurrence) and (b) the percent contribution that these categories made to the diet (percent composition) in each season (MacDonald & Mushinsky 1988; Cox 1996). Percent occurrence for a plant taxon was calculated as the number of tortoises using that taxon relative to the total number of tortoises observed feeding during that particular season. Percent occurrence thus provides an index of how commonly a particular food item was used by individuals in the population. In contrast, percent composition provides an index of the relative importance of a specific food item in the diet of the tortoises. Percent composition was calculated as the number of observations for a food item divided by the total number of feeding observations recorded for that season (MacDonald & Mushinsky 1988; Cox 1996). For example, if 10 tortoises feed on three different plant species, and 10 individuals consumed species A, 5 individuals consumed species B, and 2 individuals consumed species C, the percent occurrence for species A, B and C would be 100%, 50%, and 20% respectively. The contribution of species A to percent composition would be 59% (i.e., 10 records relative to 17 feeding observations), whereas the percent contribution for species B and C would be 29% and 12%, respectively.

3.3.3.2 Growth forms

The plant species eaten at the two sites were grouped into six major growth forms: grasses, succulents, non-succulent herbs, non-succulent shrubs, seedlings and UI plant material. In the WCNP, the summer records for *Myoporum serratum*, a tree, were included with the records for shrubs. Some of the growth forms contained fresh and dry plant material. I used the same principles as described before when calculating percent composition and occurrence for growth forms, and expressed percent composition of growth forms relative to all diet items.

3.3.3.3 Statistical analyses

Statistical tests were done with SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.) and all tests were considered significant at $P \leq 0.05$. I used contingency table analyses to test for differences in behaviour, and for differences in the frequencies of dietary food types, between sites and among seasons. Because all behavioural categories, except for

"Inactive" and "Immobile" had low frequencies, I combined all active behaviours into a single category and used only two categories ("Inactive" and "Active") in the contingency table analyses. Yates' corrections were applied when degrees of freedom equalled one. I followed the guidelines of Zar (1999) to test for bias in Chi-square contingency table analyses and tested the average expected frequency with the equation n / (rc), where n is the total records, r is the number of rows and c is the number of columns. Whenever I did multiple univariate tests, I applied the Bonferroni procedure to adjust the significance level in the family of tests across which the Type I error rate had to be controlled (Quinn & Keough 2002).

A two-way analysis of variance (ANOVA), followed by the Student-Newman-Keuls post hoc test, was used to determine the effects of site and season on the number of man-hours required during focal observations.

3.4 RESULTS

3.4.1 Tortoise behaviour

The most frequent behaviour of angulate tortoises during all seasons, except during spring at DI, was to be withdrawn into their shells (Inactive, Table 3.2). Being immobile was the second most frequent behaviour, and during spring, more than 50% of the tortoises on DI displayed this behaviour. The frequencies for the other four categories were very low, and no tortoise at the WCNP was found feeding, drinking or socialising during the quadrat scans.

The frequencies of inactive (withdrawn) and active behaviour (Table 3.2) differed significantly among the four seasons for tortoises on DI ($\chi^2_3 = 413.69$; $P < 0.0001$) and in the WCNP ($\chi^2_3 = 12.86$; $P = 0.00495$). A P value of 0.00833 was required (Bonferroni procedure) when testing for significant difference between specific seasons. Using these guidelines, the frequencies of active and inactive behaviour on DI did not differ between autumn and summer, but differed among all other seasons (all $\chi^2_1 > 65.82$; $P < 0.0001$). The only difference recorded for the WCNP was between autumn and summer ($\chi^2_1 = 9.17$; $P = 0.0025$).

Table 3.2 Behaviour frequencies of *Chersina angulata* on Dassen Island (DI) and in the West Coast National Park (WCNP), expressed as a percentage of the total number of observations (*N*) recorded when the study quadrats (2 ha) were scanned.

	Autumn	**Winter**	**Spring**	**Summer**
DI (*N* =)	316	329	374	365
Inactive	95.3	70.8	39.9	97.3
Active	4.7	29.2	60.1	2.7
Immobile	2.8	25.5	50.4	0.5
Walking	1.9	2.7	7.0	1.6
Feeding	0.0	0.3	0.3	0.0
Drinking	0.0	0.0	0.8	0.0
Socialising	0.0	0.6	1.6	0.5
WCNP (*N* =)	53	83	106	55
Inactive	77.4	91.6	88.7	98.2
Active	22.6	8.4	11.3	1.8
Immobile	18.9	8.4	10.4	1.8
Walking	3.8	0.0	0.9	0.0
Feeding	0.0	0.0	0.0	0.0
Drinking	0.0	0.0	0.0	0.0
Socialising	0.0	0.0	0.0	0.0

When testing for differences in activity levels between the WCNP and DI, the Bonferroni procedure indicated that a significance level of $P = 0.0125$ was required. There was no difference between the activity levels of angulate tortoises in the WCNP and DI during summer, but the activity levels differed in all other seasons (all $\chi^2_1 > 14.13$; $P < 0.00017$; Table 3.2).

During summer, nearly all the tortoises in the quadrats were inactive and withdrawn into their shells (Table 3.2), necessitating longer man-hours to find feeding tortoises during focal observations (Table 3.3). The effort required to find feeding tortoises differed significantly among seasons ($F_{3,7} = 118.96$; $P = 0.00129$) and the effort required in summer was higher than in all other seasons (all $P < 0.002$). At DI, the number of man-hours per feeding tortoise increased by more than an order of magnitude from spring to summer. More man-hours were also required to find feeding tortoises in the WCNP than on DI ($F_{1,7} = 75.15$; $P = 0.00323$).

Table 3.3 The number of man-hours required per feeding tortoise when doing focal observations on Dassen Island (DI) and in the West Coast National Park (WCNP).

	Autumn	**Winter**	**Spring**	**Summer**
DI	0.77	1.16	0.35	4.94
WCNP	2.70	2.30	2.23	6.93

3.4.2 Feeding observations

More feeding observations were made on DI (226) than in the WCNP (72), and at both sites, the lowest number of tortoises feeding was recorded during summer, when search effort (man-hours) was highest. There was no difference in the number of diet items (i.e., species or categories) recorded during the four seasons at the two study sites ($\chi^2_3 = 1.84$; $P = 0.606$; Tables 3.4 and 3.5).

On DI, *Trachyandra divaricata* and faeces of the European rabbit, *Oryctolagus cuniculus*, formed part of the diet of angulate tortoises throughout the year (Table 3.4). Although *T. divaricata* is a perennial, little fresh material was available during the summer and autumn months of the study. Nevertheless, the dry leaves and flower stalks of *T. divaricata* contributed 28% and 47%, respectively, to the tortoises' diet during summer and autumn. Rabbit faeces contributed more than 27% to the composition of the diet in summer and autumn. Most of the tortoises consumed seedlings (and moss) in winter and spring, and this food source comprised nearly 58% of the spring diet. Seedlings made the largest contribution to the diet overall, followed by *T. divaricata* and rabbits' faeces (Table 3.4).

Table 3.4 Percent composition (occurrence) of *Chersina angulata's* diet on Dassen Island based on focal observations. The *N* values represent the number of tortoises observed, followed by the number of objects seen eaten.

	Autumn	Winter	Spring	Summer	Totals
	N = 23, 34	*N* = 38, 77	*N* = 70, 97	*N* = 12, 18	*N* = 143, 226
Albuca flaccida		3.90(7.89)	7.22(10.00)		4.42(6.99)
Cystocapnos vesicaria			4.12(5.71)		1.77(2.80)
Grass		2.60(5.26)	1.03(1.43)		1.33(2.10)
Mesembryanthemum crystallinum		6.49(13.16)	4.12(5.71)		3.98(6.29)
Oxalis pes-caprae		1.30(2.63)			0.44(0.70)
Seedlings and moss		36.36(73.68)	57.73(80.00)		37.17(58.74)
Senecio elegans		5.19(10.53)	2.06(2.86)	5.56(8.33)	3.10(4.90)
Tetragonia fruticosa	8.82(13.04)	2.60(5.26)			2.21(3.50)
Trachyandra divaricata	[#]47.06(69.57)	15.58(31.58)	10.31(14.29)	[#]27.78(41.67)	19.03(30.07)
Urtica urens		2.60(5.26)	4.12(5.71)		2.65(4.20)
Total UI plant material	11.76(17.39)	18.18(36.84)	6.19(8.57)	38.89(58.33)	13.72(21.68)
Dry plant material	11.76(17.39)		1.03(1.43)	5.56(8.33)	2.65(4.20)
Fresh plant material		18.18(36.84)	5.16(7.14)	22.22(33.33)	10.18(16.08)
Unknown bulb				11.11(16.67)	0.88(1.40)
Total animal material	32.35(47.83)	5.19(10.53)	3.09(4.29)	27.78(41.67)	10.18(16.08)
Rabbit faeces	29.41(43.48)	5.19(10.53)	3.09(4.29)	27.78(41.67)	9.73(15.38)
Snail shell	2.94(4.35)				0.44(0.70)
Number of diet items recorded	5	11	11	6	15

[#] Feeding observations of *T. divaricata* in autumn and summer were of dried leaves and stems, in contrast with the fresh material that was eaten in winter and spring.

There were incidental observations of foraging on *Cotula* sp. and *Myoporum serratum* but not during formal focal observations.

Table 3.5 Percent composition (occurrence) of *Chersina angulata* diet in the West Coast National Park based on focal observations. The *N* values represent the number of tortoises observed, followed by the number of objects seen eaten.

	Autumn	Winter	Spring	Summer	Totals
	N = 18, 27	*N* = 9, 16	*N* = 11, 20	*N* = 6, 9	*N* = 44, 72
Apocynaceae		6.25(11.11)			1.39(2.27)
Carpobrotus edulis	3.70(5.56)				1.39(2.27)
Geranium incanum	3.70(5.56)				1.39(2.27)
Grass	18.52(27.78)	12.5(22.22)	5.00(9.09)	11.11(16.67)	12.50(20.45)
Helichrysum niveum	3.70(5.56)		5.00(9.09)		2.78(4.55)
Myoporum serratum				22.22(33.33)	2.78(4.55)
Nylandtia spinosa			5.00(9.09)		1.39(2.27)
Oncosiphon suffruticosum		6.25(11.11)			1.39(2.27)
Pelargonium sp.	3.70(5.56)	12.5(22.22)	5.00(9.09)		5.56(9.09)
Seedlings and moss		25.00(44.44)			5.56(9.09)
Senecio elegans			5.00(9.09)	11.11(16.67)	2.78(4.55)
Senecio sp.			5.00(9.09)		1.39(2.27)
Stoibrax sp.			20.00(36.36)		5.56(9.09)
Trachyandra sp.			5.00(9.09)		1.39(2.27)
Total UI plant material	59.26(88.89)	37.50(66.67)	45.00(81.82)	55.56(83.33)	50.00(81.82)
Dry plant material	51.85(77.78)		5.00(9.09)	55.56(83.33)	27.78(45.45)
Fresh plant material	7.41(11.11)	31.25(55.56)	35.00(63.64)		19.44(31.82)
Unknown angiosperm		6.25(11.11)			1.39(2.27)
Unknown herb			5.00(9.09)		1.39(2.27)
Animal material (faeces)	7.41(11.11)				2.78(4.55)
Number of diet items recorded	8	7	11	4	19

There were incidental observations of foraging on *Tetragonia fruticosa, Trichogyne verticillata, Psoralea repens, Trifolium burchellianum, Ruschia macowanii, Oxalis pes-caprae* and *Hebenstretia repens* but not during formal focal observations.

A large proportion (> 77%) of the tortoises in the WCNP were observed feeding on dry plant material during summer and autumn (Table 3.5). There was no feeding record for dry plant material in winter, and its contribution to the spring diet was very low. In winter and spring, seedlings and *Stoibrax* sp., respectively, contributed 25% and 20% to the season's diet. The WCNP tortoises consumed grass species in each season while they used *Pelargonium* sp. in three of the four seasons, and *Helichrysum niveum* and *Senecio elegans* in two different seasons. Overall, dry plant material made the largest contribution to the composition of the diet, followed by unidentified fresh plant material and grass. Nearly 10% of the tortoises were observed feeding on *Pelargonium* sp., *Stoibrax* sp. and seedlings. I recorded 19 diet items for angulate tortoises in the WCNP with the lowest number being recorded in summer and the highest number in spring (Table 3.5).

3.4.3 Growth forms

The diet of tortoises on DI did not include non-succulent shrub species, and grasses made a small contribution to their diet (Fig. 3.2). The contribution of the five plant categories (excluding UI plant material) to the tortoises' diet differed from random in each seasons (all $\chi^2_4 > 32.0$; $P < 0.001$). Herbs contributed most to the summer and autumn diets, and were the only identified plant type eaten in summer. In winter and spring, seedlings made the largest contribution to the diet but the tortoises used herbs in each of the four seasons. Overall, seedlings and herbs formed the bulk of angulate tortoises' diet on DI.

The composition of the diet on DI differed significantly between autumn and winter ($\chi^2_4 = 16.55$; $P = 0.00236$), autumn and spring ($\chi^2_4 = 27.34$; $P < 0.0001$) and between spring and summer ($\chi^2_4 = 23.63$; $P < 0.0001$). The probability of the change from winter to spring was $P = 0.0194$, and did not meet the required significance criterion of $P < 0.00833$. There were also no differences between autumn and summer, and between winter and summer diets.

The tortoises in the WCNP consumed herb and grass species in all seasons, while they used shrubs mainly in spring and succulents only in autumn (Fig. 3.3). The contribution of the five plant categories (excluding UI plant material) to the tortoises' diet differed from random only in spring ($\chi^2_4 = 13.83$; $P < 0.05$). The five plant categories did not contribute equally to the overall diet ($\chi^2_4 = 12.33$; $P < 0.05$); the contribution from herbs was higher than the expected frequency (i.e., homogeneous distribution among categories) and the contribution from succulents was lower than the expected frequency. Seasonal changes in the composition of the diet in the WCNP did not meet the required significance level.

There was a significant difference between the annual (i.e., overall) diets of angulate tortoises in the WCNP and on DI ($\chi^2_5 = 91.78$; $P < 0.0001$). The composition of the diet at the two sites also differed in autumn and in spring ($\chi^2_5 > 24.0$; $P < 0.0001$), but not in winter or summer ($P > 0.5$).

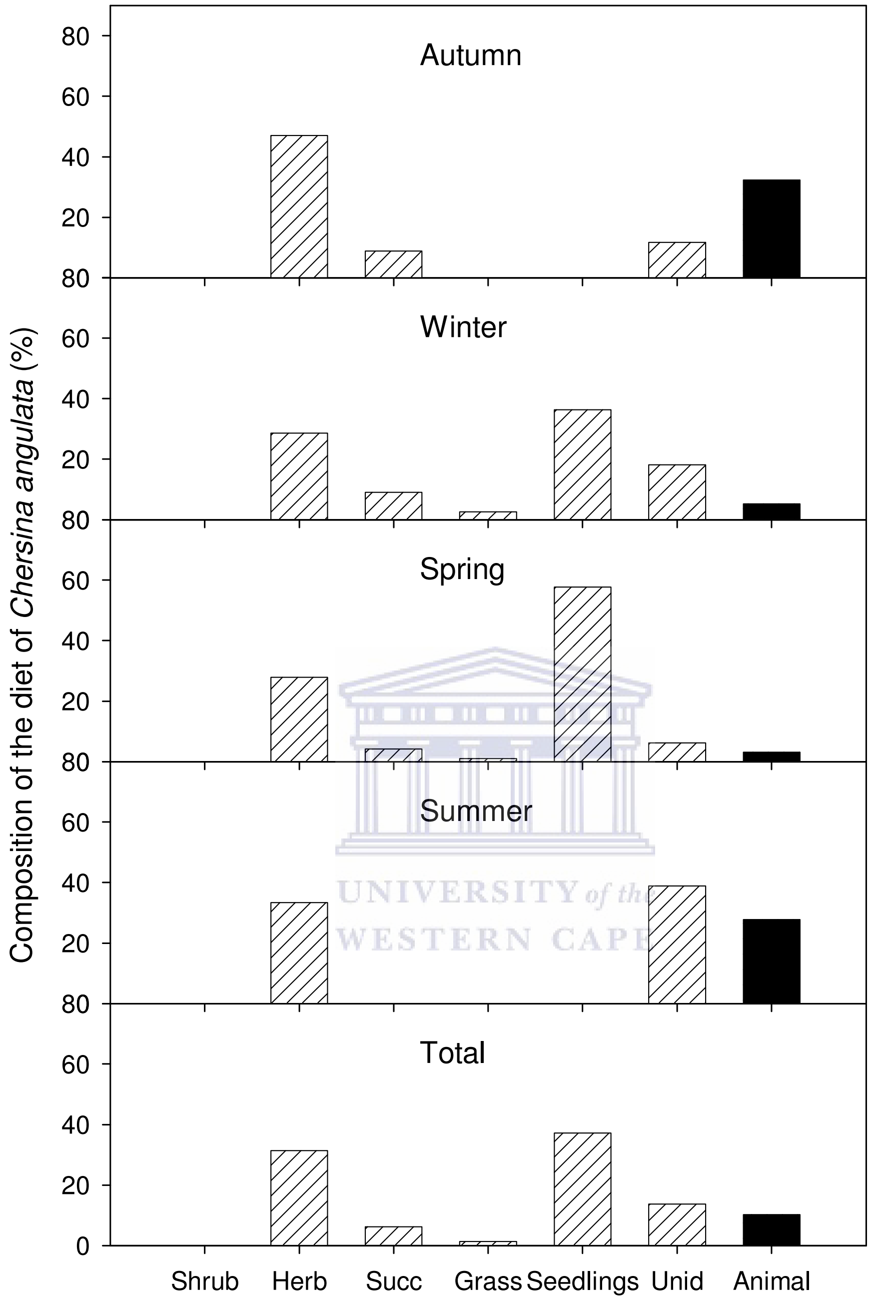


Figure 3.2 Percent composition of the diet of *Chersina angulata* on Dassen Island based on focal observations. Succ and Unid represent succulent plants and unidentified plant material, respectively. Other plant categories were non-succulent. Mosses were included in the Seedlings category. See Table 3.4 for sample sizes.

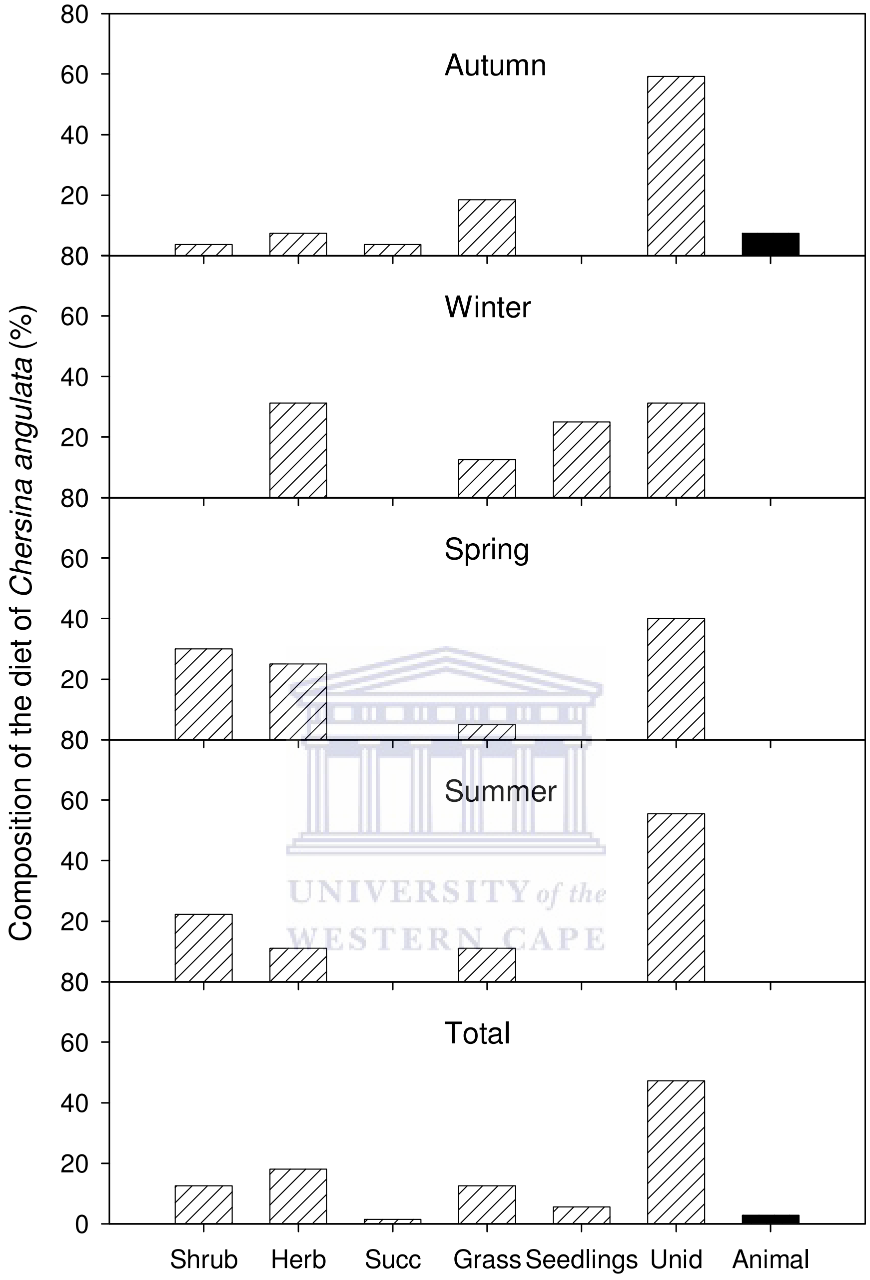


Figure 3.3 Percent composition of the diet of *Chersina angulata* in the West Coast National Park based on focal observations. Succ and Unid represent succulent plants and unidentified plant material, respectively. Other plant categories were non-succulent. Two records for tree leaves eaten in summer were included with the records for shrubs. Mosses were included in the Seedlings category. See Table 3.5 for sample sizes.

3.5 DISCUSSION

3.5.1 Activity levels and feeding

Angulate tortoises appear to maintain a low level of activity through most of the year, similar to the low activity levels that have been reported for several other chelonians, particularly species from arid regions (e.g., *Gopherus agassizii*, Nagy & Medica 1986; *Testudo horsfieldi*, Lagarde *et al*. 2003). Tortoises, being ectothermic animals, generate little heat internally and therefore depend on external heat sources to attain optimal body temperatures before activity can begin (Walker & Liem 1994; Lagarde *et al*. 2003). Low ambient temperatures thus restrict tortoise activity but high temperatures may also elicit a decrease in the level of activity if the tortoises seek cover to prevent overheating (Els *et al*. 1988; Walker & Liem 1994). In addition to the effects of temperature, seasonal changes in the availability of water and food influence the activity levels in tortoises (Rose & Judd, 1975; Gibson & Hamilton 1983; Henen 1997).

The activity levels of angulate tortoises at both study sites fluctuated with the seasons. Activity on DI was at its lowest level during summer and autumn. High temperatures and low rainfall (see Fig. 2.1), in combination with low food availability (Fig. 3.1) can explain the low activity levels of angulate tortoises during summer and autumn. In the WCNP, the activity level of *C. angulata* was low during summer but not in autumn. During autumn 1999, the first autumn rains fell just after fieldwork on DI terminated and before fieldwork started in the WCNP. The high autumn activity levels in the WCNP thus appear to be a direct consequence of the first autumn rains, rather than a response to food availability, because food was still scarce during the sampling period. An increased level of activity in response to rain has also been reported for other arid-zone tortoises such as *Gopherus agassizii* (Medica *et al.* 1980; Henen *et al.* 1998) and *Gopherus berlandieri* (Rose & Judd 1975).

The activity of angulate tortoises on DI peaked when environmental conditions were conducive to plant growth during winter and spring. The diversity and cover of plants at the two study sites increased significantly during winter and spring, but temperatures during these colder seasons may limit tortoise activity. Ramsay *et al.* (2002) found that active behaviours (e.g., feeding, fighting, courtship) occur within a restricted temperature range that corresponds closely with high ambient temperatures recorded during peak activity. In order to utilise increased food resources in the colder months, angulate tortoises might need to spend more time basking to reach body temperatures that would allow feeding activity. Keswick *et al.* (2006) reported that during spring 2004, angulate tortoises on DI spent approximately 30% of daylight hours basking. It seems probable that the tortoises would require more basking time during winter to reach optimal temperatures for feeding and subsequent digestion of food. Cloudy conditions and rainfall may limit the feeding and digestive ability of angulate tortoises during the cold and rainy season.

The different temperature regimes of the two study sites may explain why angulate tortoises in the WCNP had lower activity levels during winter and spring than the tortoises on DI had. Although maximum temperatures of the two sites differed little through winter and spring, minimum temperatures in the WCNP were consistently lower than were minimum temperatures at DI during that time of the year (see Fig. 2.1). It is possible that during winter and spring, angulate tortoises on DI managed more often to reach body temperatures that were optimal for active behaviours than was the case for tortoises in the WCNP.

Few feeding records were obtained through the quadrat scans, indicating that this method is not suitable to study the feeding ecology of angulate tortoises. It is possible that the movements of the observers disturbed the tortoises sufficiently to stop feeding so that feeding tortoises were included in the “Immobile” or “Walking” records. Low feeding frequencies, however, have been recorded for other tortoise species and *Testudo horsfieldii* spends less than 15 minutes per day foraging, despite the fact that these tortoises have to accumulate enough resources during three months to reproduce, and last through nine months of dormancy (Lagarde *et al.* 2003). Nevertheless, Keswick *et al.* (2006) found that in spring 2004, angulate tortoises on DI spent approximately 6% of daylight hours feeding. These results confirm that the quadrat scans do not reflect reliable frequencies for the feeding activities of angulate tortoises.

The focal observation method provided better records of feeding, but it required many man-hours to record sufficient data. The longer man-hours per feeding tortoise in the WCNP compared to DI can be ascribed to: (1) the low tortoise density in the WCNP compared to tortoise density on DI (M.D. Hofmeyr, unpubl. data), (2) lower visibility of tortoises in the WCNP compared to DI due to a higher percent plant cover in the WCNP than on DI (see Fig. 2.2), and (3) the low level of activity of angulate tortoises in the WCNP compared to tortoises on DI (Table 3.2). Future studies may be more efficient if the focal animals are supplied with thread-trailing devices, as in Keswick *et al.* (2006), to facilitate continuous observations of individuals.

3.5.2 Seasonal variation in diet

3.5.2.1 The wet season

Both study sites in the southwestern Cape experienced large seasonal fluctuations in temperature and rainfall, typical of a Mediterranean climate. Because of the climate, the vegetation at the study sites, and the diet of the angulate tortoises varied greatly across seasons. Autumn and winter rains stimulated plant growth and the percent plant cover at both study sites increased significantly in winter and spring (see Fig. 2.2). On DI, the availability of seedlings and mosses remained high throughout the wet season, explaining why seedlings constituted the bulk of the angulate tortoises' diet in winter and spring. The diet of the tortoises on DI included a high diversity of annual plants in winter and spring, relative to other seasons, corresponding to a high relative cover index for annual, herbaceous plants during these two seasons.

For angulate tortoises in the WCNP, seedlings formed an important diet component only in winter, the only season when seedlings had a high availability at the site. The diet of the WCNP tortoises became more diverse in spring, which was the only season when the relative cover indices of herbaceous and annual plants increased substantially in the WCNP. The different availability and consumption of annual plants in the WCNP and DI were probably a consequence of the predominantly perennial vegetation at the WCNP (Chapter 2).

The digestibility of plants is influenced largely by the fibre content of the plants, particularly the concentration of lignin in the plant tissues (Martin 1955; Mauseth 1988; Balsamo *et al.* 2004). Vertebrates are unable to digest lignified plant tissue and vertebrate herbivores rely on cellulolytic microflora in their gut to digest cellulose in their diet (Bjorndal 1987). The fibre content of plants differs widely, and the protein content of the plant tends to change inversely with the fibre content (Caughley & Sinclair 1994). Thus, more digestible plants also tend to have higher protein content. The protein and fibre content of grass and leaves change with age so that young growth generally is more digestible, with a higher protein content. The decrease in protein content with age is more pronounced for grasses than it is for the leaves of dicotyledonous plants (Caughley & Sinclair 1994). Young plants may also have high concentrations of soluble carbohydrates, which should be highly digestible (Henen *et al*. 2005). These factors probably account for the large contribution of seedlings, and other soft annual plants, to the diet of angulate tortoises during the wet season in the southwestern Cape.

Many tortoise species appear to favour annuals and herbaceous plants. Milton (1992) reported that *Stigmochelys pardalis* in the Succulent Karoo avoided woody plants and selected forbs and grasses. However, these tortoises switched their preference to succulents when green grass was no longer available. *Psammobates oculiferus* in the Kalahari selects herbaceous and succulent plants when available, and only uses grass species during periods of low rainfall when the tortoises do not have access to herbaceous plants (Rall & Fairall 1993). Desert tortoises (*Gopherus agassizii*) eat primarily fresh annuals but switch to perennials, cryptogamic soils and faeces in dry years when fresh annuals are not available (Henen 2002).

3.5.2.2 The dry season

During summer and autumn, when rainfall was low and temperatures high, percent plant cover and species diversity were lower than during the wet season (see Chapter 2). Despite DI having a milder climate than the WCNP, the low plant diversity at DI exposed the tortoises on DI to harsh conditions during the dry season. In summer and autumn, rabbit faeces and the dead leaves and flower stalks of *T. divaricata* constituted the bulk of the tortoises' diet. *Trachyandra divaricata* is a perennial plant but little fresh material was available in the dry season during the study period. However, the leaves and flower stalks of the dead plants remained as debris through summer and autumn. The dead leaves were not brittle and probably contained a small amount of moisture. During the dry season, DI often experienced incidences of fog, and the fog may have increased the water content of dead *T. divaricata* leaves. Additionally, angulate tortoises that rehydrate by drinking condensed fog (M.D. Hofmeyr, pers. comm.) are probably able to store energy when digesting dry plant matter (see Henen 1997). Yet, it is not clear what nutritional value dead *T. divaricata* provides.

Tetragonia fruticosa and *Mesembryanthemum crystallinum* were the only two plant species on DI that were available in large quantities during summer and autumn (see Table 2.1). Tortoises often took refuge under *Tetragonia fruticosa* bushes but were only observed eating young seedlings of this species and were never seen to eat parts of the adult plants. A high salt content may limit the use of this species because Els (1989) reported that *Tetragonia* sp. from DI has a sodium content of 2 693 ± 18.9 mmol kg^{-1} dry mass. *Mesembryanthemum crystallinum* is an annual plant that develops during winter and spring. Dead *M. crystallinum* plants, however, remained anchored to the ground from late summer to early winter and formed part of the plant cover on DI. The trichomes of *M. crystallinum* form bladder cells, which act as storage organs for NaCl (Adams *et al.* 1998). The salt content of adult plants can reach high levels because the concentration of salt in the bladder cells increases during conditions stressful for the plants. Juvenile *M. crystallinum* stores lower concentrations of salt in their bladder cells than mature plants do (Adams *et al.* 1998), and the tortoises probably found the young seedlings of *M. crystallinum* more palatable than the mature plants.

In summer and autumn, rabbit pellets contributed nearly 30% to the diet of angulate tortoises on DI. There have been reports of other tortoise species eating faecal material: *Geochelone pardalis* eat hyena faeces (Branch 1998), *Gopherus berlandieri* eat faeces of other tortoises and rabbit faeces (Auffenberg & Weaver 1969), and *Gopherus agassizii* eat tortoise, lizard and wood rat faeces (Henen 2002). The energy and nutritional value of rabbit faeces varies according to the age and the type of faecal pellet. The energy content of exposed rabbit pellets decreases with time due to the activities of coprophilous microflora (Angel & Wicklow 1974). Angulate tortoises were observed sniffing rabbit pellets before feeding (pers. obs.), perhaps trying to assess the nutritive value based on odours and how long the pellets have been exposed. Rabbits are hindgut fermenters and produce soft faeces that they normally re-ingest before excreting the typical hard faecal pellets (McBee 1971). The soft faeces have a high percentage of protein, most of which is bacterial cells. Hard pellets have lower protein content but the bacterial cells can contribute as much as 56% to the composition of the dry pellet (McBee 1971). Not all faecal pellets of rabbits are re-ingested and tortoises consuming select rabbit pellets probably obtain an additional source of protein (McBee 1971). The amount of protein gained from consuming rabbit faeces will depend on the type of scat consumed, but the use of rabbit pellets in the diet may aid the tortoise in acquiring additional sources of energy. By consuming rabbit pellets, tortoises could also be actively increasing their gut microflora (Angel & Wicklow 1974). The gut microflora from rabbit faeces possibly assist the tortoise to digest the cellulose of fibrous plants in the dry season.

The only season when angulate tortoises in the WCNP were observed eating faecal material was autumn, but faecal material did not make a substantial contribution to their diet. During the dry season, dry plant material and grasses formed a large proportion of the angulate tortoises' diet in the WCNP. It is not clear why dry plant material was so important in their diet, and it is not known if the normal degradation processes rendered the dead plant material more digestible. Dry plant material can be a source of energy if a tortoise is reasonably hydrated (Henen 1997); hydrated desert tortoises increase their lipid reserves while consuming dry grass.

The high relative cover index for grass species in the WCNP, particularly in autumn 1999, may have contributed to the high consumption of grasses during the dry season. *Cynodon dactylon*, one of the common grass species in the WCNP, is considered good pasture under natural conditions (Van Oudtshoorn 2002). This grass also forms part of the diet of other South African tortoises, e.g., *Psammobates geometricus* (Balsamo *et al*. 2004), and *Stigmochelys pardalis* (Mason *et al*. 1999). Although mature grass leaves may have a low protein content during the dry season, young annual grass species started growing soon after the first autumn rains.

3.5.3 Importance of the major growth forms

The vegetation composition differed strongly between the WCNP and DI. The strong perennial plant component in the WCNP persisted from year to year and presented a stable habitat in terms of plant variety and availability. In contrast, the low diversity of perennial plants and the dominance of ephemeral plant species on DI allowed wide fluctuations in plant cover with low plant diversity. It was to be expected that the different vegetation types of the WCNP and DI would influence the diet of angulate tortoises at these sites.

Herbaceous plants, including seedlings, constituted the bulk of the diet of angulate tortoises on DI throughout the year. The diet composition of tortoises in the WCNP differed from the diet composition on DI, mainly because the WCNP diet included shrubs and grasses, and was more diverse. Nevertheless, when soft herbaceous plants were available in winter and spring in the WCNP, herbaceous plants became an important component of the tortoises' diet.

There were few plant species that occurred at both study sites and the only plants observed being eaten at both sites were grasses and *Senecio elegans*. Because grass is relatively scarce on DI (Hurford 1996; pers. obs.), only a few feeding observations for grass were recorded during winter and spring, in contrast to the consumption of grass throughout the year in the WCNP. Els (1989) reported that buffalo grass (*Stenotaphrum secundatum*) is the most common diet item of angulate tortoises in the Eastern Cape. Grass thus appears to be an important diet item for *C. angulata* in different parts of its range. Nevertheless, the low consumption of grass in the WCNP during spring suggests that angulate tortoises preferred herbs and shrubs when new growth was available.

Angulate tortoises in the WCNP ate two shrub species. *Helichrysum niveum* is an ericoid shrublet, with small leaves, and had a high relative cover index through most of the year. Tortoises consumed young leaves of the shrublet when new growth developed in spring whereas the feeding observations in autumn were of mature leaves. *Nylandtia spinosa* is a low-growing shrublet with small, thick leaves. Angulate tortoises were never observed eating the leaves of *N. spinosa*, but consumed the fruits of this shrub in spring. The fleshy, red fruits are edible, but astringent (Manning & Goldblatt 1996).

The two plant species on DI with the highest relative cover index included a succulent annual (*M. crystallinum*) and a succulent shrub (*T. fruticosa*). Yet, these two species contributed little to the diet of angulate tortoises on DI. In the WCNP, one succulent herb, *Carpobrotus edulis*, contributed to the feeding records for autumn. The fleshy fruit of this plant is edible, but I have witnessed only attempts of the tortoises to tear off pierces of the thick, fleshy leaves and have not seen them eating the fruits. An incidental feeding observation was made for *Ruschia macowanii*, another succulent shrub with fleshy, but smaller leaves. The consumption of succulent plants may be an attempt by the tortoises to alleviate the water shortages during the dry season. Tortoises are known to consume succulent plants to help increase their water intake during unfavourable periods (Nagy & Medica 1986; Milton 1992; Rall & Fairall 1993; Henen 2002).

The WCNP and DI are habitats that have suffered anthropogenic disturbances to different extents in the past. The disturbance had a greater impact on DI than at the WCNP, evidenced by the ephemeral weedy growth forms that dominate the islands' vegetation. The mild climate at DI, low metabolic requirements of the tortoises, and high availability of easily digestible herbaceous species, probably made it possible for angulate tortoises to be so successful in this disturbed habitat. Additionally, it appears if the presence of the introduced European rabbit may be important to the survival of angulate tortoises during the long and hot dry season.

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4 MACROSCOPIC EVALUATION OF TORTOISE FAECES

4.1 ABSTRACT

Based upon macroscopic analysis of tortoise faeces, the diet of angulate tortoises in the West Coast National Park (WCNP) included herbs, shrubs, grasses, restios, and succulent plants. Twelve different diet items, including insect parts, were identified in the WCNP scats. The only plants that were identified each season were grass and the shrub *Nylandtia spinosa*. A large proportion of the scats could not be identified and the percent composition by mass of unidentified plant material varied seasonally between 54% and 99% for scats from the WCNP. The percent composition of unidentified plant material was even higher (96-100%) for scats of Dassen Island (DI) tortoises. Only four diet items, all herbaceous plants, could be identified in their scats. The identification of dietary items at both study sites was influenced strongly by plant part; seeds and stems were most easily recognised. Most of the unidentified material had a fibrous or pulpy appearance, indicating that most plant material was at least partially digested. Digestion of fibrous plant material was probably facilitated by cellulolytic bacteria in the large hindgut of the tortoises. Seeds formed an important constituent of the diet. Overall, seeds contributed 23% to faecal mass of WCNP tortoises and reached a maximum value of 51% in spring. On DI, seeds contributed 6% to the faecal mass with the highest value (19%) in winter. Many fruits and seeds appeared intact or only partially digested, indicating that angulate tortoises may be important agents for seed dispersal in the southwestern Cape. Tortoise scats at both study sites contained sand, with higher incidences on DI than in the WCNP. The faecal samples from DI contained sand in three of the four seasons, and the sand made up 28% of the faecal mass in spring.

4.2 INTRODUCTION

Tortoises are herbivores and require cellulolytic microflora in their alimentary tracts to digest the cell walls of plants in their diet (Bjorndal 1987). The digestive efficiency of tortoises varies considerably and is dependent mainly on the plant species ingested and their phenological stages (Bjorndal & Bolton 1993; Nagy *et al.* 1998). Tortoises do not masticate their food but tear-off small pieces from plants and consume the pieces whole (Balsamo *et al*. 2004; Strong & Fragoso 2006). Consequently, the analyses of scats from herbivorous reptiles such as leopard tortoises have shown that ingested plant material may appear to differ little from their pre-ingested state (Milton 1992).

A simple and easy method to study the diet of tortoises would be to evaluate the scats macroscopically. This method requires relatively little training as dietary items observed in scats can be compared directly to reference material collected in the animals' habitat. Milton (1992) used macroscopic evaluation of faecal samples to identify 75 species of plants in the scats of leopard tortoises in the southern Karoo, South Africa. Macroscopic evaluation is also a highly suitable method to study seed ingestion by tortoises, as has been shown for *Testudo graeca* in Spain (Cobo & Andreu 1988) and for *Geochelone carbonaria* and *G. denticulata* in northwestern Brazil (Strong & Fragoso 2006).

Chersina angulata occurs in several habitat types (Branch 1989) and is thus exposed to a variety of vegetation types and potential dietary items. Here I report seasonal changes in the diet of *C. angulata* at two study sites in the southwestern Cape, as assessed through macroscopic evaluation of the tortoises' scats.

4.3 MATERIALS AND METHODS

4.3.1 Study sites

I studied the feeding ecology of *Chersina angulata* in the West Coast National Park (WCNP, 30 000 ha, 33°13'S, 18°09'E) and on Dassen Island (DI, 222 ha, 33°25'S, 18°06'E) over four seasons from March 1999 to February 2000. Detailed descriptions of the study sites and climate are provided in Chapters 2 and 3.

4.3.2 Faecal samples

During each study period (see Table 3.1 in Chapter 3), I collected scats from angulate tortoises in and around the study quadrats for macroscopic analysis. I collected 15 faecal samples each season at each site, except in spring 1999 when only 13 samples were collected in the WCNP. When tortoises were encountered in the field and were lifted, many excreted some faecal droppings. The fresh faecal pellets were placed in 50 ml labelled vials and air-dried. Samples were labelled with the date and site at which the faecal material was collected. After the scats were dry, the samples were weighed and the vials were sealed and stored in a location devoid of moisture to prevent fungal growth on the scats.

The dried scats were too hard and compacted to be dissected without further fragmenting the brittle plant parts in the scats. Therefore, before dissecting the scats, I placed the scats in a dilute solution of hydrochloric acid and distilled water for 30 to 60 minutes to soften the faecal material. When the softened material could be teased apart, each sample was strained through three sieves (2 mm, 1 mm and 63 micron), washed with distilled water, and air-dried.

Using a dissecting microscope (Vickers Limited, Model 177359, Japan) with a maximum magnification of 45x, I sorted faecal components into leaves, fruits, seeds, seed capsules, stems, unidentified (UI) plant material, animal material, sand and stone. Subsequently, the individual pieces were sorted and identified to the species level, where possible, by comparison with reference material. Each individual group was then weighed with an analytical balance to the nearest 0.0001 mg and stored in FAA (formaldehyde : glacial acetic acid : 70% ethanol, in the proportion 0.5 : 0.5 : 9.0).

4.3.3 Macroscopic identification of plants

To aid with the macroscopic identification of plant fragments in the scats, I collected leaves, flowers and seeds of plants within and around the study quadrats throughout the year. The plant parts were stored in labelled plastic bags. Unknown plants were identified by a plant taxonomist in the Department of Biodiversity and Conservation Biology at the University of the Western Cape. The plant reference material was stored in a freezer at –18 °C until needed.

Macroscopic identification of plant fragments in scats was limited to the comparison of leaf venation patterns, laminar shape, leaf margin type, the surface texture of the plant parts, and the size and shape of the fruits and seeds. The presence of trichomes was used to identify plant parts whenever trichomes were macroscopically visible. The presence of trichomes were treated with care, however, as it was not possible to determine macroscopically if the trichomes were glandular or non-glandular (Stace 1965).

4.3.4 Data analyses

4.3.4.1 Faecal samples

Small losses of material may have occurred during processing, so I did not use the mass of the intact scats in the analysis. I summed the masses of the individual dietary items to derive a total mass for each faecal sample. Similarly, for each sample I calculated a total mass for plant material (including UI material), animal material (insect parts), and inorganic material (sand and stone). Because the size of individual faecal samples differed, I expressed each diet component as percent mass. Percent mass for individual plant items was expressed relative to the total mass for all plant items to allow direct comparisons of plant items among seasons and sites. Percent mass for animal and inorganic material, however, was expressed relative to total scat mass (plant, animal and inorganic material). For convenience, the percent mass of the scat constituents for each season and for all seasons combined was summarised as mean and 95% confidence intervals, even in instances when the distributions were non-parametric.

In addition to evaluating the tortoises' diet by percent mass, I also evaluated the results on a presence-absence basis (MacDonald & Mushinsky 1988). For comparison to results from focal observations (Chapter 3) and histological analyses (Chapter 5), the presence of a particular species in a faecal sample was regarded as a single feeding record and the different plant species or food items in a scat were regarded as separate feeding records. I calculated percent occurrence of a dietary item as the number of scats containing that particular item divided by the total number of scats collected during that season. When calculating percent composition by presence-absence, I considered all diet items and thus included animal material in the analysis. Percent composition was calculated as the records for a particular item divided by the total number of records of all plant taxa and animal items for the relevant period. The percent composition for inorganic material in the scats was calculated as the records for inorganic material divided by the total records of all items in the scats collected during the relevant period.

I used the same principles when calculating the percent composition by mass, and percent occurrence and composition by presence-absence for the plant parts and growth forms. The categories for plant parts consisted of leaves, seeds, seed capsules, stems and UI plant material. The categories for growth forms included succulents, non-succulent herbs, non-succulent shrubs, grasses and UI plant material. The single record for restioids during summer in the WCNP was combined with the grasses.

4.3.4.2 Statistical analyses

Statistical tests were done with SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.) and all tests were considered significant at $P \leq 0.05$. The data rarely satisfied assumptions of normality and homoscedasticity but log transformation often allowed parametric analyses. Whenever it was possible, I used a two-way ANOVA (F_{df}) to simultaneously test for more than one effect (e.g., site and season, or season and diet item). A two-way ANOVA was followed by the Student-Newman-Keul's (SNK) post hoc test to evaluate differences among groups for the categories of diet items, sites or seasons. When the data did not meet the assumptions for a two-way ANOVA, I used a one-way ANOVA (F_{df}) and SNK post hoc test, or a Kruskal-Wallis ANOVA (H_{df}) and Dunn's post hoc test, to evaluate the effect of season on diet items. To evaluate differences among diet items within a site and within a particular season, I used Friedman's repeated measures ANOVA (χ^2_{df}) followed by the SNK post hoc test. A Mann-Whitney Rank Sum Test ($T_{n,n}$) was used to compare diet items between sites. I used Chi-square contingency table analysis or Fisher exact test to test for differences in the frequencies (occurrences) of dietary food items, between sites and among seasons. I followed the guidelines of Zar (1999) to test for bias in Chi-square contingency table analyses and tested the average expected frequency with the equation n / (rc), where n is the total records, r is the number of rows and c is the number of columns. When using multiple univariate tests, I applied the Bonferroni procedure to adjust the significance level in the family of tests across which the Type I error rate had to be controlled (Quinn & Keough 2002).

4.4 RESULTS

4.4.1 Mass of faecal samples

Overall, the difference in faecal mass of angulate tortoises from the WCNP (N = 58) and DI (N = 60) approached significance ($F_{1,110} = 3.85$, $P = 0.052$); faecal mass differed between the two sites in summer but the differences were not significant for the other seasons (Table 4.1). There was a strong seasonal effect on faecal mass ($F_{3,110} = 13.90$, $P < 0.0001$) and an interaction between site and season ($F_{3,110} = 5.88$, $P = 0.00092$).

Overall, winter and spring faecal masses were similar, but were higher than the faecal mass of autumn and summer, while autumn faecal mass was higher than the faecal mass in summer. Faecal samples from the WCNP had a lower mass in summer than in the other seasons, whereas faecal samples from DI had a higher mass in spring than in autumn and summer.

Table 4.1 Mean mass (± CI, in grams) of scats collected from *Chersina angulata* in the West Coast National Park (WCNP; $N = 58$) and on Dassen Island (DI; $N = 60$).

	Autumn	Winter	Spring	Summer
WCNP	0.74±0.17	1.12±0.37	0.92±0.22	0.26±0.06
DI	0.56±0.11	1.13±0.47	1.38±0.39	0.71±0.20

4.4.2 Diet composition

4.4.2.1 Diet composition in the WCNP

Twelve plants species/groups were identified in the scats of tortoises from the WCNP (Table 4.2). Because the masses did not satisfy the assumptions of a two-way ANOVA, I evaluated the effects of season and plant species/groups separately. Within a season and for all seasons combined, the difference in the percent mass of the plant species/groups was highly significant (all $\chi^2_{11} > 64.6$, $P < 0.0001$), but post-hoc results showed that only the UI plant mass differed from the mass of other plant taxa. The large proportion of UI plant material, in combination with the large confidence intervals for the mean mass of individual plant taxa, rendered few statistical tests significant. The large confidence intervals of the diet items were due to wide differences in the faecal composition of individual tortoises within a season. For example, during spring in the WCNP, only three of the 13 faecal samples contained *Trichogyne verticillata*, and the percent contribution of this species to the diet (faeces) of these tortoises was 1%, 38% and 89%.

Three plant species/groups were detected each season in the tortoises' faeces: *Nylandtia spinosa*, grass and UI plant material. The seeds of *N. spinosa* contributed 17% and 10%, respectively, to the spring and summer plant mass in the faeces (Table

4.2). The percent mass of plant diet items differed significantly among seasons for UI plant material (H_3 = 31.80, P < 0.0001), *Geranium* sp. (H_3 = 14.57, P = 0.0022) and *Psoralea repens* (H_3 = 9.23, P = 0.026), and approached significance for *T. verticillata* (H_3 = 7.30, P = 0.063) and *N. spinosa* (H_3 = 7.55, P = 0.056). The percent mass for UI plant material was higher in winter than in spring and summer, and the percent mass in autumn was higher than in summer.

There was sand, but no stones, in the faecal samples of angulate tortoises from the WCNP and the sand only occurred in scats collected in autumn. Season had a significant effect on percent mass of sand (H_3 = 12.08, P = 0.0071). Only one faecal sample collected in summer contained remnants of an insect.

The diet composition, by presence-absence, of angulate tortoises in the WCNP (Table 4.3) corresponded broadly to the percent mass results. The percent composition and percent occurrence of the faecal (diet) items differed among the seasons (composition: $F_{3,36}$ = 3.90, P = 0.016; occurrence: $F_{3,36}$ = 5.30, P = 0.0039). For percent composition, winter and summer results differed significantly, whereas winter values differed from all other seasons for the occurrence data. Percent composition and occurrence varied considerably among diet items ($F_{12,36}$ = 6.48, P < 0.0001 and $F_{12,36}$ = 27.55, P < 0.0001, respectively). The percent composition of UI plant material differed from all other diet items except for *N. spinosa* and grass, while values for both *N. spinosa* and grass exceeded values for restioids and insect parts, and percent composition for grass was also larger than that of *Ruschia macowanii*. The percent occurrence of UI plant material exceeded the percent occurrence of all other groups. The percent occurrence of grass was higher than all remaining groups except for *N. spinosa*, and the percent occurrence of *N. spinosa* differed from that of *T. verticillata*, *Albuca* sp., *H. niveum*, *R. macowanii*, restioids and insects.

Table 4.2 Percent composition by mass (mean ± CI) of plants and non-plant items in the scats of *Chersina angulata* in the West Coast National Park. The *N* values represent the number of scats per season. Percentages for plant items are expressed relative to the mass of total plant material, whereas the non-plant components are expressed relative to the total mass of the scats.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=13)	Summer (*N*=15)	Totals (*N*=58)
Albuca sp. leaves	0.59±1.15	0	0.03±0.05	6.86±9.49	1.93±2.53
Cystocapnos vesicaria total	0.33±0.44	0	2.21±3.81	0.43±0.64	0.69±0.88
Capsule	0.33±0.44	0	1.65±2.84	0.43±0.64	0.57±0.67
Seeds	0	0	0.56±0.98	0	0.13±0.22
Geranium sp. seeds	0	0	10.78±10.72	0.49±0.95	2.54±2.61
Grass total	1.70±1.84	0.28±0.39	1.61±1.16	3.75±4.72	1.84±1.35
Leaves	0.79±0.95	0.28±0.39	0.47±0.61	1.15±1.67	0.68±0.52
Seeds	0.90±1.05	0	1.14±1.09	2.60±4.24	1.16±1.15
Helichrysum niveum total	0.19±0.37	0	0	0.69±0.91	0.23±0.26
Leaves	0.19±0.37	0	0	0.39±0.75	0.15±0.21
Seeds	0	0	0	0.30±0.58	0.08±0.15
Nylandtia spinosa total	3.43±4.78	0.01±0.02	17.17±12.79	13.21±14.34	8.15±5.04
Leaves	0.29±0.39	0.01±0.02	0.43±0.49	2.74±5.24	0.88±1.36
Seeds	3.14±4.72	0	16.74±12.62	10.47±13.89	7.27±4.89
Psoralea repens leaves	1.36±1.98	0	0	4.41±6.85	1.49±1.86
Restioid leaves	0	0	0	0.26±0.51	0.07±0.13
Ruschia macowanii leaves	0	0.29±0.56	0	0.19±0.38	0.12±0.17
Senecio elegans seeds	0.62±1.02	0	0.08±0.16	10.80±10.44	2.97±2.90
Trichogyne verticillata seeds	0	0	9.82±14.11	4.81±9.43	3.44±4.01
UI plant material total	91.79±6.72	99.42±0.82	58.31±15.56	54.12±16.58	76.52±7.66
Fibre or pulp	67.26±13.68	98.47±1.80	35.36±13.56	2.39±4.68	51.40±10.53
Leaves	2.87±3.59	0.08±0.12	5.76±4.52	11.81±11.19	5.11±3.32
Seeds	9.75±9.03	0.87±1.70	11.77±12.39	1.11±1.15	5.67±3.78
Stems	11.91±11.40	0	5.41±1.87	38.82±15.68	14.33±6.27
Insect parts	0	0	0	0.09±0.17	0.02±0.04
Sand	3.41±3.59	0	0	0	0.88±0.99

Table 4.3 Percent composition (occurrence) by presence-absence of plants and non-plant items in the scats of *Chersina angulata* in the West Coast National Park. The *N* values represent the number of scats per season. Percentage composition of diet items is expressed relative to the total scores for plant and animal items in the scats, whereas percent composition of sand is expressed relative to the scores for all items in the scats.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=13)	Summer (*N*=15)	Totals (*N*=58)
Albuca sp.	2.78 (6.67)	0	2.50 (7.69)	4.44 (13.33)	2.86 (6.90)
Cystocapnos vesicaria	5.56 (13.33)	0	10.00 (30.77)	4.44 (13.33)	5.71 (13.79)
Geranium sp.	0	0	12.50 (38.46)	2.22 (6.67)	4.29 (10.34)
Grass	16.67 (40.00)	10.53 (13.33)	17.50 (53.85)	11.11 (33.33)	14.29 (34.48)
Helichrysum niveum	2.78 (6.67)	0	0	6.67 (20.00)	2.86 (6.90)
Insect parts	0	0	0	2.22 (6.67)	0.71 (1.72)
Nylandtia spinosa	11.11 (26.67)	5.26 (6.67)	15.00 (46.15)	13.33 (40.00)	12.14 (29.31)
Psoralea repens	13.89 (33.33)	0	0	6.67 (20.00)	5.71 (13.79)
Restioid	0	0	0	2.22 (6.67)	0.71 (1.72)
Ruschia macowanii	0	5.26 (6.67)	0	2.22 (6.67)	1.43 (3.45)
Senecio elegans	5.56 (13.33)	0	2.50 (7.69)	8.89 (26.67)	5.00 (12.07)
Trichogyne verticillata	0	0	7.50 (23.08)	2.22 (6.67)	2.86 (6.90)
UI plant material	41.67 (100.00)	78.95 (100.00)	32.50 (100.00)	33.33 (100.00)	41.43 (100.00)
Sand	10.00 (26.67)	0	0	0	2.78 (6.90)

4.4.2.2 Diet composition on DI

Cystocapnos vesicaria was the only plant species identified in the scats for both sites. Only five plant species/groups were identifiable in the DI scats and UI plant material contributed more than 95%, each season, to the mass of plant material in the scats (Table 4.4). For all seasons combined, the percent mass differed among plant species or groups ($\chi^2_4 = 206.8$, $P < 0.0001$). The percent mass of UI plant material exceeded the percent mass of the other plant species, but the other items did not differ from one another.

The percent mass of *Urtica urens* and UI plant material differed significantly among seasons (all $H_3 > 31.8$, $P < 0.0001$). The spring mass for *U. urens* exceeded the values in the other seasons, whereas the spring mass for UI plant material was lower than in the other seasons (based on medians).

In general, the percent composition and percent occurrence by presence-absence of diet items in the scats from DI (Table 4.5) showed the same pattern as the composition by percent mass. All faecal samples contained UI plant material, and in spring, *U. urens* occurred in more than 70% of the tortoises' scats. Season had no effect on percent composition and percent occurrence, but the effect of faecal category (species or group) was significant for percent composition ($F_{4,12} = 8.30$, $P = 0.0019$) and for percent occurrence ($F_{4,12} = 7.64$, $P = 0.0027$). The percent composition and percent occurrence of UI plant material was higher than the values for all other plant groups.

The scats of angulate tortoises from DI did not contain animal material but sand/stone was present in three seasons (Table 4.4). One scat collected in winter and two scats collected in summer contained stones, while sand contributed more than 27% to the faecal mass in spring. The percent mass of sand/stone differed significantly among seasons ($H_3 = 42.87$, $P < 0.0001$) and was higher in spring than in the other seasons. More than 90% of the tortoises' scats contained sand/stone (Table 4.5).

Table 4.4 Percent composition by mass (mean ± CI) of plants and non-plant items in the scats of *Chersina angulata* on Dassen Island. The *N* values represent the number of scats per season. Percentages for plant items are expressed relative to the mass of total plant material, whereas the non-plant component is expressed relative to the total mass of the scats.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=15)	Summer (*N*=15)	Totals (*N*=60)
Albuca flaccida leaves	0.97±1.89	0	0.06±0.11	0	0.26±0.47
Cystocapnos vesicaria seeds	0	0.65±1.28	0.02±0.03	0	0.17±0.32
Trachyandra divaricata stalk	3.33±6.53	0	0	0	0.83±1.63
Urtica urens total	0	0.0043±0.0085	2.84±3.21	0	0.71±0.84
Leaves	0	0	0.15±0.20	0	0.037±0.051
Seeds	0	0.0043±0.0085	2.69±3.07	0	0.67±0.81
UI plant material total	95.70±6.67	99.34±1.29	97.09±3.19	100	98.03±1.88
Fibre or pulp	95.31±6.64	74.03±9.26	96.68±3.18	99.30±0.74	91.33±3.87
Leaves	0.11±0.19	2.29±2.31	0.028±0.037	0.21±0.41	0.66±0.62
Seeds	0.28±0.55	18.43±8.28	0.38±0.74	0.49±0.66	4.89±2.85
Stems	0	4.60±3.17	0	0	1.15±0.92
Sand/Stone	0	2.01±3.94	27.73±6.88	1.78±2.79	7.88±3.58

Table 4.5 Percent composition (occurrence) by presence-absence of plants and non-plant items in the scats of *Chersina angulata* on Dassen Island. The *N* values represent the number of scats per season. Percentage composition of plant items is expressed relative to the total scores for plant items in the scats, whereas sand or stone is expressed relative to the scores for all items in the scats.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=15)	Summer (*N*=15)	Totals (*N*=60)
Albuca flaccida	5.88 (6.67)	0	3.57 (6.67)	0	2.60 (3.33)
Cystocapnos vesicaria	0	5.88 (6.67)	3.57 (6.67)	0	2.60 (3.33)
Trachyandra divaricata	5.88 (6.67)	0	0	0	1.30 (1.67)
Urtica urens	0	5.88 (6.67)	39.29 (73.33)	0	15.58 (20.00)
UI plant material	88.24 (100.00)	88.24 (100.00)	53.57 (100.00)	100.00 (100.00)	77.92 (100.00)
Sand/Stone	0	5.56 (6.67)	33.33 (93.33)	11.76 (13.33)	18.09 (28.33)

4.4.3 Plant parts in the diet

4.4.3.1 Plant parts in the diet of tortoises in the WCNP

The percent mass of the plant part categories in the WCNP scats differed within each season and for all seasons combined (Table 4.6; all $\chi^2 > 36.4$, $P < 0.0001$). The percent mass for UI plant material was higher than the mass of all other plant parts and the percent mass of seeds exceeded the mass of the other categories. While the mass of leaves and stems did not differ, they were higher than the mass of seed capsules. In autumn and winter, percent mass for UI plant material was highest and the remaining categories did not differ, except that the mass for capsule was significantly lower than all other categories in autumn. In spring, seeds and UI plant material had the highest mass and capsule had the lowest mass. In summer, there was no difference among the mass of stems, seeds and leaves, which were all higher than the mass for UI plant material and capsule.

WCNP tortoises had leaves, seeds and UI plant material in their scats during each season (Table 4.6). The percent mass of stems differed significantly among the seasons ($H_3 = 35.68$, $P < 0.001$). Summer and spring values did not differ but the percent mass in summer was higher than in autumn and winter, and the percent mass in spring was higher than in winter (based on medians). The contribution of leaves to the diet of the tortoises differed among seasons ($F_{3.54} = 12.59$, $P < 0.0001$), with summer values higher than in the other seasons, while spring and autumn masses exceeded the percent mass in winter (all $P < 0.0079$). The percent mass of seeds in the scats was higher in spring than in all other seasons, whereas percent mass for seeds was lower in winter than in all other seasons ($F_{3.54} = 22.64$, $P < 0.0001$). Percent mass for UI plant material changed significantly with season ($H_3 = 48.38$, $P < 0.0001$); percent mass in winter was higher than summer and spring masses, while the percent mass in autumn was higher than the percent mass in summer. There was no effect of season on the percent mass of capsules ($P = 0.50$).

In spring, all the scats contained seeds and stems, while all the summer scats contained leaves and stems (Table 4.7). Although diet category had a significant effect on percent composition ($F_{5,15} = 6.11$, $P = 0.0028$) and on percent occurrence ($F_{5,15} = 4.29$, $P = 0.013$), there were few significant differences among the categories. Insect parts had lower values than those of leaves, seeds and UI plant material, and the percent composition of stems also exceeded the percent composition of insect parts. Season had no effect on percent composition or percent occurrence (all $P > 0.17$).

Table 4.6 Percent composition by mass (mean ± CI) of plant parts in the scats of *Chersina angulata* in the West Coast National Park. The *N* values represent the number of scats per season. Percentages for plant parts are expressed relative to the mass of total plant material.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=13)	Summer (*N*=15)	Totals (*N*=58)
Capsule	0.33±0.44	0	1.65±2.84	0.43±0.64	0.57±0.67
Leaves	6.09±3.81	0.66±0.81	6.69±4.30	27.80±15.09	10.43±4.87
Seeds	14.41±9.46	0.87±1.70	50.89±14.12	30.57±15.80	23.27±7.33
Stems	11.91±11.40	0	5.41±1.87	38.82±15.68	14.33±6.27
UI plant material	67.26±13.68	98.47±1.80	35.36±13.56	2.39±4.68	51.40±10.53

Table 4.7 Percent composition (occurrence) by presence-absence of plant parts and animal material in the scats of *Chersina angulata* in the West Coast National Park. The *N* values represent the number of scats per season. Percentage composition is expressed relative to the total scores for plant and animal items in the scat.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=13)	Summer (*N*=15)	Totals (*N*=58)
Capsule	4.26 (13.33)	0	3.85 (15.38)	4.26 (13.33)	3.59 (10.34)
Insect parts	0	0	0	2.13 (6.67)	0.60 (1.72)
Leaves	27.66 (86.67)	19.05 (26.67)	23.08 (92.31)	31.91 (100)	26.35 (75.86)
Seeds	25.53 (80.00)	9.52 (13.33)	25.00 (100)	27.66 (86.67)	23.95 (68.97)
Stems	10.64 (33.33)	0	25.00 (100)	31.91 (100)	19.76 (56.90)
UI plant material	31.91 (100)	71.43 (100)	23.08 (92.31)	2.13 (6.67)	25.75 (74.14)

4.4.3.2 Plant parts in the diet of tortoises on DI

The scats of angulate tortoises on DI did not contain seed capsules. The percent mass of the plant categories in the scats (leaves, seeds, stems and UI plant material) differed significantly within seasons and for all seasons combined (Table 4.8; all $\chi^2_4 > 48.2$, $P < 0.0001$). The percent mass of UI plant material was higher than the mass for all other plant parts in all seasons, while the percent mass for seeds was higher than the mass of leaves and stems in winter, spring, and overall.

There were seasonal differences in the percent mass of all plant parts (all $H_3 > 29.29$, $P < 0.0001$), except for leaves, which only approached the statistical criterion for significance ($P = 0.076$). The percent mass of UI plant material did not differ for autumn, spring and summer, but the mass for winter was lower than in the other seasons. The mean percent mass for seeds was higher in winter than in autumn and summer, and higher in spring than in autumn. The winter value for stems was higher than that of the other seasons.

Percent composition by presence-absence of plant parts in the scats of tortoises on DI (Table 4.9) did not differ significantly among seasons, but the effect of season approached significance for percent occurrence ($P = 0.064$). There were significant differences among plant parts for percent composition and percent occurrence (all $F_{3,9} > 7.50$, $P < 0.0081$); UI plant material values exceeded the values for leaves, seeds and stems. The percent occurrence values indicate that approximately 90% of the scats contained seeds during winter and spring.

4.4.3.3 Comparison between sites

For all seasons combined, the percent mass for leaves, seeds and stems was higher in tortoise scats from the WCNP than in the scats from DI, whereas DI scats had a higher mass for UI plant material than measured on WCNP scats (all $T_{58,60} > 2488$, $P < 0.0013$; Bonferroni adjusted significance level of $P = 0.0125$). Based on contingency table analysis of presence-absence counts of leaves, seeds, stems, and UI plant material, the occurrence of plant parts in the scats of WCNP and DI tortoises differed significantly in winter ($\chi^2_3 = 12.19$, $P = 0.0068$), spring ($\chi^2_3 = 13.29$, $P = 0.0040$), summer ($\chi^2_3 = 41.04$, $P < 0.0001$), and for the whole year ($\chi^2_3 = 22.22$, $P < 0.0001$). Autumn diets ($\chi^2_3 = 10.10$, $P = 0.018$) just failed significance relative to the Bonferroni adjusted P value of 0.01.

Table 4.8 Percent composition by mass (mean ± CI) of plant parts in the scats of *Chersina angulata* on Dassen Island. The *N* values represent the number of scats per season. Percentages for diet items are expressed relative to the mass of total plant material, exclusive of inorganic material.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=15)	Summer (*N*=15)	Totals (*N*=60)
Leaves	1.07±1.89	2.29±2.31	0.23±0.21	0.21±0.41	0.95±0.77
Seeds	0.28±0.55	19.09±7.97	3.09±3.07	0.49±0.66	5.74±2.88
Stems	3.33±6.53	4.60±3.17	0	0	1.98±1.84
UI plant material	95.31±6.64	74.03±9.26	96.68±3.18	99.30±0.74	91.33±3.87

Table 4.9 Percent composition (occurrence) by presence-absence of plant parts in the scats of *Chersina angulata* on Dassen Island. The *N* values represent the number of scats per season. Percentage composition of plant parts is expressed relative to the total scores for plant items in the scat, exclusive of inorganic material.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=15)	Summer (*N*=15)	Totals (*N*=58)
Leaves	15.00 (20.00)	15.22 (46.67)	15.15 (33.33)	5.00 (6.67)	13.45 (26.67)
Seeds	5.00 (6.67)	30.43 (93.33)	39.39 (86.67)	20.00 (26.67)	26.89 (53.33)
Stems	5.00 (6.67)	21.74 (66.67)	0	0	9.24 (18.33)
UI plant material	75.00 (100)	32.61 (100)	45.45 (100)	75.00 (100)	50.42 (100)

4.4.4 Growth forms in the diet

4.4.4.1 Growth forms in the diet of tortoises in the WCNP

Apart from the UI plant material, the scats of angulate tortoises in the WCNP contained grasses (including restios), succulents, non-succulent herbs, and non-succulent shrubs (Table 4.10). Succulents included *Ruschia macowanii*; herbs included *Albuca* sp., *Cystocapnos vesicaria, Geranium* sp., *Trichogyne verticillata* and *Senecio elegans*; and shrubs included *Helichrysum niveum, Nylandtia spinosa* and *Psoralea repens*.

The percent mass of the growth forms differed significantly within each season and for all seasons combined (all $\chi^2_4 > 27.73$, $P < 0.0001$). For all seasons combined, the percent mass differed among all growth forms except between shrubs and herbs (UI plant material > shrubs = herbs > grass > succulents). The autumn percent mass of UI plant material exceeded that of shrubs, and both masses were higher than that of the other growth forms. Winter percent mass was higher for UI plant material than for the other categories. In spring, the sequence for percent mass was UI plant material > herb > shrub = grass > succulent, while for summer the sequence was UI plant material > shrubs = herbs > grass > succulents.

The percent mass for grass and for succulents in the faecal samples did not differ among seasons (all $P > 0.17$), but seasonal differences were detected for herbs, shrubs and UI plant material (all $H_3 > 12.87$, $P < 0.0049$; Table 4.10). Percent mass for herbs in winter was lower than in spring and summer, whereas summer mass for shrubs exceeded winter mass. The mean percent mass of UI plant material was higher in winter than in summer and spring, while autumn values also exceeded summer values.

There was no effect of season on the percent composition by presence-absence of growth forms in the WCNP (Table 4.11), but faecal composition varied among plant categories ($F_{5,15} = 9.37$, $P = 0.00033$) with UI plant material having higher values than the other categories. Concerning percent occurrence, the effect of season just failed significance ($P = 0.080$), but the percent occurrence differed among growth forms ($F_{5,15} = 17.5$, $P < 0.00001$). The occurrence of UI plant material in the scats was higher than the occurrence of the other categories, and the occurrence of shrubs, herbs and grasses was higher than the occurrence of succulents and insect parts.

Table 4.10 Percent composition by mass (mean ± CI) of growth forms in the scats of *Chersina angulata* in the West Coast National Park. The *N* values represent the number of scats per season. Percentages for growth forms are expressed relative to the mass of total plant material.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=13)	Summer (*N*=15)	Totals (*N*=58)
Grass / restio	1.70±1.84	0.28±0.39	1.61±1.16	4.00±5.19	1.91±1.46
Herbs	1.54±1.67	0	22.92±15.40	23.38±13.80	11.58±5.65
Shrubs	5.78±4.87	0.04±0.06	17.17±12.79	23.65±16.74	11.47±5.74
Succulents	0	0.29±0.56	0	0.19±0.38	0.12±0.17
UI plant material	90.98±6.66	99.39±0.82	58.31±15.56	48.77±15.84	74.92±7.83

Table 4.11 Percent composition (occurrence) by presence-absence of growth forms and animal material in the scats of *Chersina angulata* in the West Coast National Park. The *N* values represent the number of scats per season. Percentage composition of diet categories is expressed relative to the total scores for plant and animal items in the scats.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=13)	Summer (*N*=15)	Totals (*N*=58)
Grass / restio	17.14 (40.00)	10.00 (13.33)	19.44 (53.85)	11.63 (33.33)	14.93 (34.48)
Herbs	11.43 (26.67)	0	27.78 (76.92)	23.26 (66.67)	17.91 (41.38)
Insect parts	0	0	0	2.33 (6.67)	0.75 (1.72)
Shrubs	28.57 (66.67)	10.00 (13.33)	16.67 (46.15)	25.58 (73.33)	21.64 (50.00)
Succulents	0	5.00 (6.67)	0	2.33 (6.67)	1.49 (3.45)
UI plant material	42.86 (100)	75.00 (100)	36.11 (100)	34.88 (100)	43.28 (100)

4.4.4.2 Growth forms in the diet of tortoises on DI

Most of the plant material in the scats of angulate tortoises from DI could not be identified and the all identified fragments were herbaceous (Table 4.12). Herbs made a higher contribution to the spring scats than in the other seasons (based on ranked data in a Kruskal-Wallis ANOVA; $H_3 = 27.99$, $P < 0.0001$). Percent occurrence values showed that there was UI plant material all scats and that herbaceous species occurred in 80% of the scats in spring (Table 4.13).

4.4.4.3 Comparison between sites

The mean percent mass of UI plant material was higher in the tortoise scats from DI than in the scats from the WCNP ($T_{58,60} = 2436$, $P < 0.0001$), whereas the mean percent mass for herbs was higher in the WCNP scats than in the DI scats ($T_{58,60} = 3825$, $P = 0.044$; Tables 4.10 and 4.12). The occurrence of herbs and UI plant material in the tortoises' scats from the WCNP and DI differed only in summer (Fisher exact test, $P = 0.0063$; Tables 4.11 and 4.13).

Table 4.12 Percent composition by mass (mean ± CI) of growth forms in the scats of *Chersina angulata* on Dassen Island. The *N* values represent the number of scats per season. Percentages for diet categories are expressed relative to the mass of total plant material, exclusive of inorganic material.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=15)	Summer (*N*=15)	Totals (*N*=60)
Herbs	4.30±6.67	0.66±1.29	2.91±3.19	0	1.97±1.88
UI plant material	95.70±6.67	99.34±1.29	97.09±3.19	100	98.03±1.88

Table 4.13 Percent composition (occurrence) by presence-absence of growth forms in the scats of *Chersina angulata* on Dassen Island. The *N* values represent the number of scats per season. Percentage composition of growth forms is expressed relative to the total scores for plant items in the scat.

	Autumn (*N*=15)	Winter (*N*=15)	Spring (*N*=15)	Summer (*N*=15)	Totals (*N*=60)
Herbs	11.76 (13.33)	6.25 (6.67)	44.44 (80.00)	0	20.00 (25.00)
UI plant material	88.24 (100)	93.75 (100)	55.56 (100)	100.00 (100)	80.00 (100)

4.5 DISCUSSION

4.5.1 Unidentified plant material in the scats

The scats of angulate tortoises consisted mainly of UI plant material and the number of diet items identified was relatively low, particularly on DI. During the dry season, UI plant material was dry and fibrous, whereas UI faecal material in the wet season had a pulpy texture. It seems likely that the explanation for the high incidence of UI plant material may differ for the wet and dry seasons.

At the study sites, environmental conditions during summer and autumn are hot and dry. In this winter rainfall region, plant growth in the dry season is slow or absent and plant material available to tortoises are probably quite fibrous. Plant cell walls consist largely of structural carbohydrates, such as cellulose, and with advancing cellular maturity, many plants accumulate additional cellulose and lignin in their cell walls (Robbins 1983; Huston & Pinchak 1991). Herbivorous reptiles do not synthesize enzymes to digest cellulose but have microbes in their digestive tracts to digest cellulose through fermentation (Throckmorton 1973; Bjorndal 1985; Bjorndal 1991). Lignin, in contrast, is largely indigestible even by cellulolytic bacteria and protozoa (Robbins 1983).

Mechanical breakdown facilitates the digestion of fibrous plant material by increasing the surface area available for the action of cellulolytic microbes (Robbins 1983; Caughley & Sinclair 1994). Herbivorous reptiles do not masticate their food (Sokol 1971; Throckmorton 1973; Balsamo *et al.* 2004; Strong & Fragoso 2006) but bite and tear off pieces of plant material that are ingested whole. Digestion takes place in the stomach and intestine and the large hindgut of angulate tortoises (MD Hofmeyr, pers. comm.) is probably important in the symbiotic digestion of structural plant parts. High temperatures in the dry season most likely increased the number or efficacy of gut microbes that facilitate fermentation of fibrous plants (Bjorndal 1987).

Focal observations have shown that angulate tortoises at both study sites ingest large quantities of dry plant material in the dry season (see Tables 3.4 and 3.5), similar to findings for *Gopherus agassizii* (Nagy *et al.* 1998). Dry plant materials probably have a high fibre content but the natural degradation processes may have rendered the plant material more accessible to the digestive actions of the symbiotic microbes and the tortoise's digestive enzymes. Wind blown sand can abrade the superficial layers of leaf surfaces (Cleugh *et al.* 1998) of fresh and dry plant material, to expose the softer tissues to digestion. These processes would not only facilitate digestion of dry plant material but may also have destroyed identifiable characters, contributing to the high percentage of UI plant material in scats during the dry season. On DI, rabbit faeces formed an important component of the angulate tortoise's diet during the dry season (see Chapter 3) and it is reasonable to expect that the original plant material would no longer be identifiable.

Winter rains stimulate plant growth and new plant growth has relatively little structural components, making new growth easy to digest (Robbins 1983; Huston & Pinchak 1991). The activity level of the angulate tortoises was higher in winter and spring than in the dry season (see Chapter 3) and the tortoises probably consumed large quantities of good quality food in the wet season. This may explain why dry faecal mass was higher during the wet season than during the dry season. At both study sites, the availability of annual and herbaceous plants increased substantially during the wet season (see Chapter 2), while focal studies on angulate tortoises showed a high consumption of seedlings in the wet season (see Chapter 3). The high level of UI plant material in the scats of angulate tortoises during the wet season was most likely the remnants of easily digested herbaceous plants that were consumed in large quantities.

A strong botanical training (e.g., Milton 1992), or histological analyses of faeces (see Chapter 5), should enhance the identification of plant species and parts in tortoise faeces. Nevertheless, it seems that angulate tortoises may have a relatively efficient digestive system, and select highly digestible food items when possible, so that few items in the faeces are unaltered and easily recognisable. Macroscopic scatological evaluations are valuable in dietary analyses, but this method is not very suitable for studying the diet of herbivores with efficient digestion or strong preferences for low fibre foods.

4.5.2 Diet mixing: growth forms and plant parts in the diet

Succulent plants had a low occurrence in the scats of angulate tortoises in the WCNP and were absent from the DI scats. The focal studies (see Chapter 3) also showed a low incidence of succulents in the diet despite the high relative cover of succulents on DI and a moderate abundance in the WCNP (see Fig. 2.4). The succulents in the WCNP were perennials possessing thick epidermi and were tough to the touch (pers. obs.). It may have been difficult or impossible for tortoises to tear off and consume large, easily identifiable pieces of perennial succulents because of their tough epidermi (e.g., *Carpobrotus edulis* and *Carpobrotus quadrifidus*), reducing their representation in the faeces. The slender leaves of *Ruschia macowanii* may have contributed to this succulent species being detected in the scats. The dominant succulent plants available for consumption on DI were *Mesembryanthemum crystallinum* and *Tetragonia fruticosa*. Tortoises may have avoided consuming these species due to their high concentrations of ions (e.g., *Mesembryanthemum crystallinum* concentrates potassium and sodium; Adams *et al*. 1998), which may make them unpalatable to tortoises.

The low contribution of grass to the diet of angulate tortoises was surprising because grasses form an important constituent in the diet of several tortoise species (Milton 1992; Nagy *et al*. 1998; Mushinsky *et al*. 2003). It is possible that angulate tortoises consumed mainly the young shoots of annual and perennial grasses, which would be more difficult to detect macroscopically because young shoots have higher digestibility (Huston & Pinchak 1991). Annual grasses may also be more palatable than perennial grasses because annual plants spend little or none of their resources to produce anti-herbivore defences (Cates & Orians 1975).

The relatively high values recorded for herbs and shrubs in the macroscopic evaluation are mainly due to the presence of their fruits or seeds, which often remained intact and thus were easy to identify. The shrub, *Nylandtia spinosa*, was the most prominent diet item identified in the WCNP mainly due to a high consumption the plant's fruits in spring and summer. The fruits are small enough to swallow completely, and some fruits in the scats were unaltered while others were partially digested (pers. obs.). It is known that the fruits of *N. spinosa* are edible and widely used by birds and tortoises, hence the common name of the plant, tortoise berry (Van Rooyen & Steyn 1999).

Fruits and seeds are storage tissue with high energy content, but the protein content of seeds can be low (Janzen *et al*. 1985; Caughley & Sinclair 1994). Tortoises may thus consume seeds in high quantities, when available, to satisfy their energy requirements. However, fruits and seeds often appear intact in the scats and it is not clear what the nutritional gain of the tortoise may be. As is the case for *N. spinosa*, only a certain percentage, or a certain part, of the fruits of other species may have been digested by the tortoise. This seems to be the case for *Cystocapnos vesicaria*, where the scats of angulate tortoises in the WCNP contained seeds and remnants of the capsule, but the scats from DI contained only the seeds. Although angulate tortoises may have eaten seeds *per se*, in most instances the primary diet items were probably the flower heads or unripe ovaries of the plants. In these instances, digestion of the petals, nectar, pollen and ovaries would have provided important nutrient while the seeds were left intact or partially digested. In this study, *C. angulata* consumed seeds of at least eight plant species and *C. angulata* is potentially an important agent of seed dispersal in both the WCNP and on DI. Several studies have shown that tortoises are important agents of seed dispersal (Milton 1992; Varela & Bucher 2002; Strong & Fragoso 2006) and, in a few instances, germination success of the seeds increased after passing through a tortoise's digestive system (Cobo & Andreu 1988).

The proportion of leaves and stems in the scats of angulate tortoises did not differ although leaves generally have lower fibre content than stems, and stems have lower digestibility (Huston & Pinchak 1991). It is not clear if the ingestion of stems was deliberate or incidental to the consumption of leaves. Young leaves have a higher energy and protein content than old leaves (Caughley & Sinclair 1994), and in the winter rainfall region more young leaves would be available in winter and spring than in summer. Nevertheless, the ingestion of leaves in the WCNP appears to be highest in summer. It seems likely that young leaves that were consumed in winter may form part of the large UI plant category because improved digestibility would have rendered the leaves unidentifiable.

Chersina angulata consumed a mixed diet that consisted of a variety of plant parts, different growth forms and even included animal material. The benefits of a mixed diet have been widely researched but the basis of food choice, for most species, is still poorly understood (Bjorndal 1991). The nutritional value of dietary items can be additive and the additive interdependence of diet items can become quite complex in herbivores that ingest a range of diet items (Robbins 1983). The complexity of food choice increases even more when the non-additive interactions among diet items are considered. For example, in wild ruminants fed on a mixture of grass and shrub stems the digestion of fibre increased because gut retention time increased (Robbins 1983). Non-additive interactions of diet items may play an important role in the food choice of angulate tortoises since associative effects likely occur in herbivores that ingest a mixture of plant parts and food types (Bjorndal 1991).

4.5.3 Geophagy and lithophagy

Angulate tortoises consumed sand at both study sites. The ingestion of sand (lithophagy) and stone (geophagy) has been observed in a variety of reptiles (Sokol 1971; Rhodin 1974; Mason *et al.* 1999). The abrasive properties of sand and stone against ingested plant material is thought to help increase the amount of nutrients assimilated by removing the outer epidermis and exposing the underlying soft tissues to digestive enzymes (Sokol 1971; Throckmorton 1973; Sylber 1988).

The scats of angulate tortoises in the WCNP contained sand only in autumn. The high incidence of UI plant fibre in the scats indicates that angulate tortoises in the WCNP may have consumed predominately high-fibre plants in autumn, the end of the dry season. The ingestion of sand may have facilitated digestion of fibrous plants by abrading the tough outer plant surfaces. However, the first autumn rains fell just before this field season and the tortoises may have ingested sand incidentally when they drank water.

Fourteen of the 15 spring scat samples from DI contained sand, and the sand contributed 12–54% of the faecal mass. It seems unlikely that such high quantities of sand in the faeces represent incidental ingestion. Yet, focal observations (see Chapter 3) indicated that more than 50% of the spring diet on DI consisted of seedlings and mosses, and these plants would hardly require the abrasive action of sand to facilitate digestion. If the sand was not ingested incidentally while the tortoises fed on seedlings and mosses, the sand probably served a different purpose to abrasion in the feeding ecology of DI tortoises during spring.

It is well known that mammals use salt licks (areas where ungulates actively ingest sand) to supplement elements such as sodium, magnesium and carbonates in their diet (Ayotte *et al*. 2006). The limited food choice on DI (see Chapter 2) could be responsible for the ingestion of sand in that the tortoises try to acquire minerals to address deficiencies in their diets. Alternatively or additionally, lithophagy on DI may serve the purpose to increase the presence of cellulolytic microbes in the guts of angulate tortoises, as has been suggested for other reptiles (Sokol 1971).

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5 HISTOLOGICAL EVALUATION OF TORTOISE FAECES

5.1 ABSTRACT

Microhistological analyses identified 94 plant items in the scats of angulate tortoises in the West Coast National Park (WCNP) compared to 33 plant items in the scats of Dassen Island (DI) tortoises. The diverse diet of WCNP tortoises can be ascribed to the diverse vegetation at the site, whereas the depauperate vegetation on DI offered fewer food species to these tortoises. Monocots and dicots were of equal importance in the diet of WCNP tortoises. In contrast, the diet of DI tortoises was dominated by monocotyledonous plants. At both sites, perennial plants made a larger contribution to the tortoises' diet than annual plants made. The diet of angulate tortoises included several growth forms; overall, grasses and herbs made the largest contributions, respectively, to the WCNP and DI diets. *Cynodon dactylon*, a perennial grass, was the most important diet item of WCNP tortoises, which consumed mainly the inflorescences of this grass. The perennial herb, *Trachyandra divaricata*, was the most important diet item of the DI tortoises. Shrub and succulent plant species occurred in the scats of WCNP tortoises but not in the scats of DI tortoises. The only woody plant eaten on DI was a tree species, *Myoporum serratum*. Sedge species formed part of the tortoises' diet at both sites, but inflorescences of the sedge *Ficinia nigrescens* were particularly important in the spring diet of DI tortoises. The scats of the tortoises at both study sites contained insect parts. The tortoises may have ingested the insects incidentally, but the insect tissue should nevertheless contribute to the nutrition of the tortoises. Parasite eggs in the scats were not regarded as diet items. The high parasite infestation noted for DI tortoises may be linked to the high tortoise density on DI, or the infestation may be caused by the ingestion of sand and rabbit faeces on DI.

5.2 INTRODUCTION

Food not only affects animals’ body condition but also their ability to reproduce successfully (Clark 1982; Avery *et al*. 1993; Henen 1997). A good understanding of animals’ dietary requirements will consequently improve our ability to manage animals and their associated habitats (Ferreira & Bigalke 1987; Kennett & Tory 1996; Mouden *et al*. 2006). Plants display greater fluctuations in nutrient content compared to animal material (Nagy *et al*. 1998), and the nutrient content of plant material varies among plant species as well as differs among plant parts, e.g., leaves, seeds and stems (Huston & Pinchak 1991). Herbivorous reptiles may thus select a wide range of plant species and plant parts to satisfy their nutritional needs (Hailey *et al.* 1998; Mushinsky *et al.* 2003).

Microhistological faecal analysis is one of several methods that have been used to study the diets of mammals (Bhadresa 1977; Thompson & McCourt 1981) and reptiles (Mason *et al*. 1999; Loehr 2002; Mouden 2006). This method is based on the recognition of unique microscopic features of epidermal plant fragments in the scats of herbivorous animals (Vavra & Holechek 1980). Although the method requires extensive training in epidermal preparation and a thorough knowledge of microscopic epidermal characters for the identification of plant fragments, it provides both qualitative and quantitative information of an animal’s diet (Vavra & Holechek 1980; Holechek *et al*. 1982). Diet data can also be combined with plant availability data to determine food preferences of animals.

I undertook a histological evaluation of the scats of angulate tortoises at two sites in the southwestern Cape to compare the efficacy of histological scat analysis with a) macroscopic scat analysis and b) focal studies for assessing the feeding ecology of angulate tortoises.

5.3 MATERIALS AND METHODS

5.3.1 Study sites and the collection of faecal samples

I studied the feeding ecology of *Chersina angulata* in the West Coast National Park (WCNP, 30 000 ha, 33°13’S, 18°09’E) and on Dassen Island (DI, 222 ha, 33°25’S, 18°06’E) over four seasons from March 1999 to February 2000. Detailed descriptions of the study sites and climate are provided in Chapters 2 and 3. During each study period (see Table 3.1 in Chapter 3), I collected scats from angulate tortoises in and around the study quadrats for macroscopic and histological analyses. I collected 15 faecal samples each season at each site, except in spring 1999 when only 12 samples were available for the WCNP. After completing the macroscopic evaluation of the samples (see Chapter 4), I stored each faecal sample individually in FAA (formaldehyde : glacial acetic acid : 70% ethanol, in the proportion 0.5 : 0.5 : 9.0) for histological preparation.

5.3.2 Preparation of faecal samples for histological analysis

The preserved faecal samples were removed from the FAA and allowed to air dry before each sample was homogenised in a coffee grinder. Ground faecal material was funnelled into a 10 ml vial and the grinder was brushed with a camel-hair brush to remove residual particles. The vial was labelled and three-quarter filled with FAA for storage. The coffee grinder was thoroughly cleaned with a damp paper towel before I processed the next sample.

I used a diamond cutter and ruler to cut a grid, with 1 mm graduations, into a number of glass slides. When a faecal sample was studied, I placed one to two drops of the faecal-FAA solution in the middle of the graduated slide with a pipette. A few drops of a 50:50 glycerol and water mixture were placed on the slide to help retard sample desiccation (Ferreira & Bigalke 1987). The slide was then viewed under a light microscope (Olympus CX40RF200) at 400x magnification and the epidermal fragments were identified.

5.3.3 Histological evaluation

I collected leaves, flowers and seeds of a variety of plants within and around the study quadrats throughout the study period, and collected additional material in the subsequent year in an attempt to identify some of the previously unidentified epidermi in the scats. The plant material was used to make an epidermal reference collection, which was used in the histological evaluation of the faecal samples. A detailed description of the procedures to make reference slides, and the characteristics of the plant epidermi, are provided in Chapter 7. I also made wet mounts of floral parts (anthers and corolla) to help identify pollen grains in the scats.

Because the histological evaluation of faecal samples is a time-intensive process, it was important to establish, at the outset of the study, how many epidermal fragments per scat should be counted and identified to ascertain where the cumulative number of plant taxa peaked. The objective was to count enough fragments to accurately reflect the composition of the sample, but to not waste time counting more fragments than was necessary. A preliminary analysis showed that the number of taxa levelled-off at less than 200 counts for the WCNP, and at less than 100 counts for Dassen Island. Consequently, for the analysis, I identified the first 200 fragments in each sample from the WCNP and the first 100 fragments in each sample from DI.

Some faecal samples contained large quantities of pollen or trichomes. Counting the detached trichomes and pollen would have overestimated the contribution of that specific plant to the diet. My approach was thus to use trichomes or pollen for identification only when the trichomes or pollen were still attached to epidermal fragments or floral parts, respectively.

While doing the histological analysis, I made detailed drawings of the epidermal fragments or objects that were counted but could not be identified. These drawings were subsequently compared to new reference material from the study sites for identification. Whenever possible, the diet items were identified to the species level. When I could not establish the species, genus or family, I tried to identify the growth form (e.g., grass) or establish if the plant belonged to the monocotyledons or dicotyledons. The objective was to provide individual, recognisable identities to all plant items that were considered separate species, albeit unidentified. In the end, all plant fragments that could not be categorised were combined as unidentified (UI) plant material. Some items that were counted in the scats were in fact animal material, and where possible, the animal material was identified; a few fragments were placed in a category for unknown animal material.

5.3.4 Data analyses

In order to allow direct comparison of plant items among seasons and between sites, I used percent counts, and expressed the counts of individual plant items relative to the total counts of the plant items. The counts for the animal items were expressed relative to the total counts for each scat. I calculated the mean and standard deviation of the percent counts for each diet item per season and for all seasons combined. To allow a comparison among histological, focal and macroscopic data, I evaluated the histological data also on a presence-absence basis (MacDonald & Mushinsky 1988). In these calculations, the presence of a particular plant species in a scat was regarded as a single record, whether one or several fragments per scat were counted. Percent occurrence was calculated as the number of scats in a sample that contained a particular diet item divided by the total number of scats in the sample (e.g., 15 scats per season). Similarly to the focal and macroscopic studies, I included animal material in the calculation of percent composition by presence-absence. However, I excluded the counts for parasite eggs from the animal material.

I used the same principle when calculating the percent composition and percent occurrence by presence-absence for plant types and growth forms. Two different plant type groups were identified: monocots-dicots and annuals-perennials. Growth forms were categorised as grasses, restioids, sedges, succulents, non-succulent herbs and non-succulent shrubs. Items in the scats that did not fit the listed categories were categorised as UI plant material or as animal material.

5.3.4.1 Statistical analysis

Statistical tests were done with SigmaStat 2.03 (SPSS Inc., Chicago, U.S.A.) at $\alpha = 0.05$. In most instances, the data were non-parametric despite log and square-root transformations. Consequently, I often could not use multi-factorial analysis of variance (ANOVA) to simultaneously test for more than one effect. When multiple tests were done, I used the Sequential Bonferroni procedure (Holm 1979 in Quinn & Keough 2002) to sequentially test the *P*-values against adjusted α levels.

I used Friedman's repeated measures ANOVA (χ^2_{df}) followed by the Student-Newman-Keul's (SNK) post hoc test to evaluate differences among diet items within a site and within a season. For the comparison of diet items among seasons, I used a one-way ANOVA (F_{df}) followed by the SNK test if data were parametric, and I used a Kruskal-Wallis ANOVA (H_{df}) followed by Dunn's post hoc test when the data were non-parametric. When data met parametric assumptions, I used a two-way ANOVA (F_{df}) to test simultaneously for the effects of diet item and season. Only a few diet items were shared between sites and I used either Student's *t* test (t_{df}) or Mann-Whitney Rank Sum Test ($T_{n,n}$) to compare diet items between sites. In a few instances (e.g., for presence-absence data), it was possible to do a three-way ANOVA to test simultaneously for the effects of site, season and diet category.

5.4 RESULTS

5.4.1 Diet composition in the WCNP

5.4.1.1 Diet composition within each season and overall

For all seasons combined, a total of 94 plant items and three animal items were identified in the scats of angulate tortoises from the WCNP (Table 5.1). Forty-seven plant items were identified to the species or genus level while two plant items were identified to the family level. The unidentified plant items consisted of 10 grasses, one sedge, two succulents, one herb, 24 dicots, five monocots, one unidentified fruit, and the category UI plant material. The animal material consisted of insect parts, nematode eggs and unknown animal material (Table 5.1).

A total of 17 grasses were identified in angulate tortoise scats from the WCNP; *Cynodon dactylon* ranked first in the list of diet items while three other grass species fell within the top-ten ranks. Thirteen non-succulent herbaceous species were identified. *Geranium incanum* ranked second overall while two other herbs, *Albuca* sp. and *Senecio elegans*, also fell within the top-ten ranks (Table 5.1). Nine succulent plants were identified in the scats and the succulent classified as Aizoaceae ranked third on the list. *Chersina angulata* in the WCNP consumed material from 21 non-succulent shrubs (woody plants, including the parasite plant *Septulina glauca*). *Hermannia scabra*, a low growing shrub, was the only shrub in the top-ten ranks. The epidermi of only two cyperids were identified in the scats, and both cyperids, *Ficinia nigrescens* and Sedge 1, made small contributions to the overall composition of the scats. *Thamnochortus spicigerus* was the only restioid identified and occurred in only one faecal sample. UI plant material was ranked in the fifth position on the list (Table 5.1).

When doing the statistical analysis, I considered plant and animal items separately. For all seasons combined, the contribution of the 94 plant items to the composition of the diet differed significantly ($\chi^2_{93} = 1484.0$, $P << 0.0001$). *Cynodon dactylon* made a larger contribution than any other item to the diet of WCNP angulate tortoises. The contribution of *G. incanum* was second largest, followed by Aizoaceae and UI plant material. There was no difference among the remaining plant items. The apparent contradictory result that the contribution of UI plant material exceeded the contribution of *Albuca* sp. (see Table 5.1) should be viewed in the light that the repeated measures ANOVA compared the different diet components within the same scat.

When considering individual seasons, 33 plant items were identified in autumn scats (Table 5.1). The grasses *C. dactylon* and *Lolium perenne* ranked first and second, respectively. The top-ten ranks for autumn also included two herbs, *G. incanum* and *Albuca* sp., and two shrubs, *Rhus laevigata* and *H. scabra*. The contribution of the diet items to scat composition differed significantly ($\chi^2_{32} = 145.8$, $P << 0.0001$) but only *C. dactylon* made a significantly larger contribution to the diet than the other diet items made. Winter scats contained 46 plant items (Table 5.1) and the contribution of individual items to the diet composition differed significantly ($\chi^2_{45} = 276.1$, $P << 0.0001$). The herb *G. incanum* made the largest contribution to the diet composition followed by the herb *Albuca* sp. and the grass *Pennisetum setaceum*. The contribution of the other diet items did not differ. *Cynodon dactylon* ranked only eighth in the winter diet. The spring scats were comprised of 34 plant items (Table 5.1). Grass featured prominently in the spring diet with five grass species in the top-ten ranks. There was a significant difference in the contribution of diet items to the composition of scats ($\chi^2_{33} = 150.2$, $P << 0.0001$); *C. dactylon* made a larger contribution to the diet than any other diet item, and was followed by the succulent Aizoaceae and UI plant material. There was no difference in the contribution of the remaining diet items. In summer, 52 plant items were identified in angulate tortoise scats (Table 5.1). The diet items did not contribute equally to the summer diet ($\chi^2_{51} = 184.2$, $P << 0.0001$) but only the contribution of *C. dactylon* differed significantly from the others. The succulent Aizoaceae ranked second and four herbs, *Oncosiphon suffruticosum*, *Senecio elegans*, *Albuca* sp. and Herb 1 (a creeper), were in the top-ten ranks.

5.4.1.2 Seasonal changes in the importance of diet items

Fifty-four of the 94 plant diet items in the scats were found in one season only while the number of plant items recorded for two, three and four seasons, respectively, were 18, 13 and nine. In many instances, the contribution of plant items to the diet composition of angulate tortoises in the WCNP changed with season (Table 5.1).

The most prominent diet item, *C. dactylon*, formed part of each season's diet, and the mean counts for *C. dactylon* differed among the four seasons ($H_3 = 29.61$, $P << 0.0001$); percent counts in autumn was higher than in the other seasons. Percent counts in winter scats was higher than in all the other seasons for *G. incanum* and *P. setaceum*, and winter counts for *Hebenstretia repens* exceeded autumn and summer values while winter counts for *Albuca* sp. was higher than spring counts (all $H_3 > 16.91$, $P < 0.00074$). The counts for Aizoaceae and UI plant material differed significantly among seasons (all $H_3 > 16.91$, $P < 0.00074$) and were particularly high in spring. The spring count for Aizoaceae exceeded autumn and winter values, whereas the spring count for UI plant material was higher than the autumn and summer counts, and the winter count for UI plant material was larger than the autumn count. The percent counts for *Nylandtia spinosa* was higher in summer than in winter ($H_3 = 14.38$, $P = 0.0024$).

The counts for *Avena fatua*, *Cystocapnos vesicaria*, Dicot 8, Dicot 9, Dicot 13, Dicot 22, Grass 5, *Helichrysum niveum*, *Lolium perenne*, *O. suffruticosum*, *Psoralea repens*, *Rhus laevigata*, *Ruschia macowanii*, *Ruschia* sp. and *Senecio elegans* changed among seasons (all $H_3 > 7.85$, $P < 0.05$). However, there were no post hoc differences among seasons for these species. The effect of season approached significance for *F. nigrescens*, Grass 2, Grass 7, Grass 9, *H. scabra* and Monocot 5 (all $H_3 > 7.59$, P = 0.051 to 0.055), but had no effect on the remaining plant items (all $P > 0.066$).

The contribution of animal material to the composition of angulate tortoise scats changed significantly among seasons ($H_3 = 11.98$, $P = 0.0074$) and was higher in summer than in autumn. The effect of season was significant for insect parts ($H_3 = 12.32$, $P = 0.0064$) and for nematode eggs ($H_3 = 15.22$, $P = 0.0016$) but failed significance for unknown animal material ($P = 0.057$). Insect parts had higher counts in summer than in autumn.

Table 5.1 Diet composition of *Chersina angulata* in the WCNP based on percent counts (mean ± SD) of histological fragments in the scats of 15 tortoises each season but12 tortoises in spring. Two hundred fragments were counted per scat.

Taxon	**Category**	**Autumn**	**Winter**	**Spring**	**Summer**	**Total**
Afrolimon purpuratum	D / P / S	0	0	0	0.3 ± 1.1	0.1 ± 0.6
Aizoaceae	D / P / Su	0.6 ± 0.8	2.7 ± 5.6	17.7 ± 24.8	8.7 ± 17.8	6.9 ± 15.8
Albuca sp.	M / P / H	4.0 ± 7.6	14.5 ± 18.3	0.5 ± 1.6	3.5 ± 6.1	5.9 ± 11.7
Apocynaceae	D / A / H	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Aspalathus hispida	D / P / S	0	0	0	0.8 ± 2.1	0.2 ± 1.1
Asparagus lignosus	M / P / S	0	0.1 ± 0.5	0	0	0.0 ± 0.3
Avena fatua	M / A / G	0	0	0	1.8 ± 5.7	0.5 ± 3.0
Avena sp.	M / A / G	0.3 ± 1.2	0.5 ± 1.0	1.8 ± 2.8	0.2 ± 0.4	0.6 ± 1.6
Carpobrotus edulis	D / P / Su	0	0	0	1.0 ± 3.8	0.3 ± 2.0
Carpobrotus quadrifidus	D / P / Su	0	0	0	0.0 ± 0.1	0.0 ± 0.1
Chaetobromus dregeanus	M / P / G	0	0	0	0.5 ± 1.5	0.1 ± 0.8
Chironia baccifera	D / P / S	0	0.3 ± 0.7	0	1.8 ± 6.8	0.6 ± 3.5
Chrysanthemoides monilifera	D / P / S	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Cynanchum africanum	D / P / S	0.6 ± 1.7	0	0	0.6 ± 2.1	0.3 ± 1.4
Cynodon dactylon	M / P / G	54.8 ± 21.7	4.3 ± 6.6	15.8 ± 22.2	19.3 ± 22.9	24.0 ± 27.1
Cystocapnos vesicaria	D / A / H	0	0.8 ± 1.4	0	2.2 ± 8.4	0.8 ± 4.4
Dicot 1	D	0	0	0.4 ± 1.3	0	0.1 ± 0.6
Dicot 2	D	0	0.1 ± 0.3	1.3 ± 3.6	0	0.3 ± 1.7
Dicot 3	D	0.1 ± 0.5	0	2.4 ± 8.4	0	0.5 ± 3.9
Dicot 4	D	0	0	0.1 ± 0.3	0	0.0 ± 0.1
Dicot 5	D	0	0	0.2 ± 0.6	0	0.0 ± 0.3
Dicot 6	D	0	0	0.6 ± 2.2	0	0.1 ± 1.0
Dicot 7	D	0	2.0 ± 5.2	0	1.3 ± 4.9	0.9 ± 3.7
Dicot 8	D	1.0 ± 2.5	0	0	0.1 ± 0.3	0.3 ± 1.3
Dicot 9	D	1.7 ± 4.3	0	0	0	0.4 ± 2.3
Dicot 10	D	2.7 ± 7.9	0.7 ± 2.4	0	0.6 ± 2.5	1.1 ± 4.4
Dicot 11	D	0	0	0	0.2 ± 0.7	0.1 ± 0.4
Dicot 12	D	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Dicot 13	D	4.5 ± 9.9	0	0	0	1.2 ± 5.3
Dicot 14	D	0.0 ± 0.1	0	0	0	0.0 ± 0.1
Dicot 15	D	0.1 ± 0.5	0	0.2 ± 0.4	0.1 ± 0.4	0.1 ± 0.4
Dicot 16	D	0	0	0	0.5 ± 1.6	0.1 ± 0.8
Dicot 17	D	0	1.3 ± 4.1	0	3.4 ± 9.5	1.2 ± 5.4
Dicot 18	D	0	0	0	0.1 ± 0.3	0.0 ± 0.1
Dicot 19	D	0.6 ± 1.7	0	0	0.1 ± 0.3	0.2 ± 0.9
Dicot 20	D	0	0	0	0.7 ± 2.1	0.2 ± 1.1
Dicot 21	D	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Dicot 22	D	0	0	0	2.9 ± 7.6	0.8 ± 4.0
Dicot 23	D	0.7 ± 1.8	0.8 ± 3.1	0	4.3 ± 16.6	1.5 ± 8.7
Dicot 24	D	0	0	0.2 ± 0.6	0	0.0 ± 0.3
Ehrharta villosa	M / P / G	0	0	0.2 ± 0.7	0.4 ± 1.7	0.2 ± 0.9
Ficinia nigrescens	M / P / C	0	0	0.5 ± 1.6	0	0.1 ± 0.7
Geranium incanum	D / P / H	6.1 ± 12.8	22.1 ± 15.6	0.4 ± 0.5	2.4 ± 5.1	8.2 ± 13.5
Grass 1	M / G	0.0 ± 0.1	0	0	0.4 ± 1.6	0.1 ± 0.8
Grass 2	M / G	0.2 ± 0.4	5.0 ± 12.0	5.8 ± 8.6	3.4 ± 10.6	3.5 ± 9.1
Grass 3	M / G	0.1 ± 0.5	0	0	0	0.0 ± 0.3
Grass 4	M / G	1.1 ± 4.0	0.3 ± 0.5	0	1.4 ± 2.4	0.7 ± 2.4
Grass 5	M	0.4 ± 0.8	0	0	0.1 ± 0.5	0.1 ± 0.5
Grass 6	M / G	0	1.1 ± 2.8	3.4 ± 8.2	0.4 ± 1.6	1.1 ± 4.2
Grass 7	M / G	0	0	4.9 ± 15.1	0	1.0 ± 7.0

Table 5.1 continued

Taxon	Category	Autumn	Winter	Spring	Summer	Total
Grass 8	M / G	0	0	0.5 ± 1.8	0	0.1 ± 0.8
Grass 9	M / G	0	0	2.7 ± 6.5	0	0.6 ± 3.1
Grass 10	M / G	0.1 ± 0.3	0.4 ± 1.1	0	0	0.1 ± 0.6
Gymnosporia buxifolia	D / P / S	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Hebenstretia repens	D / A / H	0.0 ± 0.1	5.6 ± 9.4	0.8 ± 1.6	0	1.6 ± 5.3
Helichrysum niveum	D / P / S	0.0 ± 0.1	0	0	3.8 ± 7.8	1.0 ± 4.3
Herb 1	D / P / H	0	0	0	3.5 ± 13.4	0.9 ± 6.9
Hermannia pinnata	D / P / S	0	0	0	0.1 ± 0.3	0.0 ± 0.1
Hermannia scabra	D / P / S	2.9 ± 8.8	5.6 ± 13.8	4.8 ± 9.4	0.2 ± 0.7	3.3 ± 9.4
Lachnospermum imbricatum	D / P / S	0	0	0	0.0 ± 0.1	0.0 ± 0.1
Lolium perenne	M / P / G	8.1 ± 15.5	0.2 ± 0.7	0.1 ± 0.3	2.0 ± 5.7	2.7 ± 8.9
Manochlamys albicans	D / P / S	0	0.1 ± 0.3	0	0	0.0 ± 0.1
Monocot 1	M	0	0.1 ± 0.4	0	0	0.0 ± 0.2
Monocot 2	M	0	0	1.2 ± 4.1	0.1 ± 0.3	0.3 ± 1.9
Monocot 3	M	0	0.2 ± 0.8	0	0	0.1 ± 0.4
Monocot 4	M	0	0.2 ± 0.5	0.0 ± 0.1	0.0 ± 0.1	0.1 ± 0.3
Monocot 5	M	0	0	0.4 ± 1.0	0	0.1 ± 0.5
Nylandtia spinosa	D / P / S	0.4 ± 1.1	0	0.6 ± 1.2	3.3 ± 5.4	1.1 ± 3.1
Oncosiphon suffruticosum	D / A / H	0	0	0	8.4 ± 20.5	2.2 ± 10.9
Osyris compressa	D / P / S	0	0	0	1.4 ± 5.4	0.4 ± 2.8
Oxalis sp.	D / A / H	0	0.6 ± 1.9	0.6 ± 1.7	0	0.3 ± 1.3
Passerina corymbosa	D / P / S	0	0.5 ± 1.9	0	0	0.1 ± 1.0
Passerina ericoides	D / P / S	0	0.2 ± 0.7	0	0	0.0 ± 0.3
Pelargonium myrrhifolium	D / P / S	0.3 ± 1.0	0	0	0.0 ± 0.1	0.1 ± 0.5
Pennisetum setaceum	M / P / G	0	11.7 ± 18.2	2.3 ± 7.5	2.2 ± 7.0	4.2 ± 11.3
Psoralea repens	D / P / S	0	3.5 ± 8.0	0	0	0.9 ± 4.3
Rhus laevigata	D / P / S	4.6 ± 9.7	0.3 ± 0.6	0	1.6 ± 3.9	1.7 ± 5.5
Rhus sp.	D / P / S	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Ruschia macowanii	D / P / Su	0.4 ± 0.7	2.9 ± 5.0	0	1.1 ± 2.6	1.2 ± 3.1
Ruschia sp	D / P / Su	0	0.4 ± 0.7	0	0	0.1 ± 0.4
Sedge 1	M / C	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Senecio elegans	D / A / H	1.3 ± 3.1	0	12.6 ± 29.9	5.3 ± 12.9	4.4 ± 15.6
Senecio maritimus	D / A / Su	0.0 ± 0.1	0	6.3 ± 21.7	2.4 ± 5.0	2.0 ± 10.2
Senecio sp.	D / H	0.1 ± 0.4	0	0	0	0.0 ± 0.2
Septulina glauca	D / P / S	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Succulent 1	D / Su	0	0	0.1 ± 0.3	0	0.0 ± 0.1
Succulent 2	D / Su	0	0.0 ± 0.1	0.3 ± 1.2	0	0.1 ± 0.5
Tetragonia sp.	D / H	0	0.1 ± 0.3	0	0	0.0 ± 0.1
Thamnochortus spicigerus	M / P / R	0	0.0 ± 0.1	0	0	0.0 ± 0.1
Trifolium burchellianum	D / P / H	0	0.0 ± 0.1	0	0	0.0 ± 0.1
UI plant material	UI	1.7 ± 5.5	10.2 ± 17.4	10.3 ± 10.9	0.7 ± 1.6	5.5 ± 11.3
Unknown fruit	UI	0	0.1 ± 0.3	0	0	0.0 ± 0.1
Zantedeschia aethiopica	M / P / H	0	0	0	0.0 ± 0.1	0.0 ± 0.1
Zygophyllum morgsana	D / P / Su	0	0	0	0.3 ± 1.2	0.1 ± 0.6
Animal material*	Am	0.1 ± 0.3	0.8 ± 0.9	1.0 ± 1.5	5.1 ± 10.1	1.8 ± 5.5
Insect parts	Am	0.1 ± 0.3	0.3 ± 0.7	0.7 ± 1.3	3.9 ± 9.5	1.3 ± 5.1
Nematode eggs	Am	0.0 ± 0.1	0	0	1.1 ± 1.7	0.3 ± 1.0
Unknown	Am	0	0.4 ± 0.8	0.3 ± 0.6	0.1 ± 0.3	0.2 ± 0.5

The different categories include: M = Monocot, D = Dicot, A = Annual, P = Perennial, G = Grass, C = Cyperid, R = Restio, Su = Succulent, H = Herb (non-succulent), S = Shrub (non-succulent), UI = Unidentified plant material, Am = Animal material. *Percent counts for animal material and its subcategories are relative to the total number of counts in the scats, whereas percent counts for plant items are relative to the total number of counts for plant material.

5.4.1.3 Diet composition based on presence-absence data

The results for the presence-absence data, percent composition and percent occurrence, corresponded roughly to the results based on counts of the diet items, although the ranking of diet items for the two procedures was not identical (Table 5.2). Both procedures illustrated the overall importance of *C. dactylon, G. incanum* and Aizoaceae in the diet of angulate tortoises in the WCNP. A two-way ANOVA to test for the effects of season and plant item on percent composition of the 41 diet items that occurred in more than one season, showed a significant effect for diet item ($F_{40,120}$ = 3.36, $P << 0.0001$) but not for season ($P = 0.80$). Percent composition for *C. dactylon* was larger than that of 25 other diet items, while percent composition for Aizoaceae and *G. incanum* exceed that of 10 and six other diet items, respectively.

For all seasons combined, four diet items occurred in the scats of at least 50% of angulate tortoises: *C. dactylon, G. incanum,* Aizoaceae, and UI plant material (Table 5.2). In autumn, more than 50% of the tortoise scats contained *C. dactylon, G. incanum, L. perenne, H. scabra* and *S. elegans*. The percent occurrence for *C. dactylon* and *G. incanum* remained high in winter, and in addition, percent occurrence for *Albuca* sp., *P. setaceum, H. repens*, Aizoaceae and UI plant material also increased to more than 50%. Percent occurrence in spring remained above 50% for *C. dactylon, G. incanum*, Aizoaceae and UI plant material, and percent occurrence for *H. scabra, Avena* sp., Grass 2 and insect parts also exceeded 50% in spring. Only four diet items featured in the scats of more than half of *Chersina angulata* in summer: *C. dactylon*, Aizoaceae, *N. spinosa* and insect parts.

A two-way ANOVA to test for the effects of season and diet item on percent occurrence, using only the 41 diet items that occurred in more than one season, showed a significant effect for diet item ($F_{40,120}$ = 3.45, $P << 0.0001$) but not for season ($P = 0.88$). Percent occurrence for *C. dactylon* was larger than that of 25 other diet items, while percent occurrence for Aizoaceae and *G. incanum* exceed that of eight and seven other diet items, respectively.

Table 5.2 Percent composition and occurrence, based on presence-absence, of diet items in the scats of *Chersina angulata* in the WCNP.

	Percent composition					**Percent occurrence**				
	Au	**Wi**	**Sp**	**Su**	**Total**	**Au**	**Wi**	**Sp**	**Su**	**Total**
Afrolimon purpuratum	0	0	0	1.2	0.3	0	0	0	13.3	3.5
Aizoaceae	5.6	4.5	10.5	6.8	6.6	46.7	53.3	100	73.3	66.7
Albuca sp.	4.0	7.3	0.9	3.7	4.3	33.3	86.7	8.3	40.0	43.9
Apocynaceae	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Aspalathus hispida	0	0	0	1.2	0.3	0	0	0	13.3	3.5
Asparagus lignosus	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Avena fatua	0	0	0	1.9	0.5	0	0	0	20.0	5.3
Avena sp.	1.6	1.7	5.3	1.9	2.4	13.3	20.0	50.0	20.0	24.6
Carpobrotus edulis	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Carpobrotus quadrifidus	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Chaetobromus dregeanus	0	0	0	1.2	0.3	0	0	0	13.3	3.5
Chironia baccifera	0	1.7	0	1.2	0.9	0	20.0	0	13.3	8.8
Chrysanthemoides monilifera	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Cynanchum africanum	2.4	0	0	1.2	0.9	20.0	0	0	13.3	8.8
Cynodon dactylon	12.1	6.8	10.5	8.7	9.2	100	80.0	100	93.3	93.0
Cystocapnos vesicaria	0	4.0	0	0.6	1.4	0	46.7	0	6.7	14.0
Dicot 1	0	0	0.9	0	0.2	0	0	8.3	0	1.8
Dicot 2	0	0.6	1.8	0	0.5	0	6.7	16.7	0	5.3
Dicot 3	0.8	0	0.9	0	0.3	6.7	0	8.3	0	3.5
Dicot 4	0	0	1.8	0	0.3	0	0	16.7	0	3.5
Dicot 5	0	0	0.9	0	0.2	0	0	8.3	0	1.8
Dicot 6	0	0	0.9	0	0.2	0	0	8.3	0	1.8
Dicot 7	0	1.7	0	0.6	0.7	0	20.0	0	6.7	7.0
Dicot 8	3.2	0	0	0.6	0.9	26.7	0	0	6.7	8.8
Dicot 9	3.2	0	0	0	0.7	26.7	0	0	0	7.0
Dicot 10	2.4	1.7	0	0.6	1.2	20.0	20.0	0	6.7	12.3
Dicot 11	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Dicot 12	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Dicot 13	4.0	0	0	0	0.9	33.3	0	0	0	8.8
Dicot 14	0.8	0	0	0	0.2	6.7	0	0	0	1.8
Dicot 15	0.8	0	1.8	0.6	0.7	6.7	0	16.7	6.7	7.0
Dicot 16	0	0	0	1.2	0.3	0	0	0	13.3	3.5
Dicot 17	0	2.3	0	1.9	1.2	0	26.7	0	20.0	12.3
Dicot 18	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Dicot 19	1.6	0	0	0.6	0.5	13.3	0	0	6.7	5.3
Dicot 20	0	0	0	1.2	0.3	0	0	0	13.3	3.5
Dicot 21	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Dicot 22	0	0	0	1.9	0.5	0	0	0	20.0	5.3
Dicot 23	1.6	0.6	0	1.2	0.9	13.3	6.7	0	13.3	8.8
Dicot 24	0	0	0.9	0	0.2	0	0	8.3	0	1.8
Ehrharta villosa	0	0	0.9	0.6	0.3	0	0	8.3	6.7	3.5
Ficinia nigrescens	0	0	1.8	0	0.3	0	0	16.7	0	3.5
Geranium incanum	7.3	8.5	6.1	4.3	6.6	60.0	100	58.3	46.7	66.7
Grass 1	0.8	0	0	0.6	0.3	6.7	0	0	6.7	3.5
Grass 2	1.6	1.7	6.1	1.9	2.6	13.3	20.0	58.3	20.0	26.3
Grass 3	0.8	0	0	0	0.2	6.7	0	0	0	1.8
Grass 4	1.6	2.3	0	3.1	1.9	13.3	26.7	0	33.3	19.3
Grass 5	3.2	0	0	0.6	0.9	26.7	0	0	6.7	8.8
Grass 6	0	1.7	3.5	0.6	1.4	0	20.0	33.3	6.7	14.0
Grass 7	0	0	1.8	0	0.3	0	0	16.7	0	3.5

Table 5.2 continued

	Percent composition					Percent occurrence				
	Au	**Wi**	**Sp**	**Su**	**Total**	**Au**	**Wi**	**Sp**	**Su**	**Total**
Grass 8	0	0	0.9	0	0.2	0	0	8.3	0	1.8
Grass 9	0	0	1.8	0	0.3	0	0	16.7	0	3.5
Grass 10	0.8	1.7	0	0	0.7	6.7	20.0	0	0	7.0
Gymnosporia buxifolia	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Hebenstretia repens	0.8	6.2	2.6	0	2.6	6.7	73.3	25.0	0	26.3
Helichrysum niveum	0.8	0	0	3.7	1.2	6.7	0	0	40.0	12.3
Herb 1	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Hermannia pinnata	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Hermannia scabra	6.5	4.0	5.3	0.6	3.8	53.3	46.7	50.0	6.7	38.6
Insect parts	0.8	2.8	5.3	6.2	3.8	6.7	33.3	50.0	66.7	38.6
Lachnospermum imbricatum	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Lolium perenne	7.3	0.6	0.9	2.5	2.6	60.0	6.7	8.3	26.7	26.3
Manochlamys albicans	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Monocot 1	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Monocot 2	0	0	0.9	0.6	0.3	0	0	8.3	6.7	3.5
Monocot 3	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Monocot 4	0	1.1	0.9	0.6	0.7	0	13.3	8.3	6.7	7.0
Monocot 5	0	0	1.8	0	0.3	0	0	16.7	0	3.5
Nylandtia spinosa	2.4	0	3.5	5.6	2.8	20.0	0	33.3	60.0	28.1
Oncosiphon suffruticosum	0	0	0	4.3	1.2	0	0	0	46.7	12.3
Osyris compressa	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Oxalis sp.	0	1.1	1.8	0	0.7	0	13.3	16.7	0	7.0
Passerina corymbosa	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Passerina ericoides	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Pelargonium myrrhifolium	0.8	0	0	0.6	0.3	6.7	0	0	6.7	3.5
Pennisetum setaceum	0	6.8	1.8	1.2	2.8	0	80.0	16.7	13.3	28.1
Psoralea repens	0	2.3	0	0	0.7	0	26.7	0	0	7.0
Rhus laevigata	5.6	2.8	0	4.3	3.3	46.7	33.3	0	46.7	33.3
Rhus sp.	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Ruschia macowanii	4.0	4.0	0	1.9	2.6	33.3	46.7	0	20.0	26.3
Ruschia sp.	0	2.8	0	0	0.9	0	33.3	0	0	8.8
Sedge 1	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Senecio elegans	6.5	0	3.5	4.3	3.3	53.3	0	33.3	46.7	33.3
Senecio maritimus	0.8	0	0.9	2.5	1.0	6.7	0	8.3	26.7	10.5
Senecio sp.	0.8	0	0	0	0.2	6.7	0	0	0	1.8
Septulina glauca	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Succulent 1	0	0	0.9	0	0.2	0	0	8.3	0	1.8
Succulent 2	0	0.6	0.9	0	0.3	0	6.7	8.3	0	3.5
Tetragonia sp.	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Thamnochortus spicigerus	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Trifolium burchellianum	0	0.6	0	0	0.2	0	6.7	0	0	1.8
UI plant material	2.4	6.2	9.6	2.5	5.0	20.0	73.3	91.7	26.7	50.9
Unknown fruit	0	0.6	0	0	0.2	0	6.7	0	0	1.8
Zantedeschia aethiopica	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Zygophyllum morgsana	0	0	0	0.6	0.2	0	0	0	6.7	1.8
Nematode eggs*	0.8	0	0	3.7	1.2	6.7	0.0	0.0	40.0	12.3

*Note that the percent composition of nematode eggs is expressed relative to the scores for all items in the scats, whereas percent composition of the diet items is expressed relative to the total scores for plant items and insect parts in the scats.

5.4.2 Diet composition on DI

5.4.2.1 Diet composition within each season and overall

For all seasons combined, I identified a total of 33 plant items and three animal items in the scats of angulate tortoises on DI (Table 5.3). Fifteen plant items were identified to the species or genus level. The UI plant items consisted of seven dicots, five grasses, four monocots, one unidentified fruit and the diet category UI plant material. The animal material consisted of insects, nematode eggs and other parasite eggs.

Nine grass species were identified in angulate tortoise scats from DI (Table 5.3) of which three species were present in the top-ten ranks. *Avena byzantina* was the highest ranked grass (third overall) followed by *Phalaris minor*, which ranked seventh overall. The epidermi of seven non-succulent herbaceous plant species were identified in the scats (Table 5.3). *Trachyandra divaricata,* a perennial herb, which was consumed throughout the year, ranked first in the diet list while *Senecio elegans* and *Albuca flaccida* were included in the top-ten ranks. Three cyperids were identified in the scats and *Ficinia nigrescens*, the highest ranked cyperid, ranked second in the diet list. Angulate tortoises on DI consumed only one woody plant species, the leaves of an introduced tree *Myoporum serratum* (Table 5.3).

When doing the statistical analysis, I considered plant and animal items separately. For all seasons combined, the contribution of the 33 plant items to the composition of the diet differed significantly (χ^2_{32} = 497.9, $P << 0.0001$). Multiple comparisons revealed that *T. divaricata* made the largest contribution to the diet, and that the contribution of *A. byzantina* exceeded the contribution of the remaining diet items, which did not differ from one another. The nature of the analysis (RM ANOVA) explains the apparent anomaly that the contribution of *A. byzantina* exceeding the contribution of *F. nigrescens* (see Table 5.3).

When considering individual seasons, 15 plant items were identified in the autumn scats (Table 5.3) and the contribution of the diet items to the scat composition differed significantly (χ^2_{14} = 87.8, $P << 0.0001$); *T. divaricata* made a larger contribution than all other diet items and there was no difference among the other diet items. Thirteen plant items were identified in the winter scats, including epidermal fragments of an unidentified fruit. The plant items in the winter scats differed significantly (χ^2_{12} = 87.4, $P << 0.0001$); the contribution of *T. divaricata* was larger than all other plant items and the contribution of Dicot 5 exceeded the remaining contributions.

The spring scats contained 17 plant items (Table 5.3) and the contribution of the plant items to the scat composition differed significantly ($\chi^2_{16} = 115.6$, $P << 0.0001$). The cyperid *F. nigrescens* made the largest contribution to the diet, while the percent counts for *A. byzantina* and *T. divaricata* did not differ but exceeded that of all remaining plant items. Summer scats were comprised of 16 plant items (Table 5.3). There was a significant difference in the contribution of plant items to the composition of scats ($\chi^2_{15} = 56.0$, $P << 0.0001$) but only *T. divaricata* made a larger contribution than the other plant items to the summer scats.

5.4.2.2 Seasonal changes in the importance of diet items

Fifteen of the 33 plant items in angulate tortoise scats on DI were found in one season only while the number of diet items recorded for two, three and four seasons, were 11, 4 and 3, respectively. In many instances, the contribution of plant items to the DI diet changed with season (Table 5.3).

Trachyandra divaricata formed part of each season's diet and the counts for *T. divaricata* differed among the seasons ($F_{3,56} = 9.63$, $P < 0.0001$). The autumn and winter counts did not differ but exceeded the spring and summer counts, which were similar. The mean counts for *A. byzantina* differed among seasons ($H_3 = 19.86$, $P = 0.00018$) with higher values in spring than in winter. Season also influenced the counts for *P. minor* ($H_3 = 14.59$, $P = 0.0022$) with summer counts being larger than the counts for winter. *Ficinia nigrescens* and the unknown fruit occurred in the scats in only one season, spring and winter respectively (Table 5.3), but the effect of season was significant for both diet items ($H_3 > 30.97$, $P << 0.00001$). Dicot 5 had higher counts in winter than in the other seasons ($H_3 = 48.48$, $P << 0.0001$).

The counts for *Bromus pectinatus*, Dicot 1, Dicot 2, Grass 1, Grass 2, Grass 4, *Hemimeris racemosa*, *M. serratum*, *Oxalis* sp. and *Zantedeschia aethiopica* all changed among seasons (all $H_3 > 8.28$, $P < 0.041$) but there were no post hoc differences for these plants. Season had no significant effect on the remaining plant species (all $P > 0.070$).

The scats of angulate tortoises on DI contained animal material throughout the year (Table 5.3), with significant differences among seasons ($F_{3,56} = 10.58$, $P < 0.0001$). Spring and winter counts did not differ and exceeded counts for autumn and summer.

Season had an effect on parasite eggs (H_3 = 11.76, P = 0.0082), nematode eggs ($F_{3,56}$ = 6.20, P = 0.0010) and insect parts (H_3 = 17.13, P = 0.00066). There were no post hoc differences for parasite eggs but counts for nematode eggs were higher in spring than in autumn and winter and higher in summer than in autumn. For insect parts, the winter and spring counts did not differ but the counts for these seasons were higher than the counts in autumn.

Table 5.3 Diet composition of *Chersina angulata* on DI based on percent counts (mean ± SD) of histological fragments in the scats of 15 tortoises per season. One hundred fragments were counted per scat.

Taxon	Category	Autumn	Winter	Spring	Summer	Annual
Albuca flaccida	M / P / H	12.2 ± 32.3	3.0 ± 11.7	3.7 ± 10.6	0	4.7 ± 18.1
Avena byzantina	M / A / G	4.2 ± 9.0	0.2 ± 0.8	11.5 ± 9.4	10.9 ± 17.9	6.7 ± 11.8
Avena sp.	M / A / G	0.8 ± 2.0	0.1 ± 0.3	0	3.4 ± 7.7	1.1 ± 4.1
Bromus pectinatus	M / A / G	0.7 ± 2.1	0	0	4.9 ± 7.3	1.4 ± 4.2
Cyperus sp.	M / C	0	0.5 ± 2.0	0	0	0.1 ± 1.0
Dicot 1	D	0	0	3.0 ± 8.4	0	0.7 ± 4.3
Dicot 2	D	0	0	3.0 ± 4.4	2.2 ± 4.3	1.3 ± 3.3
Dicot 3	D	0	0	1.2 ± 2.7	1.0 ± 2.3	0.5 ± 1.8
Dicot 4	D	2.5 ± 9.6	1.3 ± 2.2	0	0.9 ± 2.7	1.2 ± 5.0
Dicot 5	D	0.3 ± 1.0	13.6 ± 12.9	0	0	3.5 ± 8.6
Dicot 6	D	0	0	0	0.8 ± 3.1	0.2 ± 1.5
Dicot 7	D	0	0	0	0.1 ± 0.3	0.0 ± 0.1
Ficinia nigrescens	M / P / C	0	0	48.8 ± 27.9	0	12.2 ± 25.3
Grass 1	M / G	0.3 ± 1.3	3.4 ± 5.6	0	0	0.9 ± 3.2
Grass 2	M / G	0	0	2.3 ± 3.9	5.3 ± 20.4	1.9 ± 10.4
Grass 3	M / G	0	0	0.1 ± 0.3	0	0.0 ± 0.2
Grass 4	M / G	0	0	5.5 ± 10.8	0	1.4 ± 5.8
Grass 5	M / G	0	0	0.1 ± 0.3	0	0.0 ± 0.1
Hemimeris racemosa	D / A / H	0	0	2.3 ± 4.3	0	0.6 ± 2.3
Isolepis antarctica	M / A / C	0	0	1.3 ± 3.9	0	0.3 ± 2.0
Monocot 1	M	0.1 ± 0.3	0	0	±	0.0 ± 0.1
Monocot 2	M	0	0	0.2 ± 0.8	0	0.1 ± 0.4
Monocot 3	M	0	1.1 ± 4.2	0	0	0.3 ± 2.1
Monocot 4	M	0.3 ± 0.8	0	0	0.1 ± 0.3	0.1 ± 0.4
Myoporum serratum	D / P / T	12.2 ± 24.2	0	0	10.9 ± 26.0	5.8 ± 18.3
Oxalis sp.	D / A / H	0.3 ± 0.9	0	0	2.7 ± 5.6	0.7 ± 3.0
Phalaris minor	M / A / G	0.7 ± 1.5	0	3.8 ± 6.5	12.4 ± 21.6	4.2 ± 12.1
Senecio elegans	D / A / H	0.1 ± 0.3	2.1 ± 5.3	1.8 ± 7.0	18.5 ± 31.7	5.6 ± 17.7
Trachyandra divaricata	M / P / H	65.4 ± 38.0	59.5 ± 34.9	11.1 ± 13.3	22.0 ± 20.0	39.5 ± 36.4
UI plant material	UI	0.1 ± 0.3	0.9 ± 2.4	0	0	0.2 ± 1.2
Unknown fruit	UI	0	14.2 ± 21.3	0	0	3.5 ± 12.1
Urtica urens	D / A / H	0	0.2 ± 0.7	0	0	0.0 ± 0.4
Zantedeschia aethiopica	M / P / H	0	0	0.3 ± 1.2	4.1 ± 9.6	1.1 ± 5.0
Animal material*	Am	1.1 ± 1.6	7.7 ± 8.0	12.0 ± 9.8	4.3 ± 3.4	6.3 ± 7.6
Insects	Am	0.3 ± 0.8	1.9 ± 2.0	5.1 ± 8.0	0.4 ± 0.6	1.9 ± 4.5
Nematode eggs	Am	0.8 ± 1.3	2.8 ± 3.7	6.3 ± 5.6	3.9 ± 3.4	3.4 ± 4.2
Parasite eggs	Am	0	3.0 ± 6.1	0.6 ± 1.1	0	0.9 ± 3.3

The different categories include: M = Monocot, D = Dicot, A = Annual, P = Perennial, G = Grass, C = Cyperid, H = Herb (non-succulent), S = Shrub (non-succulent), T = Tree, UI = Unidentified plant material, Am = Animal material. *Percent counts for animal material and its subcategories are relative to the total number of counts in the scats, whereas percent counts for plant items are relative to the total number of counts for plant material.

5.4.2.3 Diet composition based on presence-absence data

The results for the presence-absence data, percent composition and percent occurrence, corresponded roughly to the results based on counts of the diet items although the ranking of diet items for the two procedures was not identical (Table 5.4). For both data types, *T. divaricata* ranked first. When simultaneously evaluating the effects of season and diet item on the 19 diet items that occurred in more than one season, percent composition showed a significant effect for diet item ($F_{18,54} = 3.81$, $P < 0.0001$) but not for season ($P = 0.51$). Percent composition for *T. divaricata* was larger than that of all other diet items.

In every season, more than 85% of the scats contained *T. divaricata* while all scats in spring had fragments of *F. nigrescens*. Insect parts, *A. byzantina*, *P. minor*, *H. racemosa*, Dicot 2, Dicot 5, Grass 4, and Unknown fruit occurred in at least one season in more than 50% of the scats. For the 19 diet items that occurred in more than one season, season did not have an effect on percent occurrence ($P = 0.61$), but diet item influenced percent occurrence ($F_{18,54} = 3.80$, $P < 0.0001$). Percent occurrence for *T. divaricata* exceeded all other occurrences.

Table 5.4 Percent composition and occurrence, based on presence-absence, of diet items in the scats of *Chersina angulata* on DI.

	Percent composition					Percent occurrence				
Taxon	**Au**	**Wi**	**Sp**	**Su**	**Annual**	**Au**	**Wi**	**Sp**	**Su**	**Annual**
Albuca flaccida	3.8	1.4	2.9	0	1.9	13.3	6.7	20.0	0	10.0
Avena byzantina	13.5	1.4	12.4	10.1	9.4	46.7	6.7	86.7	53.3	48.3
Avena sp	5.8	1.4	0	5.1	2.6	20.0	6.7	0	26.7	13.3
Bromus pectinatus	3.8	0	0	7.6	2.6	13.3	0	0	40.0	13.3
Cyperus sp	0	1.4	0	0	0.3	0	6.7	0	0	1.7
Dicot 1	0	0	2.9	0	1.0	0	0	20.0	0	5.0
Dicot 2	0	0	7.6	5.1	3.9	0	0	53.3	26.7	20.0
Dicot 3	0	0	2.9	3.8	1.9	0	0	20.0	20.0	10.0
Dicot 4	1.9	6.8	0	3.8	2.9	6.7	33.3	0	20.0	15.0
Dicot 5	1.9	19.2	0	0	4.9	6.7	93.3	0	0	25.0
Dicot 6	0	0	0	1.3	0.3	0	0	0	6.7	1.7
Dicot 7	0	0	0	1.3	0.3	0	0	0	6.7	1.7
Ficinia nigrescens	0	0	14.3	0	4.9	0	0	100	0	25.0
Grass 1	1.9	9.6	0	0	2.6	6.7	46.7	0	0	13.3
Grass 2	0	0	4.8	1.3	1.9	0	0	33.3	6.7	10.0
Grass 3	0	0	1.0	0	0.3	0	0	6.7	0	1.7
Grass 4	0	0	7.6	0	2.6	0	0	53.3	0	13.3
Grass 5	0	0	1.0	0	0.3	0	0	6.7	0	1.7
Hemimeris racemosa	0	0	7.6	0	2.6	0	0	53.3	0	13.3
Insect	5.8	15.1	10.5	6.3	9.7	20.0	73.3	73.3	33.3	50.0
Isolepis antarctica	0	0	1.9	0	0.6	0	0	13.3	0	3.3
Monocot 1	1.9	0	0	0	0.3	6.7	0	0	0	1.7
Monocot 2	0	0	1.0	0	0.3	0	0	6.7	0	1.7
Monocot 3	0	1.4	0	0	0.3	0	6.7	0	0	1.7
Monocot 4	3.8	0	0	1.3	1.0	13.3	0	0	6.7	5.0
Myoporum serratum	13.5	0	0	6.3	3.9	46.7	0	0	33.3	20.0
Oxalis sp	3.8	0	0	5.1	1.9	13.3	0	0	26.7	10.0
Phalaris minor	7.7	0	6.7	11.4	6.5	26.7	0	46.7	60.0	33.3
Senecio elegans	1.9	6.8	1.0	6.3	3.9	6.7	33.3	6.7	33.3	20.0
Trachyandra divaricata	26.9	17.8	13.3	16.5	17.5	93.3	86.7	93.3	86.7	90.0
UI plant material	1.9	4.1	0	0	1.3	6.7	20.0	0	0	6.7
Unknown fruit	0	12.3	0	0	2.9	0	60.0	0	0	15.0
Urtica urens	0	1.4	0	0	0.3	0	6.7	0	0	1.7
Zantedeschia aethiopica	0	0	1.0	7.6	2.3	0	0	6.7	40.0	11.7
Nematode eggs*	10.7	13.2	11.9	14.0	12.5	40.0	66.7	86.7	80.0	68.3
Other parasite eggs*	0	6.6	4.6	0	3.1	0	33.3	33.3	0	16.7

*Note that the percent composition of nematode and other parasite eggs is expressed relative to the scores for all items in the scats.

5.4.3 Comparison of diet items in WCNP and DI scats

Only three plant species occurred in the scats at both sites: *Ficinia nigrescens*, *Senecio elegans* and *Zantedeschia aethiopica*. The scats at both sites also contained UI plant material, insect parts, and parasite eggs. Parasite eggs in the WCNP scats were from nematodes, whereas parasite eggs in DI scats included nematode eggs plus the eggs of other unidentified parasites.

Ficinia nigrescens occurred only in angulate tortoise scats collected during spring, when counts in DI scats were substantially larger than counts in WCNP scats ($T_{12,15} = 78$, $P << 0.0001$). Angulate tortoises from DI consumed *S. elegans* in every season, whereas this plant did not occur in WCNP scats collected in winter. After applying the Bonferroni correction, the counts for *S. elegans* did not differ between the two sites, within a particular season or for all seasons combined (all $P > 0.033$). *Zantedeschia aethiopica* did not occur in autumn or winter scats, but was found in DI scats during spring, and in scats from both sites in summer. There was no difference in the counts for *Z. aethiopica* between sites in spring, summer or all seasons combined (all $P > 0.0947$). Scats from the WCNP contained UI plant material in every season, whereas scats from DI did not have UI plant material in spring or summer. Autumn and summer values for UI plant material did not differ between the two sites (all $P > 0.23$) but the counts were higher in WCNP scats than in DI scats in winter ($T_{15,15} = 168$, $P = 0.0078$), spring ($T_{12,15} = 251$, $P << 0.0001$) and for all seasons combined ($T_{57,60} = 4137$, $P << 0.0001$).

The counts for animal material in angulate tortoise scats were influenced by site ($F_{1,109} = 36.01$, $P << 0.0001$) and season ($F_{3,109} = 10.02$, $P << 0.0001$), and there was a significant interaction between site and season ($F_{3,109} = 5.79$, $P = 0.0010$). The counts were higher in DI scats than in WCNP scats for winter, spring and overall, but the counts did not differ significantly between the sites in autumn or summer. In DI scats, spring values for animal material were higher than summer values, and autumn scats had lower values than in all other seasons. For scats from the WCNP, summer counts for animal material exceeded the autumn counts.

With regard to the subcomponents of animal material, there was no difference between the counts for insect part in DI and WCNP scats for autumn, spring, summer and all seasons combined (all $P > 0.031$), but in winter DI scats had higher counts than WCNP scats had ($T_{15,15} = 298$, $P = 0.0069$). The scats of *Chersina angulata* in DI had more nematode eggs than the scats of tortoises from the WCNP had in spring ($T_{12,15} = 90$, P

<< 0.0001), winter ($T_{15,15}$ = 308, P = 0.0019), summer ($T_{15,15}$ = 175, P = 0.0170), and for all seasons combined ($T_{57,60}$ = 2352, P << 0.0001), but the counts for nematode eggs did not differ in autumn (P = 0.095). Similar results were found when all parasite eggs (nematode and other eggs) in the scats of DI angulate tortoises were compared with parasite eggs (only nematodes) in the scats of angulate tortoises from the WCNP.

5.4.4 Plant growth forms in the diet of angulate tortoises in the WCNP

5.4.4.1 The contribution of growth forms to seasonal diets

Six plant growth forms were identified in the scats of angulate tortoises in the WCNP but because there was only one count for a restioid, I combined the restioid with the sedges. The scats also contained UI plant material (Table 5.5). Overall, there was a significant difference among the contribution of plant growth forms to angulate tortoises' diet (χ^2_5 = 126.4, P << 0.0001). The relative presence among the growth forms was: grass > herb > UI plant material > shrub = succulent > sedge/restio.

The contribution of growth forms to the autumn diet differed significantly (χ^2_4 = 28.2, P <<0.0001), with the counts for grass being larger than that of the other categories. The growth forms in the scats differed in winter (χ^2_5 = 47.7, P << 0.0001) and the ranking among the growth forms had the sequence: herb > grass > UI plant material > shrub = succulent > sedge/restio. In spring the relative presence among the growth forms was: grass = UI plant material > succulent = herb > shrub > sedge/restio (χ^2_5 = 35.3, P << 0.0001). There was no difference among the contribution of the growth forms to the summer scats (P = 0.21).

The contribution of grass to the diet of angulate tortoises in the WCNP changed over the seasons ($F_{3,53}$ = 7.58, P = 0.00026); percent counts in autumn were higher than in winter and summer. Season also had an effect on herbs ($F_{3,53}$ = 7.67, P = 0.00024), and in this instance, the winter value for herbs was larger than in the other seasons. Seasonal comparisons of counts for succulents showed significant differences ($F_{3,53}$ = 6.66, P = 0.00067); spring and summer values were higher than value for autumn, while the spring value was also higher than the winter value. Season had no effect on the contributions of UI plant material, shrubs and sedge/restio to the scat composition of WCNP angulate tortoises (all P > 0.181).

5.4.4.2 Percent occurrence and percent composition

Nearly all angulate tortoises had grass and herbs in their scats in each season whereas at most 17% of the tortoises had fragments of sedge/restio in their scats (Table 5.6). Growth form had a strong effect on percent occurrence ($F_{6,18} = 25.7$, $P << 0.0001$) and on percent composition ($F_{6,18} = 20.8$, $P << 0.0001$), but season had no effect (all $P > 1.0$). Grass, herbs, UI plant material, succulents and shrubs had higher values than insect parts and sedge/restio, while values for insect parts exceeded that of sedge/restio.

Table 5.5 Diet composition based on percent counts (mean ± SD) of plant growth forms in the scats of angulate tortoises in the WCNP.

Growth form	**Autumn**	**Winter**	**Spring**	**Summer**	**Annual**
Grass	65.2 ± 23.0	23.4 ± 22.5	37.5 ± 27.7	32.1 ± 28.3	39.7 ± 29.5
Herb	11.6 ± 13.4	43.7 ± 21.6	14.8 ± 29.1	25.3 ± 27.2	24.3 ± 26.0
Sedge/restio	0	0.1 ± 0.2	0.5 ± 1.6	0	0.1 ± 0.7
Shrub	8.8 ± 12.7	10.8 ± 18.4	5.5 ± 10.3	14.0 ± 15.4	10.0 ± 14.7
Succulent	1.0 ± 1.1	6.1 ± 7.1	24.4 ± 29.1	13.5 ± 17.8	10.6 ± 18.2
UI plant material	13.3 ± 16.0	15.8 ± 17.6	17.3 ± 13.1	15.1 ± 23.6	15.2 ± 17.8

Table 5.6 Percent composition and occurrence based on presence-absence of plant growth forms and insect parts in the scats of angulate tortoises in the WCNP.

	Percent composition					**Percent occurrence**				
Growth form	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
Grass	24.6	20.0	19.4	18.7	20.5	100	100	100	93.3	98.2
Herb	21.3	20.0	17.7	18.7	19.4	86.7	100	91.7	93.3	93.0
Insect parts	1.6	6.7	9.7	13.3	8.1	6.7	33.3	50.0	66.7	38.6
Sedge/restio	0	2.7	3.2	0	1.5	0	13.3	16.7	0	7.0
Shrub	19.7	17.3	11.3	17.3	16.5	80.0	86.7	58.3	86.7	78.9
Succulent	14.8	14.7	19.4	16.0	16.1	60.0	73.3	100	80.0	77.2
UI plant material	18.0	18.7	19.4	16.0	17.9	73.3	93.3	100	80.0	86.0

5.4.5 Plant growth forms in the diet of angulate tortoises on DI

5.4.5.1 The contribution of growth forms to seasonal diets

Four plant growth forms were identified in the scats of *Chersina angulata* on DI (Table 5.7). As for the WCNP, the scats also contained UI plant material. Overall, there was a significant difference among the contribution of plant growth forms to angulate tortoises' diet ($\chi^2_4 = 87.6$, $P << 0.0001$). All the categories differed from one another and the sequence from largest to smallest was: herbs > grass > UI plant material > sedge > tree.

The contribution of growth forms to the composition of the scats differed in autumn ($F_{4,56} = 33.4$, $P << 0.0001$), winter ($\chi^2_4 = 45.0$, $P << 0.0001$), spring ($F_{4,56} = 38.2$, $P << 0.0001$) and summer ($F_{4,56} = 23.1$, $P << 0.0001$). In autumn, herbs made a larger contribution than any other category, and the contribution of grass and tree exceeded the contribution of sedge. The sequence of importance in the winter scats was: herbs > UI plant material > grass > sedge = tree, and the sequence in spring scats was: sedge > grass = herbs > UI plant material > tree. The summer contributions of herbs and grasses did not differ but exceeded the contribution of all other categories. Additionally, the percent counts for UI plant material was larger than for sedges but the remaining categories did not differ.

The contribution that grasses made to the diet of angulate tortoises on DI changed with the seasons ($F_{3,56} = 15.1$, $P << 0.0001$). Spring and summer counts for grasses were similar and were larger than autumn and winter counts. Sedges were only found in spring and winter scats, and spring values differed significantly from the other seasons ($H_3 = 54.9$, $P << 0.0001$). Epidermi for the tree species were found in two of the four seasons and, although season influenced the counts ($H_3 = 15.3$, $P = 0.0016$), there were no significant post hoc differences. The contribution of herbs to the composition of angulate tortoise scats changed with season ($F_{3,56} = 12.6$, $P << 0.0001$); autumn, winter and summer values were larger than spring values, while autumn values were also larger than summer values. Season also influenced the counts for UI plant material ($F_{3,56} = 9,8$, $P < 0.0001$); winter counts were higher than in the other seasons.

5.4.5.2 Percent occurrence and percent composition

Herbs were prominent in angulate tortoise scats on DI, with high percent occurrences in every season (Table 5.8). Results of a two way ANOVA for percent occurrence revealed no effect of season (*P* = 0.31) but growth forms displayed an effect ($F_{5,15}$ = 4.32, *P* = 0.012); percent occurrence for herbs was larger than for tree and sedge. Similarly, season had no effect on percent composition (*P* = 1.0) but growth forms had an effect ($F_{5,15}$ = 4.45, *P* = 0.011); the percent composition for herbs was larger than for tree and sedge.

Table 5.7 Diet composition based on percent counts (mean ± SD) of plant growth forms in the scats of angulate tortoises on DI.

Growth form	Autumn	Winter	Spring	Summer	Annual
Grass	6.7 ± 11.3	3.6 ± 5.5	23.2 ± 16.7	36.8 ± 30.7	17.6 ± 22.5
Herbs	77.9 ± 28.9	64.8 ± 31.4	19.3 ± 19.0	47.2 ± 29.5	52.3 ± 34.9
Sedge	0	0.5 ± 2.0	50.1 ± 27.1	0	12.7 ± 25.5
Tree	12.2 ± 24.2	0	0	10.9 ± 26.0	5.8 ± 18.3
Ul plant material	3.1 ± 10.5	31.0 ± 32.3	7.4 ± 9.5	5.1 ± 5.4	11.7 ± 20.8

Table 5.8 Percent composition and occurrence based on presence-absence of plant growth forms in the scats of angulate tortoises on DI.

	Percent composition					Percent occurrence				
Growth form	Au	Wi	Sp	Su	Ann	Au	Wi	Sp	Su	Ann
Grass	21.6	18.4	22.7	30.6	23.4	53.3	60.0	100	100	78.3
Herbs	40.5	28.6	22.7	28.6	28.9	100	93.3	100	93.3	96.7
Insects	8.1	22.4	16.7	10.2	14.9	20.0	73.3	73.3	33.3	50.0
Sedge	0	2.0	22.7	0	8.0	0	6.7	100	0.0	26.7
Tree	18.9	0	0	10.2	6.0	46.7	0	0	33.3	20.0
Ul plant	10.8	28.6	15.2	20.4	18.9	26.7	93.3	66.7	66.7	63.3

5.4.6 Comparison of growth forms in WCNP and DI tortoise scats

Overall, the scats of angulate tortoises in the WCNP contained higher counts for grasses ($T_{57,60}$ = 4198, P << 0.0001), shrubs/tree ($T_{57,60}$ = 4311, P << 0.0001) and UI plant material ($T_{57,60}$ = 3808, P = 0.015) than the scats of tortoises on DI contained. In contrast, overall counts for DI scats were higher than counts for WCNP scats were for herbs ($T_{57,60}$ = 2560, P << 0.0001) and sedges ($T_{57,60}$ = 2995, P = 0.045). There were no succulents in the scats from DI.

The counts for grasses in the scats of angulate tortoises in the WCNP were higher than in the scats of DI tortoises in autumn ($T_{15,15}$ = 124, P << 0.0001) and in winter ($T_{15,15}$ = 140, P << 0.0001), while these counts did not differ in spring (P = 0.11) and in summer (P = 0.67). Herbs made a much larger contribution to angulate tortoise diets for DI compared to the WCNP for autumn (t_{28} = 8.06, P << 0.0001), winter (t_{28} = 2.15, P = 0.041), spring ($T_{12,15}$ = 127, P = 0.048) and summer (t_{28} = 2.12, P = 0.043). I compared the shrub counts in the WCNP scats with the tree counts in the DI scats and found higher values for WCNP scats than for DI scats in winter ($T_{15,15}$ = 135, P << 0.0001), spring ($T_{12,15}$ = 221, P = 0.011) and summer ($T_{15,15}$ = 289, P = 0.020), while the values did not differ in autumn (P = 0.254).

Sedges were not present at either of the sites in autumn and summer and the counts in the scats did not differ in winter (P = 0.80). Spring counts for sedges were substantially higher in DI scats than in WCNP scats ($T_{12,15}$ = 78, P << 0.0001). The counts for UI plant material did not differ in winter (P = 0.121) and summer (P = 0.33), but were higher in WCNP scats than in DI scats in autumn ($T_{15,15}$ = 172, P = 0.013) and spring ($T_{12,15}$ = 218, P = 0.016).

A three-way ANOVA, that considered the effects of site, season and growth form for percent composition (presence-absence), showed a significant effect for growth form ($F_{4,12}$ = 14.06, P < 0.0001), but not for season or site (all P > 0.13). Similarly, results for percent occurrence showed no effect for season (P = 0.10), approached significance for site (P = 0.069) and showed a strong effect for growth form ($F_{5,15}$ = 17.94, P < 0.0001). In both instances, the relationship among the growth forms were: herb = grass = UI plant material > shrub / tree = insect parts > sedge.

5.4.7 Plant types in the diet of WCNP angulate tortoises

5.4.7.1 Monocotyledons and dicotyledons in WCNP scats

The scats of angulate tortoises in the WCNP contained monocots and dicots in every season (Fig. 5.1). For all seasons combined, the counts for monocots and dicots were similar, but were higher than the counts for UI plant material were ($\chi^2_2 = 65.8$, $P << 0.0001$). The relationship among the plant types in autumn was: monocots > dicots > UI plant material ($F_{2,28} = 41.47$, $P << 0.0001$), whereas the relationship in winter and spring was: monocot = dicot > UI plant material (winter: $F_{2,28} = 9.67$, $P = 0.00064$; spring: $F_{2,22} = 5.62$; $P = 0.011$). In summer, dicots had the highest count, and the count for monocots was higher than the count for UI plant material ($F_{2,28} = 62.9$, $P < 0.0001$).

The importance of the diet categories changed with season (Fig. 5.1). The contribution of monocots to the diet of angulate tortoises in the WCNP was higher in autumn than in all other seasons ($F_{3,53} = 5.48$, $P = 0.0023$). In contrast, the contribution of dicots to the autumn diet was lower than its contribution to the diet in all other seasons ($F_{3,53} = 4.99$, $P = 0.0040$). The counts for UI plant material were higher in spring than in autumn and summer, while winter counts also exceeded autumn counts ($H_3 = 21.07$, $P = 0.00010$).

All angulate tortoise scats had fragments of monocots and dicots in every season (Table 5.9). Season had no effect on percent occurrence or composition (all $P > 0.32$) but diet item had an effect on percent occurrence ($F_{3,9} = 9.21$, $P = 0.0042$) and composition ($F_{2,6} = 6.06$, $P = 0.036$). In both instances, the counts for dicots and monocots were similar and exceeded the counts for UI plant material and insect parts; the latter two categories did not differ.

5.4.7.2 Annuals and perennials in WCNP scats

Every season I recorded high values for perennials in the scats of angulate tortoises in the WCNP (Fig. 5.2). For all seasons combined, the count for perennials was higher than for annuals and UI plant material and the count for UI plant material was higher than the counts were for annuals ($\chi^2_2 = 51.2$, $P << 0.0001$). The same trend was evident in autumn and winter (autumn: $F_{2,28} = 118.1$; winter: $\chi^2_2 = 18.75$; all $P < 0.0001$). Spring counts for perennial and UI plant material did not differ and their counts were higher than the count for annuals ($F_{2,22} = 4.40$, $P = 0.025$). The summer count for perennials was higher than the counts for annuals and UI plant material were ($\chi^2_2 = 8.37$, $P = 0.015$).

The counts for perennials and annuals changed significantly with season (perennial: $F_{3,53} = 6.49$, $P = 0.00080$; annual: $F_{3,53} = 5.06$, $P = 0.0037$) but season had no effect on UI plant material ($P = 0.10$). Values for perennials were higher in autumn than in spring and summer, and also higher in winter than in spring. Annuals had lower counts in autumn than in all the other seasons.

All the scats of angulate tortoises in the WCNP contained perennials in every season (Table 5.10). Season had no effect on percent occurrence or percent composition (all $P > 0.063$) but percent occurrence and composition were influenced by diet item (all $F_{3,9} > 11.76$, $P < 0.0018$); the values for insect parts were lower than values for the other categories.

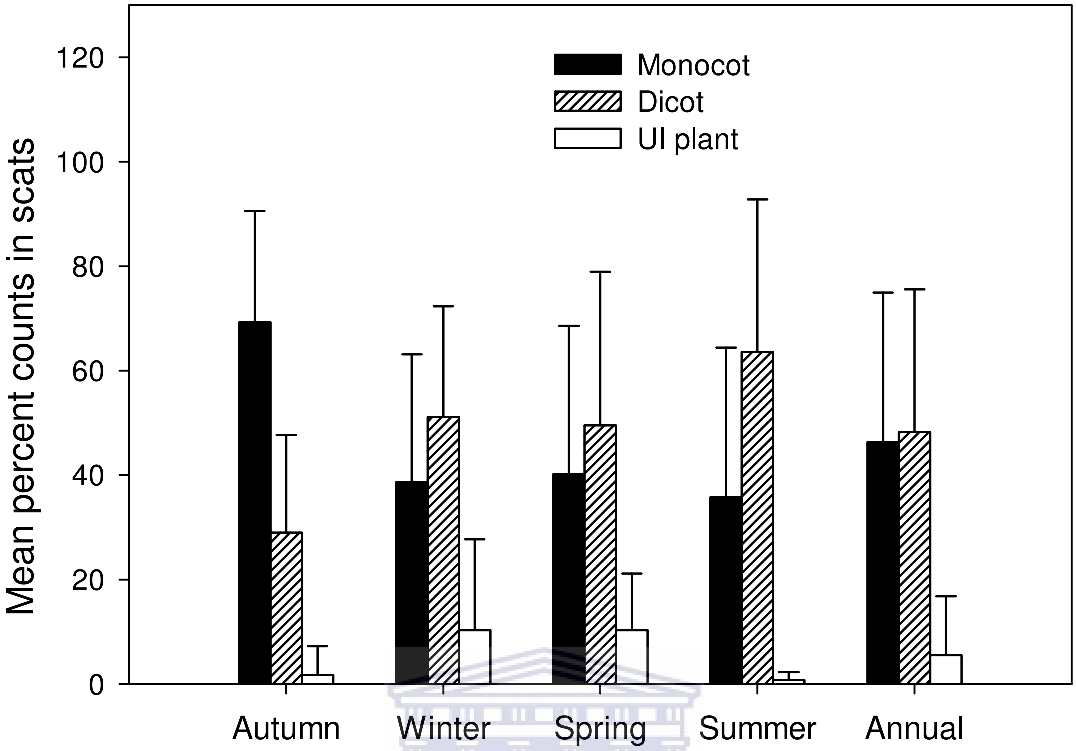

Figure 5.1 Diet composition based on percent counts (mean ± SD) of monocotyledons and dicotyledons in the scats of angulate tortoises in the WCNP.

Table 5.9 Percent composition and occurrence based on presence-absence of monocotyledons, dicotyledons and insect parts in the scats of angulate tortoises in the WCNP.

	Percent composition					Percent occurrence				
Plant type	**Au**	**Wi**	**Sp**	**Su**	**Total**	**Au**	**Wi**	**Sp**	**Su**	**Total**
Dicot	44.1	32.6	29.3	34.1	34.5	100	100	100	100	100
Insect parts	2.9	10.9	14.6	22.7	13.3	6.7	33.3	50.0	66.7	38.6
Monocot	44.1	32.6	29.3	34.1	34.5	100	100	100	100	100
UI plant material	8.8	23.9	26.8	9.1	17.6	20.0	73.3	91.7	26.7	50.9

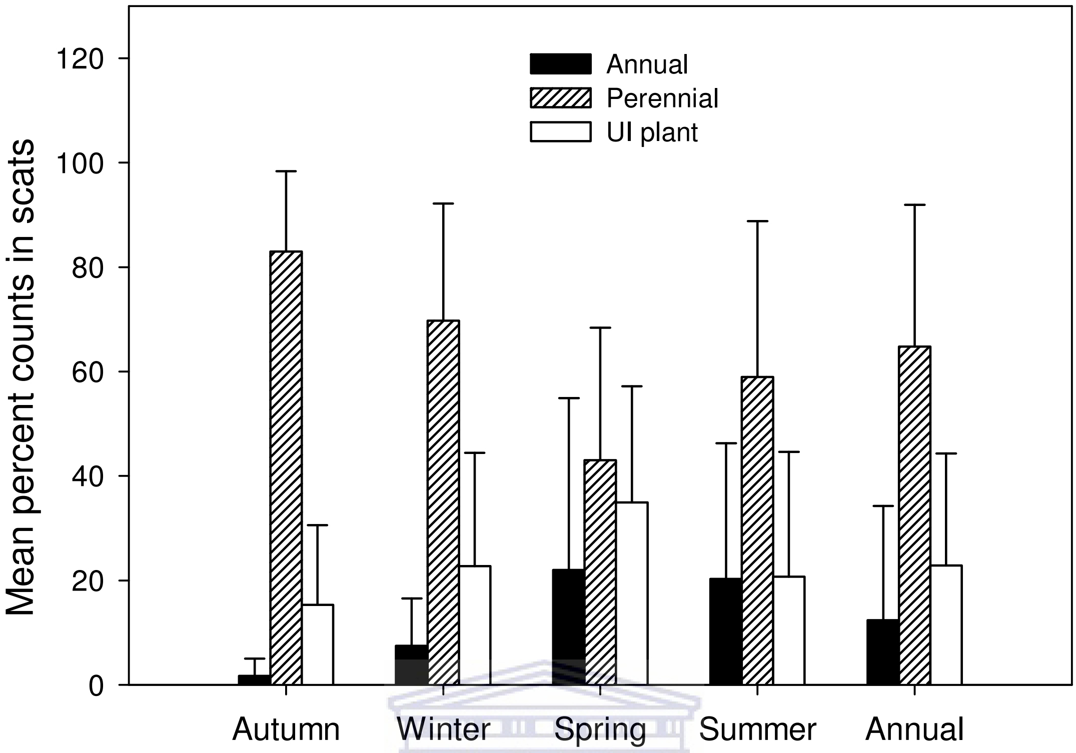

Figure 5.2 Diet composition based on percent counts (mean ± SD) of annuals and perennials in the scats of angulate tortoises in the WCNP.

Table 5.10 Percent composition and occurrence based on presence-absence of annuals, perennials and insect parts in the scats of angulate tortoises in the WCNP.

	Percent composition					Percent occurrence				
Plant types	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
Annual	23.7	27.7	26.8	26.4	26.3	60.0	86.7	91.7	93.3	82.5
Insect parts	2.6	10.6	14.6	18.9	12.3	6.7	33.3	50.0	66.7	38.6
Perennial	39.5	31.9	29.3	28.3	31.8	100	100	100	100	100
UI plant material	34.2	29.8	29.3	26.4	29.6	86.7	93.3	100	93.3	93.0

5.4.8 Plant types in the diet of DI angulate tortoises

5.4.8.1 Monocotyledons and dicotyledons in DI scats

The diet of angulate tortoises on DI consisted largely of monocots (Fig. 5.3), and for all seasons combined, the contribution of all the diet items differed significantly ($\chi^2_2 = 78.3$, $P << 0.0001$). The count for monocots was highest, followed by dicots, while the count for UI plant material was the lowest.

The contribution of monocots, dicots and UI plant material to the scats differed significantly within each season (autumn: $\chi^2_2 = 25.08$, winter: $\chi^2_2 = 12.88$, spring: $\chi^2_2 = 25.56$, summer: $\chi^2_2 = 22.8$, all $P < 0.0016$) but the relative importance of the categories was not the same. During autumn the order was: monocot > dicot > UI plant material. The winter sequence was: monocot > dicot = UI plant material, largely due to the increase in UI plant material. The sequence of importance for spring was: monocot > dicot > UI plant material. In summer, the counts for monocots and dicots were similar, and both were higher than the count for UI plant material (monocot = dicot > UI plant material).

The contribution of the categories changed with the seasons (Fig. 5.3). Seasonal comparisons of monocots displayed a significant effect ($H_3 = 11.24$, $P = 0.011$) and autumn counts exceeded summer counts. The importance of dicots changed with the season ($F_{3,56} = 4.32$, $P = 0.0082$) and the count for dicots was higher in summer than in autumn and spring. The winter count for UI plant material was larger than the counts in all other seasons ($H_3 = 36.03$, $P << 0.0001$).

All the scat samples on DI contained monocots (Table 5.11). Season did not influence percent occurrence or composition (all $P > 0.13$) but plant type had an effect (all $F_{3,9} > 8.76$, $P < 0.0049$). There were higher counts for monocots and dicots than for UI plant material, and a higher count for monocots than for insects.

5.4.8.2 Annuals and perennials in DI scats

Every season, epidermi of annual and perennial plants were present in angulate tortoise scats (Fig. 5.4). For all seasons combined, perennial plants had higher counts than annuals and UI plant material had, and the latter two categories did not differ (χ^2_2 38.9, $P << 0.0001$). The same trend was detected in autumn ($\chi^2_2 = 25.3$, $P < 0.0001$) and spring ($F_{2,42} = 29.4$, $P << 0.0001$). In winter, the relationship among the categories was: perennial > UI plant material > annual ($F_{2,28}$ = 20.87, P <0.0001), whereas in summer the relationship was: perennial = annual > UI plant material (χ^2_2 = 10.38, P = 0.0056).

The counts for the annual and perennial categories changed with the seasons (annual: $F_{3,56}$ = 25.24, perennial: H_3 = 22.8, UI plant material: $F_{3,56}$ = 14.88, all $P < 0.0001$). For annual plants, summer values were the highest, and spring values were higher than autumn and winter values; the latter two did not differ. For perennial plants, autumn had the largest value while winter and spring values did not differ but exceeded the value in summer. For UI plant material, the winter and spring counts were similar, but were higher than the summer and autumn counts; summer counts exceeded autumn counts.

Percent occurrence of the annual and perennial categories (Table 5.12) was not influenced by season (P = 0.14) or by plant type (P = 0.11). Similarly, season and category did not affect percent composition (all $P > 0.14$).

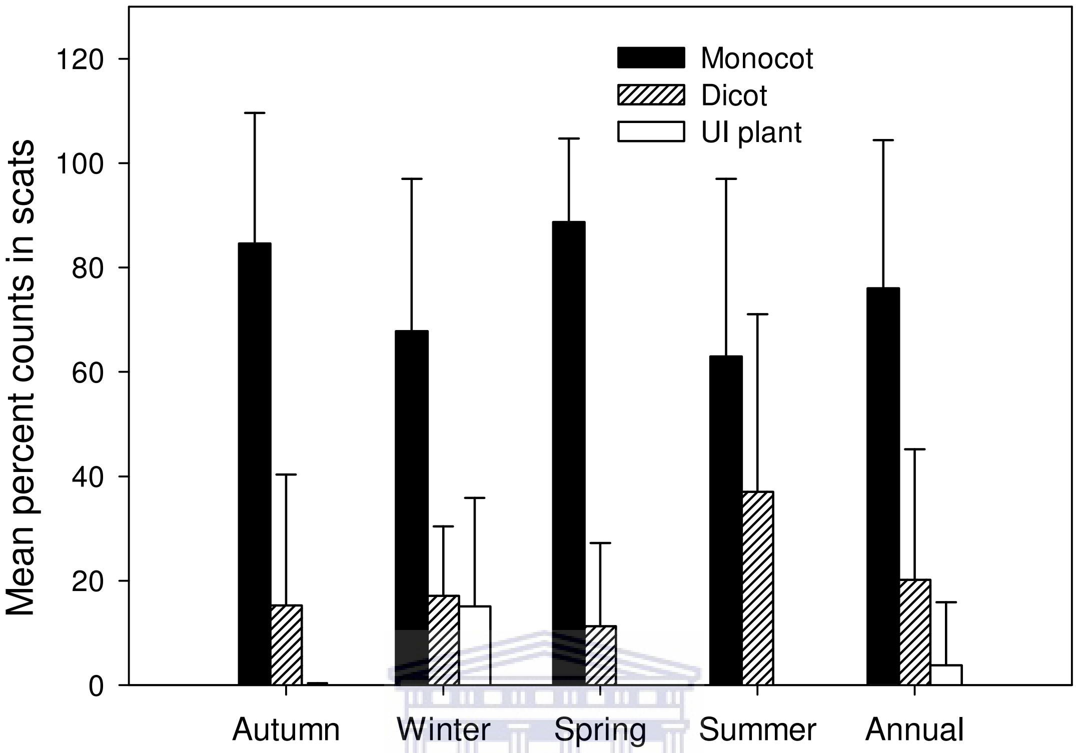

Figure 5.3 Diet composition based on percent counts (mean ± SD) of monocotyledons and dicotyledons in the scats of angulate tortoises on DI.

Table 5.11 Percent composition and occurrence based on presence-absence of monocotyledons, dicotyledons and insect parts in the scats of angulate tortoises on DI.

	Percent composition					**Percent occurrence**				
Plant type	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
Dicot	29.6	27.5	31.6	42.9	32.5	53.3	93.3	80.0	100	81.7
Insects	11.1	21.6	28.9	14.3	19.9	20.0	73.3	73.3	33.3	50.0
Monocot	55.6	29.4	39.5	42.9	39.7	100	100	100	100	100
UI plant	3.7	21.6	0	0	7.9	6.7	73.3	0	0	20.0

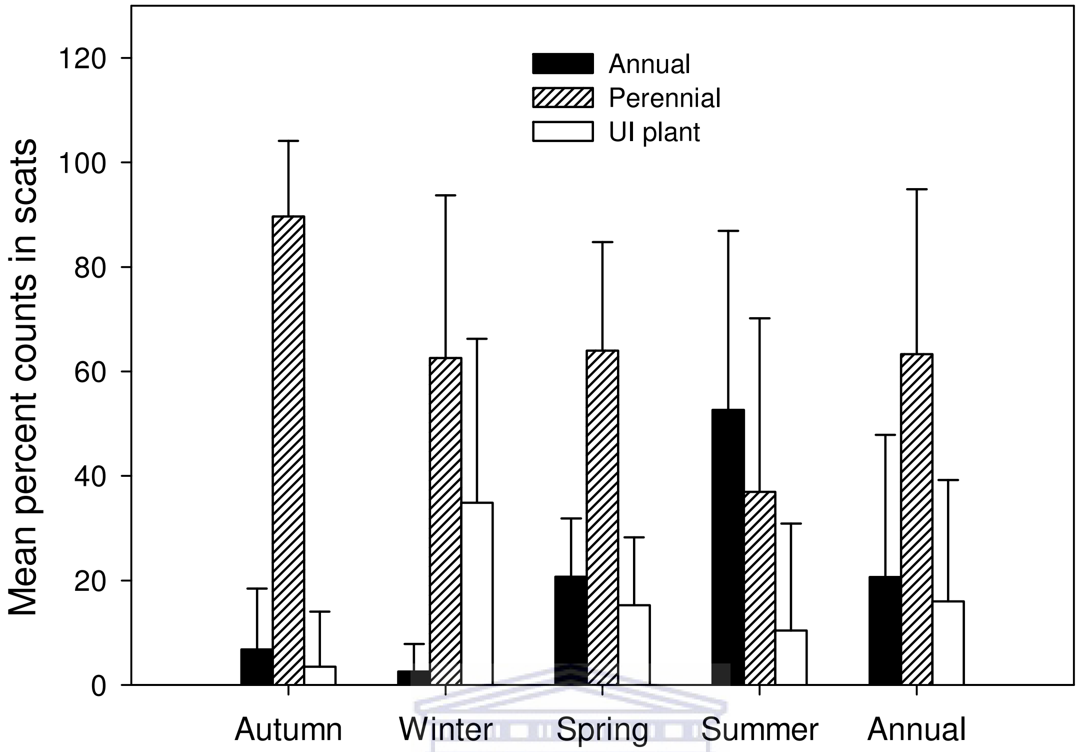

Figure 5.4 Diet composition based on percent counts (mean ± SD) of annuals and perennials in the scats of angulate tortoises on DI.

Table 5.12 Percent composition and occurrence based on presence-absence of annuals, perennials and insect parts in the scats of angulate tortoises on DI.

	Percent composition					Percent occurrence				
Plant types	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
Annual	26.7	14.9	27.3	34.9	25.7	53.3	46.7	100	100	75.0
Insects	10.0	23.4	20.0	11.6	17.1	20.0	73.3	73.3	33.3	50.0
Perennial	50.0	29.8	27.3	30.2	32.6	100	93.3	100	86.7	95.0
UI plant material	13.3	31.9	25.5	23.3	24.6	26.7	100	93.3	66.7	71.7

5.4.9 Comparisons between sites

5.4.9.1 Comparisons for monocotyledons and dicotyledons

Monocots were more prevalent in angulate tortoise scats from DI than in angulate tortoise scats from the WCNP for all seasons combined ($T_{57,60}$ = 2362, $P << 0.0001$), autumn ($T_{15,15}$ = 294, $P = 0.011$), winter (t_{28} = 2.97, $P = 0.0061$), spring (t_{25} = 5.62, $P < 0.0001$) and summer ($T_{15,15}$ = 293, $P = 0.013$). In contrast, the percent counts for dicots were higher in the WCNP than on DI (overall: $T_{57,60}$ = 4401, $P << 0.0001$; autumn: $T_{15,15}$ = 171, $P = 0.011$; winter: t_{28} = 5.26, $P < 0.0001$; spring: t_{25} = 4.32, $P = 0.00022$; summer: $T_{15,15}$ = 174, $P = 0.016$). The percent counts for UI plant material was higher in the WCNP than on DI for all seasons combined ($T_{57,60}$ = 3852, $P = 0.0077$) and in spring ($T_{12,15}$ = 251, $P << 0.0001$), but there was no difference between the sites during winter and spring (all P > 0.21).

A three-way ANOVA on percent occurrence data showed no effect of site or season (all $P > 0.068$), but showed an effect of diet category ($F_{3,9}$ = 20.7, $P = 0.00022$). Similarly, diet category had a significant effect on percent composition ($F_{3,9}$ = 22.52, $P = 0.00016$), and there was no effect of site or season (all $P > 0.99$). For percent composition and percent occurrence, the values for monocots and dicots did not differ but exceeded the values for UI plant material and insect parts.

5.4.9.2 Comparisons for annuals and perennials

Percent counts for annuals were higher in scats from DI than from the WCNP only in summer (t_{28} = 2.91, $P = 0.0070$), while the counts did not differ in the other seasons and for all seasons combined (all $P > 0.022$). There was no difference for percent counts of perennials between the two sites (all $P > 0.026$). The percent counts for UI plant material were higher in scats from the WCNP than in scats from DI in autumn, spring and for all seasons combined (autumn: $T_{15,15}$ = 157, $P = 0.0018$; spring: t_{25} = 2.87, $P = 0.0083$; overall: $T_{57,60}$ = 3838, $P = 0.0097$), but did not differ in winter and summer (all $P > 0.064$).

Percent composition was not influenced by site or season, but was influenced by diet item ($F_{3,9}$ = 10.77, $P = 0.0025$); percent composition of annuals, perennials and UI plant material was higher than the percent composition of insect parts. Percent occurrence, however, was influenced by diet category ($F_{3,9}$ = 12.64, $P = 0.0014$) and by season ($F_{3,9}$ = 4.65, $P = 0.032$), but not by site ($P = 0.37$). Percent occurrence for perennials was higher than for insect parts, and percent occurrence was higher in spring than in autumn.

5.5 DISCUSSION

5.5.1 Importance of different plant types

The importance of monocotyledonous and dicotyledonous plants in the diet of angulate tortoises differed between the two study sites. Overall, *C. angulata* consumed similar quantities of monocots and dicots in the WCNP even though monocots made up only 30% of the diet plant species, whereas on DI, monocots made up 61% of the diet plant species and contributed larger quantities to the tortoises' diet than the dicots did. In general, the leaves of dicots have a higher nutritive value than the leaves of monocots have, but this beneficial effect is offset by secondary compounds, such as tannins, which often accumulate in dicotyledonous plants (Huston & Pinchak 1991). These factors should influence the selection of monocots or dicots by tortoises, provided the plant diversity of the environment, such as in the WCNP, allows the tortoises a wide choice. The low plant diversity on DI (Hurford 1996) provided the angulate tortoises with few choices, particularly during the dry season.

Perennial and annual plant species consumed included varieties of both monocot and dicot plant species. At both study sites, perennial plants formed a significantly larger part of angulate tortoise diets over all seasons compared to annual plants. Perennials represent a stable, reliable source of plant material that is always available for tortoise consumption. Perennial plant types included grasses, restios, sedges, herbs, shrubs and succulents. Long-lived perennial plants invest more resources into the production of anti-herbivore defences to deter herbivores from consuming them (Cates & Orians 1975). The production of secondary compounds, such as lignin and suberin, are responsible for the strengthening of plant tissues, making the plants more difficult to digest (Briske 1991; Balsamo et al. 2004). Perennial plant material would thus be easier to detect in scats compared to annual plants, and it seems likely that the consumption of annual plants may have been underestimated, particularly on DI.

Angulate tortoises on DI had to deal with wide fluctuations in the availability of plants due to the ephemeral nature of vegetation on the island (Hurford 1996). The consumption of ephemeral, annual species may have benefited angulate tortoises because annuals often have higher digestible nutrient contents compared to established perennial plants (Cates & Orians 1975). First successional plants species are the first colonisers in a disturbed habitat. They grow and mature quickly, investing little if any resources in anti-herbivore defences (Cates & Orians 1975). Angulate tortoises would thus gain higher levels of nutrients from these plants compared to perennials. Annual plants were present in low levels in *C. angulata* scats for three out of four seasons, but equalled the contribution of perennial plants in summer. The high digestibility of annual plants compared to perennial plants may have contributed to annuals being under-represented in the scats. The importance of perennials in the diet of angulate tortoises on DI was largely due to their high consumption of a dominant species, *Trachyandra divaricata*, over all seasons.

5.5.2 Growth forms and important diet plants

Perennial grass species comprised the most important growth form in the diet of angulate tortoises in the WCNP, while annual grasses contributed significantly to the DI diet during spring and summer. Els (1989) reported that buffalo grass contributes 25% to the diet of angulate tortoises in the Eastern Cape. Grasses also form an important component in the diets of several other tortoise species (Macdonald & Mushinsky 1988; Milton 1992; Rall & Fairall 1993; Nagy *et al*. 1998; Henen 2002). Grasses generally have a lower nutritive value than most forbs and shrubs (Huston & Pinchak 1991), thus it is somewhat surprising that grasses seem to be so important in the diet of several tortoise species. However, consuming grasses appears useful for lipid storage and achieving energy surpluses, at least for desert tortoises (Henen 1997).

Cynodon dactylon was the most important diet item of angulate tortoises in the WCNP. The tortoises consumed this perennial grass throughout the year, with a particularly high consumption in autumn. *Cynodon dactylon* is a short, creeping grass, which makes all plant parts easily accessible to angulate tortoises. This grass provides good fodder, and flowers from early spring to late autumn (Van Oudtshoorn 1999). The epidermal fragments identified for *C. dactylon* were mainly from the bracts of inflorescences, indicating that the long flowering season made this species a particularly useful diet plant. Balsamo *et al*. (2004) evaluated the biomechanical properties of food plants used by geometric tortoises and found that the leaves of *C. dactylon* have a low failure load, which would make it easy for small tortoises to tear pieces off the plant. Other important diet grasses in the WCNP included *Lolium perenne*, a highly palatable grass (Van Oudtshoorn 1999), and *Pennisetum setaceum*, which provide poor pasture because the leaves are course and tough (Van Oudtshoorn 1999). The angulate tortoises consumed *P. setaceum* mainly in winter when the leaves were probably younger and softer. It is also possible that increased water availability in winter may have enabled angulate tortoises to better digest coarse plant material, as tortoises require water to digest dry plants (Nagy *et al.* 1998).

Although grasses had a patchy distribution on Dassen Island, annual grasses were important in the diet of angulate tortoises. Animals are thought to gain more nutrients from ingesting fast-growing annual plants than from perennial plants because the perennial plants divert resources into the production of structural material (low digestibility) and anti-herbivore defences, which would make them less palatable to herbivores (Cates & Orians 1975; Huston & Pinchak 1991). Annual plants, such as the grasses *Avena byzantina* and *Phalaris minor*, would therefore divert fewer resources into the production of anti-herbivore defences than perennial grasses do, which might make annual grasses more palatable to angulate tortoises. Nevertheless, *P. minor* is not considered a palatable grass (Van Oudtshoorn 1999), and its high consumption in summer may be linked to the flowering season, which covers spring and summer (Van Oudtshoorn 1999). In contrast, *Avena byzantina* is regarded as palatable and is cultivated for grain and fodder (Animal feed resources information system).

Herbaceous plants constituted the most important growth form in the diet of angulate tortoises on DI, and was the growth form that made the largest contribution to the WCNP diet in winter. Herbaceous species, in general, are more digestible than grasses and shrubs, and often have a high protein and phosphorous content (Huston & Pinchak 1991). The wet season stimulates the germination and growth of new annual plants, and new growth of perennial plants, and the younger plant parts provided angulate tortoises with a potentially more nutritious source of food compared to tougher, more mature plant material consumed during the dry season (Huston & Pinchak 1991). The high digestibility of soft plant material may have contributed to the lower quantities of herbaceous plant material identified in diets during spring. Plant parts such as flower petals are probably more digestible than leaves. Flowers tended to fall apart during the process of removing epidermi for producing reference slides (pers. obs.). A high digestibility of flowers may have caused an under-representation of herbaceous plant material in the diets of angulate tortoises in this study.

The herbaceous perennial, *Geranium incanum*, was the second most important diet plant of angulate tortoises in the WCNP. This low-growing plant forms a dense carpet, which would be easily accessible to tortoises. The plant flowers from spring to autumn (Joffe 2003), but the high consumption of *G. incanum* in winter indicates that the tortoises probably consumed mainly new leaves, which developed after the rainfall season commenced. The herb, *Senecio elegans,* was present in high quantities in angulate tortoise scats in the WCNP during spring. *Senecio elegans* has soft leaves, which have been described as becoming succulent when growing near the coast (Kidd 2002). *Chersina angulata* probably gained not only nutrients from these soft leaves but also access to an additional source of water. This may also be the case for *C. angulata* on DI, where *S. elegans* formed an important diet component in summer.

The perennial herb *Trachyandra divaricata* was the most important diet plant of angulate tortoises on DI. All parts of this plant are considered edible (Manning 2003), although consumption of *T. divaricata* has been linked to lipofuscin storage disease in sheep (Newsholme *et al.* 1985). *Trachyandra divaricata* forms new leaves at the start of the rainfall season in late autumn (pers. obs.) and the tortoises fed extensively on the fresh leaves in winter. During the dry season (summer and autumn), the condition of the plants deteriorate, and the leaves may even die-off during particularly dry years (pers. obs.). This was the situation during the study period, when the angulate tortoises consumed high quantities of dry *T. divaricata* leaves in autumn. *Albuca flaccida* also featured prominently in the autumn diet of angulate tortoises. This fleshy-leaved geophyte was observed growing between the branches of *Tetragonia fruticosa*, which probably protected this geophyte from unfavourable conditions and grazing pressure, and enabled it to persist after flowering in spring. It is not clear, however, if the high consumption of *A. flaccida* in autumn was of new leaves, or if the tortoises consumed old leaves that persisted until autumn.

Angulate tortoises consumed *Zantedeschia aethiopica*, a geophyte possessing moderately fleshy leaves but containing oxalic acid (van Wyk *et al.* 2002). Oxalic acid in large concentrations can be harmful to animals and the consumption of leaves from *Z. aethiopica* is known to cause distress if ingested (van Wyk *et al.* 2002). Only epidermi of floral parts of *Z. aethiopica* were identified in scats. The ingested floral parts may contain lower concentrations of oxalic acid compared to leaves, making them more palatable to angulate tortoises. The fleshy fruits of this plant are also popular with birds (Joffe 2003).

Angulate tortoises on DI did not consume shrubs or succulent plants, whereas both growth forms were represented in the WCNP diet. *Hermannia scabra* is a low-growing shrublet and both the leaves and flowers (winter and spring; Manning & Goldblatt 1996) would have been within reach of angulate tortoises. *Rhus laevigata* was an important diet plant in autumn, when the tortoises probably fed on the fruits of the plant. The low levels of shrubs identified in tortoise scats may be because of the height restrictions faced by tortoises, which feed at a lower level than larger herbivores such as cows and sheep (Rall & Fairall 1993). Angulate tortoises were thus restricted to feed from the lower branches of shrubs, and on the leaves or fruits that dropped to the ground. On DI, the consumption of leaves from the tree, *Myoporum serratum*, made a significant contribution to the dry season's diet of angulate tortoises. *Myoporum serratum* is an evergreen tree species that was introduced to DI (Hurford 1996), and is recorded as being a tree xerophyte (Gindel 1969). *Chersina angulata* might have consumed *M. serratum* as a last resort when more nutritious plant material was unavailable in the environment.

Succulent plant species dominated the study site on DI (see Chapter 2), but the diet of angulate tortoises on DI did not include succulents, although the tortoises experienced long periods of low rainfall during summer and autumn. Milton (1992) found that leopard tortoises change their diet from grasses to succulents during the summer months when green grass was no longer available. It is possible that a high concentration of ions, or other toxic substances, precluded the used of succulent plants on DI. *Mesembryanthemum crystallinum*, an abundant succulent on DI, concentrates ions in its tissues in response to drought conditions; potassium and or sodium are commonly concentrated in specialised trichomes modified to form bladder cells (Adams *et al*. 1998). The concentration of these ions may have contributed to these plants being unpalatable to angulate tortoises.

In the WCNP, succulents increased in the diet of angulate tortoises during spring and summer. Although it is possible that the low value recorded during the driest season, autumn, is due a high digestibility of succulent species, a more likely explanation is that angulate tortoises do not rely on succulent plants to supplement water during the dry season. The spring scats of angulate tortoises in the WCNP contained large quantities of a succulent species that could be classified only to the family Aizoaceae. This small plant was not present in the study quadrats, and was scarce at the study site. The succulent plant *Carpobrotus edulis* has tough fleshy leaves and edible fruits (Roux & Schelpe 1994; Manning & Goldblatt 1996), and has a high abundance in the WCNP. Despite its palatability, this plant was not detected in the scats of angulate tortoises, perhaps because angulate tortoises do not have the bite strength to tear off large enough pieces from *C. edulis*. Succulent species that appeared in their diet, e.g., *Senecio maritimus* and *Ruschia macowanii*, have smaller leaves that would be easier for these tortoises to bite and tear.

Angulate tortoises avoided restios, except that one tortoise in the WCNP appeared to have sampled small quantities of *Thamnochortus spicigerus*, a common but tough plant. On DI, the sedge *Ficinia nigrescens*, a small tufted perennial that flowers from late autumn to spring (Manning & Goldblatt 1996), was a very important diet plant in spring. Most of the epidermi observed in the scats were from floral parts of *F. nigrescens*, indicating that *C. angulata* avoided consuming the tougher stems but favoured the inflorescences. Baard (1990) reported that two sedge species contributed 2% to the diet of geometric tortoises at the Elandsberg Private Nature Reserve.

The scats of *C. angulata* at both study sites contained low quantities of UI plant material. This indicates that the bulk of material identified in the scats could at least be classified to the level of genus or plant type. The lower level of UI plant material observed in DI scats was partly due to the low plant diversity on the island, which limited the potential to overlook inconspicuous plants in the environment when collecting specimens for reference slides. The high plant diversity on the mainland made it easier to overlook less common plant species. The low levels of UI plant material recorded in scats also indicate that microscopic faecal analysis is an effective method to determine the diet of angulate tortoises.

5.5.3 Animal material in the scats

The scats of angulate tortoises at both study sites contained insect parts, but it is not clear if the insects were eaten deliberately, or were ingested incidentally. Angulate tortoises were never observed actively seeking and ingesting insects, and the tortoises are probably too slow to seek and capture most insects. It seems more likely that angulate tortoises incidentally ingested insects while consuming plant organs such as flowers. Insects have been observed also in the scats of other tortoises and turtles (Bjorndal 1991; Milton 1992; Spencer *et al.* 1998). Even if the ingestion of insects was incidental, the animal material probably contributed to the nutrition of angulate tortoises and may have provided nutrients that might not be obtained from plant material. It is possible that *C. angulata* selected plant parts covered in insects to acquire additional sources of nutrients such as animal protein.

An indirect interaction practiced by angulate tortoises with other animals was the consumption of faecal material. Faecal material excreted by an animal may contain material edible to other animals, such as seeds (Logiudice 2001). This excreted edible material may serve as a source of food to other animals, which risk infection by faecal parasites or pathogens when eating the faeces (Logiudice 2001). Parasite infection caused through the ingestion of faecal material has been observed in animals consuming racoon faeces (Logiudice 2001; Evans 2002). Racoons infested with the parasitic roundworm *Baylisascaris procyonis* pass their infection to other animals through contaminated faeces.

The scats of angulate tortoises at both study sites contained parasite eggs, but the level of infestation on DI was particularly high, perhaps as a consequence of the high tortoise density on DI. Most internal parasites are host-specific but parasites may be transferred between different animal species through the consumption of faeces that contain viable parasite eggs (Logiudice 2001; Evans 2002). The practice of coprophagy by angulate tortoises may have contributed to the high level of infection observed amongst these tortoises. *Chersina angulata* were not observed consuming their own scats but rather those of other animals such as the European rabbit on DI. The island also hosts a number of breeding seabird colonies from which *C. angulata* may consume faecal material. Focal studies (see Chapter 3) showed that angulate tortoises on DI consumed rabbit faeces mostly during the dry season, in summer and autumn. This does not correspond with the highest level of parasite infestation, which occurred in spring. Thus, there may not be an immediate link between coprophagy and parasite infestation on DI.

It is interesting to note that angulate tortoises on DI had significantly higher levels of sand in the scats than tortoises in the WCNP had, and that the incidence of sand in their scats peaked in spring (see Chapter 4). There may thus be an association between sand ingestion and parasite infestation in *C. angulata*. It is known that there is a direct correlation between geophagy and geohelminth infections in humans (Saathoff *et al*. 2002).

5.6 REFERENCES

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6 FEEDING STRATEGIES AND METHODOLOGIES

6.1 ABSTRACT

The diet of angulate tortoises consisted mainly of angiosperms, but also included mosses, mushrooms, insects, snails, and animal faeces. Seventy-two diet plants, in 32 different families, were identified to the genus level. The histological method provided the most comprehensive diet list, but macroscopic evaluation of faecal samples and focal observations provided information about the feeding strategies of angulate tortoises that could not be obtained by histological scat analysis. Tortoises in the WCNP and DI had 12 and 11 principal food plants, respectively, of which most were principal food items in one season only. Most principal food items were grass or herb species. Over the whole year, four principal food items were distinguished for WCNP tortoises and five principal food items were distinguished for DI tortoises. *Cynodon dactylon* was a principal food species in the WCNP for three of the four seasons, whereas on DI, *Trachyandra divaricata* was a principal food item in every season. Although the number of principal food items of angulate tortoises did not differ between the two sites, the tortoises in the WCNP had a more diverse diet than the tortoises on DI had. Most plant species, however, occurred in low frequencies in the scats, and it seems likely that the tortoises sampled some of these plants to test their potential as new food items or to monitor changes in their nutrient content. Two preference indices, forage ratio and Manly's α, were calculated to assess food selection of angulate tortoises. Manly's α appeared to be a more conservative index because the forage ratio indicated positive selection for substantially more plant species than Manly's α did. Plants, which were selected out of proportions to their availability, included principal food items as well as plants with low frequencies in the diet. The latter category may have been selected because the plants contained specific nutrients that the tortoises required. The tortoises showed a strong aversion for some of the abundant plant species, which may be very fibrous, have a high salt content, or may be poisonous. The proportional similarity index was 0.31 and 0.16 for tortoises in the WCNP and DI, respectively, indicating that angulate tortoises are selective feeders and not generalist feeders, despite the tortoises inhabiting a variety of habitat types.

6.2 INTRODUCTION

Foraging ecology provides critical information about factors that influence the survival of animals. In the past, most foraging studies were simply descriptive, but in recent years, the focus shifted from diet lists to analytical evaluations that improve understanding of the cause and effect basis of foraging (Robbins 1983). The optimal foraging strategy represents a balance between the costs and benefits associated with foraging: costs include factors such as the energy and time spent searching for food, while benefits include factors such as long-term reproductive success (Robbins 1983). Foraging strategies differ among species, and some animals, food generalists, have broad diets, whereas food specialists are highly selective and ignore most of the food items they encounter (Smith & Remington 1996).

Food selection can be driven by a number of factors, e.g., availability of the food item, its palatability, accessibility and profitability (Smith & Remington 1996). It is often found that a few plant species constitute the bulk of a herbivore's diet while a range of other species are present in small quantities (Robbins 1983). This may be a consequence of a generalist herbivore's habit to often sample available food items in order to monitor changes in nutrient content and secondary plant compounds (Robbins 1983; Dearing & Schall 1992). Consequently, food selection may be influenced by food nutrient levels (Henen *et al*. 2005; Tracy *et al.* 2006). Experimental studies have shown that when birds are given food choices, they select a diet with the most favourable amino acid composition within 16 hours (Murphy & King 1987). Furthermore, populations of the same species could achieve the same nutritional balance from the food types available in different habitats (Dearing & Schall 1992).

Habitat destruction and transformation pose significant threats to the continued existence of many animals, including tortoise species of South Africa (Gardner *et al*. 1999; Hofmeyr *et al*. 2006). The effective conservation and management of animals require an understanding of the animals' habitats and their foraging ecology (Norton 1983). In this chapter, I used data on the availability of food resources and the diet composition of angulate tortoises (reported in Chapters 2 and 5, respectively) to evaluate seasonal changes in food preferences and aversions of *C. angulata* at two study sites in the southwestern Cape. I also assessed the efficacy of three different methods, focal observations, macroscopic faecal analysis, and histological analysis of scats, which were used to evaluate the feeding strategies of angulate tortoises.

6.3 MATERIALS AND METHODS

6.3.1 Principal food items and cumulative percentages in the scats

Principal food species are food items that contribute substantially to the diet of an animal (Mason *et al*. 1999). In this analysis, I followed the example of Mason *et al.* (1999) to regard plant taxa that have an average frequency greater than 5% in the diet as principal food. I used the data for the histological evaluation of the faecal samples to represent the proportion of each plant taxon in the diet. Although the category unidentified plant material contributed more than 5% to the WCNP scat composition in winter, spring and overall (see Table 5.1), I did not regard this category as principal food. The scats from DI had low percentages of unidentified plant material (see Table 5.3). When I calculated cumulative percentages for the plant taxa in the scats, I first ranked the taxa from the largest percentage to the lowest percentage, but placed the unidentified plant category last in the list.

6.3.2 Preference indices

Several methods are available to calculate food preferences of animals. I calculated two preference indices for angulate tortoises; forage ratio (Gerald 1966) and Manly's α (Chesson 1978). The forage ratio (FR) simply compares usage of a diet item with availability. A FR of 1.0 indicates that the food item is used in the same proportion as its availability in the environment. In contrast, a FR > 1.0 indicates preference for the food item and a FR < 1.0 indicates avoidance of the food item (Gerald 1966).

$$\mathrm{FR}_i = \frac{p_i}{q_i} \qquad \text{……………………. [1]}$$

Where FR_i = Forage ratio for species *i*

p_i = Percentage / proportion of species *i* in the diet

q_i = Percentage / proportion of species *i* available in the environment

The FR does not take the availability and use of other food items in the environment into consideration, whereas Manly's preference index (α_i) indicates an animal's preference for a specific food item relative to the other food items available in the environment (Chesson 1978, 1983). When the consumer does not influence the abundance of the food item in the environment, α_i can be estimated as the ratio of the food item *i* in the diet to the food item *i* in the environment (thus the FR_i), scaled to the sum of the ratios for all diet items, so that the sum of $\alpha_i = 1.0$.

$$\alpha_i = \frac{p_i / q_i}{\sum_{i=1}^{m} p_i / q_i} \qquad \text{……………………} [2]$$

Where α_i = Manly's preference index for food type *i*

m = Number of food species available

When the animal is using the available food items in the environment at random, α_i would be identical for all food items ($\alpha_i = 1/m$), consequently $\alpha_i > 1/m$ indicates selection whereas $\alpha_i < 1/m$ indicates avoidance (Chesson 1978, 1983; Krebs 1999).

I used the data for the histological evaluation of the faecal samples to represent the proportion of plant species in the diet. For these calculations, I excluded the animal material in the faecal samples and calculated the percentage for each plant species/category relative to the plant material in the faeces. I combined all grass species identified in the histological evaluation, except *Ehrharta villosa*, to correspond with availability data for grass.

The availability of plant species at the study sites was calculated as relative cover indices (RCI; see Chapter 2). In order to use RCI in the calculation of preference indices, I had to convert RCI to percentages so that availability data and consumption data were measured on the same scale. I calculated the total RCI of each 5x5 m cell and expressed each plant species/category in that cell as a percentage of the total RCI for that cell. The average percentage for each plant species/category was then calculated from all cells for each season and for the four seasons combined (annual). The four seasons used in the calculations corresponded with the four seasons for which faecal samples were collected and analysed.

Trachyandra divaricata was an important diet item for angulate tortoises on Dassen Island. During autumn 1999, *T. divaricata* was available as debris and not as live plant material. Debris was not included in the analyses of the vegetation composition presented in Chapter 2, but for the percent availability of each plant species/category in this chapter, I included debris when calculating the RCI of *T. divaricata*.

Many plant species identified in the faecal analyses were not identified in the plant surveys. I made the assumption that these plant species were scarce in the environment, and for each season when these species occurred in the diet, I assigned a standard percent availability value that was smaller than the lowest value recorded for any species in the vegetation surveys (Mason *et al*. 1999).

In order to determine if the preference or avoidance of plants was statistically significant, I used a Mann-Whitney Rank Sum Test ($T_{n,n}$) to compare use (mean p_i) with availability (mean q_i).

6.3.3 Niche breadth

Feinsinger *et al*. (1981) suggested that "niche breadth be defined as the degree of similarity between the frequency distribution of resources used by members of a population and the frequency distribution of resources available to them". I used the Proportional Similarity Index (PSI) proposed by Feinsinger *et al*. (1981) to estimate if *C. angulata* is a generalist or a specialist feeder (Mason *et al.* 1999; Lagarde *et al*. 2003). The PSI can range from 1.0 for a generalist feeder, when the population uses resources in proportion to their availability, to a minimal q_i for a highly selective feeder, which exclusively feeds on the rarest resources (Feinsinger *et al*. 1981).

$$\text{PSI} = 1 - 0.5 \sum_{i=1}^{m} \left| p_i - q_i \right| \qquad \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots \text{[3]}$$

When calculating the PSI for tortoises at each study site and each season, I used the records of plants detected in the faeces and plants identified in the vegetation surveys.

6.3.4 Comparison of focal, macroscopic and histological data

In order to evaluate the level of correspondence among the results for the focal, macroscopic and histological methods, I used one-way repeated measures ANOVA to compare percent composition over four seasons for the diet items that were detected by all three methods.

6.4 RESULTS

6.4.1 Cumulative percentages and principal food items

Overall, six plant taxa contributed 50%, and 22 taxa contributed 80%, to the scat composition in the WCNP (Fig. 6.1a). The number of taxa required to reach the 80% mark changed with season, and was six, 11, 12, and 17, respectively, in autumn, winter, spring and summer. For angulate tortoises on DI, two plant taxa made up 50%, and eight taxa made up 80% of the annual scat composition (Fig. 6.1b). The number of taxa that contributed 80% to the scat composition was lower in autumn and winter (three taxa) than in spring and summer (six taxa).

Twelve plant taxa in the WCNP were identified as principal food items of angulate tortoises (Table 6.1). The contribution of these items to the diet differed seasonally, and most taxa were categorised as principal food in one season only. *Cynodon dactylon*, however, was a principal food species in three seasons, while *Senecio elegans*, *Geranium incanum*, and the unknown succulent (Aizoaceae) qualified in two seasons. When the contribution of the plant taxa was considered over the whole year, four principal food items were distinguished in the WCNP. Angulate tortoises on DI had 11 principal food items in their diet (Table 6.1). *Trachyandra divaricata* qualified as a principal food item in each season, while *Avena byzantina* and *Myoporum serratum* were principal food items in two seasons each. For the whole year, five diet species were categorised as principal food items. The number of principal food plants recorded each season did not differ between the WCNP and DI ($P = 0.29$, Chi-square test).

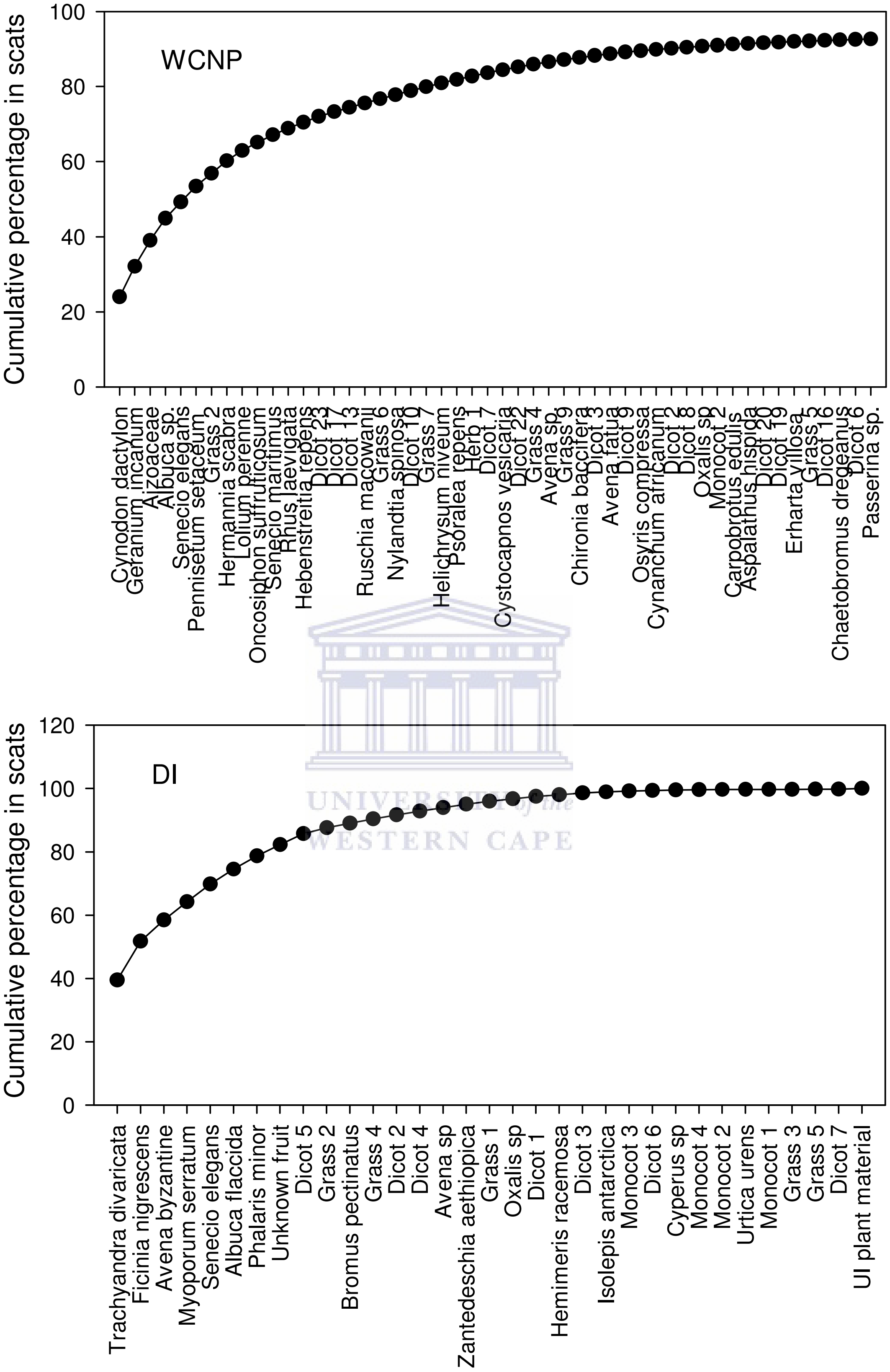

Figure 6.1 Cumulative percentages for plant taxa in the scats of angulate tortoises from the West Coast National Park (only the first 50 taxa) and Dassen Island over one annual cycle.

Table 6.1 Principal food species of angulate tortoises in the West Coast National Park and on Dassen Island. Plant species that contributed more than 5% to the diet in a particular season (in bold) were considered principal food items.

Sample	Au	Wi	Sp	Su	Ann
West Coast National Park					
Aizoaceae	0.6	2.7	**17.7**	**8.7**	**6.9**
Albuca sp	4.0	**14.5**	0.5	3.5	**5.9**
Cynodon dactylon	**54.8**	4.3	**15.8**	**19.3**	**24.0**
Geranium incanum	**6.1**	**22.1**	0.4	2.4	**8.2**
Grass 2	0.2	5.0	**5.8**	3.4	3.5
Hebenstreitia repens	0.0	**5.6**	0.8	0.0	1.6
Hermannia scabra	2.9	**5.6**	4.8	0.2	3.3
Lolium perenne	**8.1**	0.2	0.1	2.0	2.7
Oncosiphon suffruticosum	0.0	0.0	0.0	**8.4**	2.2
Pennisetum setaceum	0.0	**11.7**	2.3	2.2	4.2
Senecio elegans	1.3	0.0	**12.6**	**5.3**	4.4
Senecio maritimus	0.0	0.0	**6.3**	2.4	2.0
Dassen Island					
Albuca flaccida	**12.2**	3.0	3.7	0.0	4.7
Avena byzantina	4.2	0.2	**11.5**	**10.9**	**6.7**
Dicot 5	0.3	**13.6**	0.0	0.0	3.5
Ficinia nigrescens	0.0	0.0	**48.8**	0.0	**12.2**
Grass 2	0.0	0.0	2.3	**5.3**	1.9
Grass 4	0.0	0.0	**5.5**	0.0	1.4
Myoporum serratum	**12.2**	0.0	0.0	**10.9**	**5.8**
Phalaris minor	0.7	0.0	3.8	**12.4**	4.2
Senecio elegans	0.1	2.1	1.8	**18.5**	**5.6**
Trachyandra divaricata	**65.4**	**59.5**	**11.1**	**22.0**	**39.5**
Unknown fruit	0.0	**14.2**	0.0	0.0	3.5

6.4.2 Dietary preferences of tortoises in the WCNP

Selection indices were calculated for 77 plant taxa (grass species combined) in the WCNP (Table 6.2). The forage ratios (FR) revealed that angulate tortoises used most plant taxa out of proportion to their abundance. Manly's preference index appears to be more conservative and for all seasons combined, only 14 of the 77 plant taxa were selected. The number of taxa that appeared to be selected according to the FR and Manly's α, respectively, were 21 and six taxa in autumn, 29 and seven taxa in winter, 22 and four taxa in spring, and 34 and nine taxa in summer.

It was possible to statistically evaluate selection and avoidance of 25 plant taxa, for which both availability and utilization data were recorded (Table 6.1). When the diet for the entire year was considered, angulate tortoises showed a preference for *G. incanum*, *S. elegans* and grasses (all $T_{57,2683} > 93245$; $P < 0.011$) and avoided *C. edulis*, *E. villosa*, *H. niveum* and *R. laevigata*. The statistical values for the other taxa were not significant (all $P > 0.078$), indicating that the use of these diet items were not used out of proportion with their availability.

Statistical tests on 19 plant taxa available in autumn showed that angulate tortoises selected *G. incanum*, *R. laevigata*, *S. elegans* and grasses (all $T_{15,379} > 4051$; $P < 0.012$), and avoided *E. villosa* and *H. niveum* (all $T_{15,379} > 1944$; $P < 0.019$). The results approached significance (avoidance) for *C. edulis* ($T_{15,379} = 2115$; $P = 0.0501$). In winter, 24 taxa were analysed, of which three were selected (*C. vesicaria*, *G. incanum* and grasses; all $T_{15,768} > 8568$; $P < 0.0020$), and three were avoided (*C. edulis*, *E. villosa* and *R. macowanii*; all $T_{15,768} > 4177$; $P < 0.050$). The spring data of 22 plants showed that *G. incanum* and grasses were selected (all $T_{12,768} > 7250$; $P < 0.0001$), and that *E. villosa* was avoided ($T_{12,768} = 3133$; $P = 0.045$). During summer, 21 plant taxa were available and the tortoises selected *G. incanum*, *O. suffruticosum*, *S. elegans* and grasses (all $T_{15,768} > 8317$; $P < 0.0090$) while they avoided *E. villosa* ($T_{15,768} = 3920$; $P < 0.024$).

Table 6.2 Seasonal variation in the preference indices, Forage ratio and Manly's α, of angulate tortoises in the West Coast National Park. Values in bold indicate selection (>1.0 for Forage ratio and > 1/*m* for Manly's α) and the asterisks indicate for which dietary items Mann-Whitney tests could be done. For convenience, Manly's α is shown as a percentage rather than a fraction of 1.0.

	Forage ratio					**Manly's α**				
Plant taxon	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
*Afrolimon purpuratum**	0.0	0.0	0.0	0.2	0.1	0.0	0.0	0.0	0.0	0.0
Aizoaceae	**28.4**	**137.6**	**890.9**	**451.5**	**347.9**	2.8	**7.4**	**46.5**	**23.0**	**21.2**
Albuca sp.	**201.9**	**720.0**	**23.2**	**177.4**	**295.6**	**19.7**	**38.7**	1.2	**9.0**	**18.1**
Apocynaceae		**1.7**			0.4		0.1			0.0
Aspalathus hispida				**38.7**	**9.8**				2.0	0.6
*Asparagus lignosus**	0.0	**6.7**			**3.2**	0.0	0.4			0.2
*Carpobrotus edulis**	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0
Carpobrotus quadrifidus				**1.8**	0.4				0.1	0.0
*Chironia baccifera**	0.0	**4.6**		**41.3**	**12.0**	0.0	0.2		2.1	0.7
*Chrysanthemoides monilifera**	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Cynanchum africanum	**28.4**			**33.4**	**16.1**	2.8			1.7	1.0
*Cystocapnos vesicaria**		**42.0**	0.0	**112.4**	**8.0**		2.3	0.0	**5.7**	0.5
Dicot 1			**19.0**		**4.0**			1.0		0.2
Dicot 2		**3.4**	**65.3**		**14.7**		0.2	3.4		0.9
Dicot 3	**6.7**		**122.2**		**27.7**	0.7		**6.4**		**1.7**
Dicot 4			**6.3**		**1.3**			0.3		0.1
Dicot 5			**8.4**		**1.8**			0.4		0.1
Dicot 6			**31.6**		**6.7**			1.6		0.4
Dicot 7		**102.4**		**65.0**	**43.8**		**5.5**		**3.3**	**2.7**
Dicot 8	**51.7**			**3.5**	**14.7**	**5.1**			0.2	0.9
Dicot 9	**85.1**				**22.8**	**8.3**				**1.4**
Dicot 10	**135.1**	**36.9**		**33.4**	**54.5**	**13.2**	2.0		1.7	**3.3**
Dicot 11				**8.8**	**2.2**				0.4	0.1
Dicot 12		**1.7**			0.4		0.1			0.0
Dicot 13	**225.2**				**60.3**	**22.0**				**3.7**
Dicot 14	**1.7**				0.4	0.2				0.0
Dicot 15	**6.7**		**8.4**	**5.3**	**4.9**	0.7		0.4	0.3	0.3
Dicot 16				**19.3**	**4.9**				1.0	0.3
Dicot 17		**63.8**		**175.7**	**61.6**	0.0	**3.4**		**8.9**	**3.8**
Dicot 18				**3.5**	0.9				0.2	0.1
Dicot 19	**31.7**			**3.5**	**9.4**	3.1			0.2	0.6
Dicot 20				**36.9**	**9.4**				1.9	0.6
Dicot 21		**1.7**			0.4		0.1			0.0
Dicot 22				**151.1**	**38.4**				**7.7**	**2.3**
Dicot 23	**33.4**	**40.3**		**228.4**	**77.7**	3.3	2.2		**11.6**	**4.7**
Dicot 24			**8.4**		**1.8**			0.4		0.1
*Erharta villosa**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
*Ficinia nigrescens**	0.0	0.0	**1.9**	0.0	0.3	0.0	0.0	0.1	0.0	0.0

Table 6.2 continued

	Forage ratio					Manly's α				
Plant taxon	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
*Geranium incanum**	**2.7**	**55.1**	0.9	**2.2**	**9.6**	0.3	**3.0**	0.0	0.1	0.6
Grass*	**2.6**	**2.7**	**2.7**	**3.6**	**3.2**	0.3	0.1	0.1	0.2	0.2
*Gymnosporia buxifolia**		0.1	0.0	0.0	0.0		0.0	0.0	0.0	0.0
Hebenstretia repens	**1.7**	**276.9**	**37.9**		**82.2**	0.2	**14.9**	2.0		**5.0**
*Helichrysum niveum**	0.0	0.0	0.0	0.3	0.1	0.0	0.0	0.0	0.0	0.0
Herb 1				**175.7**	**44.7**				**8.9**	**2.7**
Hermannia pinnata				**3.5**	0.9				0.2	0.1
Hermannia scabra	**145.1**	**282.0**	**242.2**	**8.8**	**167.5**	**14.2**	**15.1**	**12.6**	0.4	**10.2**
Lachnospermum imbricatum				**1.8**	0.4				0.1	0.0
*Manochlamys albicans**	0.0	**3.4**	0.0		0.6	0.0	0.2	0.0		0.0
Monocot 1		**5.0**			**1.3**		0.3			0.1
Monocot 2			**59.0**	**3.5**	**13.4**			3.1	0.2	0.8
Monocot 3		**10.1**			**2.7**		0.5			0.2
Monocot 4		**10.1**	**2.1**	**1.8**	**3.6**		0.5	0.1	0.1	0.2
Monocot 5			**19.0**		**4.0**			1.0		0.2
*Nylandtia spinosa**	0.1	0.0	0.1	0.4	0.2	0.0	0.0	0.0	0.0	0.0
*Oncosiphon suffruticosum**	0.0		0.0	**4.4**	**1.3**	0.0		0.0	0.2	0.1
*Osyris compressa**		0.0	0.0	**17.0**	**6.0**		0.0	0.0	0.9	0.4
Oxalis sp.		**30.2**	**29.5**		**14.3**		1.6	1.5		0.9
*Passerina corymbosa**	0.0	0.9	0.0	0.0	0.2	0.0	0.0	0.0	0.0	0.0
Passerina ericoides		**8.4**			**2.2**		0.5			0.1
Pelargonium myrrhifolium	**13.3**			**1.8**	**4.0**	1.3			0.1	0.2
*Psoralea repens**		**3.3**	0.0	0.0	0.5		0.2	0.0	0.0	0.0
*Rhus laevigata**	**2.5**	0.1	0.0	0.2	0.3	0.2	0.0	0.0	0.0	0.0
Rhus sp.		**1.7**			0.4		0.1			0.0
*Ruschia macowanii**	0.1	0.8	0.0	0.2	0.3	0.0	0.0	0.0	0.0	0.0
Ruschia sp.*	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Sedge 1		**1.7**			0.4		0.1			0.0
*Senecio elegans**	**12.3**	0.0	**1.9**	**3.1**	**1.3**	1.2	0.0	0.1	0.2	0.1
Senecio maritimus	**1.7**		**315.9**	**126.5**	**99.6**	0.2		**16.5**	**6.4**	**6.1**
Senecio sp.	**5.0**				**1.3**	0.5				0.1
*Septulina glauca**		0.8			0.7		0.0			0.0
Succulent 1			**4.2**		0.9			0.2		0.1
Succulent 2		**1.7**	**16.8**		**4.0**		0.1	0.9		0.2
Tetragonia sp.		**3.4**			0.9		0.2			0.1
*Thamnochortus spicigerus**	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
*Trifolium burchellianum**		**1.7**	0.0		**1.1**		0.1	0.0		0.1
Zantedeschia aethiopica				**1.8**	0.4				0.1	0.0
Zygophyllum morgsana				**15.8**	**4.0**				0.8	0.2

6.4.3 Dietary preferences of tortoises on Dassen Island

The FR showed that over the annual cycle, angulate tortoises selected 18 of the 27 diet plants on DI out of proportion to their availability (Table 6.3). For the same period, Manly's α indicated that only five taxa were selected. The number of plant items selected seasonally, according to the FR and Manly's α respectively, were eight and three taxa in autumn and in winter, 12 and two taxa in spring, and 10 and three taxa in summer. Statistical analysis showed that for all seasons combined, angulate tortoises selected *T. divaricata* and *S. elegans*, and avoided *U. urens* (all $T_{60,3071} > 63440$; $P < 0.013$). *Urtica urens* was not present in the environment in autumn and summer, but the plant was avoided in winter and spring (all $T_{15,768} > 1199$; $P < 0.0001$). The tortoises selected *T. divaricata* in each season (all $T_{15,768} > 8283$; $P < 0.0054$), and they selected *S. elegans* in winter and in summer (all $T_{15,768} > 7789$; $P < 0.027$).

Table 6.3 Seasonal variation in the preference indices, Forage ratio and Manly's α, of angulate tortoises on Dassen Island. Values in bold indicate selection (>1.0 for Forage ratio and > 1/*m* for Manly's α) and the asterisks indicate for which dietary items Mann-Whitney tests could be done. For convenience, Manly's α is shown as a percentage rather than a fraction of 1.0.

	Forage ratio					**Manly's α**				
Species	**Au**	**Wi**	**Sp**	**Su**	**Ann**	**Au**	**Wi**	**Sp**	**Su**	**Ann**
Albuca flaccida	**121.6**	**30.2**	**37.0**		**47.2**	**34.9**	10.1	4.2		**8.9**
Anagalis arvensis		0.0			0.0		0.0			0.0
Cyperus sp.		**5.1**			**1.3**		1.7			0.2
Cystocapnos vesicaria			0.0		0.0			0.0		0.0
Dicot 1			**29.7**		**7.4**			3.4		1.4
Dicot 2			**30.2**	**22.0**	**13.0**			3.4	2.8	2.5
Dicot 3			**11.5**	**10.4**	**5.5**			1.3	1.3	1.0
Dicot 4	**24.7**	**12.5**		**9.5**	**11.7**	7.1	4.2		1.2	2.2
Dicot 5	**2.7**	**136.0**			**34.7**	0.8	**45.4**			**6.5**
Dicot 6				**8.0**	**2.0**				1.0	0.4
Dicot 7				0.7	0.2				0.1	0.0
Ficinia nigrescens			**488.2**		**122.1**			**55.5**		**23.0**
Grass	**67.4**	**36.5**	**232.4**	**367.8**	**176.0**	**19.3**	**12.2**	**26.4**	**47.1**	**33.2**
Hemimeris racemosa			**23.1**		**5.8**			2.6		1.1
Isolepis antarctica			**13.2**		**3.3**			1.5		0.6
Mesembryanthemum crystallinum	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Monocot 1	0.7				0.2	0.2				0.0
Monocot 2			**2.1**		0.5			0.2		0.1
Monocot 3		**10.9**			**2.7**		3.6			0.5
Monocot 4	**2.8**			0.7	0.9	0.8			0.1	0.2
Myoporum serratum	**121.6**			**108.8**	**57.6**	**34.8**			**13.9**	**10.9**
Oxalis sp.	**3.4**			**26.5**	**7.5**	1.0			3.4	1.4
*Senecio elegans**	0.7	**20.7**	**1.2**	**184.6**	**15.2**	0.2	6.9	0.1	**23.6**	2.9
Tetragonia fruticosa	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
*Trachyandra divaricata**	**3.4**	**47.9**	**7.2**	**1.6**	**4.5**	1.0	**16.0**	0.8	0.2	0.8
*Urtica urens**		0.0	0.0		0.0		0.0	0.0		0.0
Zantedeschia aethiopica			**3.1**	**40.7**	**11.0**			0.4	5.2	2.1

6.4.4 Niche breadth in the WCNP and DI

The PSI values of angulate tortoises in the WCNP and on DI were low in all seasons and overall (Table 6.4). A two-way ANOVA showed that season had no effect on PSI values (P = 0.27), but PSI values of tortoises in the WCNP were higher than the values were on DI ($F_{1,3}$ = 78.8; P = 0.0030).

Table 6.4 Seasonal changes in the Proportional Similarity Index of angulate tortoises in the West Coast National Park and on Dassen Island.

	Au	Wi	Sp	Su	Ann
WC National Park	0.31	0.27	0.29	0.26	0.31
Dassen Island	0.19	0.16	0.12	0.15	0.16

6.4.5 The diet of *Chersina angulata* and methodologies

The three study methods used to evaluate the feeding ecology of angulate tortoises did not generate similar diet lists; substantially more diet species were identified through the microscopic method than through focal studies or macroscopic analysis. The diet of *C. angulata* included 72 plants that were identifiable to the genus level, and also included mosses (Phylum: Bryophyta), mushrooms (Phylum: Basidiomycota), insects, snails and animal faeces. The 72 angiosperms belonged to 32 different plant families (Table 6.5).

Table 6.5 Food plants (Y), and plants not eaten (N) by *Chersina angulata* in the West Coast National Park and Dassen Island. Only plants identified to the genus level were included in the list. Food items (L=leaves, S=seeds, f=flowers, St = stem) were identified through focal studies (F), macroscopic (M) and histological (H) evaluation of faeces, and incidental observations (O).

Study site	Family	Species	Food	L	S	f	F	M	H	O
WCNP	Aizoaceae	*Carpobrotus edulis*	Y	L			F		H	
WCNP	Aizoaceae	*Carpobrotus quadrifidus*	Y	L					H	
DI	Aizoaceae	*Mesembryanthemum crystallinum*	Y	L			F			
WCNP	Aizoaceae	*Ruschia macowanii*	Y	L				M	H	O
WCNP	Aizoaceae	*Ruschia* sp.	Y	L					H	
DI WCNP	Aizoaceae	*Tetragonia fruticosa*	Y	L			F			O
WCNP	Aizoaceae	*Tetragonia* sp.	Y	L					H	
WCNP	Amaranthaceae	*Manochlamys albicans*	Y	L					H	
WCNP	Anacardiaceae	*Rhus laevigata*	Y	L	S				H	
WCNP	Anacardiaceae	*Rhus* sp.	Y		S				H	
WCNP	Apiaceae	*Stoibrax capense*	Y	L			F			O
WCNP	Apocynaceae	*Cynanchum africanum*	Y	L					H	O
DI WCNP	Araceae	*Zantedeschia aethiopica*	Y			f			H	
WCNP	Asparagaceae	*Asparagus lignosus*	Y	L					H	
DI	Asphodelaceae	*Trachyandra divaricata*	Y	L			F	M	H	
WCNP	Asphodelaceae	*Trachyandra* sp.	Y	L			F			
WCNP	Asteraceae	*Chrysanthemoides monilifera*	Y	L					H	
DI WCNP	Asteraceae	*Cotula sp.*	Y	L						O
WCNP	Asteraceae	*Helichrysum niveum*	Y	L	S		F	M	H	
WCNP	Asteraceae	*Lachnospermum imbricatum*	Y	L					H	
WCNP	Asteraceae	*Oncosiphon suffruticosum*	Y	L	S	f	F		H	
WCNP	Asteraceae	*Pteronia uncinata*	Y			f				O
WCNP	Asteraceae	*Senecio burchellii*	Y	L						O
DI WCNP	Asteraceae	*Senecio elegans*	Y	L		f	F	M	H	
DI WCNP	Asteraceae	*Senecio maritimus*	Y	L		f			H	
WCNP	Asteraceae	*Senecio sp.*	Y	L			F		H	
WCNP	Asteraceae	*Trichogyne verticillata*	Y	L	S			M		O
DI WCNP	Boraginaceae	*Amsinckia calycina*	Y			f				O
WCNP	Celastraceae	*Gymnosporia buxifolia*	Y	L					H	
DI	Cyperaceae	*Cyperus* sp.	Y	L					H	
DI WCNP	Cyperaceae	*Ficinia nigrescens*	Y	L				M	H	
DI	Cyperaceae	*Isolepis antarctica*	Y	L					H	
WCNP	Fabaceae	*Aspalathus hispida*	Y	L					H	
WCNP	Fabaceae	*Psoralea repens*	Y	L				M	H	O
WCNP	Fabaceae	*Trifolium burchellianum*	Y	L					H	O
DI WCNP	Fumariceae	*Cystocapnos vesicaria*	Y	L	S		F	M	H	
WCNP	Gentianaceae	*Chironia baccifera*	Y	L					H	
WCNP	Geraniaceae	*Erodium moschatum*	Y	L		f				O
WCNP	Geraniaceae	*Geranium incanum*	Y	L	S	f	F	M	H	
WCNP	Geraniaceae	*Pelargonium myrrhifolium*	Y			f			H	
WCNP	Geraniaceae	*Pelargonium* sp.	Y			f	F			
DI	Hyacinthaceae	*Albuca flaccida*	Y	L			F	M	H	

Table 6.5 continued

Study site	**Family**	**Species**	**Food**	**L**	**S**	**f**	**F**	**M**	**H**	**O**
WCNP	Hyacinthaceae	*Albuca* sp.	**Y**	L				M	H	
WCNP	Loranthaceae	*Septulina glauca*	**Y**	L					H	
DI WCNP	Myoporaceae	*Myoporum serratum*	**Y**	L			F		H	O
DI WCNP	Oxalidaceae	*Oxalis pes-caprae*	**Y**			f	F			O
DI WCNP	Oxalidaceae	*Oxalis* sp.	**Y**	L					H	
WCNP	Plumbaginaceae	*Afrolimon purpuratum*	**Y**			f			H	
DI	Poaceae	*Avena byzantina*	**Y**		S				H	
WCNP	Poaceae	*Avena fatua*	**Y**	L	S				H	
DI WCNP	Poaceae	*Avena sp*	**Y**	L					H	
DI	Poaceae	*Bromus pectinatus*	**Y**	L					H	
WCNP	Poaceae	*Chaetobromus dregeanus*	**Y**		S				H	
WCNP	Poaceae	*Cynodon dactylon*	**Y**	L	S				H	
WCNP	Poaceae	*Erharta villosa*	**Y**	L	S				H	
WCNP	Poaceae	*Lolium perenne*	**Y**	L	S				H	
WCNP	Poaceae	*Pennisetum setaceum*	**Y**	L	S				H	
DI	Poaceae	*Phalaris minor*	**Y**	L					H	
WCNP	Polygalaceae	*Nylandtia spinosa*	**Y**	L	S		F	M	H	
DI	Primulaceae	Anagalis arvensis	**Y**			f				O
WCNP	Restionaceae	*Thamnochortus spicigerus*	**Y**	L					H	
WCNP	Rosaceae	*Cliffortia filifolia*	**Y**	L						O
WCNP	Santalaceae	*Osyris compressa*	**Y**	L					H	
WCNP	Santalaceae	*Thesidium* sp.	**Y**	St						O
WCNP	Scrophulariaceae	*Hebenstretia repens*	**Y**	L					H	O
DI	Scrophulariaceae	*Hemimeris racemosa*	**Y**	L					H	
WCNP	Sterculiaceae	*Hermannia pinnata*	**Y**	L					H	
WCNP	Sterculiaceae	*Hermannia scabra*	**Y**	L					H	
WCNP	Thymelaeaceae	*Passerina corymbosa*	**Y**	L					H	
WCNP	Thymelaeaceae	*Passerina ericoides*	**Y**	L					H	
DI	Urticaceae	*Urtica urens*	**Y**	L	S		F	M	H	
WCNP	Zygophyllaceae	*Zygophyllum morgsana*	**Y**	L					H	
DI		Mosses	**Y**				F			
DI		Mushrooms	**Y**							O
DI WCNP		Animal faeces	**Y**				F			O
DI WCNP		Insect parts	**Y**					M	H	
DI		Snail shells	**Y**				F			
WCNP	Aizoaceae	*Conicosa pugioniformis*	N							
DI	Aizoaceae	*Dorotheanthus* sp.	N							
WCNP	Amaranthaceae	*Atriplex semibaccata*	N							
DI WCNP	Amaranthaceae	*Chenopodium album*	N							
WCNP	Amaryllidaceae	*Haemanthus coccineus*	N							
WCNP	Anacardiaceae	*Rhus glauca*	N							
WCNP	Anacardiaceae	*Rhus lucida*	N							
WCNP	Anthericaceae	*Chlorophytum undulatum*	N							
WCNP	Apiaceae	*Torilis arvensis*	N							
WCNP	Asparagaceae	*Asparagus rubicundus*	N							
WCNP	Asteraceae	*Berkheya armata*	N							
WCNP	Asteraceae	*Felicia hyssopifolia*	N							
DI WCNP	Asteraceae	*Sonchus oleraceus*	N							

Table 6.5 continued

Study site	Family	Species	Food	L	S	f	F	M	H	O
WCNP	Asteraceae	*Stoebe* sp.	N							
WCNP	Ebenaceae	*Diospyros austro-africana*	N							
WCNP	Euphorbiaceae	*Euphorbia burmanii*	N							
WCNP	Euphorbiaceae	*Euphorbia mauritanica*	N							
WCNP	Euphorbiaceae	*Euphorbia peplus*	N							
WCNP	Fabaceae	*Aspalathus* sp.	N							
WCNP	Hyacinthaceae	*Ornithogalum thyrsoides*	N							
WCNP	Hypoxidaceae	*Spiloxene capensis*	N							
WCNP	Iridaceae	*Babiana ringens*	N							
DI	Iridaceae	*Homeria flaccida*	N							
WCNP	Lamiaceae	*Ballota africana*	N							
WCNP	Lamiaceae	*Salvia africana-lutea*	N							
DI WCNP	Malvaceae	*Malva parviflora*	N							
WCNP	Menispermaceae	*Cissampelos capensis*	N							
DI WCNP	Molluginaceae	*Pharnaceum exiguum*	N							
WCNP	Oxalidaceae	*Oxalis obtusa*	N							
DI	Poaceae	*Avena barbata*	N							
WCNP	Poaceae	*Bromus diandrus*	N							
WCNP	Rhamnaceae	*Phylica ericoides*	N							
WCNP	Rhamnaceae	*Phylica thunbergiana*	N							
WCNP	Rutaceae	*Agathosma* sp.	N							
WCNP	Santalaceae	*Osyris* sp.	N							
WCNP	Solanaceae	*Lycium* sp.	N							
WCNP	Solanaceae	*Lycium tetrandrum*	N							
WCNP	Solanaceae	*Lyperia lychnidea*	N							
WCNP	Zygophyllaceae	*Zygophyllum flexuosum*	N							

Only five diet categories of angulate tortoises in the WCNP were indicated by all three methods: *Geranium incanum, Helichrysum niveum, Nylandtia spinosa, Senecio elegans* and UI plant material. Percent composition results obtained through the focal, macroscopic and histological methods differed significantly for *Nylandtia spinosa* ($F_{2,6}$ = 24.42, P = 0.0013) and for UI plant material ($F_{2,6}$ = 9.64, P = 0.013), but not for the other three diet species (all $P > 0.22$). For *N. spinosa*, percent composition determined through macroscopic evaluation was higher than percent composition determined through focal and histological evaluation, while the results for the latter two methods did not differ. The percent composition of UI plant material was higher for the focal and macroscopic methods than for the histological method. A further eight diet items were detected by two of the three methods: *Albuca* sp., Apocynaceae, *Carpobrotus edulis*, *Cystocapnos vesicaria*, *Oncosiphon suffruticosum*, *Psoralea repens*, T*rachyandra* sp. and insects.

On DI, four diet items were detected by all three methods: *Albuca flaccida*, *Trachyandra divaricata*, *Urtica urens* and UI plant material. Percent composition of *T. divaricata* obtained through the focal and histological methods was higher than the percent composition obtained through macroscopic evaluation ($F_{2,6}$ = 11.09, P = 0.0097). In contrast, the macroscopic method gave the largest percent composition for UI plant material ($F_{2,6}$ = 57.40, P = 0.00012). There was no difference among the results of the three methods for *A. flaccida* and *U. urens* (all P > 0.33). Two other species, *Oxalis* sp. and *S. elegans*, were detected by two of the three methods.

For angulate tortoises in the WCNP, the histological method detected a higher percent composition for grass ($F_{2,6}$ = 5.25, P = 0.048) and for succulents ($F_{2,6}$ = 42.81 P = 0.00028) than the focal or macroscopic method detected. There was no difference in the percent composition of herbs and shrubs (all P > 0.69) detected by the three methods. Similarly, the percent composition for herbs in the diet of angulate tortoises on DI did not differ among the three methods.

6.5 DISCUSSION

6.5.1 Principal, preferred and avoided plants

Despite the WCNP having much wider plant diversity than DI, the number of principal food items in the diets of angulate tortoises from these sites did not differ. This finding suggests that a few, well chosen, plant species can probably provide most of the nutritional requirements of the tortoises. The diet of tortoises in the WCNP was nevertheless more diverse than the diet on DI was, but most plant species occurred in low quantities in the faeces. It seems likely that many of the food items with low frequencies represent plants that the tortoises sampled to monitor changes in plant composition, or to test potentially new food plants that they encountered (Robbins 1983; Dearing & Schall 1992). It is also possible that some food items with low frequencies contained specific nutrients that the tortoises needed.

Most of the principal food items at both sites were grasses or herbs. Grasses were eaten out of proportion to availability in every season. The strong selection for grasses throughout the year indicates that the digestive system of angulate tortoises probably processed grasses effectively so that the tortoises gained sufficient energy and nutrients from this resource. The ingestion of grasses was probably particularly important to tortoise survival during the dry season when soft, edible herbaceous plants were in short supply. Grasses also form an important part of other tortoises' diets, e.g., desert tortoises, leopard tortoises and gopher tortoises (Macdonald & Mushinsky 1988; Milton 1992; Nagy *et al*. 1998).

The low diversity and highly ephemeral nature of plants on DI probably influenced the food choices made by angulate tortoises. Their principal and preferred plants were predominately soft and herbaceous in nature. Annual plants, which include growth forms such as grasses and herbs, invest little resources in anti-herbivore defences and can contain higher levels of nutrients compared to perennial plant species (Cates & Orians 1975). Herbaceous plants generally have high nutritive value, which may be offset by high levels of secondary compounds (Huston & Pinchak 1999). The access to annual and herbaceous plants probably helped angulate tortoises to survive and reproduce successfully on DI. Angulate tortoises in the WCNP also displayed high levels of preferences for herbaceous plants.

Chersina angulata appears to avoid tough plants such as perennial shrubs and restios, and the principal food plants at the two sites included only one shrub and one tree species. No restio or cyperid species was used as a principal dietary item by angulate tortoises in the WCNP, probably due to the tougher and more fibrous nature of these plants. Nevertheless, angulate tortoises on DI showed a high preference for the sedge *Ficinia nigrescens* during spring, when they fed on the flowers. Not all plants that were avoided (consumption low relative to availability) were tough and fibrous. *Urtica urens* was abundant on DI during the wet season but was used at low levels, probably because the stinging emergences cause irritation of the skin (Bromilow 2001).

6.5.2 Generalist or specialist feeder?

Chersina angulata consumed a large number of plant species when the vegetation in their environment was diverse (e.g., in the WCNP), but they did not necessarily select abundant plants. Two highly abundant plant species in the WCNP, *E. villosa* and *C. edulis*, were avoided. Similarly, *C. angulata* on DI avoided the most abundant species *M. crystallinum* and *T. fruticosa*. Many plants eaten by angulate tortoises were consumed in disproportion to their availability, and the tortoises' diet included many rare plant species that were not recorded in the study quadrats. These findings suggest that *C. angulata* may be a specialist feeder, which was confirmed by the low PSI values for the tortoises at both sites.

The Proportional Similarity Indices of angulate tortoises in the WCNP and on DI were 0.31 and 0.16, respectively, and were lower than values reported for tortoises that are considered midway between specialist and generalist herbivores (0.497 for *Stigmochelys pardalis*, Mason *et al*. 1999; and 0.55 for *Testudo horsfieldi*, Lagarde *et al*. 2003). The PSI of *C. angulata* corresponded closer to that of *Testudo graeca* graeca (0.20), which was recorded in an arid and overgrazed zone in Morocco (Mouden *et al.* 2006). The result that *C. angulata* is a specialist feeder contradicts the perception of Boycott & Bourquin (2000) that these tortoises are generalist feeders just because they occupy a large variety of habitat types.

Season had no effect on foraging niche breadth of angulate tortoises, indicating that the animals remained selective feeders even when the availability of food species in the habitat changed. The highly specialised feeding pattern of DI tortoises was probably due to the low diversity and ephemeral nature of the plants on the island. The ephemeral nature of plants resulted in high cover values for plant species during the wet seasons and lower values during the dry seasons. The most abundant plants on DI appear to be unpalatable and the tortoises had a restricted choice of palatable and nutritious plants. The greater diversity of food plants in the WCNP allowed more choice and can explain the higher PSI values for WCNP tortoises.

6.5.3 Evaluation of the three methods to study diet

Focal observations, macroscopic analysis and histological analysis had different levels of success in cataloguing the diet of angulate tortoises and their preferences for specific food items. In this study, the focal and macroscopic methods recorded substantially lower diversities of food items than the histological method did, but those two methods supplied other information that could not be gained by the histological method.

Since angulate tortoises are relatively small animals, the height and density of vegetation, particularly in the WCNP, made it difficult to observe feeding tortoises without alarming them. Furthermore, the tortoises often fed under bushes or in thick grass patches, which compromised the identification of food plants and the plant parts consumed. Nevertheless, focal observation provided a wider diet list than was obtained by macroscopic scat analysis, and the focal method brought to light that rabbit faecal pellets made a substantial contribution to the diet of angulate tortoises on DI.

Macroscopic scat analysis provided useful data on the range and frequencies of plant parts used by angulate tortoises. Macroscopic analysis revealed that seeds formed an important dietary component of angulate tortoises, and that *C. angulata* may be an important agent of seed dispersal. Seed epidermi, for the majority of plant species, were difficult to identify in histological scat analysis and the latter method thus did not supply useful information on plant parts in the diet.

The histological analysis of angulate tortoises' scats provided the most extensive list of food plants consumed by the tortoises, which emphasised the inadequacies of the other two methods. The histological method may underestimate some food plants (e.g., soft plant material), and overestimate others (e.g., grasses), but the range of food plants identified made it possible to evaluate food preferences and aversions, and foraging niche breadth of angulate tortoises.

6.5.4 Implications for the conservation of *Chersina angulata*

The fact that *C. angulata* is a specialist feeder should be taken into account in the conservation of the species. The narrow foraging niche breadth of *C. angulata* may influence the survival of the tortoises if they have to compete with domestic ungulates or large, wild herbivores that may have the same food preferences. The restricted food choices of angulate tortoises on DI mean that great care should be taken when conserving *C. angulata* in this nature reserve. The continued availability of herbaceous plants would be critical to the survival of this population.

The improved understanding of the foraging ecology of angulate tortoises will benefit animals reared in captivity, or as part of conservation programmes. Knowledge of the tortoises' preference for specific food types can be used to supply captive bred animals with wider food choices. If this knowledge is combined with information on the nutrient content of preferred food plants, the tortoises can be provided the most nutritious plant species, which will help the tortoises to survive better in captivity, and increase their chances to reproduce successfully.

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7 GENERAL CONCLUSIONS

Scientific studies often advance understanding by elucidating detailed mechanisms that answer research questions, and by revealing knowledge gaps that provoke further scientific inquiry. My dissertation has advanced our understanding of *Chersina angulata* feeding ecology and has revealed nutritional ecology gaps plaguing our understanding of angulate tortoises and other ectothermic herbivores. Yet, we are far from a comprehensive understanding of the nutritional ecology of most organisms (Robbins 1993).

Here I intend to elaborate on some of these gaps and concerns, and suggest future studies that may address these concerns. Also, by evaluating inherent physiological abilities of ectotherms, and distributions of flora and fauna, we may grasp better the elements critical to the feeding or nutritional ecology of angulate tortoises and other animals. Ultimately in this synthesis, I suggest, and hope we implement, ways to conserve angulate tortoises and their ecosystems.

7.1 METHODOLOGICAL IMPROVEMENTS AND FUTURE STUDIES

To understand feeding and nutritional ecology, we must do more than generate a list of food items for a species (Rall & Fairall 1993; Robbins 1993). However, it is much more difficult to quantify how selective animals feed, how much food they eat or require, and how animals balance intake of various, and varying, foodstuffs to meet nutrient requirements. To complicate matters, nutrient requirements may vary between sexes and among individuals, developmental stages, reproductive states, seasons, habitats and activity levels (Nagy 1987 & 2001; Robbins 1993).

My dissertation demonstrates seasonal and habitat (by proxy of site) influences, and to a degree, individual variation (individual scats). However, these two sites represent only a small portion of the species' range and habitat types (see Heterogeneity, below). We would benefit from similar detailed analyses in the Succulent Karoo and Thicket of the Eastern Cape. These are other *C. angulata* habitats, which have disparate plant species (food and refugial), physiognomies, climates and other ecosystem influences (e.g., predation). Desert tortoises (*Gopherus agassizii*) are also exposed to considerable variation in plant species and plant condition across the species' range (Hansen *et al.* 1976, Nagy & Medica 1986; Esque 1994; Avery 1998; Henen 2002, Oftedal 2002 and others). This variation will have important ecological, physiological and conservation implications.

We may also enhance our understanding of *C. angulata* feeding or nutritional ecology by improving, and then applying, my current methods, and by using powerful methods, such as nutrient balance trials and isotope methods, to quantify food and nutritional requirements (Nagy & Medica 1986; Henen 1997; Oftedal *et al*. 2002). Integrating these methods in a well-designed, multifaceted study is necessary to provide a detailed and accurate evaluation. Each of the three methods I used has advantages and disadvantages. Some disadvantages may be overcome if all three methods are used simultaneously, especially if faeces can be collected from individuals monitored in focal observations. Attaching faecal collection bags (e.g., Avery *et al.* 1993) may help, but focal observations usually provide numerous opportunities to collect fresh samples from active tortoises (QI Joshua, pers. obs.). One caveat is that long, gut transit times in tortoises (e.g., 10 to 60 days, Meienberger *et al*. 1993; Nagy *et al*. 1998) would require matching faecal samples to prior days or weeks of focal observations. Sufficient observation hours, and sample sizes for faecal analyses, will improve quantitative estimates of the composition of the diet for each population. This would be an expensive and time intense venture.

Additionally, the three methods can be improved to limit error. Error is reduced primarily by increasing methodological and statistical power. The speed, accuracy and precision of the histological method may be improved by using computer imaging software, having an extensive collection of reference slides (accounting for variation among species, morphological structures and phenological stages), using fresh scats (not preserved), and using gentle solutions when preparing soft epidermi (Vavra & Holechek 1980). Focal observations may be improved largely by increased sample size and sampling effort (Chapters 2 & 6), observing tortoises not influenced by monitors (habituated tortoises may facilitate accurate observations of foraging), and using observers extremely well trained in the local flora. Experts on the local flora would also increase the accuracy and speed of identifying species, plant parts and phenological stages of plants in the macroscopic faecal analyses.

Additional studies - Controlled nutrient balance trials would reveal the importance of gut microflora to cellulose digestion, free-fatty acid metabolism, and vitamin and energy absorption (Robbins 1993). Such studies may indicate the motivation for coprophagy, and whether the dung of European rabbits (e.g, Dassen Island) is an adequate or superlative substitute for the dung of the dassies that inhabited Dassen Island before Europeans altered the South African landscape. Similar trials may reveal whether ingested sand is incidental to foraging, supports mineral balance (Ayotte *et a*l. 2006), aids abrasion and digestion of plant cell walls and fibre (Chapter 4), or helps eliminate gut parasites (Logiudice 2001; Evans 2002; Chapter 5).

The results of nutrient balance trials are most useful within the context of the absolute food and nutrient requirements of free-ranging angulate tortoises. The food and nutrient requirements of free-ranging vertebrates and invertebrates have been quantified with various isotopic methods, with the doubly-labelled water method perhaps the most versatile and accurate technique for terrestrial vertebrates (Nagy 2001). Knowing these absolute requirements would also quantify how important gut microflora and sand ingestion are to free-ranging angulate tortoises at Dassen Island, the West Coast National Park, and sites where human influences are negligible. Doubly-labelled water studies have elucidated key metabolic advantages ectothermic vertebrates use to endure and succeed in harsh or limiting environments (Bennett & Nagy 1977; Nagy 1983, 2001; Peterson 1996a&b; Henen 1997). These advantages may be instrumental to the success of tortoises and other ectothermic herbivores. Such advantages may help angulate tortoises in disturbed environments, or in conservation efforts requiring physiological exaptations and acclimation to new or changing environments.

7.2 ECTOTHERM PHYSIOLOGY AND BEHAVIOUR

The angulate tortoise has a wide distribution, and in some regions, has high population densities (Boycott & Bourquin 2000; MD Hofmeyr, unpublished data). Consequently, *C. angulata* appears to have adapted, or been adaptable (exapted), to endure and reproduce among a range of climates and environments, some of which are harsh and exemplify temporal and spatial heterogeneity of resources (e.g, the Succulent Karoo; Milton *et al.* 1997). This apparent success may be due, largely, to the angulate tortoise‘s ectothermic physiology, behaviour and activity levels (see Pough *et al*. 2004).

Ectotherms may require only 3% of the energy that similarly sized endotherms use (Pough *et al*. 2004), enabling ectotherms to succeed in low productivity environments, and environments where food and water vary considerably in time and space. Low daily energy requirements are due to a) using external heat sources to maintain body temperature while active, b) reducing body temperature and metabolic rates at night when ambient temperature is low and basking is not possible, and c) reducing activity (see Bennett & Nagy 1977 and Pough *et al*. 2004). Angulate tortoises bask (Keswick *et al*. 2006) like desert tortoises and many other reptiles, so they should conserve considerable energy in the costs of thermoregulation. Furthermore, under laboratory conditions, their heating rate exceeds their cooling rate, which should expedite heating while basking, and retard cooling when inactive or in refugia. (Els 1989)

The Q_{10} effect on ectotherm metabolism, where metabolic rates double approximately with 10 °C increases in body temperature (Schmidt-Nielsen 1997), may confer considerable energy savings to angulate tortoises. Except for opportunities for basking and associated cooling and heating lags, body temperatures of angulate tortoises should approximate ambient temperature. Consequently, metabolic costs should be reduced greatly at night when angulate tortoises are inactive in refugia (under vegetation), cool days without sunshine (e.g., foggy days on Dassen Island), or days when tortoises remain inactive within their refugia (Bennett & Nagy 1977; Pough *et al*. 2004). Angulate tortoises in refugia with partial sunshine may have elevated body temperatures compared to those without partial exposure; these elevated temperatures might facilitate digestion without exposing tortoises to wind or predators (Keswick *et al*. 2006). Conversely, partial exposure at night could cause body temperatures to drop due to radiative heat loss to the cold night sky.

Angulate tortoises may also reduce metabolism, conserving reserves, by not being active every day. By remaining inactive in refugia for days (Nagy & Medica 1986), or even longer adverse periods (e.g., droughts), desert tortoises (*Gopherus agassizii*) can reduce field metabolic rates (i.e., daily energy expenditures) by 90% compared to similar seasons in favourable years (Henen 1997, Henen *et al*., 1998). Desert tortoises may be active every three days, on average, during the active season, and only aboveground 5% of the year; they brumate (winter dormancy) for about five months each year (Nagy & Medica 1986; Henen 1997). Angulate tortoises can be active at low ambient temperatures in winter and spring (Ramsay *et al*. 2002; Keswick *et al*. 2006). If their corresponding body temperatures are also low, the Q_{10} effect on metabolic rates may help them conserve energy. The same effect would apply to nighttime metabolism, when angulate tortoises reside in refugia, or even daytime metabolism on days angulate tortoises remain inactive within their refugia (Keswick *et al*. 2006). Remaining inactive may confer savings beyond Q_{10} effects, but empirical studies are necessary to quantify activity costs separate from temperature effects. If empirical studies demonstrate metabolic savings of ectothermy in *C angulata*, we may employ these savings in conserving the species (e.g., reducing body temperatures and activity during translocation projects should reduce depletion of nutrient reserves).

Ectothermy probably confers great physiological tolerance to angulate tortoises, as it appears to do for desert tortoises (Nagy & Medica 1986; Peterson 1996a, b; Henen 1997, 2002). Desert tortoises are highly opportunistic in acquiring food and water to replenish and build body stores (water, lipids and protein), and very conservative with metabolism and reserves when environmental conditions are unfavourable. They are also extremely tolerant to dehydration and other changes in body condition (Nagy & Medica 1986; Peterson 1996a, b; Henen 1997, 2002). Their ability to relax or relinquish homeostasis enables them to endure extended droughts without food or water. As ectothermic herbivores, angulate tortoises probably share, to a degree, many of the physiological and behavioural traits facilitating survival and reproduction in desert tortoises.

On a mass specific basis, ectotherms have lower metabolic requirements, and higher production efficiencies than endotherms (Pough *et al*. 2004). Of the energy they consume, ectotherms convert more into tissue (growth or reproduction) than endotherms convert. This is largely because ectotherms spend less energy maintaining their body temperatures for activity (Pough *et al*. 2004). One ecological consequence is that, compared to endotherms, ectotherms tend to require less food to produce the same mass or number of offspring. Some ectotherms can produce offspring in habitats that have low production levels (Louw & Seely 1982; Henen 1997; Pough *et al*. 2004).

Herbivores often do well in low production habitats because the biomass of primary producers is higher than that of the primary consumers (see Louw & Seely 1982); there is potentially more food available (biomass) to herbivores than to carnivores. Since tortoises are not as mobile as most birds and mammals, particularly migratory species, they must cope with local vagaries (temporal and spatial) and their consequences on nutrient availability. Desert tortoises deal with such vagaries by relaxing homeostasis (tolerating large nutrient imbalances), decoupling nutrient balances (e.g, water, electrolyte, protein and lipids; Nagy & Medica 1986; Peterson 1996a; Henen 1997), reducing nutrient losses, and judiciously allocating resources towards maintenance or reproduction (Henen 1997). The desert tortoise might be, to a degree, an ecological equivalent of angulate tortoises. It would be worthwhile to know to what extent angulate tortoises share the same physiological abilities and life history traits exhibited by *Gopherus agassizii*.

7.3 HETEROGENEITY AND SELECTIVITY INFLUENCES IN FEEDING ECOLOGY

Angulate tortoises may have the greatest number of individuals and, one of the widest distributions of southern African tortoise species (Boycott & Bourquin 2000). What is the basis of the angulate tortoise's successful inhabitation of the wide range of habitats in the Cape Floristic Kingdom (CFR) and Succulent Karoo (SK)? The climate of the CFR is moderated somewhat by coastal climate influences, yet there is considerable variation (spatial) in rainfall levels and predictability from the Western Cape to the Eastern Cape (Schulze 1997; Hofmeyr *et al*. 2005). Inland or continental climate influences also impose strong seasonal variation on rainfall and temperature regimes in the Succulent Karoo where angulate tortoises are also found (Schulze 1997). Ectothermy, herbivory (see above), and a nearly aseasonal or continuous reproductive pattern (Hofmeyr 2004), are probably essential to the survival and reproductive success of angulate tortoises in such disparate environments.

How important is feeding ecology to the species' success in these habitats? On the surface, data from captive tortoises, plus the extremely broad range, suggest that angulate tortoises may succeed by being dietary generalists (Boycott & Bourquin 2000). However, my data (Chapter 6) indicate that *C. angulata* at Dassen Island and the West Coast National Park were dietary specialists, and specialised more than Horsfield's tortoises (Lagarde *et al*. 2003) and leopard tortoises (Mason *et al*. 1999), the latter sympatric with *C. angulata* in parts of the species' distributions. Data from my study are not inconsistent with data across the species' range, if we consider scale of analysis. Angulate tortoises may specialise on plant species within a region, but each region or habitat has distinct flora, often with little overlap with other habitats. In fact, diets differed between DI and WCNP, probably due to little overlap in flora at the two sites (Chapter 2). Literature for desert tortoises (*Gopherus agassizii*), which inhabit a wide range and disparate habitats among the Colorado, Mojave, Sinaloan and Sonoran Deserts, also indicate specialisation on a few species of the local flora (Hansen *et al*. 1976, Nagy & Medica 1986; Esque 1994; Avery 1998; Henen 2002, Oftedal 2002), with little dietary overlap among sites. The same pattern may apply to Horsfield's tortoise and other species with wide distributions.

We need to evaluate degree of dietary specialisation of angulate tortoises in other portions of its range, such as in Namaqualand, the Karoo and in the Eastern Cape (e.g., Thicket). Furthermore, reverse transplant and common garden experiments may indicate whether dietary specialisation has genetic components, including behavioural tendencies of food choice, and physiological or digestive tolerances to certain plants. Such studies may also provide information important to understanding the evolution of lineages within *C. angulata* (Daniels *et al*. 2007). Furthermore, our species lists, faecal analyses and proportional similarity indices provide some information about feeding ecology. We must also understand the biomechanical constraints (Balsamo *et al*. 2004), and nutritional consequences (Meienberger *et al*. 1993; Nagy *et al*. 1998; Oftedal 2002, Oftedal *et al*. 2002; Henen *et al*. 2005), affecting dietary specialisation.

Understanding the digestive physiology and physiological tolerance of *C. angulata* may be useful in addressing whether dietary specialisation is either inherent to a population, or a behavioural and physiological exaptation of tortoises. There are very few distinct or unique dietary requirements among vertebrates, at least at the level of cellular physiology (Oftedal 2002). Nutritional distinctions (adaptations?) among chelonian species may occur at tissue or whole-animal levels of organisation (e.g., the importance of the urinary bladder to osmoregulation; Dantzler & Schmidt-Nielsen 1966), and be related mostly to a matter of degree (e.g., the hydration and dehydration tolerance of *Gopherus agassizii*) or scale (e.g., degree of fermentation possible by large or small species). Whether dietary specialisation has a genetic basis may be important for designing conservation action plans.

Although angulate tortoises were dietary specialists within each season, their diets, particularly the principle dietary items at the WCNP, changed among seasons. This suggests that angulate tortoises may adapt their diet to nutritional needs, food availability, or both. Desert tortoises opportunistically forage on different foodstuffs, e.g., different species, plant parts or phenological stages of species, in different seasons (Nagy & Medica 1986; Henen 1997, 2002; Oftedal 2002). At least part of these shifts have benefits for nutrient balances, although the prime nutritional benefits may vary among seasons or years (e.g., for growth or building protein or lipid reserves; Nagy & Medica 1986; Henen 1997). If angulate tortoises have physiological abilities similar to *G. agassizii*, *C. angulata* may capitalise upon food availability changes among seasons. Likewise, angulate tortoises may limit food choices, activity and food consumption during drier periods (see Henen 1997, 2002) to minimise use of nutrients or nutrient reserves.

Dassen Island tortoises represent an intriguing population. Although human influences have greatly altered Dassen Island's flora and fauna, the population densities represent one of the highest population densities of any tortoise species (MD Hofmeyr, unpublished data). This density may be due, in part, to a lack of non-avian predators and a relatively mild climate with substantial fogs that provide tortoises with water (MD Hofmeyr, unpublished data). Relative to nearby mainland populations, Dassen Island has a depauperate flora (Hurford 1996), and the tortoises subsist on only some of the plants available. Still, angulate tortoises were very common at Dassen Island. Dassen Island tortoises may be useful for transplant or common garden experiments (see above), the results of which may be important to conservation action plans anticipating regional aridification (Rutherford *et al*. 1999).

7.4 CONSERVATION OF ANGULATE TORTOISES

Because angulate tortoises are relatively numerous in South Africa, they are not on the IUCN's Red List (IUCN 2007). Yet, South Africa restricts trade of angulate tortoises, or any of its tortoises. Nonetheless, angulate tortoises are poached for the international pet trade (BT Henen, MD Hofmeyr & EHW Baard, unpublished manuscript; EHW Baard, pers. comm.), sometimes by the hundreds. These numbers are likely small in comparison to the thousands of road kills that must occur annually in South Africa (MD Hofmeyr & BT Henen, pers. comm.). Both of these numbers may pale in comparison to those killed or displaced by destruction of habitat for housing and agriculture, and due to altered fire regimes (Knight 1991; Baard & de Villiers 2000). In the WCNP in 2000, more than 200,000 angulate tortoises were killed in one fire that lasted only a couple of days (M.D. Hofmeyr & E.H.W. Baard, unpublished data). Consequently, altered fire regimes (Baard & de Villiers 2000) may be responsibly for inordinately high mortality rates, from direct fire-killed tortoises and eggs (in nests), severely burned- or smoke-damaged tortoises, destroyed refugia and food sources, and subsequently altered reproductive cycles and recruitment rates for surviving populations. Fires are natural to the CFR, but their frequency may be unnatural (Baard & de Villiers 2000). Impending climate change may also aridify substantial parts of the Succulent Karoo and CFR (Rutherford *et al*. 1999, and Chapter One), perhaps limiting the tortoise food and refugial plants throughout most of the current range of angulate tortoises.

Since the long-term future is uncertain for South Africa's tortoises, it is critical that we act now to minimise these impacts. Developing assurance colonies and evolutionary corridors, plus developing translocation projects, may be the most effective means of protecting individual and genetic diversity of angulate tortoises. Assurance colonies are essentially captive populations of tortoises that hold sufficient numbers of tortoises to retain the genetic integrity and diversity represented in wild populations. This may require several colonies to represent the different regions and clades of angulate tortoises (Daniels *et al*. 2007). If large fires or other disasters occur, natural or manmade, these colonies can be used to help repopulate wild areas. They will also facilitate in translocating tortoises, helping develop and support husbandry techniques while transporting tortoises to areas where *C. angulata* has been extirpated, and in areas reclaimed for restoring tortoise populations.

Landscape-scale management is necessary if we are to manage the effects of human population growth and associated infrastructure and agriculture projects. Corridors should help maintain connection among isolated or highly fragmented populations. Angulate tortoises, like most tortoises, do not move extreme distances (Branch 1984), so corridors would serve on an evolutionary scale, helping maintain gene flow among regions. For these corridors, it would be critical to maintain the integrity of the ecosystem structure and dynamics for angulate tortoises. This would include maintaining the large diversity of food and refuge plants for *C. angulata*.

My dissertation identifies principle and preferred food items necessary to support *C. angulata* populations in the southwestern Cape, and documents the relative abundance of food and non-food plants that help characterise suitable habitat. Such information may be useful for managing plant species diversity and abundance, and the overall physiognomy of *C. angulata* habitat. Similar data should be collected, as soon as possible, for other populations of angulate tortoises, especially different habitats along the southern Coast, in the Eastern Cape (Thicket), up the West Coast of South Africa (e.g., Namaqualand), and the Little Karoo. Such information would be useful for maintaining plant diversity for specific populations, and for identifying possible substitute habitats for translocated tortoises, suitable avenues for corridors, and locales where head-start programs and assurance colonies can be developed.

Dietary specialists - If we find that the dietary specialisation of angulate tortoises is genetically determined, then we will need to cultivate dietary species for each population. However, there is no evidence of this specialisation, and many pet *C. angulata* survive and reproduce on a variety of non-native plants. Consequently, there may be great opportunities to apply translocation, assurance colony and corridor programs to conserve angulate tortoises.

Angulate tortoises may be able to learn to eat novel plant species that the tortoises might encounter at translocation sites, sites recovering from fires, revegetation sites, or in corridors. Similarly, offspring that hatch or mature in new locations may quickly learn to eat the local flora; this could be important for translocation and assurance colony projects. In such situations, supplementing the local flora with additional, nutritious plants, should facilitate survival and growth of the tortoises, and may reduce dispersal movements in attempt to find food. Dispersal may expose tortoises to anthropogenic or natural hazards as individuals explore a new area. Thus, it is important to know the best types of plants to provide, and ensure that the habitat has them.

Many tortoises eat grasses (desert tortoises, leopard tortoises, *C. angulata*, *P geometricus*, *T. horsfieldi*) and annual herbs (this study; Nagy & Medica 1986; Milton 1992; Rall & Fairall 1993; Esque 1993, Henen 2002; Lagarde *et al*. 2003; Henen *et al*. 2005). These plant types can be important sources of water, energy, electrolytes and protein (Nagy & Medica 1986; Oftedal 2002; Henen *et al*. 2005). In fact, the ratio of water and protein to potassium may be a major influence on food choice in tortoises (see Oftedal 2002; Oftedal et al. 2002). This is probably related to the ability to excrete excess potassium, if the diet has sufficient water and protein, or if the animal is well hydrated. This selectivity is not known for *C. angulata*. Additionally, the concentration of soluble carbohydrates and phosphorus in plants may influence tortoise food choice (Henen *et al*. 2005).

Consequently, knowing the nutritive value of plants is important. We need to know the nutrient content and digestibility of foods. Furthermore, knowing the biomechanical properties of potential food items may influence whether they should be fostered as food sources for angulate tortoises (Balsamo *et al*. 2004). Another complication is whether to substitute new, potentially invasive, species. Although some evidence indicates that exotic species, under controlled conditions (Nagy *et al*. 1998), may be as nutritious as native food species, it is not known whether the same applies in the wild. Furthermore, invasive exotics can have detrimental effects on the ecosystem's species diversity, species composition, and fire regime (Brooks 1999).

Ecosystem processes, disturbance and subsidies - Protecting ecosystem processes may effectively manage suitable food species for angulate tortoises. Fire is inherent to Fynbos (Cowling *et al*. 1997), where *C. angulata* can be common. Fire may remove overgrowth and may open areas for the growth of annual plant species. These annuals and open spaces may benefit angulate tortoises while serving part of the natural ecosystem. If natural fire regimes can be maintained, without disrupting normal plant and animal function, then allowing natural fires may be the most efficient way to maintain food plants and habitat for angulate tortoises. At the same time, this process should provide for more than just one species.

Disturbance due to fire or other natural processes may be complemented, in some circumstances, with anthropogenic disturbances. Disturbances at Dassen Island and the West Coast National Park seem to promote 'weedy' species at these sites (Chapter 2; Dean & Milton 1991, Yeaton *et al*. 1993). If these weedy species can support angulate tortoises, as at Dassen Island, they may serve at least a temporary conservation function. They may substitute for fire disturbance, and may generate quality forage for angulate tortoises in translocation and corridor projects. Nonetheless, we must protect natural environments from invasive exotics that alter the ecosystem and fail conservation programs.

Symbiotic functions should also be considered, or investigated, for translocation and corridor projects. Angulate tortoises may distribute seeds via their faeces. Thus, faeces from source populations might help generate suitable flora at destinations of translocated animals, or along corridors. In addition, if coprophagy is important to inoculate gut microflora, then transporting faeces may help tortoises inoculate their gut flora and aid digestion at translocation sites.

Finally, 'subsidies' to predators on angulate tortoises, such as pied crows or ravens, should be minimised or eliminated. Humans provide numerous food and water resources or 'subsidies' to predators (e.g., pied crows or ravens; Boarman 2003). These resources, such as open landfills, refuse bins, littered motorways, excessively irrigated lawns and agricultural fields, support the survival, growth and reproduction of predator populations, increasing predation upon tortoises. Many juvenile angulate tortoises are killed at roosts, fence posts or other manmade structures or clearings (M.D. Hofmeyr & B.T. Henen, unpublished observations) in the West Coast National Park. Similar subsidies cause unusually high densities of common ravens (*Corvus corax*) and desert tortoise mortalities in the Mojave Desert (Boarman 2003). Conservation efforts for angulate and desert tortoises are likely to fail without controlling populations of subsidised predators.

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8 APPENDIX 1: EPIDERMAL CHARACTERS OF PLANTS

8.1 ABSTRACT

The epidermal and cuticular characters of 18 monocotyledonous and 63 dicotyledonous plants were examined to identify informative characters that group these plants into taxonomic units or plant types, and to construct identification keys for these plants. The epidermal cells of monocots had a parallel arrangement whereas the epidermal cells of dicots did not have a systematically structured appearance. Both groups, however, contained exceptions, and additional characters were required to reliably separate the monocots from the dicots. Important characters that aided in separating taxonomic units included the shape of the anticlinal wall, the type of periclinal surface, the shape of stomata, the type and number of cells surrounding the stoma, and the different types of trichomes. Monocots in general had a smooth cuticle, paracytic stomata and no glandular trichomes. The Poaceae were characterised by costal / intercostal zones, sinuous anticlinal walls, dumb-bell shaped stomatal guard cells, and prickle hairs. Many dicot species had cuticle striations, and dicots generally had anomocytic stomatal complexes. Eighteen different trichome shapes were distinguished for the dicots but a simple trichome shape occurred most frequently. Key characters of the succulents included the absence of trichomes, thick stomatal walls, and the absence of cuticular striations. A good character to distinguish between herbs and shrubs was the relatively small stomatal length-to-width ratios of shrubs. Herbaceous plants were characterised by the presence of anomocytic stomatal complexes, sinuous anticlinal walls, and glandular trichomes. Two separate epidermal keys were constructed, one for the Monocotyledoneae and one for the Dicotyledoneae.

8.2 INTRODUCTION

Plant taxonomy not only allows for the cataloguing of plants but also aids in determining the evolutionary and genetic interrelationships of plants. Macroscopic plant features have been utilised extensively in plant taxonomy (Stace 1965). When identifying plants from stored leaf material, taxonomists often use characters such as the shape of the leaf lamina, venation patterns, petiole features, and the shape of the leaf base and apex (Leaf Architecture Working Group 1999; Singh 2004). Relative to the macroscopic studies of plant leaves, microscopic studies of leaf epidermi have only recently gained importance as an alternative method to identify plants (Stace 1965). Plant taxonomists use a number of characters to identify leaf epidermi; the most important characters include the cell shape, stomatal complex type, and the trichome structure and distribution (Stace 1965; Mauseth 1988; Stenglein *et al*. 2003; Singh 2004).

Both macroscopic and microscopic techniques have their merits and shortcomings. Macroscopic studies do not require specialised equipment and it is easy to identify most plant features with a hand lens. However, identification keys based on macroscopic features often require additional characters from sources such as flowers and fruit, which are available only at certain times of the year (Jarvie & Stevens 1998). Microscopic studies, in contrast, require the use of specialised equipment, but leaf material for the analysis is generally available throughout the year.

In microscopic studies, the arrangement of epidermal cells on the leaves helps distinguish the monocotyledons from the dicotyledons. The epidermal cells of monocotyledons are often elongated and arranged in parallel rows along the parallel veins (Ellis 1979; Mauseth 1988). In some monocotyledons, the cells overlying the parallel veins, the costal cells, differ substantially from the epidermal cells between the veins so that distinct costal and intercostal zones can be distinguished (Ellis 1979; Fig. 7.1; see Glossary). These zones emphasize the structured appearance of monocotyledonous epidermi. Dicotyledonous plants, in contrast, do not have such an ordered appearance. Dicots generally have reticulate veins with a random distribution of the trichomes and stomata over the epidermis, and modified cells along the margins of the leaf (Dunn *et al*. 1965; Stace 1965; Croxdale 2000). In some dicot species, cuticle striations may be confined to the cells overlying the veins (Stace 1965; Mauseth 1988).

The ordinary epidermal cells have a variety of shapes, which include round to rectangular cells, or the cell outline can be irregular. Poaceae can have long cells that alternate with short cells; the short cells often have distinct taxonomic characters and can differentiate into silica cells and cork cells (Mauseth 1988). The silica bodies inside silica cells can be useful taxonomic characteristics of grasses, but may occur also in other monocotyledons (Ellis 1979; Mauseth 1988). The shape of the anticlinal walls is often responsible for the overall appearance of epidermal cells in surface view. The anticlinal walls show a variety of shapes such as straight (Fig. 7.2), curved, undulate and sinuous (Fig. 7.1). Undulate anticlinal walls have only one peak and trough per wall whereas sinuous anticlinal walls have a number of peaks and troughs per cell wall (Christophel *et al*. 1996). The external environment is known to influence the shape of a plant's anticlinal walls (Stenglein *et al*. 2003). Increased salt stress in the external environment, for example, is known to increase the waviness, or number of undulations, on anticlinal walls (Curtis & Lauchli 1987).

The cuticle covers the periclinal walls (Fig. 7.2) of epidermal cells. In some instances, the cuticle has complex patterns (striations or wrinkles), which may be limited to the surface of a single cell, or may extend over several epidermal cells (Stace 1965). The periclinal walls of epidermal cells can be smooth and featureless, or the cells may have ridges, or bear projections, the trichomes (Stace 1965; Singh 2004). Trichomes are hair-like structures, with an epidermal origin, that project markedly from the periclinal surface (Mauseth 1988). These projections can consist of a single cell or a number of cells, which can be branched or unbranched (Mauseth 1988; Singh 2004). Trichomes are classified as glandular when they secrete a substance such as water, salt, mucilage, adhesives or irritants (e.g., in *Urtica urens*). Non-glandular trichomes lack a secretory function (Mauseth 1988). Trichomes can have a variety of shapes and appear as spines, thorns, prickles, hairs, warts, papillae and emergences (Mauseth 1988; Singh 2004; Figs. 7.1 & 7.2). The type, shape and distribution of trichomes have been used successfully in plant taxonomy, e.g., to distinguish the different taxa in the genus *Solanum* (Edmonds 1982) and to distinguish among genera in the family Combretaceae (Singh 2004). In the Poaceae, prickles are usually associated with costal cells, whereas intercostal cells may have hooks, papillae, and or macro hairs. The presence of papillae is especially useful for distinguishing monocotyledonous species (Pridgeon 1982). Many plants contain a single type of trichome, but a single plant leaf may also possess a variety of trichome types (Stace 1965; Larkin *et al.* 1997).

The stomatal pores open on the surface of the epidermis and two guard cells surround each pore (Fig. 7.2). The structure formed by the two guard cells and stomatal pore is called a stoma (plural = stomata; Stace 1965; Mauseth 1988; Salisbury & Ross 1992). Two basic types of guard cells are distinguished: dumb-bell shaped guard cells occur in grasses (Fig. 7.1) and sedges while other plant groups have crescent-shaped guard cells (Mauseth 1988). Epidermal cells surrounding the guard cells can be unspecialised, with no distinguishing characters from the surrounding epidermal cells (Stace 1965; Mauseth 1988). Modified epidermal cells adjacent to the guard cells are called subsidiary cells (Fig. 7.2; Salisbury & Ross 1992). The stoma and surrounding epidermal cells are collectively called the stomatal complex (Stace 1965; Mauseth 1988). Many different stomatal complexes have been described (see Glossary). An anomocytic stomatal complex has no obvious subsidiary cells whereas other complexes are categorised by the number and arrangement of subsidiary cells. For example, in the paracytic complex one or more subsidiary cell is aligned parallel with a guard cell (Fig. 7.2; Stace 1965; Salisbury & Ross 1992; Singh 2004).

The stomata often have a random distribution over the leaf surface but in some instances, they form clusters, or are aligned parallel with the pattern of the epidermal cells (Mauseth 1988). In many plants, the stomata are more numerous on the abaxial than on the adaxial surfaces of leaves, requiring an evaluation of both surfaces. A certain stomatal complex type may be typical for a plant taxon, but several plant families have more than one stomatal complex type (Metcalf & Chalk 1957; Gopal & Shah 1970).

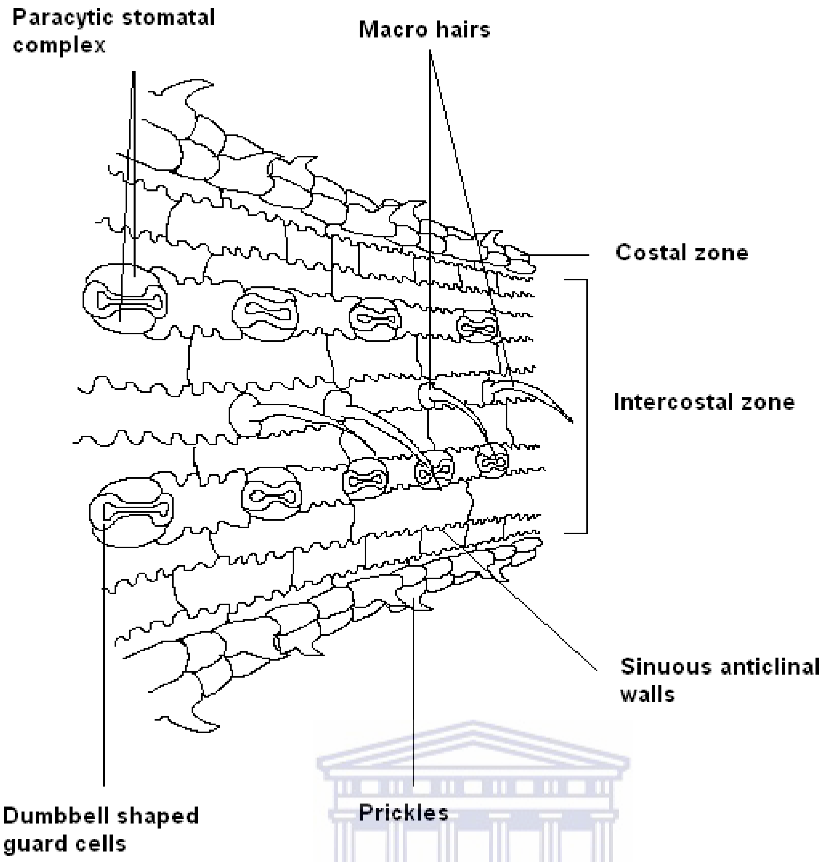

Figure 8.1 Epidermal characters of the Poaceae.

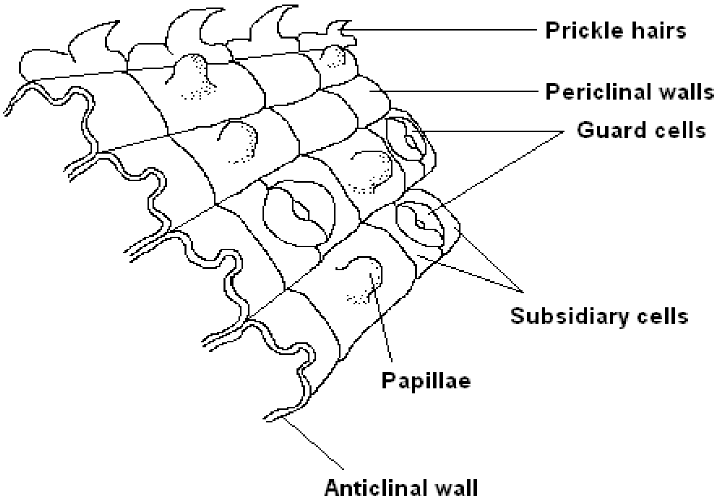

Figure 8.2 Epidermal characters on a hypothetical leaf epidermis.

The epidermal characteristics of plants can be used in a variety of ways. The most obvious being plant identification, taxonomic research and phylogenetic investigations (Stace 1965; Yukawa *et al*. 1992). Paleobotanists utilize epidermal characters, such as the structure of anticlinal walls (Krings & Kerp 1998), to classify the remains of prehistoric plants. They also study the cuticle impressions left behind on sandstone (Stace 1965; Guignard *et al.* 2004) or the fossilized remains of plants (Stace 1965). The classification of plant material based on cuticle and epidermal characters can also serve as a valuable tool in the study of peat stratigraphy, pharmacognostical analyses, and animal diet research (Stace 1965; Stace 1989).

Microscopic techniques can be used to identify food plants from the epidermal fragments in animal scats. It is relatively easy to collect scat samples from large numbers of animals, at different times of the year, and at different sites. Scat analysis thus offers a way to gain a comprehensive record of the diet plants used by a particular animal. When the diet study is combined with a record of plant species availability, ecologists can determine which plants are selected, avoided, or form the principal food items during different times of the year. This knowledge can help managers identify habitats that should be given a high priority when determining suitable areas for conservation.

Despite the advantages of using histology in animal diet research, few studies used this technique (Stewart 1967; Holechek *et al*. 1982; Loehr 2002; Mouden *et al*. 2006). One important reason is that the sheer number of epidermal characters available for identification can overwhelm researchers with no botanical background (Jarvie & Stevens 1998). If identification keys of the epidermal characters of plant taxa in South Africa become readily available, more scientists will be able to evaluate the food requirements of the rich herbivore fauna in this country. In this thesis, I evaluated the feeding ecology of angulate tortoises at two study sites in the southwestern Cape. The aims of this particular chapter are to:

(a) Identify epidermal characters that are reliable and easy to use when identifying a range of plant taxa in the southwestern Cape
(b) Compare epidermal characters of species within the same genus to determine characters common to that genus
(c) Determine if epidermi of different plant types show trends for specific characters
(d) Use the epidermal characters analysed to construct identification keys that can assist future users with plant identification.

8.3 MATERIALS AND METHODS

8.3.1 Study site and sampling

Most plant samples were collected between January 1999 and February 2000 in the West Coast National Park (WCNP) and Dassen Island (DI). Some plant material was lost during a power failure and I collected additional reference material during 2003 and 2004. Leaf material was collected from mature perennial and annual plants. Upon collection, samples were sealed in plastic bags, clearly marked, and refrigerated (ca. 5 °C) for short-term storage, or frozen (-20 °C) for long-term storage. A plant taxonomist at the University of the Western Cape identified the unknown plants.

I collected a variety of herbs, shrubs and grasses in the WCNP. Dassen Island is a highly disturbed habitat composed mainly of ephemeral weeds (Hurford 1996). This restricted the time when certain plants could be collected for epidermal analysis. From DI, I collected a variety of annual plants and three perennial plants, *Tetragonia fruticosa*, *Trachyandra divaricata* and *Myoporum serratum*.

8.3.2 Epidermal preparation

In general, I prepared epidermi from the abaxial and adaxial sides of leaves except for certain delicate plants where I could remove the epidermis from only one side. To distinguish between the abaxial and adaxial epidermi, I marked the surface of the leaf with a permanent marker before processing the leaf. For a few species, the ink flaked off and thus it is not known if the histology was determined from the abaxial or adaxial surfaces of these species. Epidermal fragments were taken midway between the apex and base of the leaf, and the fragments included the central portion and margins of the leaf. The leaf margins of some species have epidermal characters that can help identify the species and are thus important in plant epidermal taxonomy (Stace 1965). Including the leaf margins also facilitated the removal of the epidermis from the underlying parenchyma.

I used the epidermal scraping method outlined in Metcalfe (1960) and Zuloaga *et al.* (1993) to prepare epidermal samples. Before scraping the epidermis from the leaf, the leaf fragments were placed in a petri dish and floated in a weak solution of domestic bleach and water (3.5% m/v sodium hypochlorite - NaOCl). Domestic bleach acts as a softening agent and lubricant when scraping unwanted plant material from the epidermis. The leaf fragments were removed from the bleach solution when the epidermis started to separate from the underlying parenchymatous tissue. This process required approximately 15 minutes for delicate plants (e.g., *Senecio elegans*) and between 15 and 30 minutes for tougher plants (e.g., *Chrysanthemoides monilifera*).

The softened plant fragments were placed in a petri dish with distilled water and inspected under a dissecting microscope. Any parenchymatous material adhering to the abaxial or adaxial epidermi was scraped away with a flexible needle, and subsequently with a camel hairbrush, if necessary (Metcalfe 1960). The ease of removing parenchymatous tissue from plant epidermi varied from species to species. Epidermi prepared from shrubs were easier to make than epidermi from herbaceous material. When all the parenchymatous material was removed, the epidermis was washed in water and preserved. All epidermal preparations were preserved in individual vials containing FAA (formaldehyde : glacial acetic acid : 70% ethanol, in the proportion 0.5 : 0.5 : 9.0) and subsequently mounted on glass microscope slides using Haupt's adhesive (1 g gelatine + 100 ml distilled water + 2 g phenol crystals + 15 ml glycerol).

The plant epidermi were stained for 24 to 48 hours in safranin epidermal stain solution (4 g safranin + 22 ml methyl cellosove + 100 ml 95% alcohol + 100 ml distilled water + 4 g sodium acetate + 8 ml formaldehyde), and subsequently rinsed (once or twice) with distilled water (formula for stain modified from Metcalfe & Chalk 1983). I used a light microscope to examine the epidermi for correct staining. Shrubs, grasses, restioids and succulents stained more strongly than did soft herbs, which often under-stained. Over-stained epidermi were discarded if the excess stain could not be leached out of the epidermis. The epidermi that were salvaged by leaching-out excess stain were restained. When herbaceous epidermi could not be stained in the normal manner, I floated the epidermal fragment directly on a drop of the safranin stain. This procedure dramatically improved the chance that soft herbaceous epidermi stained properly.

After staining, the plant epidermi were placed through successive concentrations of ethanol (70%, 90% and absolute ethanol) to desiccate the plant epidermis. The duration of each dehydration stage could vary from a few minutes to one hour, depending on the type of plant. The ethanol leached the stain within minutes from herbaceous material, so the thin-walled epidermi of herbaceous leaves were left for only a few minutes in each dehydration stage. Preparations from plants with relatively thick epidermi could be left in the dehydration solution for up to one hour with no visible change in the stain intensity.

The alcohol used in the dehydration process is not miscible with the mountant. Xylene is miscible with the mountant and the epidermal samples remained overnight in 100% Xylene to be cleared. The cleared slides were permanently mounted with two drops of DPX mountant and the slides were subsequently air-dried for seven days before being used.

8.3.3 Microscopic analysis

Stained epidermal preparations were examined with an Olympus CX40RF200 light microscope at 400x magnification in order to distinguish the cuticle and epidermal characters. For each epidermis I recorded the arrangement of the epidermal cells, the shape of the anticlinal walls, the structure of the cuticle and periclinal walls, stomatal shape and stomatal complex type, and the type and shape of the trichomes. The shapes of trichomes were determined visually and terminologies used to distinguish between shapes were based on Payne (1978). Where no suitable term existed to classify a trichome's shape, a new term was created (e.g., flame or rod shaped).

For each dicotyledonous plant species, I measured the length and width (microns) of 15 stomata on the abaxial and adaxial surfaces, when both surfaces were available. The objective was to ascertain if stoma size could aid in the construction of a plant identification key of the dicots. Stomatal shapes were classified according to their length-to-width ratios. These measurements were recorded from a single specimen and thus do not represent the range of the population. For these measurements, I used an Olympus CX40RF200 light microscope (400x magnification) equipped with a calibrated ocular.

When all characters were recorded, I took digital pictures of the abaxial and adaxial surfaces. The epidermi were photographed on a Leica DMLS compound microscope with an attached video camera system. This system malfunctioned however, whereafter I used an Olympus BX50 compound microscope with an attached Olympus DP11 digital camera to photograph the remaining epidermi. Images were recorded and converted to a digital format with Leica Lida Imaging software (version 1.50).

In some instances, the surface view of the epidermi did not provide a clear, three-dimensional view of the trichomes and stomata. When focussing could not provide sufficient depth, it was difficult to distinguish short trichomes (unicellular and multicellular) from the surrounding cells. If the neck cells of the trichome could not be seen, it was difficult to determine if the trichome was glandular or non-glandular. Short, glandular trichomes can be unicellular or multicellular, but often this feature could not be determined from the surface view. Stomata can be level with the epidermal surface or sunken, as in xerophytic plants (Stace 1965). It was not always clear if stomata were sunken when focussing did not provide sufficient depth of view. Improper staining of the epidermi aggravated this problem and prevented the identification of some stomatal complexes.

The abaxial surface of *Atriplex semibaccata* and *Salvia africana-lutea* stained incorrectly and I could only record stomata measurements on these slides. Observing epidermal characters for *Salvia africana-lutea* was particularly difficult as the sheer numbers of trichomes present obscured the unspecialised epidermal cells underneath. The process of dehydrating the epidermi also influenced the shape of trichomes for *Salvia africana-lutea*. Trichomes appeared to be squashed in ways associated with dehydration. In such instances, trichomes were indicated as present only, if no other characters could be distinguished.

8.3.4 Data analysis and the construction of identification keys

The quantitative stomata data (length and width) were summarized as means and ranges for each species. To develop an objective estimate of stoma shape, I calculated the length-to-width ratio for each individual stoma and presented the ratios as means. Using length-to-width ratios of the guard cells, I identified four stomatal shapes among the dicotyledonous plants. The shapes were round, round to elliptical, elliptical, and rectangular. Round-shaped stomata had length-to-width ratios between 0.99 and 1.14. Round-to-elliptical stomata had ratios of 1.15 to 1.24 compared with elliptical stomata that had ratios between 1.26 and 1.44. Rectangular-shaped stomata had length-to-width ratios of 1.46 to 1.93.

The taxonomic software program DELTA (version 1.04) was used to develop an identification key based on the microscopic characters of the plants. After finding very low resolution in the key, I developed two separate keys based on the two major plant groups, the Monocotyledoneae and the Dicotyledoneae. I used the venation pattern of these groups to classify each plant species into either group. The epidermal and cuticle characters of the groups were then used to develop two separate keys, to the genus level, in the program DELTA.

Before DELTA constructs an identification key, the program first determines which character is the most informative. As a first step, DELTA eliminates all characters that are present in only a single taxon. The remaining characters are then evaluated using a comparison function and the most informative character (with the lowest value) is used to divide the dataset into a number of subsets (Dallwitz *et al.* 2000). The remaining characters are used to further divide the subsets. This process is continued until either no suitable character is left or each subset only contains one taxon (Dallwitz *et al.* 2000).

The dataset for the monocots included 14 characters (Table 7.1) but the DELTA program used only 13 characters to construct the epidermal key for the Monocotyledoneae. The original dataset for dicots included 15 characters (Table 7.1), but the key based on these characters was not satisfactory because some plant species occurred more than once in the key. After determining which characters were problematic, I excluded five characters from the dataset, and in the final analysis, DELTA used the remaining 10 characters to construct a key for the Dicotyledoneae. The characters included were those that represented the most complete data set, i.e., those characters that were present for most of the plant species. The DELTA program did not respond well to gaps in data and, in some instances where a character could not be placed in a specific category and was simply recorded as present, I had to manipulate the key manually. Additionally, plant species belonging to the same genus but appearing in distant positions on the identification key were manually moved closer together to aid the grouping of genera belonging to the same family.

For various reasons, I cannot provide detailed epidermal descriptions of all the plants that were identified in the histological scat evaluation (Chapter 5). For example, the epidermi of *Hebenstreitia repens and Pelargonium myrrhifolium* consistently under-stained, despite several attempts, and although it was possible to identify epidermal fragments in the scats, it was not possible to discern sufficient characters to warrant inclusion in this chapter. Because of under-staining, stomatal measurements were not recorded from *Passerina vulgaris* and the adaxial leaf epidermal surface of *Manochlamys albicans*. No stomatal measurements were recorded from the epidermal preparations of *Lachnospermum imbricatum, Passerina ericoides, Phylica ericoides* and *Phylica thunbergiana* as no stomata were present on the prepared epidermi. No stomatal complex types could be recorded for *Salvia africana-lutea*, as the epidermal cells around the stomata did not stain properly. The dehydration process affected the trichomes on the epidermis of *Salvia africana-lutea* and the shrivelled appearance of the trichomes made it impossible to determine their shape.

Table 8.1 Leaf epidermal and cuticle characters considered for the identification keys of monocotyledonous and dicotyledonous plants at the West Coast National Park and Dassen Island, South Africa. Character states are defined in the Glossary and character states not used for the keys are marked by an asterisk.

	Characters	Character states
Monocotyledoneae		
1	Arrangement of cells on leaf	Parallel / random
2	Costal and intercostal zones	Present / absent
3	Anticlinal wall shape	Straight / curved / sinuous / data absent
4	Anticlinal wall thickness	Thin / thickened (visual estimation)
5	Cuticle appearance	Smooth / striate
6	Stomatal guard cell shape	Dumb-bell / elliptical
7	Stomata complex type	Anomocytic / paracytic
8	Subsidiary cells	Present / absent
9	Number of stomata rows	1 / 2 / 3 / 1 or 2 / 2 or 3 / 4 or 5
10	Intercostal cells between stomata	Six different states for intercostal cell length relative to costal cell length
11	Trichome types	Macro hairs / prickles / macro hairs and prickles / papillae / none
12	Macro hair distribution	Margins / intercostal zones /costal zones / combinations
13	Prickle hair distribution	Margins / intercostal zones / costal zones / combinations
14	Number of subsidiary cells*	0 / 2
Dicotyledoneae		
1	Arrangement of cells on leaf	Parallel / random
2	Cuticle	Smooth / striate / wrinkled
3	Cuticle striations	On a single cell / spanning a number of cells
4	Subsidiary cells	Present / absent
5	Stomatal complex type	Anomocytic / anomotetracytic / anisocytic / amphibrachyparacytic / brachyparacytic / cyclocytic / paracytic
6	Polar thickening of guard cells	Present / absent
7	Trichomes	Present / absent
8	Trichome type	Glandular / non-glandular / both types
9	Number of trichome types	1 / 2
10	Trichome shape and special adaptations	Anvil / acerate / attenuate / bladder cells / cruciate / filiform / flagelliform / flame / hirsute / prickles / ornithorhynchous / papillae / peltate / rod / stellate / serpentine / sunken / stinging emergences
11	Trichome location*	Margins / randomly over the epidermis
12	Trichome distribution*	Abaxial / adaxial / both surfaces
13	Epidermal cells around stomata*	The numbers 3 to 8
14	Stomatal complex distribution*	Abaxial / adaxial / both surfaces
15	Anticlinal wall shape*	Straight / curved / undulate / sinuous / combinations

8.4 RESULTS AND DISCUSSION

8.4.1 Monocotyledoneae

8.4.1.1 Cell pattern and shape

I evaluated epidermal characters of 18 monocotyledonous plant taxa belonging to eight different families (Table 7.2). The epidermal cells of all the monocotyledonous plants, except *Zantedeschia aethiopica*, had a parallel arrangement, which appears to be a reliable histological character to separate the monocots from the dicots. For *Z. aethiopica*, the epidermal cells had a random arrangement, as found in dicotyledonous plants (Plate 1). Exceptions like *Z. aethiopica* can be problematic, as no epidermal character clearly distinguished this species from the dicots.

The nine Poaceae species evaluated had costal / intercostal zones (Plates 10-16), consistent with the findings of Metcalfe (1960) and Ellis (1979). However, in contrast to the findings of these authors, the epidermi of *Cyperus* sp. did not have costal / intercostal zones (Plates 3 and 4). Among the geophytes, only *Trachyandra divaricata* had the costal / intercostal arrangement (Plate 2). The presence of costal / intercostal zones are thus strongly indicative of the Poaceae. The stomata of most but not all the monocots were arranged in rows. Stace (1965) considers the distribution and frequency of stomata to be of significant systematic and diagnostic value to help distinguish between the monocots and the dicots.

The cuticles of all monocotyledons were smooth (Table 7.2), except for *Avena barbata*, *Bromus diandrus*, *Phalaris minor*, *Asparagus lignosus* and *Z. aethiopica*, which had striation patterns on the cuticle that stretched over a number of epidermal cells. The cuticle striation of *Z. aethiopica* covered a number of unspecialised cells, while the cuticle striation of *P. minor* covered unspecialised epidermal cells in the costal zones but not in the intercostal zones. A few light cuticle striations were observed over the unspecialised epidermal cells of *A. barbata* in the intercostal zones.

The anticlinal wall shape of many taxa appeared straight, or straight to curved (Table 7.2), whereas most taxa in the Cyperaceae (Plates 5-6) and Poaceae families had sinuous cell walls (Plates 10-11, 13, 15-16). The long cells in the intercostal zones were rectangular with numerous undulations at regular intervals. The sinuous anticlinal walls together with the rectangular shape of the intercostal long cells gave a good indication of either the Poaceae or Cyperaceae. The undulations of the sinuous anticlinal walls of monocots appeared smaller and more consistent in frequency and size than those of the dicots.

8.4.1.2 Stomatal complexes and trichomes

Two stomatal shapes were observed for the monocotyledonous plants (Table 7.2). Dumb-bell shaped stomatal guard cells occurred in all the Poaceae (Plates10-13 and 15-16), while the remainder of the plant species had elliptical stomata (Plates 1-4, 7-8, 9 and 17). Several authors reported that dumb-bell shaped guard cells characterise the Poaceae and Cyperaceae (Ellis 1979; Mauseth 1988; Salisbury & Ross 1992; Singh 2004). The dumb-bell shape is caused by differential thickening of guard cell walls, which are thin-walled at the ends and thickened towards the centre (Ellis 1979; Mauseth 1988). Dumb-bell shaped guard cells were not found in the dicots (see next section) so this characteristic is thus reliable to separate monocots from dicots.

The monocotyledons had only two stomatal complex types. Three taxa had anomocytic stomata, characterised by the absence of subsidiary cells around the guard cells (Plate 23). The majority of the monocots had paracytic stomata, where one subsidiary cell was found parallel to each guard cell. In the Poaceae and Cyperaceae, the stomata were confined to the intercostal zones (Plates 5-6, 10-13 and 15-16).

None of the monocotyledonous plants had glandular trichomes but three non-glandular trichome types, papillae, prickles and macro hairs, were represented. Papillae were observed on the periclinal surfaces of the leaves of *Asparagus lignosus* and *Thamnochortus spicigerus* (Plate 17). The papillae were distributed all over the epidermis of *T. spicigerus* whereas the distribution of the papillae was clumped on some portions of the leaf of *A. lignosus*. The presence of prickle hairs and macro hairs is of great importance in the classification of the Poaceae and Cyperaceae (Metcalfe 1960). In this study, prickle hairs (Plate 10) were limited to the Poaceae, whereas macro hairs (Plate 11) occurred in the Poaceae and in one geophyte, *Spiloxene capensis*. The Cyperaceae did not have prickle hairs, in contrast to the findings of Metcalfe (1960).

8.4.2 Dicotyledoneae

8.4.2.1 Cell pattern and shape

I evaluated 63 dicotyledonous plant taxa belonging to 30 different families (Table 7.3). The epidermal cells of the dicotyledonous plants were not arranged in an orderly fashion and the cells appeared to have a random distribution. My samples, however, included dicotyledonous species that did not conform to this arrangement. The dicots *Thesidium* sp. and *Cliffortia filifolia* showed a parallel arrangement of epidermal cells but the epidermal cells were not grouped into costal and intercostal zones (Plate 84 and 86). Although the parallel and random arrangement of epidermal cells are strongly linked to the monocotyledonous and dicotyledonous groups, respectively, the exceptions show that this feature is not infallible and that additional characteristics should be considered to separate these groups.

In contrast to the pattern in monocots, nearly half of the dicots had striations on the cuticle (Table 7.3). The cuticular striations most often overlapped a number of cells but four species, *Helichrysum niveum*, *Myoporum serratum, Agathosma* sp. and *Phylica thunbergiana*, had striations confined within the boundaries of a cell. The value of cuticle striations confined to certain epidermal cells were especially useful when viewing *Myoporum serratum* (Plate 76) and *Zygophyllum morgsana* epidermal preparations, as I was unable to identify other epidermal characters that were confined to these species.

In most dicots, the periclinal walls were smooth and featureless and the features were identical for the abaxial and adaxial surfaces**.** Three dicot species had trichomes that were modified to form bladder cells on their periclinal walls. Two of these species belonged to the Aizoaceae, *Dorotheanthus* sp. and *Mesembryanthemum crystallinum* (Plate 20). The third plant species, *Atriplex semibaccata*, belonged to Chenopodiaceae and possessed trichomes only on the abaxial surfaces of the leaf epidermi. One dicot, the shrublet *Psoralea repens*, had papillae on the periclinal walls of the unspecialised cells (Plate 67-68).

Most of the dicotyledonous plants had similar anticlinal wall characteristics on the abaxial and adaxial sides of the leaf (Table 7.3). However, the anticlinal walls of dicots varied substantially in shape, which made it difficult to limit descriptions to specific shapes, as much information can be lost by this practice. A descriptive term such as sinuous does not take into consideration how frequently the undulations occur along the anticlinal walls of the cell, the size of undulations, and the overall shape of the cell. In this study, severely sinuous anticlinal walls sometimes obscured the overall shape of the cells.

The use of anticlinal wall shape as a diagnostic feature, nevertheless, had some merit. For example, the anticlinal walls of the Aizoaceae were straight to curved (Plates 18-19 & Plates 21-24), giving the unspecialised cells of *Carpobrotus* and *Ruschia* a hexagonal shape. In general, the epidermi of these two genera appeared quite similar. The anticlinal walls of *Euphorbia peplus* showed areas of irregular thickening resembling beads (Plate 66), which facilitated identification of this species. Furthermore, *Agathosma* sp. characteristically had thick, dark-staining anticlinal walls (Plate 85). The anticlinal walls observed for *Carpobrotus* spp. and *Ruschia* spp. supported the findings of Stace (1965) that xerophytic plants have a tendency to bear straight anticlinal walls.

8.4.2.2 Stomatal complexes

Stomatal length and width measurements (Table 7.4) showed large variations for many plant species. These measurements were obtained from one leaf of one plant, and the variation among the leaves of the plant, and within the species, will probably be larger. Stomatal length-to-width ratios provide an objective assessment of the different stomatal shapes.

In this study, the mean length-to-width ratios of the stomata (abaxial, abaxial, or both) ranged from 0.99 to 1.93 with 89.7% of the taxa having ratios between 1.1 and 1.5. Consequently, the stomata of most dicots had an elliptical shape. The stomatal ratio of species within a genus showed close correspondence for the congenerics of *Rhus*, *Hermannia* and *Senecio*. This corresponds with the findings that the stomata of *Heracleum mantegazzianum*, *H. sphondylium* and their hybrid have similar measurements (i.e., lengths and widths; Arora *et al.* 1982), supporting the idea that stomatal length-to-width ratio is a useful diagnostic feature in plant taxonomy.

I distinguished seven different stomatal complex types in the dicotyledons (Table 7.5). The anomocytic complex (e.g., Plate 47) occurred most often (67%) followed by the brachyparacytic complex (13%; Plate 21). The paracytic stomatal complex, which occurred in most of the monocotyledons, was found only in the three *Rhus* spp. (Plates 25-30), and in the parasite plant *Septulina glauca* (Plate 74). The other four stomatal complex types had a limited distribution among the different taxa. The majority of plant epidermi had only one stomatal complex type on a leaf surface. Two of the three parasitic plants (*Septulina glauca* and *Thesidium* sp.) had more than one stomatal complex type on a single plant leaf or stem. In certain *Carpobrotus* spp. and *Ruschia* spp., the stomata appeared sunken, which is considered an adaptation to drought conditions (Mauseth 1988). The wide distribution of some stomatal complex types among plants limits the diagnostic value of this feature although the stomatal complex types with low occurrences can be useful to distinguish specific plant species.

8.4.2.3 Trichomes

Over 60% of the dicot species had trichomes, most of which had a simple structure, were non-glandular, and resembled hairs (Table 7.5). The observation of Mauseth (1988) that non-glandular, unicellular trichomes are very common among plants supports my findings. The majority of trichomes had smooth surfaces devoid of any striations or ornamentation but there were exceptions, such as *Trifolium burchellianum*, which had bulbous outgrowths on the surface of the trichomes. The prevalence of simple trichomes in different plants limits the usefulness of this feature.

Of the four complex trichome types, a four-armed (cruciate) and seven-armed (stellate) type occurred on *Hermannia pinnata* and *H. scabra*, respectively, while *Oxalis obtusa* and *Psoralea repens* had an anvil-shaped trichome type (Plate 67) and *Septulina glauca* a peltate-shaped trichome type. The cruciate and stellate trichome types made it possible to distinguish between *H. pinnata* and *H. scabra* as the epidermi of these two species were very similar. The complex trichome types were very useful diagnostic features.

I found 18 different varieties of trichome shapes (including those with special adaptations) for the dicotyledonous plant species (Table 7.5 & Glossary). For the majority of leaves examined, the trichomes were distributed over the entire epidermis and were not confined to specific areas. In *Felicia hyssopifolia* and *Cliffortia filifolia,* the trichomes were found mainly along the leaf margins, and in *F. hyssopifolia*, only one or two cells attached to the trichome base cell remained in the epidermal preparation. When the trichomes were limited to the leaf margins, the tips often broke off during sample preparation.

Four species, *Hermannia pinnata, H. scabra, Urtica urens,* and *Erodium moschatum*, had glandular and non-glandular trichomes. Both trichome types occurred on the abaxial and adaxial surfaces of these plants. *Chrysanthemoides monilifera* was the only species with sunken glandular trichomes (Plates 36-37). Stinging emergences occur in a number of families (Mauseth 1988) but are best known in the Urticaceae (Stace 1965; Thurston 1974). In this study, *Urtica urens* was the only plant bearing stinging emergences (Plate 96).

8.4.3 Identification keys

A variety of epidermal characters was evaluated to construct identification keys for monocotyledonous plants (Table 7.6) and dicotyledonous plants (Table 7.7) that occur in the southwestern Cape. The use of histological characters to construct identification keys for plants is not an easy process and the difficulties encountered were highlighted in this chapter. Nevertheless, the usefulness of epidermal keys in various science disciplines by far outweighs the problems associated with this method.

8.4.4 Growth forms

For most of the succulent plants examined, the epidermal cell walls were fairly straight with curved corners. The anticlinal wall shape of these genera supports the deduction of Stace (1965) that straight anticlinal cell walls on leaf epidermi are common to xeromorphic plants. The periclinal walls of most succulents were smooth, although some succulent species had faint cuticular striations. The epidermal arrangement of the succulents, particularly the *Carpobrotus* genus, showed no association with the leaf venation patterns. The stomata of succulents had thicker walls and stained darker than the surrounding cells. Some succulents had sunken stomata. None of the succulent plant epidermi possessed trichomes.

Many herbaceous plants had sinuous anticlinal walls whereas this character had a limited occurrence among the shrub species. The number of undulations varied from one per cell wall to many undulations, as in Apocynaceae (Plates 31-32). All the herbaceous plants had anomocytic stomatal complexes, whereas the shrubs had four additional stomatal complex types. The length-to-width ratios of the stomata of shrubs appeared small compared to the ratios of the herbs, succulents and parasitic plants (Table 7.4). One shrub, *Psoralea repens* had a very high ratio. When this shrub was removed from the data, the ratio, of the adaxial surfaces, for shrubs was significantly smaller that the ratios for the other four groups (One way ANOVA untransformed data – $F_{3,39} = 9.944$, $P = 0.00005$). Most of the herbs and shrubs had trichomes, but glandular trichomes were more prevalent among the herbaceous plants than among the shrubs. In shrubs, the epidermal cells overlying the veins were distinctive from the epidermal cells among the veins, whereas in herbaceous plants the difference between these cell types was less defined or absent. Xerophytic plants also have little or no venation pattern on their epidermal cells (Stace 1965).

8.4.5 Recommendations

The descriptions and keys in this chapter focussed on the leaf characteristics of monocotyledonous and dicotyledonous plants. However, herbivores may also eat the flowers and/or fruits of the plants. For ecological studies, it may be important to know which part of the plant the animal eats and in which proportions the different plant structures are used. I made epidermal preparations of flowers and seeds whenever it was possible to remove epidermal fragments from the seeds. This procedure is recommended for dietary studies.

Although Martin (1955) stated that one epidermal surface often suffices for plant species identification in faecal samples, my recommendation is to prepare, whenever possible, epidermi from the abaxial and abaxial sides of leaves. Some plant species have diagnostic characters on one side of the leaf only, and if this side has not been prepared, one would not be able to identify the plant.

A thorough research of the literature is necessary before a histological study should be undertaken because the sheer number and subcategories of epidermal characters can be overwhelming and confusing. Additionally, it is important to experiment with different staining procedures, because improper staining can make it impossible to identify particular diagnostic features. These problems can lead to incorrect identification.

Further study is necessary to evaluate the potential importance of subsidiary cell shape as an aid in the identification of plant epidermi. Stomatal complex type alone was not very effective due to considerable overlap in occurrence among plant genera and species. The shape of subsidiary cells together with the stomatal complex type may prove to be of greater value in identifying plant epidermi.

It is preferable to use fresh plant material to make epidermal preparations. Some epidermal characters may not be intact in dry or decaying leaf material. Blowing sand can abrade the leaf surface and may remove the trichomes, which are important characters in plant identification. Fresh plant material should be sealed in a plastic bag and can be kept at 5 °C for a number of days without adversely affecting the epidermal characters. For long-term storage, however, the plants should be frozen at –20 °C. Representative structures of the plant should also be dried, labelled, and stored for future reference.

Table 8.2 Cuticle and epidermal characteristics from the midsections of leaves (stems of restioids) of the Monocotyledoneae.

Family	Genus and species	Anticlinal surface	Stomatal shape	Subsidiary cells	Stomatal complex	Stomatal rows	Size of cells between stomata	Prickle hair distribution	Macro hair distribution
Araceae									
	*Zantedeschia aethiopica**†	Straight to curved	Elliptical	0	Anomocytic	Absent	Absent	Absent	Absent
Asparagaceae									
	*Asparagus lignosus**†#	Straight to curved	Elliptical	0	Anomocytic	Absent	Absent	Absent	Absent
Asphodelaceae									
	Trachyandra divaricata	Straight to curved	Elliptical	2	Paracytic	3	Shorter than costal cells	Absent	Absent
Cyperaceae									
	Cyperus sp.*	Straight	Elliptical	0	Anomocytic	0	Absent	Absent	Absent
	Ficinia nigrescens	Sinuous	Elliptical	0	Anomocytic	1 or 2	Shorter than costal cells	Absent	Absent
	Isolepis antarctica	Sinuous	Elliptical	2	Paracytic	1 or 2	Longer than costal cells	Absent	Absent
Hyacinthaceae									
	*Albuca flaccida**	Straight	Elliptical	2	Paracytic	Absent	Absent	Absent	Absent
Hypoxidaceae									
	*Spiloxene capensis**TR	Straight to curved	Elliptical	2	Paracytic	Absent	Absent	Absent	Margins
Poaceae									
	Avena barbata†	Straight to sinuous	Dumb-bell	2	Paracytic	1 or 2	Similar to or longer than costal cells	Margins and costal zones	Costal zones
	Avena fatua	Sinuous	Dumb-bell	2	Paracytic	1 or 2	Shorter to or equal in size to costal cells	Absent	Absent
	Bromus diandrus†	Straight	Dumb-bell	2	Paracytic	2	Cannot determine	Margins	Costal and intercostal zones

Table 8.2 continued

Family	Genus and species	Anticlinal surface	Stomatal shape	Subsidiary cells	Stomatal complex	Stomatal rows	Size of cells between stomata	Prickle hair distribution	Macro hair distribution
	Bromus pectinatus	Straight	Dumb-bell	2	Paracytic	2	Similar to shorter than costal cells	Absent	Absent
	Chaetobromus dregeanus	Straight	Dumb-bell	2	Paracytic	2	Similar to shorter than costal cells	Margins, costal and intercostal zones	Margins and intercostal zone
	Cynodon dactylon	Sinuous	Dumb-bell	2	Paracytic	2	Shorter than costal cells	Margins	Absent
	Ehrharta villosa	Curved to sinuous	Dumb-bell	2	Paracytic	4 or 5	Shorter than costal cells	Margins	Costal and intercostal zones
	Lolium perenne	Sinuous	Dumb-bell	2	Paracytic	2 or 3	Longer than costal cells	Absent	Absent
	Phalaris minor†	Sinuous	Dumb-bell	2	Paracytic	Indistinct	Similar to costal zones	Absent	Absent
Restionaceae									
	*Thamnochortus spicigerus**#	Straight to curved	Elliptical	2	Paracytic	Absent	Absent	Absent	Absent

* Epidermal cells were not divided into costal and intercostal zones; † Striations on the cuticle; # Taxa bear papillae on their periclinal surfaces; [TR] Trichomes present on the periclinal surface. *Zantedeschia aethiopica* was the only monocotyledon with randomly orientated epidermal cells in contrast to the parallel arrangements of the other monocots. *Pennisetum setaceum* was not included in the list because of the poor quality of the reference material.

Table 8.3 Cuticle and epidermal characteristics from the midsections of leaves of the Dicotyledoneae.

Family	Genus and species	Plant type	Leaf surface	Anticlinal wall shape	Cuticle surface		
					Appearance	Striations	Location of striations
Aizoaceae							
	Carpobrotus edulis	Su	One side	Straight to curved	Smooth		
	Carpobrotus quadrifidus	Su	One side	Straight to curved	Smooth		
	Conicosia pugioniformis	Su	One side	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
	Dorotheanthus sp.	Su	One side	Curved	Smooth		
	Mesembryanthemum crystallinum	Su	One side	Straight to curved	Smooth		
	Ruschia macowanii	Su	One side	Straight to curved	Smooth		
	Ruschia sp.	Su	One side	Straight to curved	Smooth		
	Tetragonia sp.	Su	Ab	Straight to curved	Light striation	Overlap cells	Striations confined to cells around stomata
Anacardiaceae							
	Rhus glauca	Sh	Ab and Ad	Curved	Smooth		
	Rhus laevigata	Sh	Ab and Ad	Straight (ad); curved (ab)	Smooth		
	Rhus lucida	Sh	Ab and Ad	Straight (ad); curved (ab)	Light striation (ab); smooth (ad)	Overlap cells	Unspecialised epidermal cells
Apocynaceae							
	Unknown	H	Ab and Ad	Sinuous	Light striation	Overlap cells	Small groups of striations with smooth areas between successive groups
	Cynanchum africanum	Sh	Ab and Ad	Straight to curved	Heavily wrinkled	Overlap cells	Unspecialised epidermal cells
Asteraceae							
	Berkheya armata	H	One side	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
	Chrysanthemoides monilifera	Sh	Ab and Ad	Straight to curved	Smooth		

Table 8.3 continued

Family	Genus and species	Plant type	Leaf surface	Anticlinal wall shape	Cuticle surface		
					Appearance	Striations	Location of striations
	Felicia hyssopifolia	Sh	Ab and Ad	Straight to curved	Light striation	Overlap cells	Striations confined to cells around stomata (Ad); Striations not restricted and occur over all unspecialised epidermal cells (Ab)
	Helichrysum niveum	Sh	One side	Sinuous	Smooth to striate	Within a cell	Striations confined to cells around stomata
	Lachnospermum imbricatum	Sh	Entire leaf	Curved	Smooth		
	Oncosiphon suffruticosum	H	One side	Sinuous	Light striation	Overlap cells	Unspecialised epidermal cells
	Pteronia uncinata	Sh / Su	Entire leaf	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells, overlapping edges of stomata
	Senecio burchelli	Sh	Ad	Straight to curved	Smooth		
	Senecio elegans	H	Ab and Ad	Straight to curved (ad); straight to sinuous (ab)	Light striation	Overlap cells	Unspecialised epidermal cells
	Senecio maritimus	H	Ab and Ad	Straight to slightly undulate (ad); undulate to sinuous (ab)	Light striation	Overlap cells	Venation cells and trichome base cells
	Sonchus oleraceus	H	Ab and Ad	Sinuous (ad); curved to sinuous (ab)	Smooth		
	Trichogyne verticillata	H	Ab and Ad	Curved to undulate	Smooth		
Celastraceae							
	Gymnosporia buxifolia	Sh	Ab and Ad	Curved (rarely straight)	Smooth		
Chenopodiaceae							
	Atriplex semibaccata	Sh	Ad	Straight to curved	Smooth		
	Chenopodium album	H	Ad	Straight to slightly undulate (ad); Undulate (ab)	Lightly wrinkled / striate abaxially	Overlap cells	Unspecialised epidermal cells
	Manochlamys albicans	Sh	Ab and Ad	Straight to curved	Smooth		

Table 8.3 continued

Family	Genus and species	Plant type	Leaf surface	Anticlinal wall shape	Cuticle surface		
					Appearance	Striations	Location of striations
Ebenaceae							
	Diospyros austro-africana	Sh	Ab and Ad	Straight to slightly curved	Smooth		
Euphorbiaceae							
	Euphorbia burmannii	Su	Stem	Curved	Smooth		
	Euphorbia mauritanica	Su	One side	Straight to curved	Smooth		
	Euphorbia peplus	Su	Ab and Ad	Straight to curved (ad); sinuous (ab)	Smooth		
Fabaceae							
	Psoralea repens	Sh	Ab and Ad	Straight to curved	Smooth		
	Trifolium burchellianum	H	Ab	Sinuous	Smooth		
Fumariceae							
	Cysticapnos vesicaria	H	Ab and Ad	Curved to undulate	Smooth		
Gentianaceae							
	Chironia baccifera	Sh	Ab	Sinuous	Smooth		
Geraniaceae							
	Erodium moschatum	H	One side	Sinuous	Light striation	Overlap cells	Unspecialised epidermal cells
	Geranium incanum	Sh	Ab and Ad	Curved (ad); curved to undulate (Ab)	Light striation	Overlap cells	Unspecialised epidermal cells
Lamiaceae							
	Salvia africana-lutea	Sh	Ab	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
Loranthaceae							
	Septulina glauca	Pa / Sh	One side	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
Menispermaceae							
	Cissampelos capensis	Sh	Ab and Ad	Straight / slightly curved (ad); undulate (ab)	Smooth		

Table 8.3 continued

Family	Genus and species	Plant type	Leaf surface	Anticlinal wall shape	Cuticle surface		
					Appearance	Striations	Location of striations
Myoporaceae							
	Myoporum serratum	T	One side	Straight to curved	Light striation	Within a cell	Mainly confined to cells around stomata
Oxalidaceae							
	Oxalis obtusa	H	Ab and Ad	Straight to slightly curved	Smooth		
Plumbaginaceae							
	Afrolimon purpuratum	Sh	Ab and Ad	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
Polygalaceae							
	Nylandtia spinosa	Sh	One side	Straight to slightly curved	Smooth		
Primulaceae							
	Anagalis arvensis	H	Ab and Ad	Sinuous	Light striation	Overlap cells	Unspecialised epidermal cells
Rhamnaceae							
	Phylica thunbergiana	Sh	Ad	Straight	Light striation	Within a cell	Unspecialised epidermal cells
	Phylica ericoides	Sh	Ab and Ad	Straight	Smooth		
Rosaceae							
	Cliffortia filifolia	Sh	Entire leaf	Curved to slightly undulate	Smooth		
Rutaceae							
	Agathosma sp.	Sh	Entire leaf	Straight to curved	Light striation	Within a cell	Unspecialised epidermal cells
Santalaceae							
	Osyris compressa	Pa / Sh	Ab	Curved, rarely straight	Smooth		
	Thesidium sp.	Pa / Sh	Stem	Straight to curved	Smooth		

Table 8.3 continued

Family	Genus and species	Plant type	Leaf surface	Anticlinal wall shape	Cuticle surface		
					Appearance	Striations	Location of striations
Scrophulariaceae							
	Amsinckia calycina	H	Ab and Ad	Straight to curved (ad); undulate to sinuous (ab)	Smooth		
	Hemimeris racemosa	H	Ad	Sinuous	Smooth		
Solanaceae							
	Lycium afrum	Sh	Entire leaf	Curved	Light striation	Overlap cells	Unspecialised epidermal cells
Sterculiaceae							
	Hermannia pinnata	Sh	Entire leaf	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
	Hermannia scabra	Sh	Ad	Straight to curved	Light striation	Overlap cells	Unspecialised epidermal cells
Thymelaeaceae							
	Passerina sp.	Sh	Entire leaf	Curved to undulate	Smooth		
	Passerina vulgaris	Sh	Entire leaf	Curved / undulate to slightly sinuous	Smooth		
	Passerina ericoides	Sh	Entire leaf	Curved / undulate to slightly sinuous	Smooth		
Urticaceae							
	Urtica urens	H	Ab	Sinuous	Smooth		
Zygophyllaceae							
	Zygophyllum morgsana	Sh / Su	Ab and Ad	Straight to curved	Smooth to lightly striate	Overlap cells	Confined to cells around stomata

Su = succulent, Sh = shrub, H = herb, Pa = parasite, T = tree, Ab = abaxial and Ad = adaxial. For *Agathosma* sp., the anticlinal walls of cells surrounding the stomata were thicker than the walls of the cells not in contact with stomata. For *Euphorbia peplus*, the anticlinal walls had thickened areas resembling beads.

Table 8.4 Mean length and width (µm), and mean length-to-width ratios of 15 stomata on the adaxial and abaxial leaf surfaces, respectively, of the Dicotyledoneae.

Family	Genus and species	Adaxial					Abaxial				
		Mean length	Range for length	Mean width	Range for width	Ratio (L/W)	Mean length	Range for length	Mean width	Range for width	Ratio (L/W)
Aizoaceae											
	Carpobrotus edulis[#]	28	25 - 32	22	17 - 25	1.30	n/a		n/a		
	Carpobrotus quadrifidus[#]	40	32 - 49	23	20 - 30	1.76	n/a		n/a		
	Conicosia pugioniformis[#]	38	30 - 47	26	20 - 33	1.48	n/a		n/a		
	Dorotheanthus sp.[#]	33	27 - 40	27	20 - 36	1.24	n/a		n/a		
	Mesembryanthemum crystallinum	22	19 - 28	18	15 - 20	1.27	n/a		n/a		
	Ruschia macowanii[#]	27	25 - 32	17	10 - 21	1.68	n/a		n/a		
	Ruschia sp.[#]	30	26 - 35	29	27 - 31	1.07	n/a		n/a		
	Tetragonia sp.	n/a		n/a			47	33 - 64	36	31 - 47	1.31
Anacardiaceae											
	Rhus glauca						26	22 - 35	24	20 - 30	1.09
	Rhus laevigata						29	25 - 35	25	22 - 27	1.18
	Rhus lucida						28	25 - 32	25	20 - 31	1.13
Apocynaceae											
	Unknown	31	25 - 37	21	17 - 26	1.48	n/a		n/a		
	Cynanchum africanum	23	20 - 27	22	19 - 27	1.06	25	21 - 27	23	20 - 25	1.07
Asteraceae											
	Berkheya armata	25	20 - 27	18	15 - 22	1.39	n/a		n/a		
	Chrysanthemoides monilifera	33	30 - 37	30	25 - 35	1.11	32	30 - 35	30	27 - 35	1.07
	Felicia hyssopifolia	18	15 - 21	18	15 - 20	1.03	19	15 - 21	17	15 - 20	1.11
	Helichrysum niveum	21	20 - 23	21	16 - 25	1.05	n/a		n/a		

Table 8.4 continued

		Adaxial					Abaxial				
Family	Genus and species	Mean length	Range for length	Mean width	Range for width	Ratio (L/W)	Mean length	Range for length	Mean width	Range for width	Ratio (L/W)
	Oncosiphon suffruticosum	27	25 - 30	20	15 - 25	1.35	n/a		n/a		
	Pteronia uncinata	40	37 - 47	37	32 - 40	1.10					
	Senecio burchelli	30	25 - 37	23	20 - 27	1.33	n/a		n/a		
	Senecio elegans	43	25 - 57	30	20 - 42	1.44	39	28 - 49	30	25 - 36	1.34
	Senecio maritimus	32	25 - 37	24	20 - 30	1.36	28	22 - 35	25	21 - 30	1.16
	Sonchus oleraceus	27	22 - 35	22	20 - 25	1.21	21	17 - 25	16	12 - 19	1.31
	Trichogyne verticillata	24	20 - 30	20	17 - 23	1.21	n/a		n/a		
Celastraceae											
	Gymnosporia buxifolia	27	26 - 30	25	22 - 27	1.09	25	22 - 27	19	15 - 22	1.30
Chenopodiaceae											
	Atriplex semibaccata	23	20 - 27	18	16 - 20	1.30	21	17 - 27	16	12 – 17	1.33
	Chenopodium album	26	25 - 30	20	17 - 23	1.31	25	20 - 30	20	17 - 23	1.23
	Manochlamys albicans	n/a		n/a			20	17 - 25	17	15 – 20	1.18
Ebenaceae											
	Diospyros austro africana	28	25 – 32	19	15 – 25	1.46	26	20 – 32	20	16 – 25	1.30
Euphorbiaceae											
	*Euphorbia burmannii**	30	27 – 32	27	25 – 32	1.10					
	Euphorbia mauritanica	37	28 – 47	31	22 – 37	1.22	n/a		n/a		
	Euphorbia peplus						18	15 – 21	12	10 – 15	1.53
Fabaceae											
	Psoralea repens	18	12 – 21	9	7 – 12	1.93	19	14 – 30	12	9 – 17	1.65
	Trifolium burchellianum	n/a		n/a			25	23 - 27	18	15 - 20	1.41

Table 8.4 continued

Family	Genus and species	Adaxial					Abaxial				
		Mean length	Range for length	Mean width	Range for width	Ratio (L/W)	Mean length	Range for length	Mean width	Range for width	Ratio (L/W)
Fumariceae											
	Cysticapnos vesicaria						33	25 – 37	27	22 – 33	1.22
Gentianaceae											
	Chironia baccifera	n/a		n/a			52	43 – 56	39	37 – 42	1.34
Geraniaceae											
	Erodium moschatum	24	21 - 27	16	15 - 17	1.47					
	Geranium incanum	27	23 - 30	22	20 - 25	1.21	27	22 - 32	21	20 - 22	1. 27
Lamiaceae											
	Salvia africana lutea	n/a		n/a			18	15 - 22	16	12 - 20	1.13
Loranthaceae											
	Septulina glauca	40	30 - 49	25	19 - 27	1.65	n/a		n/a		
Menispermaceae											
	Cissampelos capensis	n/a		n/a			27	25 - 32	25	22 - 27	1.10
Myoporaceae											
	Myoporum serratum	34	27 - 40	20	12 - 25	1.81	33	28 - 37	21	15 - 25	1.63
Oxalidaceae											
	Oxalis obtusa	21	16 - 25	16	12 - 19	1.31	25	22 - 27	20	17 - 22	1.23
Plumbaginaceae											
	Afrolimon purpuratum	36	31 - 38	34	30 - 40	1.06	34	30 - 40	35	25 - 42	0.99
Polygalaceae											
	Nylandtia spinosa $^{\#}$	28	25 - 32	25	22 - 27	1.14	n/a		n/a		
Primulaceae											
	Anagalis arvensis	48	32 - 62	32	30 - 36	1.48	42	37 - 49	32	27 - 37	1.33

Table 8.4 continued

Family	Genus and species	Adaxial					Abaxial				
		Mean length	Range for length	Mean width	Range for width	Ratio (L/W)	Mean length	Range for length	Mean width	Range for width	Ratio (L/W)
Rosaceae											
	Cliffortia filifolia$^{\#}$	33	27 - 37	30	26 - 35	1.07	n/a		n/a		
Thymelaeaceae											
	Passerina sp.$^{\#}$	31	28 - 37	27	25 - 35	1.17	n/a		n/a		
Rutaceae											
	Agathosma sp.	33	30 - 37	30	27 - 35	1.12	n/a		n/a		
Santalaceae											
	Osyris compressa	n/a		n/a			29	25 - 37	26	20 - 30	1.17
	Thesidium sp.*	37	32 - 41	24	21 - 27	1.53					
Scrophulariaceae											
	Amsinckia calycina	29	23 - 33	22	20 - 27	1.36	33	30 - 35	24	20 - 28	1.39
	Hemimeris racemosa	45	40 - 52	31	25 - 37	1.46	n/a		n/a		
Solanaceae											
	Lycium afrum	33	28 - 40	27	22 - 31	1.20					
Sterculiaceae											
	Hermannia pinnata	22	20 - 25	19	17 - 21	1.15	n/a		n/a		
	Hermannia scabra	22	20 - 26	21	20 - 23	1.07	n/a		n/a		
Urticaceae											
	Urtica urens	n/a		n/a			22	19 - 25	18	15 - 21	1.27
Zygophyllaceae											
	Zygophyllum morgsana	35	27 - 40	28	25 - 30	1.27	36	27 - 47	28	22 - 30	1.29

$^{\#}$Unable to distinguish between the abaxial and adaxial surfaces of the leaf due to the shape of the leaf. **Thesidium* sp. and *Euphorbia burmannii* measurements were taken from the stem.

Table 8.5 Stomatal and trichome characteristics from the midsections of leaves of the Dicotyledoneae.

Family	Genus and species	Plant type	Leaf surface	Stomata shape	Stomatal complex	Subsidiary and non-subsidiary cells	Trichome structure	Trichome type	NG trichome shape
Aizoaceae									
	Carpobrotus edulis	Su	One side	Elliptical	Brachyparacytic	2	None		
	Carpobrotus quadrifidus	Su	One side	Rectangular	Brachyparacytic	2	None		
	Conicosia pugioniformis	Su	One side	Rectangular	Anomocytic	2	None		
	Dorotheanthus sp.	Su	One side	Round to Elliptical	Anomocytic	2 to 4	Simple	NG	Bladder cells
	Mesembryanthemum crystallinum	Su	One side	Elliptical	Anomocytic	2 to 4	Simple	NG	Bladder cells
	Ruschia macowanii	Su	One side	Rectangular	Brachyparacytic	2	None		
	Ruschia sp.	Su	One side	Round	Brachyparacytic	2	None		
	Tetragonia sp.	H	Ab	Elliptical	Anomocytic	5	None		
Anacardiaceae									
	Rhus glauca$^{\#}$	Sh	Ad and Ab	Round	Paracytic	2	Simple	NG	Rod
	Rhus laevigata$^{\#}$	Sh	Ad and Ab	Round to Elliptical	Paracytic	2	Simple	NG	Hirsute
	Rhus lucida$^{\#}$	Sh	Ad and Ab	Round	Paracytic	2	Simple	NG	Rod
Apocynaceae									
	Unknown	H	Ab	Rectangular	Anomocytic	3 to 4	None		
	Cynanchum africanum	H	Ad and Ab	Round	Anomocytic	4 to 8 (ab); 4 to 6 (ad)	Multicellular	NG	Acerate
Asteraceae									
	Berkheya armata	H	One side	Elliptical	Anomocytic	4 to 6	Present	NG	Filiform with swollen base
	Chrysanthemoides monilifera	Sh	Ad and Ab	Round	Anomocytic	4 to 5	Simple	G	
	Felicia hyssopifolia	Sh	Ad and Ab	Round	Anomocytic	3 to 6 (ad) / 3 to 5 (ab)	Simple	Tips broken	

Table 8.5 continued

Family	Genus and species	Plant type	Leaf surface	Stomata shape	Stomatal complex	Subsidiary and non-subsidiary cells	Trichome structure	Trichome type	NG trichome shape
	Helichrysum niveum	Sh	One side	Round	Anomotetracytic	4 to 5 striate and sinuous	Multicellular	NG	Serpentine
	Oncosiphon suffruticosum	H	One side	Elliptical	Anomocytic	4 to 5	Multicellular	G	
	Pteronia uncinata	Sh /Su	Entire leaf	Round	Anomocytic	3 to 6	Present		
	Senecio burchelli	Sh	Ad	Elliptical	Anomocytic	3 to 4	Present		
	Senecio elegans	H	Ad and Ab	Elliptical	Anomocytic	3 to 5	Simple	G	Flagelliform
	Senecio maritimus	H	Ad and Ab	Round to Elliptical	Anomocytic	3 to 5	Simple	G	Flagelliform
	Sonchus oleraceus	H	Ad and Ab	Round to Elliptical	Anomocytic	3 to 5	None		
	Trichogyne verticillata	H	Ad and Ab	Round to Elliptical (ad); none (ab)	Anomocytic	3 to 5	Simple	NG	Flagelliform
Celastraceae									
	Gymnosporia buxifolia	Sh	Ad and Ab	Round	Anomocytic	4 to 7 (ad); 4 to 6 (ab)	None		
Chenopodiaceae									
	Atriplex semibaccata	Sh	Ad	Elliptical	Anomocytic	3 to 4	Present	NG	Bladder cells (ab)
	Chenopodium album	H	Ad and Ab	Elliptical	Anomocytic	4 to 5	Multicellular	G	
	Manochlamys albicans	Sh	Ad and Ab	Round to Elliptical (Ab)	Anomocytic (Ab and Ad)	4 to 5	Present		
Ebenaceae									
	Diospyros austro africana	Sh	Ad and Ab	Rectangular	Brachyparacytic	2	Simple	NG	Flame
Euphorbiaceae									
	Euphorbia burmannii	Su	Stem	Round	Anisocytic to anomotetracytic	3 to 4	None		

Table 8.5 continued

Family	Genus and species	Plant type	Leaf surface	Stomata shape	Stomatal complex	Subsidiary and non-subsidiary cells	Trichome structure	Trichome type	NG trichome shape
	Euphorbia mauritanica	Su	One side	Round to Elliptical	Anomocytic	3 to 5	None		
	Euphorbia peplus#	Su	Ad and Ab	Rectangular	Anomocytic	3 to 4	None		
Fabaceae									
	Psoralea repens	Sh	Ad and Ab	Rectangular	Anomocytic	4 to 7	Simple / Multicellular	NG	Anvil / Papillose
	Trifolium burchellianum	H	Ab	Elliptical	Anomocytic	3 to 4	Simple	NG	Acerate / Bosselated
Fumariceae									
	Cysticapnos vesicaria#	H	Ad and Ab	Round to Elliptical	Anomocytic	2 to 5	None		
Gentianaceae									
	Chironia baccifera	Sh	Ab	Elliptical	Anomocytic	3 to 4	None		
Geraniaceae									
	Erodium moschatum	H	Ad and Ab	Elliptical	Anomocytic	3 to 5	Simple / Multicellular	G / NG	Attenuate
	Geranium incanum	Sh	Ad and Ab	Round to Elliptical (ad); Elliptical (ab)	Anomocytic	3 to 4	Present		
Lamiaceae									
	Salvia africana-lutea	Sh	Ab	Round	n/a	n/a	Multicellular	NG	n/a
Loranthaceae									
	Septulina glauca	Pa	One side	Rectangular	Anomocytic, paracytic and brachyparacytic	2	Present	NG	Peltate
Menispermaceae									
	Cissampelos capensis	Sh	Ad and Ab	None (ad); round (ab)	Anomocytic	4 to 5	None		

Table 8.5 continued

Family	Genus and species	Plant type	Leaf surface	Stomata shape	Stomatal complex	Subsidiary and non-subsidiary cells	Trichome structure	Trichome type	NG trichome shape
Myoporaceae									
	Myoporum serratum	T	One side	Rectangular	Anomocytic	3 to 4	Simple	G	
Oxalidaceae									
	Oxalis obtusa	H	Ab	Elliptical	Anomocytic	4 to 6	Mullticellular	NG	Anvil
Plumbaginaceae									
	Afrolimon purpuratum	Sh	Ad and Ab	Round	Cyclocytic	3 to 4	None		
Polygalaceae									
	Nylandtia spinosa	Sh	One side	Round	Cyclocytic	3 to 8	Simple	NG	Attenuate
Primulaceae									
	Anagalis arvensis	H	Ad and Ab	Rectangular	Anomocytic	3 to 4	Simple	G	
Rhamnaceae									
	Phylica ericoides	Sh	Ad and Ab	n/a	n/a	n/a	None		
	Phylica thunbergiana	Sh	Ad	n/a	n/a	n/a	Simple	NG	Acerate
Rosaceae									
	Cliffortia filifolia	Sh	One side	Round	Anomotetracytic	4 to 5	Simple	NG	Prickles
Rutaceae									
	Agathosma sp.	Sh	Entire leaf	Round	Anomocytic	5 to 6	Simple	NG	Attenuate
Santalaceae									
	Osyris compressa	Pa	Ab	Round to Elliptical	Brachyparacytic	2	None		
	Thesidium sp.	Pa	Stem	Rectangular	Brachyparacytic and amphibrachyparacytic	2 to 4	None		
Scrophulariaceae									
	Amsinckia calycina	H	Ad and Ab	Elliptical	Anomocytic	3 to 4	Simple	NG	Hirsute
	Hemimeris racemosa	H	Ad	Rectangular	Anomocytic	3 to 4	Simple	G	

Table 8.5 continued

Family	Genus and species	Plant type	Leaf surface	Stomata shape	Stomatal complex	Subsidiary and non-subsidiary cells	Trichome structure	Trichome type	NG trichome shape
Solanaceae									
	Lycium afrum	Sh	Entire leaf	Round to Elliptical	Anomocytic	4	Present		
Sterculiaceae									
	Hermannia pinnata	Sh	Entire leaf	Round to Elliptical	Anomocytic	4 to 6	Simple to four-armed	G / NG	Cruciate
	Hermannia scabra	Sh	Ad	Round	Anomocytic	4 to 5	Seven-armed	G / NG	Stellate
Thymelaeaceae									
	Passerina sp.	Sh	Entire leaf	Round to Elliptical	Anomocytic to anomotetracytic	4 to 5	None		
	Passerina vulgaris	Sh	Entire leaf	Elliptical	Anomocytic	4 to 5	Simple / multicellular	NG	Ornithorhynchous
	Passerina ericoides	Sh	Entire leaf	Elliptical					
Urticaceae									
	Urtica urens	H	Ab	Elliptical	Anomocytic	3 to 4	Simple	G / NG	Hirsute and attenuate
Zygophyllaceae									
	Zygophyllum morgsana	Sh / Su	Ad and Ab	Elliptical	Anomocytic	4 to 7 (ad); 4 to 8 (ab)	None		

T = tree, Su = succulent, Sh = shrub, Pa = parasite, H = herb, Ad = adaxial, Ab = abaxial, G = glandular, NG = non-glandular, Simple = unbranched, single-armed trichomes, *Two trichome types present, †Trichomes only on abaxial side, #Stomata only present on the abaxial epidermal surface of leaf.
Chrysanthemoides monilifera is the only plant species with sunken, glandular trichomes. *Felicia hyssopifolia* and *Cliffortia filifolia* are the only two species with trichomes distributed along the margins of their leaves. More than 80% of stomata were orientated in the same direction for *Amsinckia calycina*, *Anagallis arvensis, Chironia baccifera*, *Oncosiphon suffruticosum* and *Passerina* sp.

Table 8.6 Identification key of the Monocotyledoneae

1(0)	Trichome types	
	Prickles	*Cynodon dactylon*
	Prickles and macro hairs	2
	None	4
	Macro hairs	11
	Papillae	12
2(1)	Anticlinal walls thin; striate cuticle surface	3
	Anticlinal walls thickened; smooth cuticle surface	*Erharta villosa*
3(2)	Macro hairs along costal and intercostal zones; prickles along leaf margins	*Bromus diandrus*
	Macro hairs along costal zones; prickles along leaf margins and costal zones	*Avena barbata*
4(1)	Anticlinal wall shape	
	Straight	5
	Sinuous	9
5(4)	Subsidiary cells present; paracytic stomatal complex	6
	Subsidiary cells absent; anomocytic stomatal complex	8
6(5)	Anticlinal walls thin	7
	Anticlinal walls thickened, dark staining	*Trachyandra divaricata*
7(6)	Guard cells dumb-bell shaped; costal and intercostal zones distinguished	*Bromus pectinatus*
	Guard cells elliptical; no costal and intercostal zones	*Albuca flaccida*
8(5)	Cuticle surface smooth; parallel arrangement of unspecialised epidermal cells	*Cyperus* sp.
	Cuticle surface striated; random arrangement of unspecialised epidermal cells	*Zantedeschia aethiopica*
9(4)	Size of inter-stomatal cells relative to costal cells	
	Similar to costal cells	*Phalaris minor*
	Shorter or similar to costal cells	*Avena fatua*
	Shorter than costal cells	*Ficinia nigrescens*
	Longer than costal cells	10

Table 8.6 continued

10(9)	Anticlinal walls thin; dumb-bell shaped guard cells; two or three intercostal stomatal rows	*Lolium perenne*
	Anticlinal walls thickened; elliptical guard cells; one intercostal stomatal row	*Isolepis antarctica*
11(1)	Dumb-bell shaped guard cells; costal and intercostal zones distinguished; macro hairs on leaf margins and intercostal zones	*Chaetobromus dregeanus*
	Elliptical guard cells; no costal and intercostal zones; macro hairs on leaf margins	*Spiloxene capensis*
12(1)	Straight anticlinal wall; striated cuticle; subsidiary cells absent; stomatal complex anomocytic	*Asparagus lignosus*
	Straight to curved anticlinal wall; cuticle surface smooth; subsidiary cells present; stomatal complex paracytic	*Thamnochortus spicigerus*

Terminology derived from Brown & Johnson (1962), Ellis (1979), and Dávila & Clark (1990).

Table 8.7 Identification key of the Dicotyledoneae

1(0)	Random distribution of epidermal cells; single stomatal complex type	
	Anomocytic	2
	Brachyparacytic	8
	Paracytic	12
	Anomotetracytic	13
	Cyclocytic	15
	Random distribution of epidermal cells; more than one stomatal complex type	
	Anomocytic and anomotetracytic	6
	Anisocytic and anomotetracytic	7
	Anomocytic, paracytic and brachyparacytic	18
	Parallel epidermal cells; brachyparacytic and amphibrachyparacytic stomatal complex types	*Thesidium* sp.
2(1)	Cuticle surface	
	Smooth	3
	Striate	16
	Wrinkled	21
3(2)	Trichomes present but not identified	
	Anticlinal walls straight to curved	*Senecio burchelli*
	Glandular trichomes	
	Trichomes project above epidermal surface; anticlinal walls sinuous	*Hemimeris racemosa*
	Sunken glandular trichomes; anticlinal walls straight to curved	*Chrysanthemoides monilifera*
	Non-glandular trichomes	4
	Trichomes absent	5
4(3)	One trichome shape or specialised trichome type	
	Acerate	*Trifolium burchellianum*
	Anvil	*Oxalis obtusa*
	Flagelliform	*Trichogyne verticilata*
	Hirsute	*Amsinckia calycina*
	Ornithorhynchous	*Passerina vulgaris*
	Bladder cells	*Atriplex semibaccata* *Dorotheanthus* sp. *Mesembryanthemum crystallinum*
	Stinging emergences	*Urtica urens*
	Two trichome shapes present	
	Anvil and papillae	*Psoralea repens*

Table 8.7 continued

5(3)	Anticlinal wall shape	
	Straight to curved	*Zygophyllum morgsana,* *Euphorbia mauritanica,* *Manochlamys albicans*
	Round to curved	*Gymnosporia buxifolia*
	Curved to sinuous (ad) and sinuous (ab)	*Sonchus oleraceus*
	Straight, slightly curved to undulate	*Cissampelos capensis*
	Sinuous	*Chironia baccifera*
	Straight to curved (ad) and sinuous (ab)	*Euphorbia peplus*
	Curved to undulate	*Cysticapnos vesicaria*
6(1)	Cuticle surface smooth; trichomes absent; anticlinal walls curved to undulate	*Passerina* sp.
7(1)	Cuticle surface smooth; trichomes absent; anticlinal walls curved	*Euphorbia burmanii*
8(1)	Cuticle surface smooth	
	Trichomes present	9
	Trichomes absent	10
9(8)	Non-glandular, flame shaped trichomes	*Diospyros austro africana*
10(8)	Stomatal polar regions not thickened	11
	Stomatal polar regions thickened; anticlinal walls curved (epidermal cells appear round)	*Osyris compressa*
11(10)	Anticlinal walls straight to curved (epidermal cells appear hexagonal)	*Carpobrotus edulis,* *Carpobrotus quadrifidus,* *Ruschia macowanii, Ruschia* sp.
12(1)	Leaf epidermal surfaces hypostomatic (ab); cuticle surface smooth; non-glandular trichomes	
	Trichome shape hirsute; anticlinal walls straight (ad) and curved (ab)	*Rhus laevigata*
	Trichomes rod shaped; anticlinal walls curved	*Rhus glauca*
	Trichomes rod shaped; anticlinal walls straight (ad) and curved (ab); cuticle surface smooth (ad) and striate (ab)	*Rhus lucida*
13(1)	Non-glandular trichomes	14
14(13)	Prickles; cuticle surface smooth; anticlinal walls curved to undulate	*Cliffortia filifolia*
	Serpentine-shaped trichomes; cuticle surface smooth to striate; anticlinal walls sinuous	*Helichrysum niveum*

Table 8.7 continued

15(1)	Cuticle surface smooth; non-glandular, attenuate trichomes; anticlinal walls straight to slightly curved	*Nylandtia spinosa*
	Cuticle surface lightly striated; trichomes absent; anticlinal walls straight to curved	*Afrolimon purpuratum*
16(2)	Trichomes present and identified	17
	Trichomes present but not identified	
	Polar regions of stomata not thickened	
	Anticlinal walls curved	*Lycium afrum*
	Anticlinal walls curved (ad) and curved to undulate (ab)	*Geranium incanum*
	Anticlinal walls straight to curved	*Pteronia uncinata*
	Polar regions of stomata thickened; anticlinal walls straight to curved	*Felicia hyssopifolia*
	Trichomes absent; polar regions of stomata not thickened	
	Anticlinal walls straight to curved	*Conicosa pugioniformis,* *Tetragonia* sp. *Zygophyllum morgsana*
	Anticlinal walls sinuous	*Asclepadiaceae*
17(16)	Non-glandular trichome shape	
	Attenuate	20
	Flagelliform	
	Anticlinal walls straight to curved (ad); straight to sinuous (ab)	*Senecio elegans*
	Anticlinal walls straight to undulate (ad) and undulate to sinuous (ab)	*Senecio maritimus,*
	Stellate; anticlinal walls straight to curved	*Hermannia scabra*
	Cruciate; anticlinal walls straight to curved	*Hermannia pinnata*
	Filiform with swollen base; anticlinal walls straight to curved	*Berkheya armata*
	Glandular trichomes	19
18(1)	Cuticle striations overlap a number of cells; non-glandular, peltate trichomes; anticlinal walls straight to curved	*Septulina glauca*
19(17)	Cuticle striations overlap a number of cells; anticlinal walls sinuous	*Oncosiphon suffruticosum,* *Anagalis arvensis*
	Cuticle striations confined to within a cell; anticlinal walls straight to curved	*Myoporum serratum*

Table 8.7 continued

20(17)	Non-glandular and glandular trichomes; cuticle striations overlap a number of cells; stomatal polar regions not thickened; anticlinal walls sinuous	*Erodium moschatum*
	Cuticle striations confined within a cell; stomatal polar regions thickened; anticlinal walls straight to curved	*Agathosma* sp.
21(2)	Cuticle wrinkled; non-glandular, acerate trichomes; anticlinal walls straight to curved	*Cynanchum africanum*
	Cuticle lightly wrinkled or striate; glandular trichomes; anticlinal walls straight to undulate	*Chenopodium album*

References to anticlinal or periclinal surfaces concern the unspecialised epidermal cells. Terminology derived from Stace (1965), Thurston (1974), Payne (1978) and Leaf Architecture Working group (1999).

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8.6 GLOSSARY

Abaxial The lower surface of the leaf

Adaxial The top surface of the leaf

Anticlinal wall Cell wall giving the cell its shape in surface view. This wall is perpendicular to the surface of the leaf.

- **Curved** The corners where cell walls meet are curved, giving the cell a rounded appearance.
- **Round** The anticlinal wall surrounding the unspecialised epidermal cell has a rounded shape.
- **Sinuous** More than one undulation per cell wall.
- **Straight** The epidermal cell outline appears straight.
- **Undulate** Typically only one undulation (one peak and trough) per cell wall. Undulations need not be of uniform size.

Costal cells Epidermal cells above the leaf veins in monocots

Cuticle The cuticle is composed of cutin and forms a continuous layer over all the leaf epidermal cells.

Hypostomatic Stomata found on either the abaxial or the adaxial side of the leaf but never on both sides.

Intercostal cells Epidermal cells located between the leaf veins of monocots, e.g., the Poaceae.

Periclinal wall Cell wall parallel to the leaf surface, normally lying at 90° to the anticlinal wall.

- **Smooth** The surface of the cell is featureless.
- **Striate** Parallel grooves located on the cuticle surface. Striations may overlay a single epidermal cell, or may stretch over a number of cells.

Polar regions The areas where the two guard cells end. Some plant species have thickened epidermi associated with these areas.

Stomata The structure responsible for leaf transpiration including both guard cells and the stomatal pore.

Stomatal complex Structure formed by two guard cells and adjacent epidermal cells.

- **Amphibrachyparacytic** Two subsidiary cells per guard cell, arranged parallel to the long axis of the guard cell. They do not enclose the guard cell.

GLOSSARY continued

Anisocytic A single ring of three cells enclosing the guard cells.

Anomocytic No subsidiary cells surround the guard cells.

Anomotetracytic Three to five subsidiary cells surround the guard cell.

Brachyparacytic Two subsidiary cells lie parallel to the long axis of the guard cells, but do not completely enclose the guard cells.

Cyclocytic A single ring of five or more modified cells enclosing the guard cells.

Paracytic Each guard cell has one or more subsidiary cells that lie parallel to it.

Stomatal ledge A layer of cuticle encircling a stoma, forming a single rim that encloses both guard cells.

Stomatal shape

Bar-shaped Rectangular in shape.

Dumb-bell shaped guard cells Characteristic of the Poaceae and Cyperaceae where the guard cells are thin walled along the edges and thickened towards their centres.

Elliptical "Shaped like an ellipse." (Hornsby 1987)

Oblong Stomata have an acute (narrow) elliptical shape.

Round Each guard cell forms a crescent shape around the stomatal pore giving the stomata a rounded appearance.

Subsidiary cells Modified epidermal cells adjacent to the guard cells.

Trichomes Hair-like groups of cells, projecting markedly out of the epidermis.

Trichome type:

Branched Trichome is subdivided to form a more complex structure.

Simple A trichome composed of a single cell, most commonly shaped like a hair.

Glandular Possess a secretory function.

Non-glandular Do not possess any ability to secrete substances.

Emergence Type of trichome derived from the epidermal and sub-epidermal cell layers, e.g., stinging emergences.

Macro hair Larger than prickles, and normally have modified intercostal long cells associated with their bases.

Papillose Finger-like epidermal projections emanating from the periclinal wall of normal epidermal cells.

Prickles Modified costal cells, which may have a variety of shapes, e.g., sharp spines or barbs. Typically, found in the Poaceae and Cyperaceae.

GLOSSARY continued

Trichome shape:

Acerate Trichome is shaped like a needle.

Anvil Trichome possesses the form of an anvil. Roughly forming the shape of a T with a short base.

Attenuate A long trichome slowly tapering to a point.

Bosselated Covered by small protuberances or knobs.

Cruciate Taking the shape of a cross.

Filiform Trichomes possess a thread-like appearance.

Flagelliform Trichomes possess a whip-like shape.

Flame Spindle-shaped with wavy anticlinal walls.

Hirsute Trichomes are long and stiff.

Ornithorhynchous Trichome has the shape of a bird's beak.

Peltate Trichomes with flattened heads derived from either a single or a number of cells. The trichome may either lack a stalk, being directly attached to the epidermis, or may be attached to the epidermis by means of a stalk.

Rod Blunt-tipped trichomes in the shape of a rod.

Serpentine The trichome is sinuate in appearance.

Stellate The trichome is subdivided into the shape of a star.

Xeromorphic Plants adapted to living in arid conditions and displaying characters such as a thick cuticle, spines, and succulence.

Terminology based on definitions from Stace (1965), Thurston (1974), Payne (1978), Ellis (1979), Hornsy (1987), Mauseth (1988), Linder *et al.* (1990), Yukawa *et al*. (1992), Christophel *et al.* (1996), Leaf Architecture Working group (1999).

8.7 PLATES OF EPIDERMAL CHARACTERS

8.7.1 Monocotyledoneae

Family: Araceae

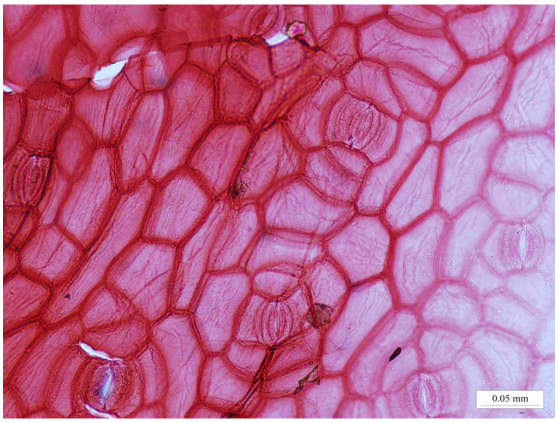


Plate 1: *Zantedeschia aethiopica* abaxial surface (200x): Epidermal cells have a random distribution over the leaf's surface.

Family: Asphodelaceae

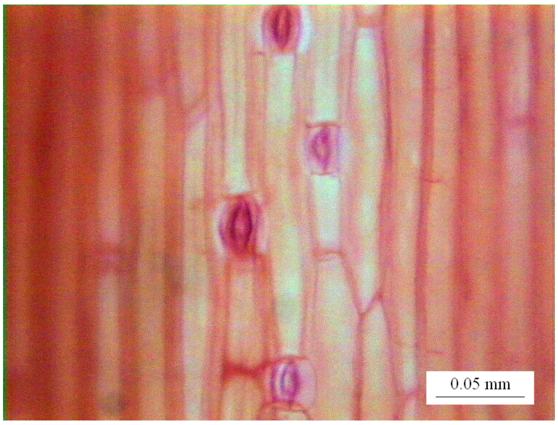


Plate 2: *Trachyandra divaricata* (400x): Epidermal cells arranged in costal / intercostal zones, as in the Poaceae. Stomata occur in the intercostal zones and are arranged into three rows

Family: Cyperaceae

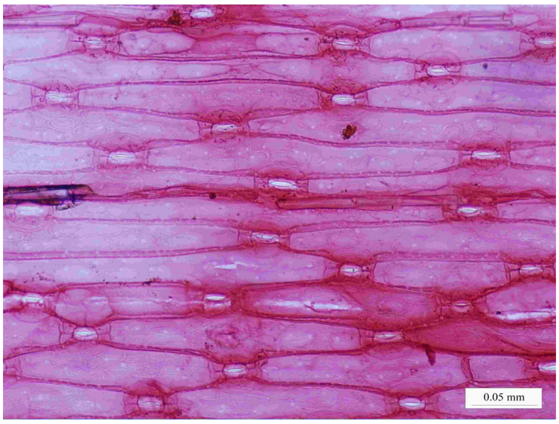


Plate 3: *Cyperus* sp. adaxial surface (200x): The epidermi are not divided into costal and intercostal zones.

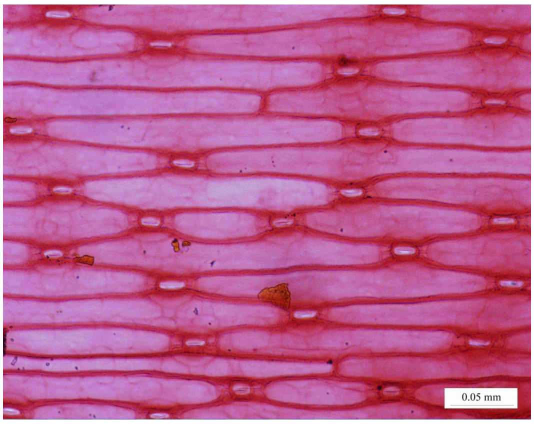


Plate 4: *Cyperus* sp. abaxial surface (200x): Elliptical-shaped stomata are visible.

Family: Cyperaceae - continued

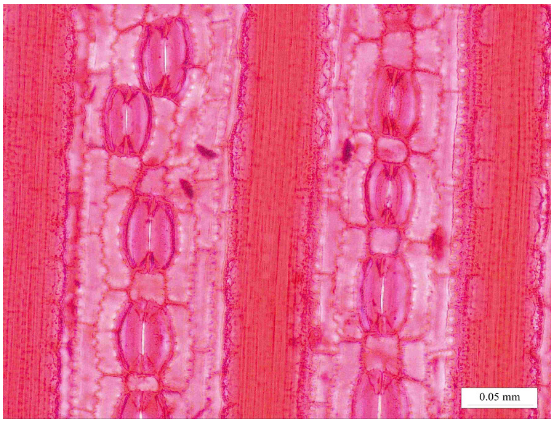
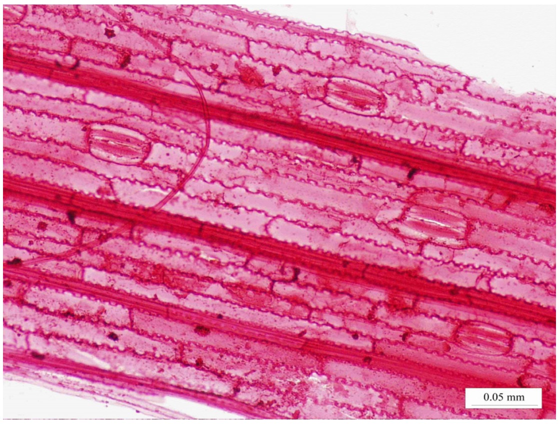
	

Plate 5: *Ficinia nigrescens* stem (400x): The epidermal cells are clearly divided into costal and intercostal zones.	Plate 6: *Isolepis antarctica* stem (200x): Paracytic stomatal complexes are visible in the intercostal zones.

Family: Hyacinthaceae

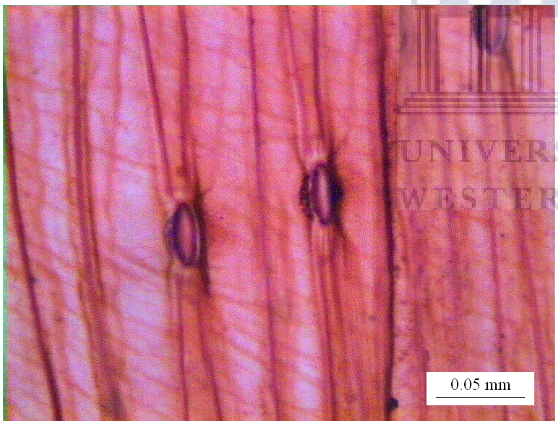
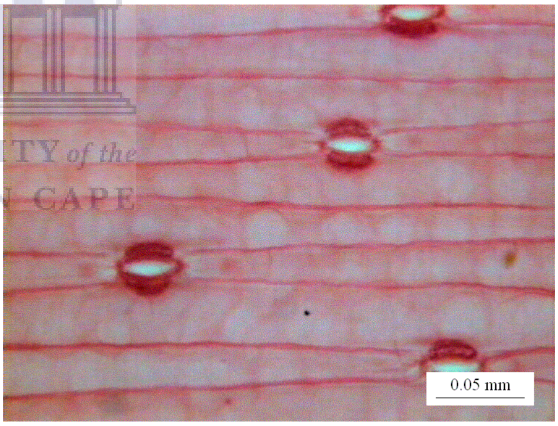
	

Plate 7: *Albuca flaccida* adaxial surface (400x): Epidermis is slightly overstained, which makes it difficult to identify stomatal complexes. Unspecialised epidermal cells with straight walls are partially visible.	Plate 8: *Albuca flaccida* abaxial surface (400x): Paracytic stomatal complexes are visible with elliptically shaped stomata.

Family: Hypoxidaceae

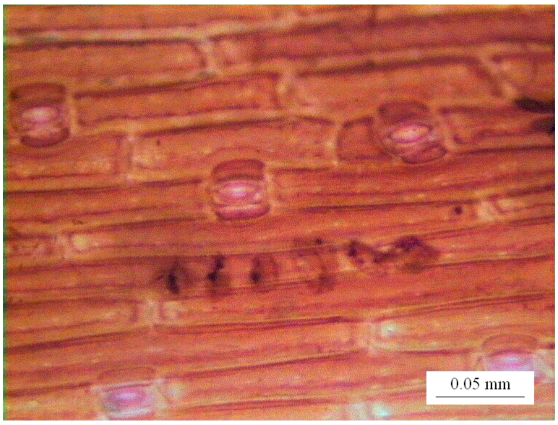


Plate 9: *Spiloxene capensis* stem (400x): Paracytic stomatal complexes present on stem epidermis.

Family: Poaceae

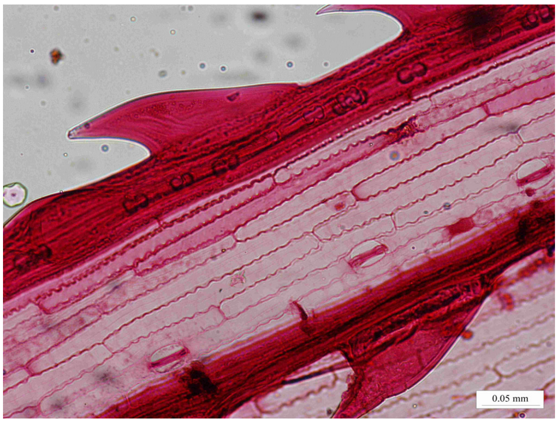


Plate 10: *Avena barbata* abaxial surface (400x): Prickles only observed in the costal zones and on margins of leaves.

Family: Poaceae

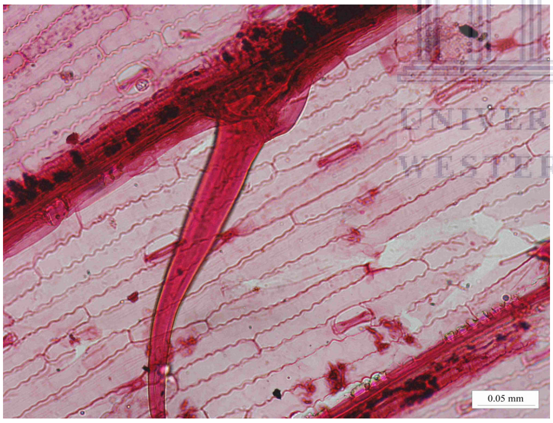


Plate 11: *Avena barbata* abaxial surface (400x): Macro hairs only observed on the costal zones and not on the leaf margins.

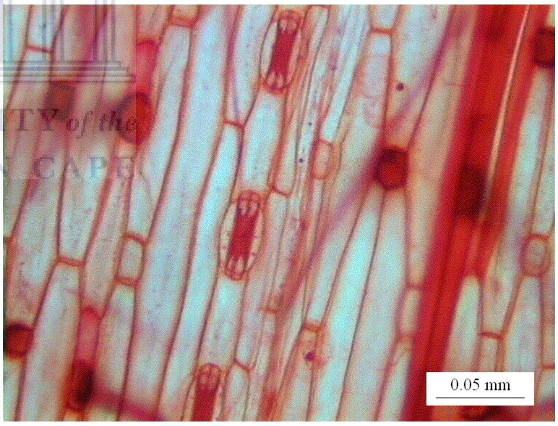


Plate 12: *Chaetobromus dregeanus* adaxial surface (400x): Trichome base cells are visible in the intercostal zones.

Family: Poaceae - continued

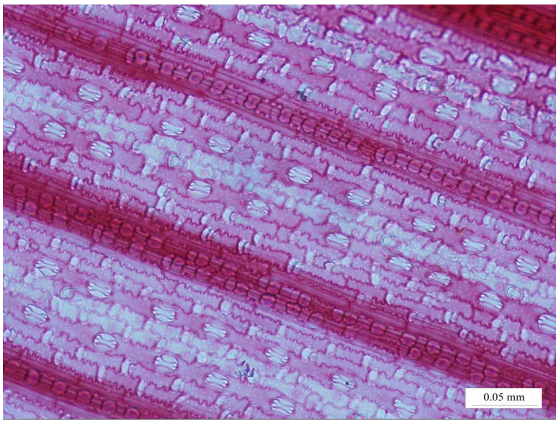
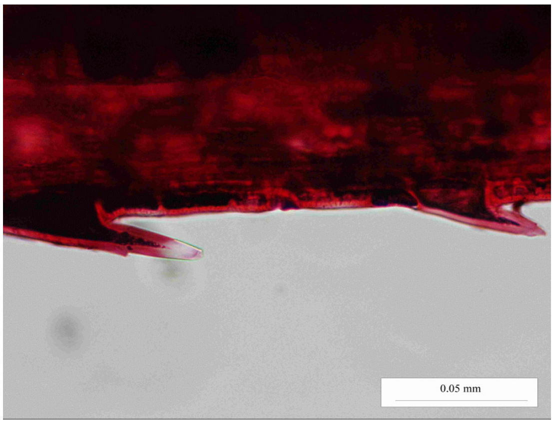
	

Plate 13: *Cynodon dactylon* (200x): The leaf epidermis is divided into costal and intercostals zones with two stomatal rows in the intercostals zones.	Plate 14: *Cynodon dactylon* abaxial surface (400x): Side view of two angular prickles on the leaf margin.

Family: Poaceae

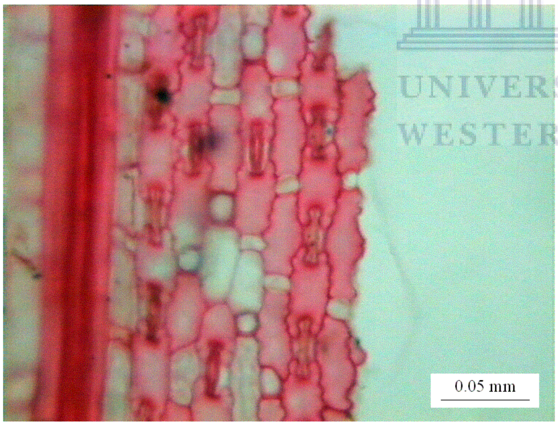
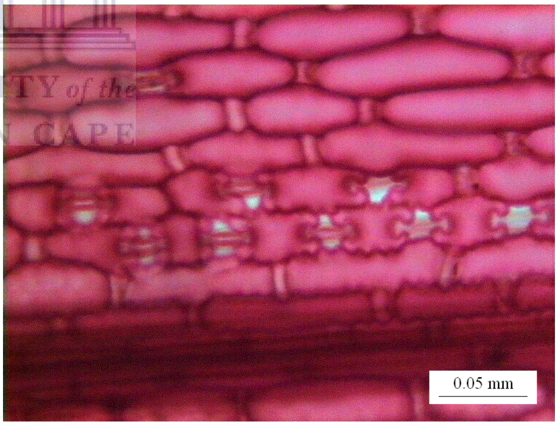
	

Plate 15: *Ehrharta villosa* adaxial surface (400x): Dumb-bell shaped guard cells visible in the intercostal zones.	Plate 16: *Ehrharta villosa* abaxial surface (400x): Epidermal cells in the intercostal zones have curved to sinuous anticlinal walls.

Family: Restionaceae

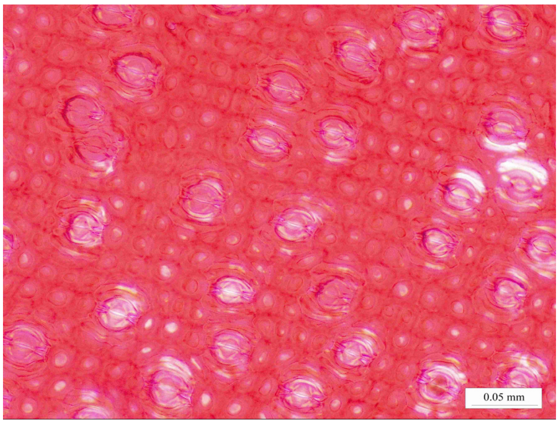


Plate 17: *Thamnochortus spicigerus* stem (200x): Thick, dark-staining epidermal cells visible on the epidermal surface. Light-staining areas are paracytic stomatal complexes among the unspecialised epidermal cells.

8.7.2 Dicotyledoneae

Family: Aizoaceae

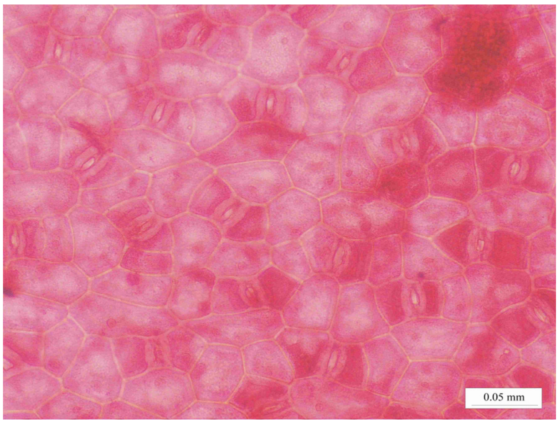
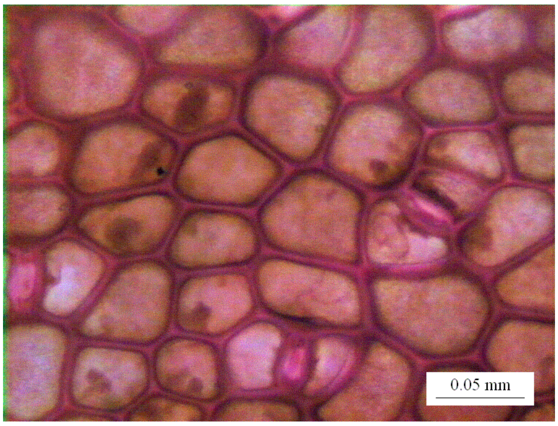
	

Plate 18: *Carpobrotus edulis* leaf (200x): Incorrectly stained epidermi highlighting the problems encountered with using the safranin stain. Brachyparacytic stomatal complexes are visible on the epidermal preparation.	Plate 19: *Carpobrotus quadrifidus* leaf (400x): Periclinal surface smooth, with no striations.

Family: Aizoaceae

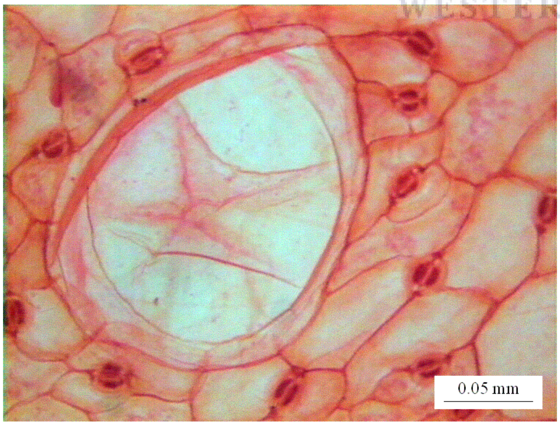
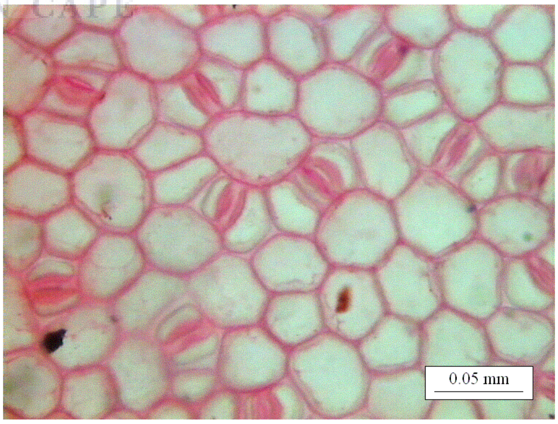
	

Plate 20: *Mesembryanthemum crystallinum* leaf (400x): Surface view of a trichome modified to form a bladder cell.	Plate 21: *Ruschia macowanii* leaf (400x): Surface view of brachyparacytic stomatal complexes.

Family: Aizoaceae - continued

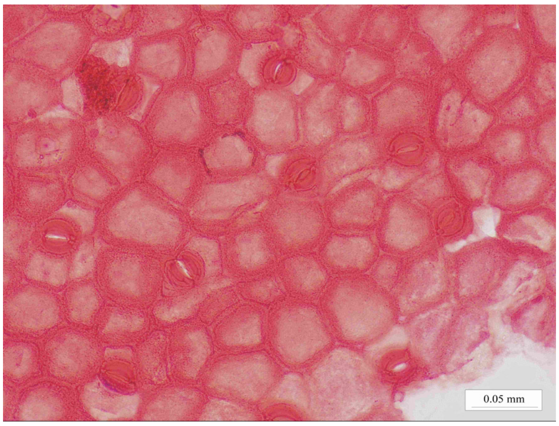


Plate 22: *Ruschia* sp. leaf (200x): Unspecialised epidermal cells with straight to curved anticlinal walls.

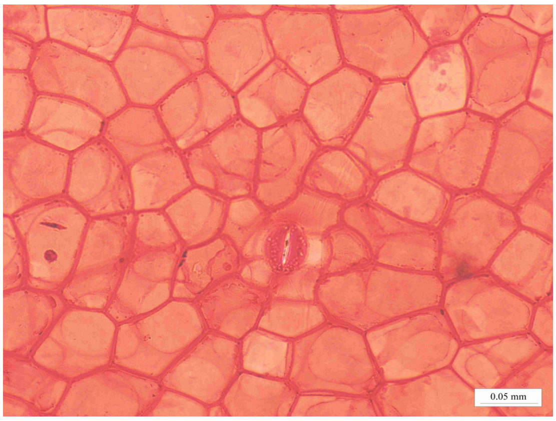


Plate 23: *Tetragonia* sp. abaxial surface (200x): Anomocytic stomatal complexes visible on epidermal surface.

Family: Aizoaceae

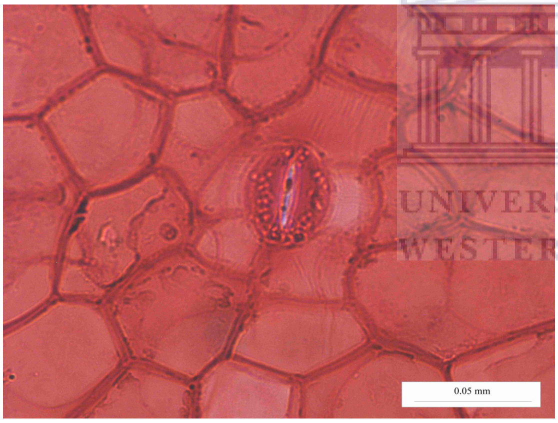


Plate 24: *Tetragonia* sp. abaxial surface (400x): Unspecialised epidermal cells have straight to curved anticlinal walls. Light striations confined to epidermal cells adjacent to stomata.

Family: Anacardiaceae

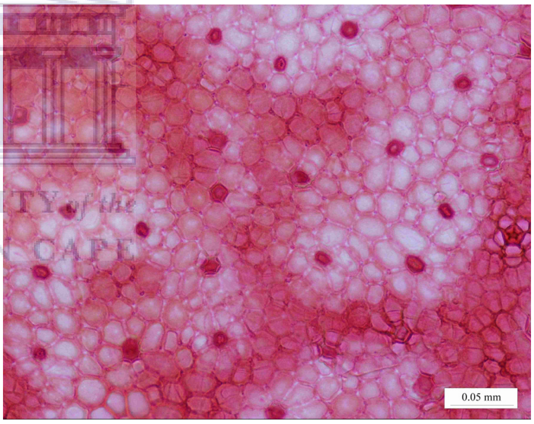


Plate 25: *Rhus glauca* adaxial surface (200x): Dark-staining oval areas are short trichomes on the epidermal surface.

Family: Anacardiaceae - continued

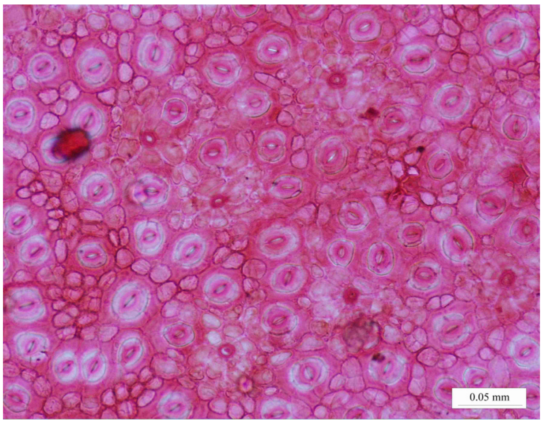
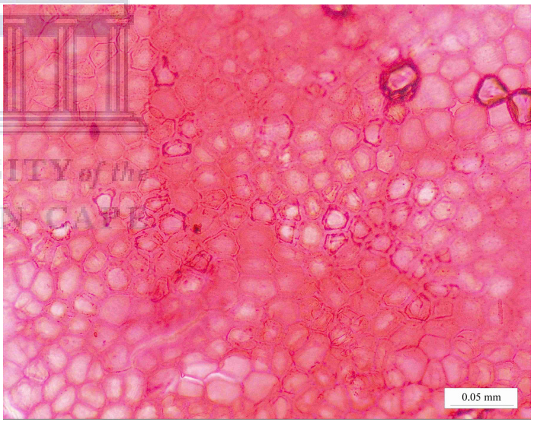


Plate 26: *Rhus glauca* abaxial surface (200x): Numerous paracytic stomatal complexes visible on the epidermal preparation.	Plate 27: *Rhus laevigata* adaxial surface (200x): Stomata absent on adaxial epidermal surface.

Family: Anacardiaceae

	
Plate 28: *Rhus laevigata* abaxial surface (200x): Paracytic stomatal complexes clearly visible.	Plate 29: *Rhus lucida* adaxial surface (200x): Numerous, tightly packed unspecialised epidermal cells visible on the epidermal surface.

Family: Anacardiaceae - continued

Plate 30: *Rhus lucida* abaxial surface (200x): Subsidiary cells stained lighter than the surrounding unspecialised epidermal cells, which made it easier to identify the stomatal complexes.

Family: Apocynaceae

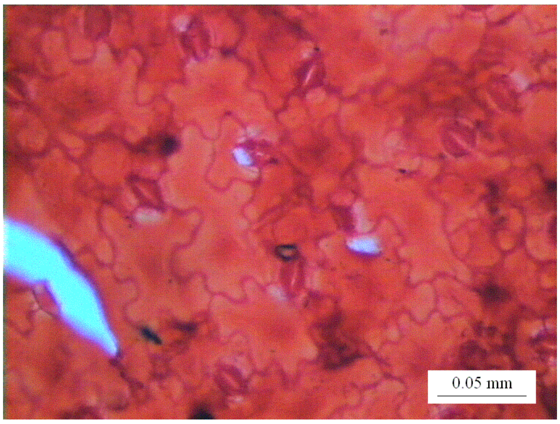


Plate 31: Unknown Apocynaceae adaxial surface (400x): Numerous irregularly shaped, unspecialised epidermal cells with sinuous walls visible on the epidermal surface.

Family: Apocynaceae

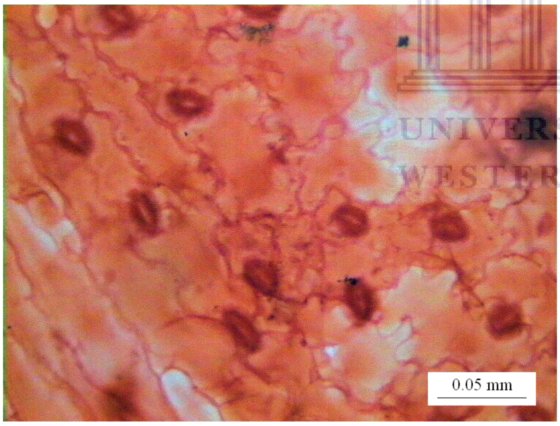


Plate 32: Unknown Apocynaceae abaxial surface (400x): Anomocytic stomatal complexes interspersed among unspecialised epidermal cells.

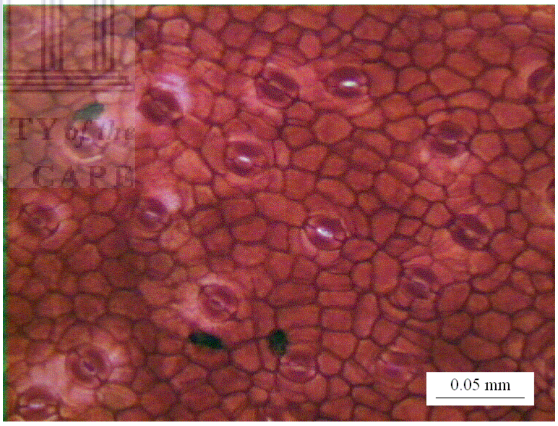


Plate 33: *Cynanchum africanum* adaxial surface (400x): Dark-staining unspecialised epidermal cells with straight to curved anticlinal walls.

Family: Asteraceae

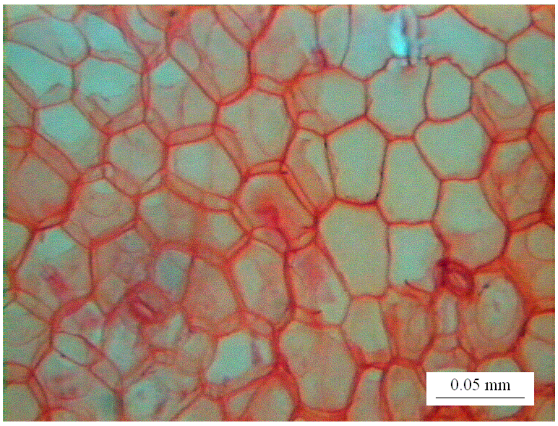


Plate 34: *Berkheya armata* adaxial surface (400x): Numerous unspecialised epidermal cells with straight to curved anticlinal walls on the epidermal surface.

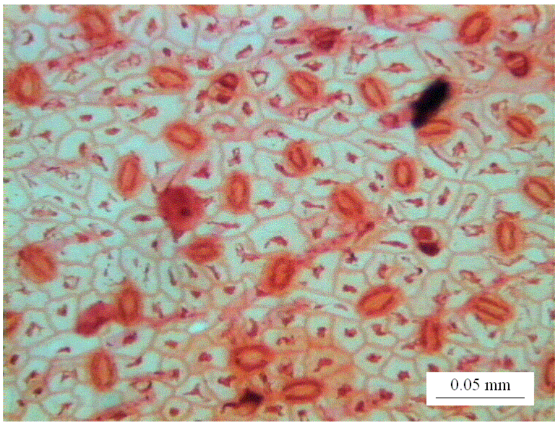


Plate 35: *Berkheya armata* abaxial (400x): Epidermal preparation displaying elliptical shaped stomata.

Family: Asteraceae

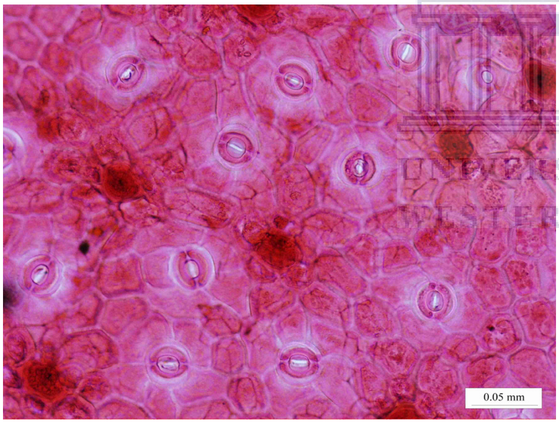


Plate 36: *Chrysanthemoides monilifera* adaxial surface (200x): Dark-stained areas show the locations of sunken glandular trichomes

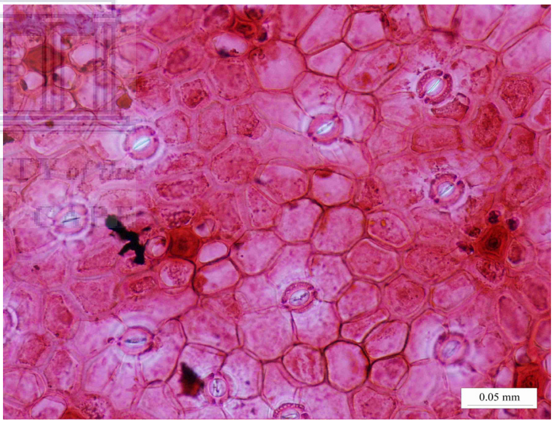


Plate 37: *Chrysanthemoides monilifera* abaxial surface (200x): Anomocytic stomatal complexes visible on the epidermal preparation.

Family: Asteraceae - continued

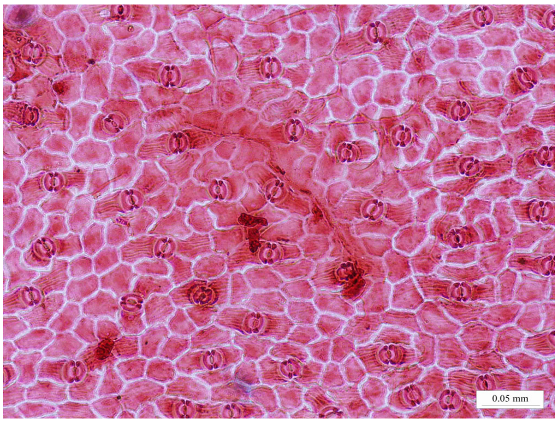
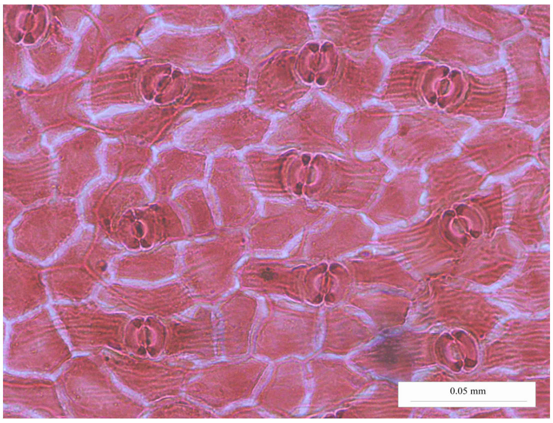
	

Plate 38: *Felicia hyssopifolia* adaxial surface (200x): Unspecialised epidermal cells with straight to curved anticlinal walls.	Plate 39: *Felicia hyssopifolia* adaxial surface (400x): Cuticle striations mostly confined to unspecialised epidermal cells adjacent to stomata.

Family: Asteraceae

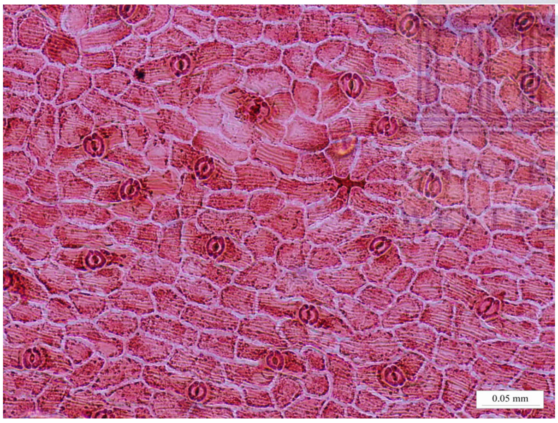
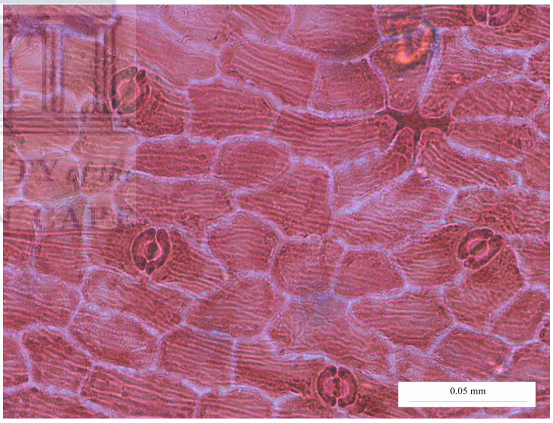
	

Plate 40: *Felicia hyssopifolia* abaxial surface (200x): Anomocytic stomatal complexes visible on the epidermal surface.	Plate 41: *Felicia hyssopifolia* abaxial surface (400x): Cuticle striations overlap a number of unspecialised epidermal cells.

Family: Asteraceae (Continued)

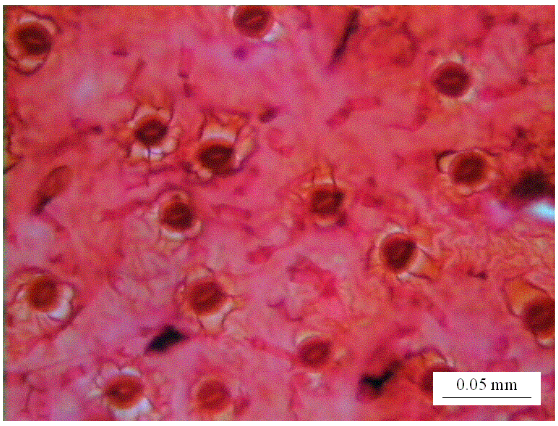


Plate 42: *Helichrysum niveum* leaf surface (400x): Epidermal characteristics partially obscured by numerous non-glandular, whip-like trichomes, which increase the difficulty to identify stomatal complexes and unspecialised epidermal cells.

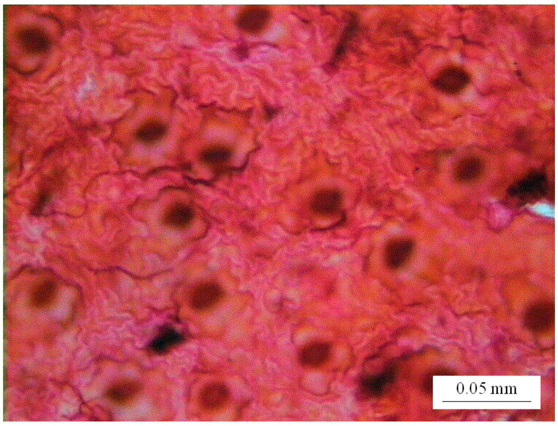


Plate 43: *Helichrysum niveum* leaf surface (400x): Anticlinal walls of unspecialised epidermal cells show uneven undulations along the anticlinal cell walls, after removal of trichomes.

Family: Asteraceae

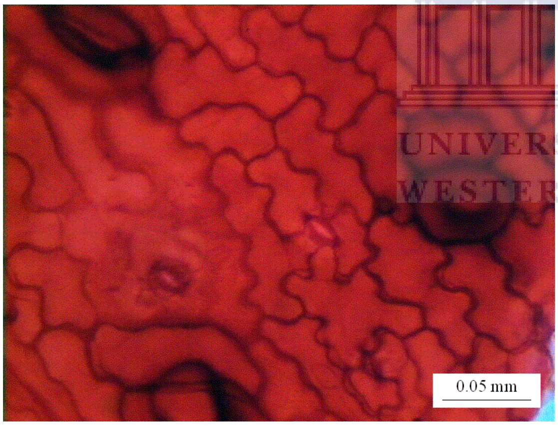


Plate 44: *Oncosiphon suffruticosum* leaf surface (400x): Unspecialised epidermal cells have sinuous anticlinal cell walls.

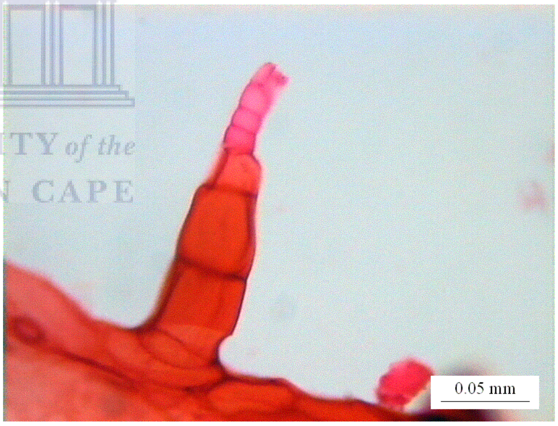


Plate 45: *Oncosiphon suffruticosum* leaf surface (400x): Large multicellular trichome with the tip broken off.

Family: Asteraceae - continued

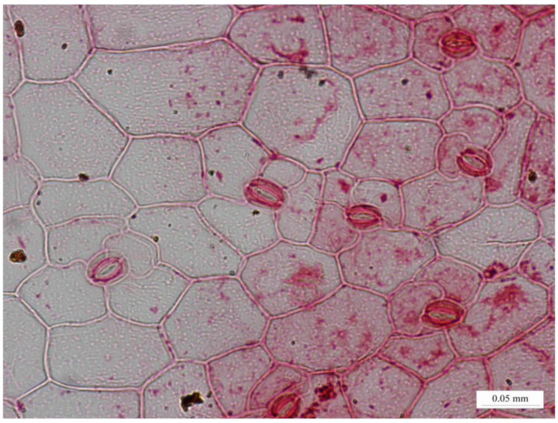


Plate 46: *Senecio burchelli* adaxial surface (200x): Unspecialised epidermal cells have straight to curved anticlinal walls, with smooth periclinal surfaces.	Plate 47: *Senecio burchelli* adaxial surface (400x): Elliptical shaped stomata surrounded by unspecialised epidermal cells (anomocytic).

Family: Asteraceae

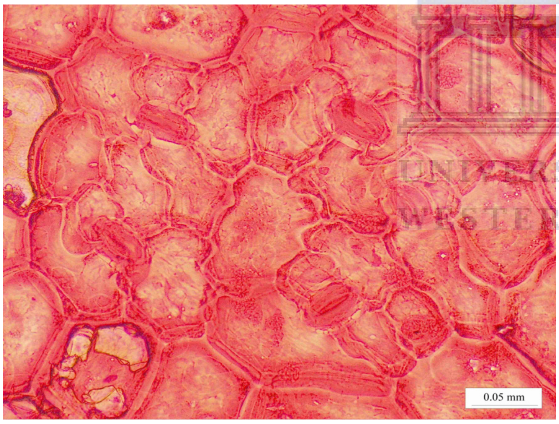
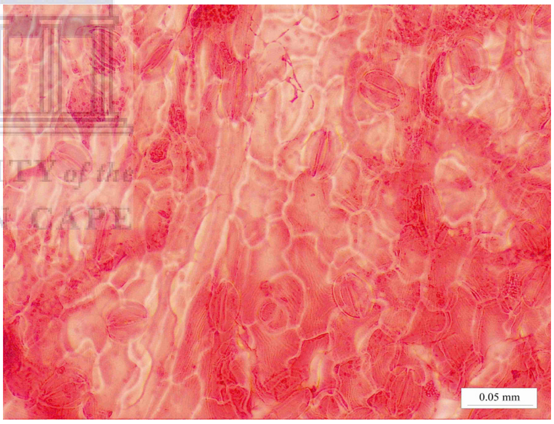
	

Plate 48: *Senecio elegans* adaxial surface (200x): unspecialised epidermal cells with straight to curved anticlinal walls.	Plate 49: *Senecio elegans* abaxial surface (200x): Unspecialised epidermal cells with straight to sinuous anticlinal walls.

Family: Asteraceae - continued

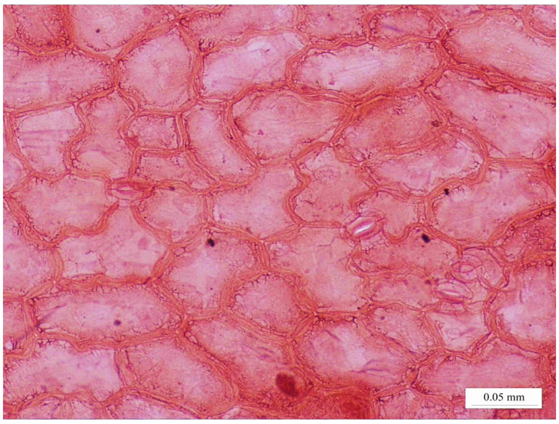
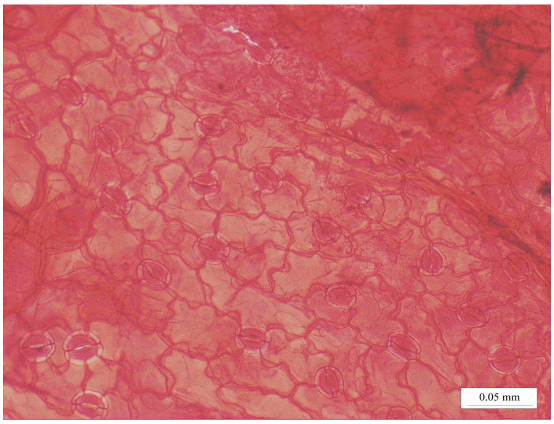
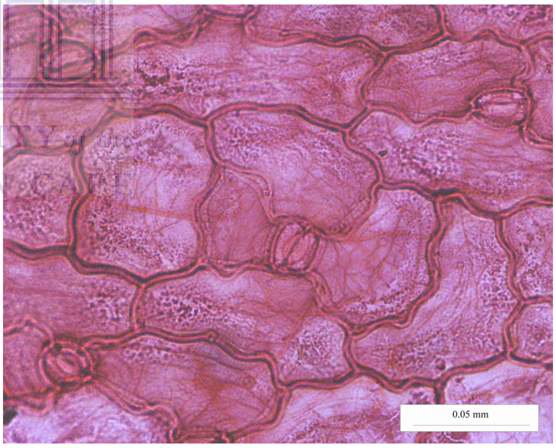
	

Plate 50: *Senecio maritimus* adaxial surface (200x): Unspecialised epidermal cells around anomocytic stomatal complexes have straight to slightly undulate anticlinal walls	Plate 51: *Senecio maritimus* abaxial surface (200x): Unspecialised epidermal cells with undulate to sinuous anticlinal walls.

Family: Asteraceae

	
Plate 52: *Sonchus oleraceus* abaxial surface (200x): Unspecialised epidermal cells with curved to sinuous anticlinal walls.	Plate 53: *Sonchus oleraceus* abaxial surface (400x): Elliptical shaped stomata surrounded by unspecialised epidermal cells (anomocytic).

Family: Asteraceae - continued

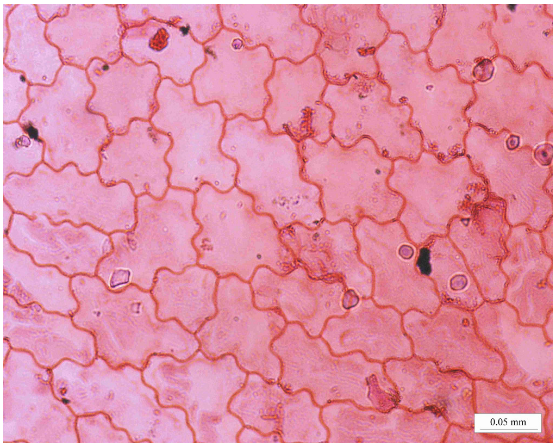
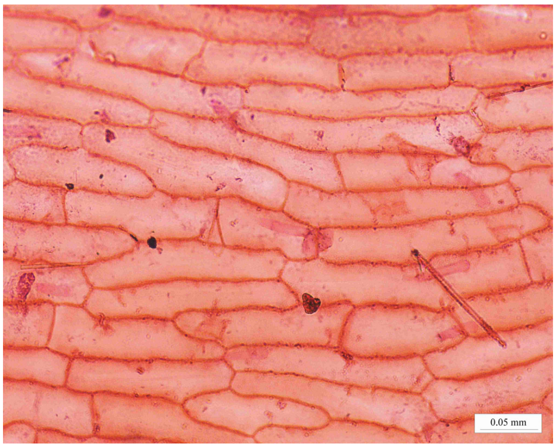
	

Plate 54: *Sonchus oleraceus* adaxial surface (200x): Unspecialised epidermal cells with sinuous anticlinal walls.	Plate 55: *Trichogyne verticillata* abaxial surface (400x): Unspecialised epidermal cells with curved to undulate anticlinal walls and smooth periclinal surfaces.

Family: Chenopodiaceae

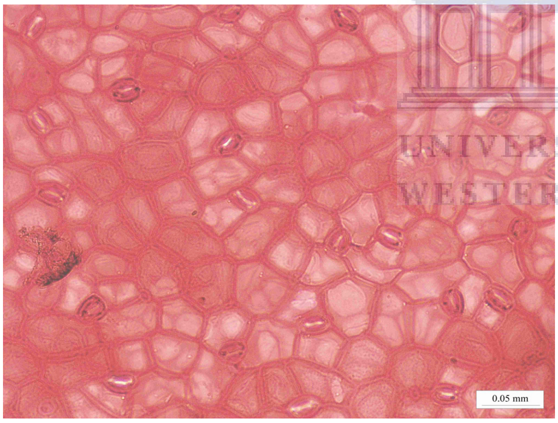
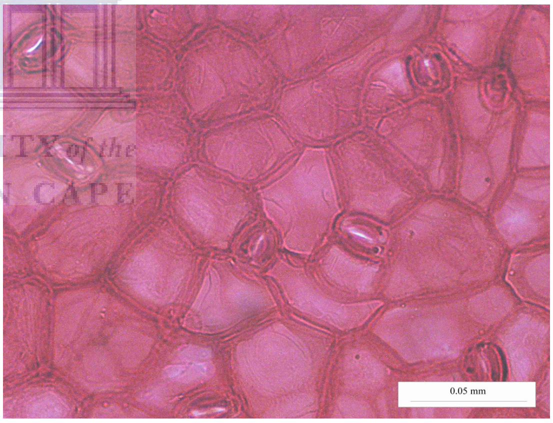
	

Plate 56: *Atriplex semibaccata* adaxial surface (200x): Numerous anomocytic stomatal complexes visible. Epidermi slightly over-stained but stomatal complex type and characteristics of unspecialised cells still visible.	Plate 57: *Atriplex semibaccata* adaxial surface (400x): Increased magnification of epidermal areas with anomocytic stomatal complexes. Unspecialised epidermal cells adjacent to guard cells have smooth periclinal walls with straight to curved anticlinal walls.

Family: Chenopodiaceae - continued

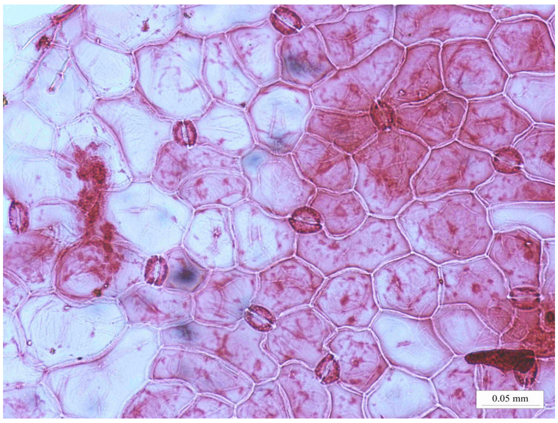


Plate 58: *Chenopodium album* adaxial surface (200x): Unspecialised epidermal cells with straight to slightly undulate anticlinal walls.	Plate 59: *Chenopodium album* adaxial surface (400x): Increased magnification of anomocytic stomatal complexes highlights the absence of subsidiary cells. Guard cells stained stronger than the surrounding unspecialised epidermal cells.

Family: Chenopodiaceae	Family: Ebanaceae

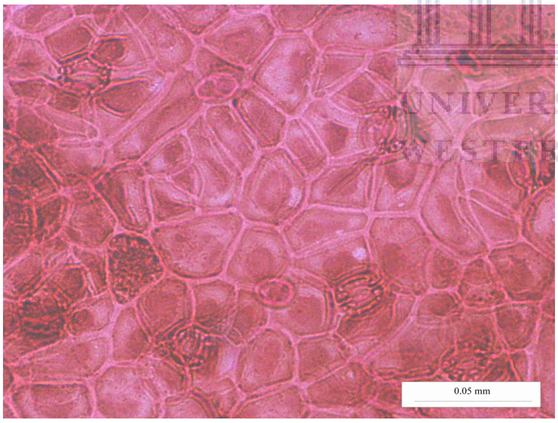
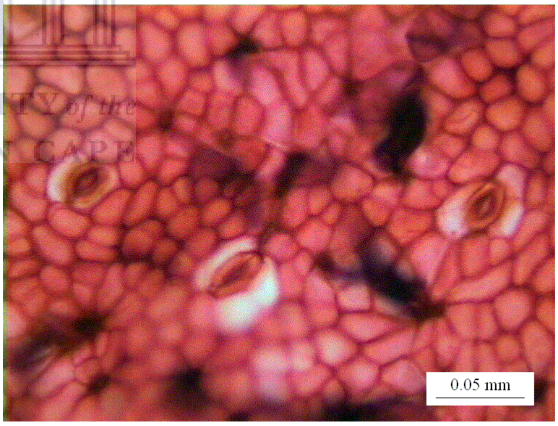

	

Plate 60: *Manochlamys albicans* abaxial surface (400x): Anomocytic stomatal complexes on the epidermis. Unspecialised epidermal cells have smooth periclinal surfaces.	Plate 61: *Diospyros austro-africana* adaxial surface (400x): Light-staining subsidiary cells reveal paracytic stomatal complexes on the epidermal preparation. Subsidiary cells are irregularly shaped in contrast with the subsidiary cells of species belonging to the family Poaceae.

Family: Ebanaceae - continued

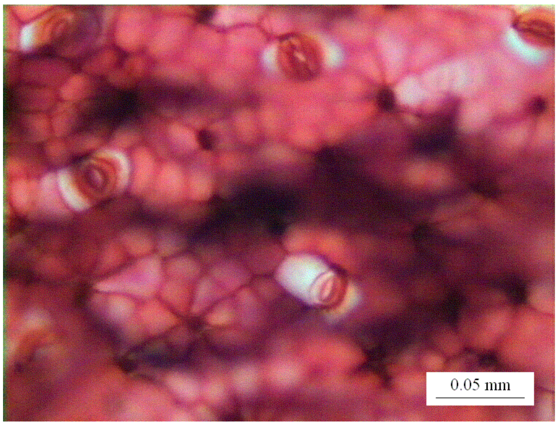


Plate 62: *Diospyros austro-africana* abaxial surface (400x): Numerous trichomes on the epidermis obscure the view but paracytic stomatal complexes and unspecialised epidermal cells still visible.

Family: Euphorbiaceae

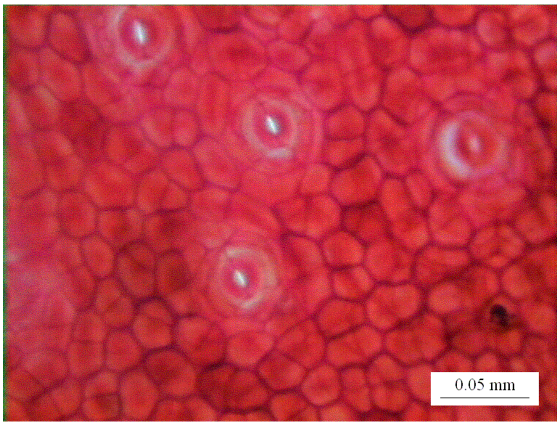


Plate 63: *Euphorbia burmannii* leaf surface (400x): Epidermis has rare characters, such as anisocytic to anomotetracytic stomatal complexes, which help to differentiate between different plant species.

Family: Euphorbiaceae

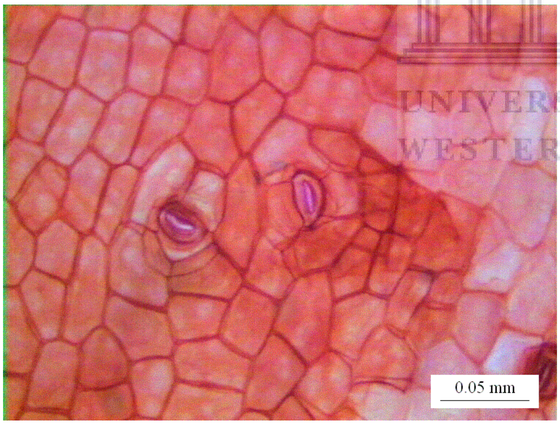


Plate 64: Euphorbia *mauritanica* leaf surface (400x): Guard cells surrounded by unspecialised epidermal cells (anomocytic complex) with smooth periclinal walls.

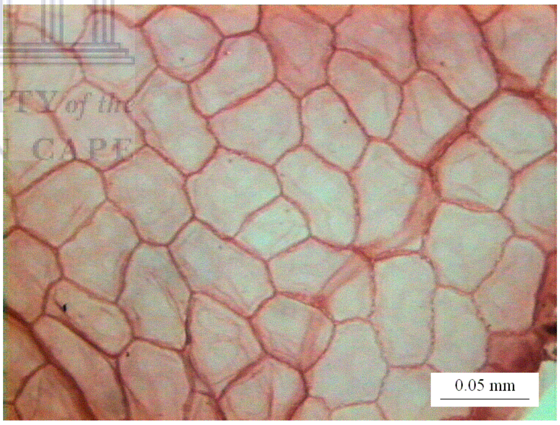


Plate 65: *Euphorbia peplus* adaxial surface (400x): Epidermis has no stomata. Unspecialised epidermal cells have straight to curved anticlinal walls.

Family: Euphorbiaceae - continued

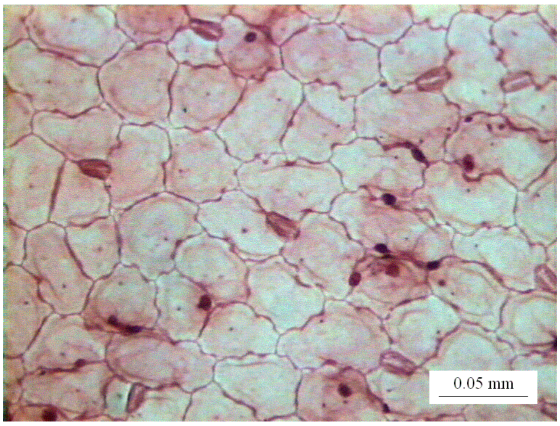


Plate 66: *Euphorbia peplus* adaxial surface (400x): Unspecialised epidermal cells have sinuous anticlinal walls with thickening areas along the anticlinal wall, characteristic for this species.

Family: Fabaceae

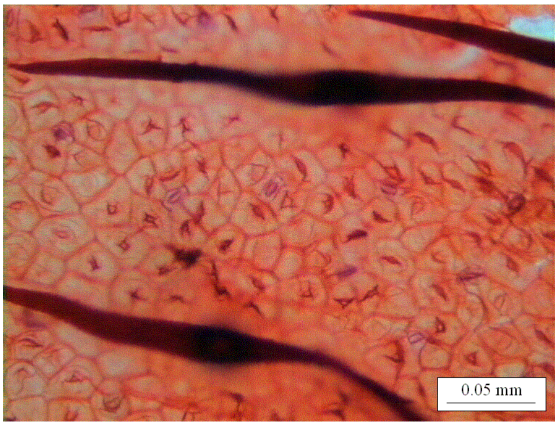


Plate 67: *Psoralea repens* adaxial surface (400x): Epidermis has both papillae and anvil-shaped trichomes. Small papillae are visible on the periclinal surfaces of most unspecialised epidermal cells. The presence of both trichome types help to separate *P. repens* from other species.

Family: Fabaceae

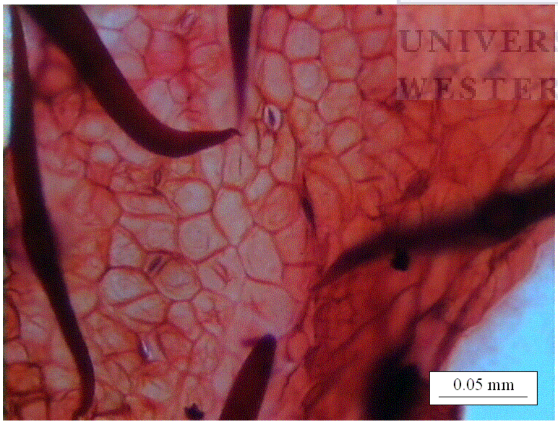


Plate 68: *Psoralea repens* adaxial surface (400x): Increased magnification shows the straight to curved anticlinal walls of the unspecialised epidermal cells, common to many different plant species and genera.

Family Fumariaceae

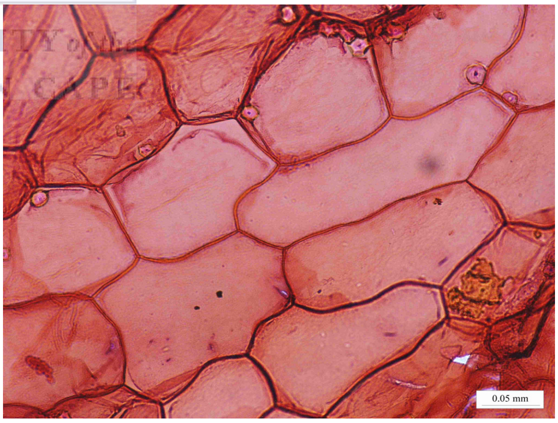


Plate 69: *Cysticapnos vesicaria* leaf surface (200x): Epidermal surface has no stomata. The large, unspecialised epidermal cells, with curved to undulate anticlinal walls, help distinguish *C. vesicaria* from other species.

Family: Gentianaceae

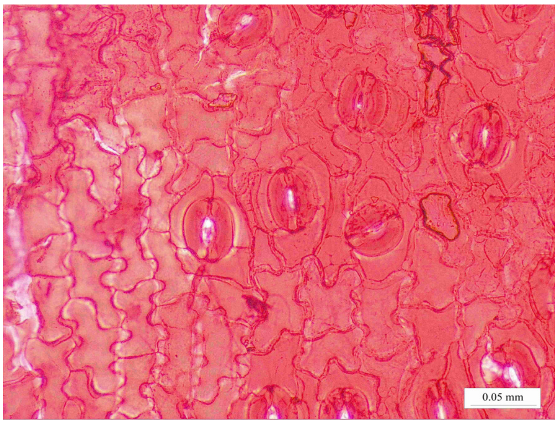


Plate 70: *Chironia baccifera* leaf surface (200x): Relatively large guard cells surrounded by numerous unspecialised, sinuous-walled epidermal cells.

Family: Geraniaceae

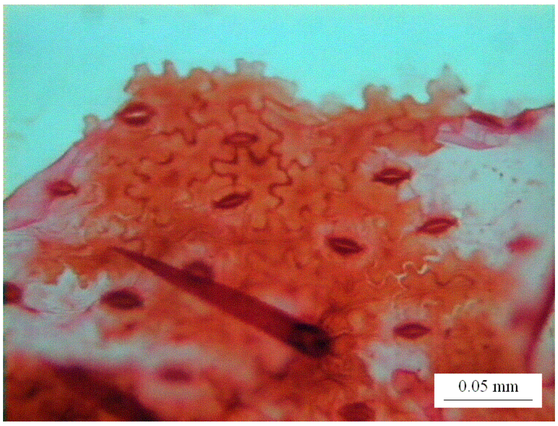


Plate 71: *Erodium moschatum* leaf surface (400x): Over-scraping of the epidermis to remove parenchymatous tissue resulted in areas devoid of stain. However, it is still possible to identify anomocytic stomatal complexes and a non-glandular trichome on the epidermal surface.

Family: Geraniaceae

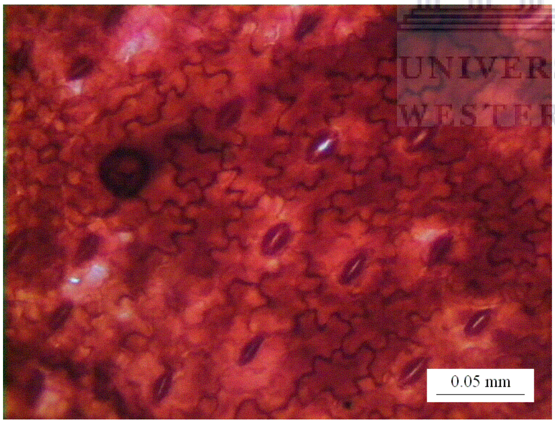


Plate 72: *Erodium moschatum* leaf surface (400x): Numerous unspecialised epidermal cells with sinuous anticlinal walls visible.

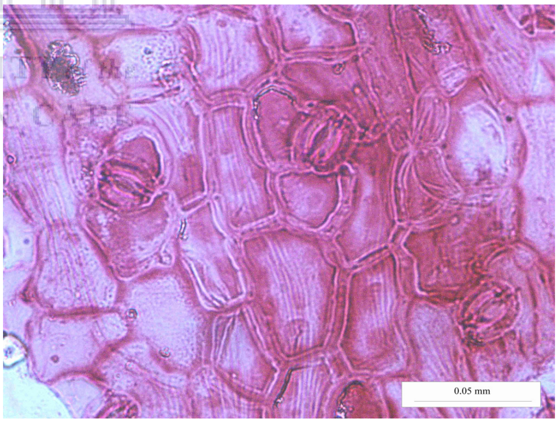


Plate 73: *Geranium incanum* abaxial surface (400x): Light cuticle striations present over the periclinal walls of unspecialised epidermal cells.

Family: Loranthaceae

	
Plate 74: *Septulina glauca* leaf surface (400x): Trichomes were removed to show the paracytic to brachyparacytic stomatal complexes.	Plate 75: *Septulina glauca* leaf surface (400x): Peltate trichomes obscure the epidermis beneath. Peltate trichomes are characteristic to this species.

Family: Myoporaceae

Family: Oxalidaceae

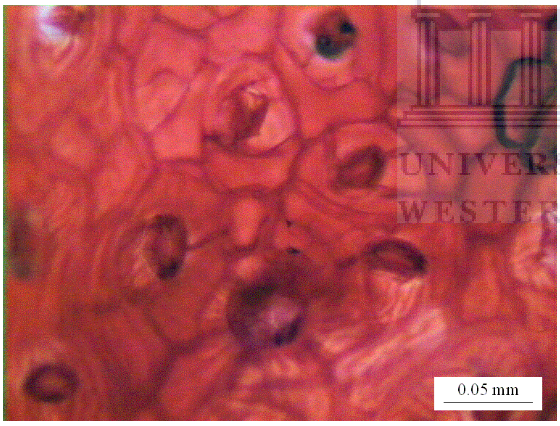
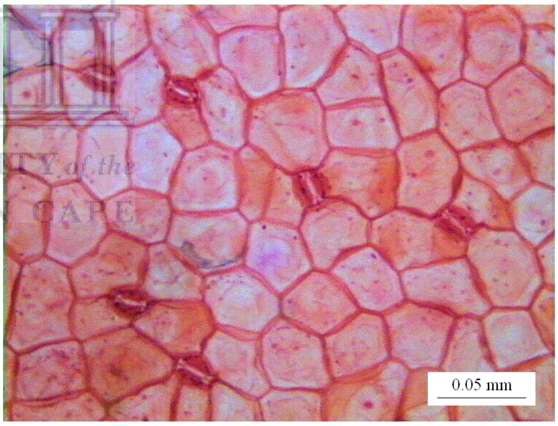
	

Plate 76: *Myoporum serratum* leaf surface (400x): Cuticular striations are visible on the periclinal surface of unspecialised epidermal cells that surround anomocytic stomatal complexes.	Plate 77: *Oxalis obtuse* adaxial surface (400x): Anomocytic stomatal complexes surrounded by unspecialised epidermal cells with straight to curved anticlinal walls.

Family: Oxalidaceae (Continued)	Family: Plumbaginaceae

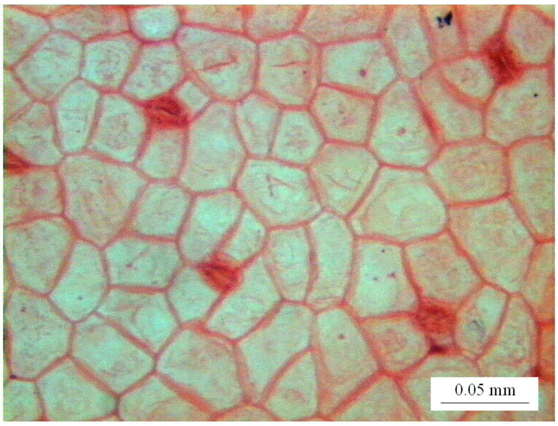
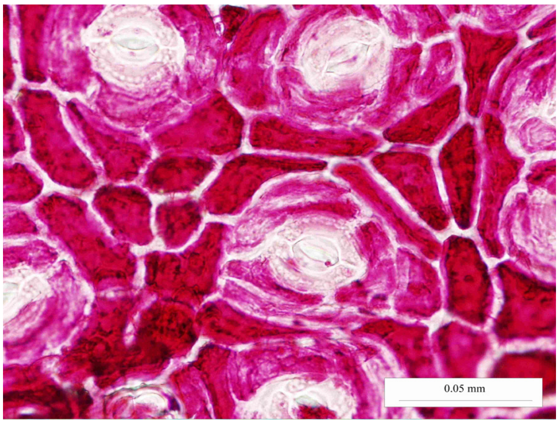

	

Plate 78: *Oxalis obtuse* abaxial surface (400x): Elliptically shaped stomata surrounded by four to five unspecialised epidermal cells.	Plate 79: *Afrolimon purpuratum* adaxial surface (400x): Cyclocytic stomatal complexes are visible.

Family: Plumbaginaceae	Family: Polygalaceae

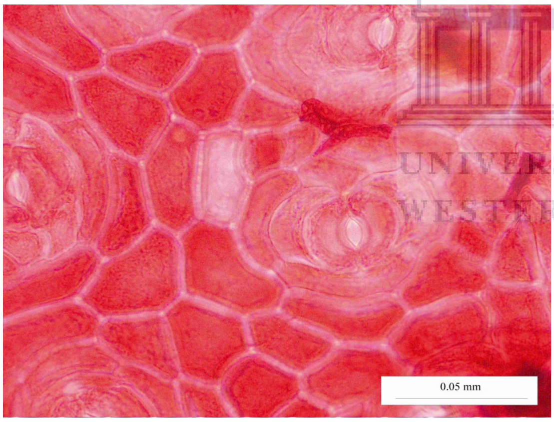



Plate 80: *Afrolimon purpuratum* abaxial surface (400x): Cyclocytic stomatal complexes are visible. The unspecialised epidermal cells stained stronger than the subsidiary cells around the guard cells	Plate 81: *Nylandtia spinosa* leaf surface (400x): A resin filled stoma is visible on the epidermal surface

Family: Primulaceae

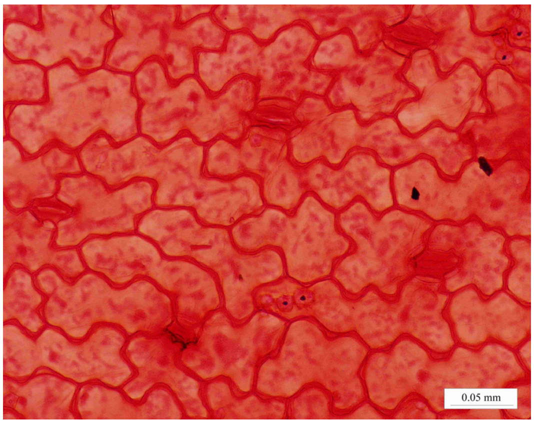


Plate 82: *Anagalis arvensis* adaxial surface (200x): Anomocytic stomatal complexes and irregularly shaped unspecialised epidermal cells with sinuous anticlinal walls.

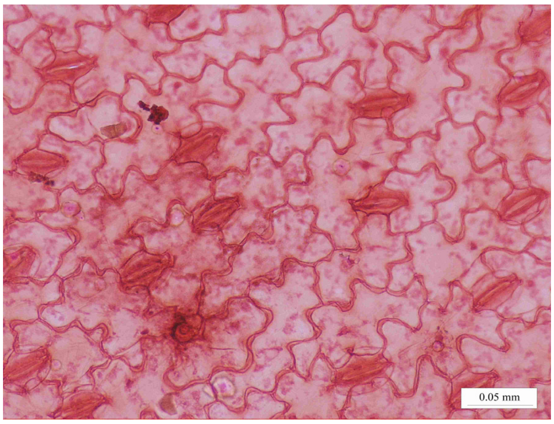


Plate 83: *Anagalis arvensis* abaxial surface (200x): Anomocytic stomatal complexes and irregularly shaped unspecialised epidermal cells with sinuous anticlinal walls.

Family: Rosaceae

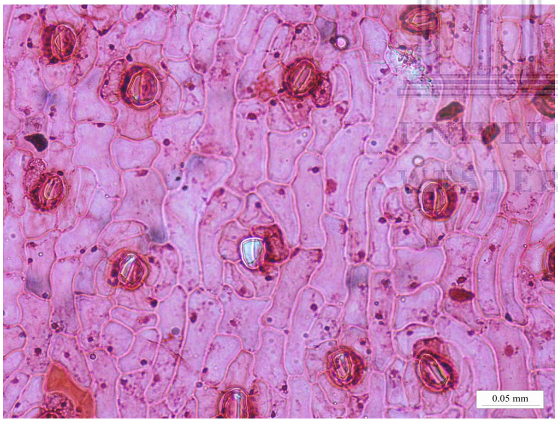


Plate 84: *Cliffortia filifolia* leaf surface (200x): Curved to undulate anticlinal walls clearly visible.

Family: Rutaceae

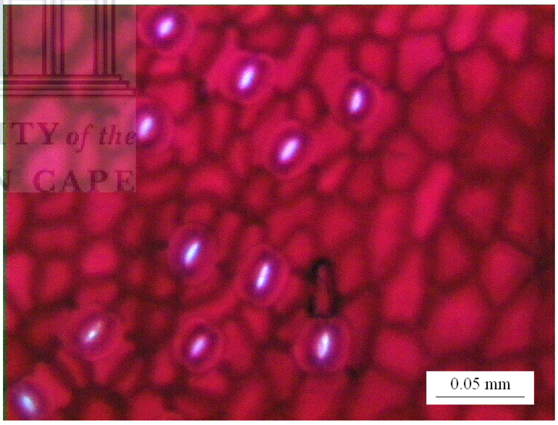


Plate 85: *Agathosma* sp. (400x): Thick-walled epidermal cells stained very strong.

Family: Santalaceae

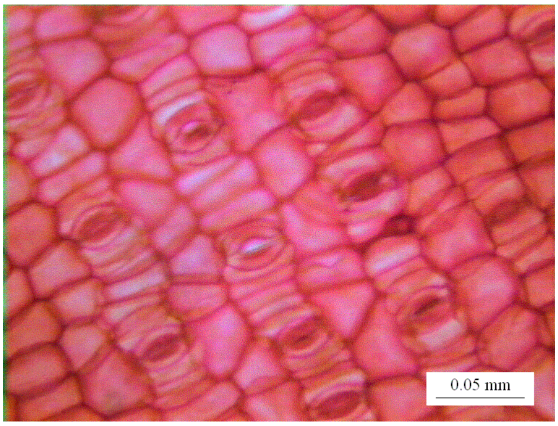


Plate 86: *Thesidium* sp. stem (400x): Amphibrachyparacytic stomatal complexes are distributed parallel to each other. Epidermal cells display a parallel distribution over the epidermal surface.

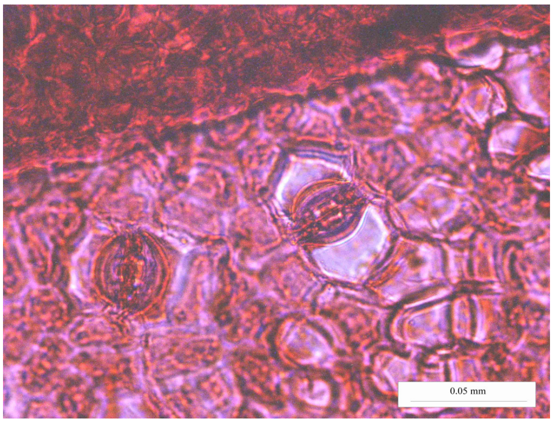


Plate 87: *Osyris compressa* adaxial surface (400x): Subsidiary cells do not completely enclose stomata (brachyparacytic stomatal complexes).

Family: Scrophulariaceae

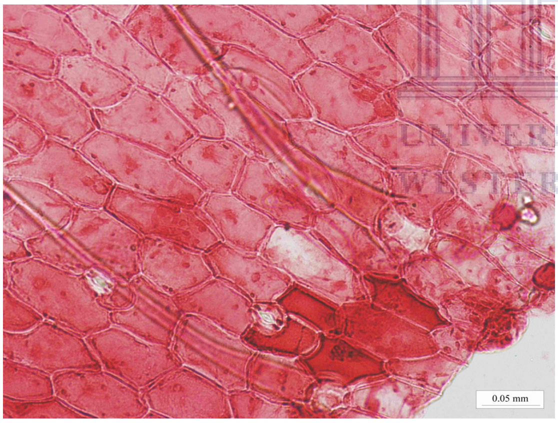


Plate 88: *Amsinckia calycina* adaxial surface (200x): Epidermis with stiff hirsute trichomes.

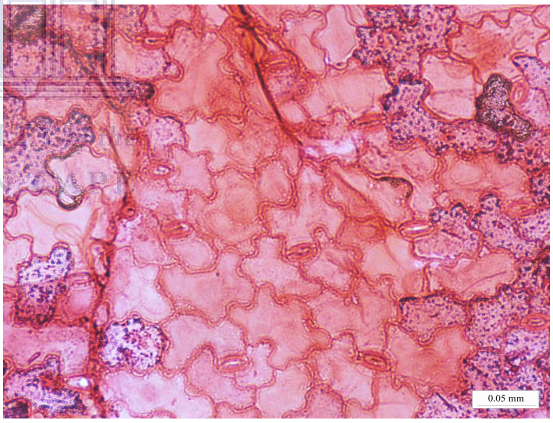


Plate 89: *Amsinckia calycina* abaxial surface (200x): Dark grey areas caused by crystallisation of stain on the epidermis obscure the periclinal surfaces.

Family: Scrophulariaceae - continued

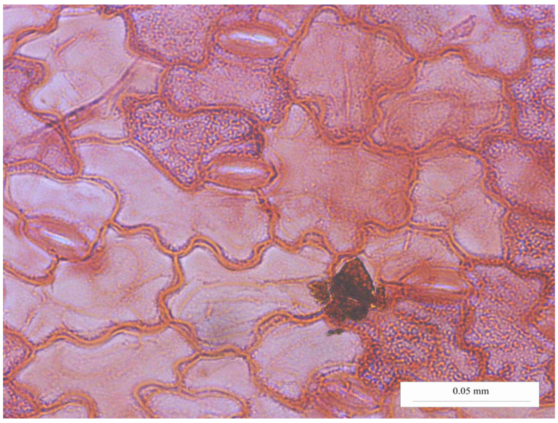


Plate 90: *Amsinckia calycina* abaxial surface (400x): Irregularly shaped unspecialised epidermal cells with sinuous anticlinal walls.

Plate 91: *Hemimeris racemosa* adaxial surface (200x): Irregularly shaped unspecialised epidermal cells with sinuous anticlinal walls and a trichome with its glandular tip broken off.

Family: Scrophulariaceae

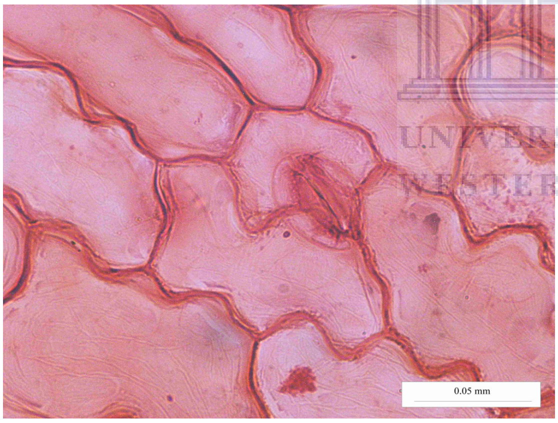


Plate 92: *Hemimeris racemosa* adaxial surface (400x): An anomocytic stomatal complex surrounded by unspecialised epidermal cells.

Family: Sterculiaceae

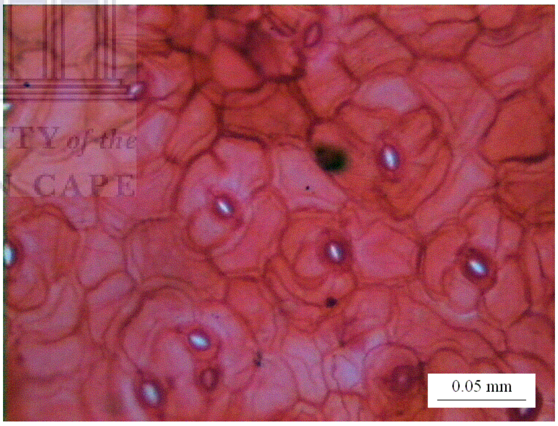


Plate 93: *Hermannia pinnata* leaf epidermal surface (400x): Anomocytic stomatal complexes on the epidermis. No trichomes visible due to epidermal scraping.

Family: Sterculiaceae - continued	Family: Urticaceae

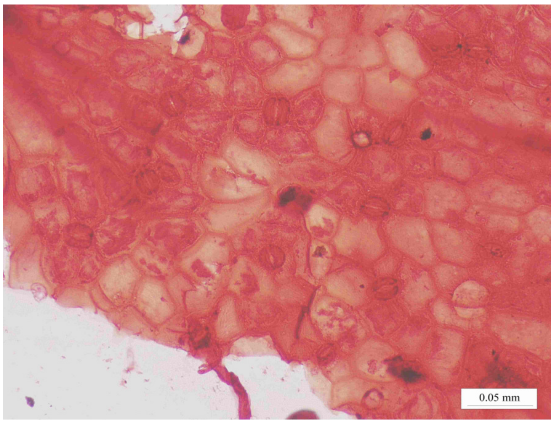
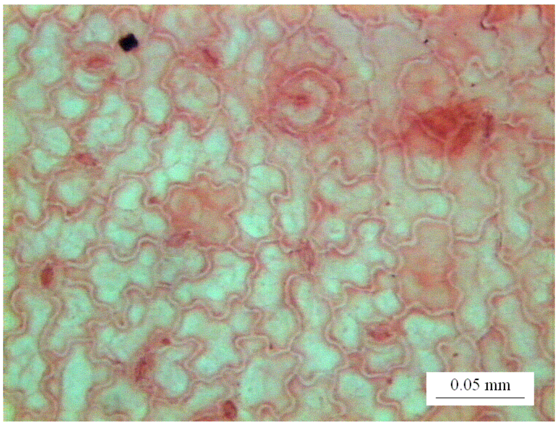
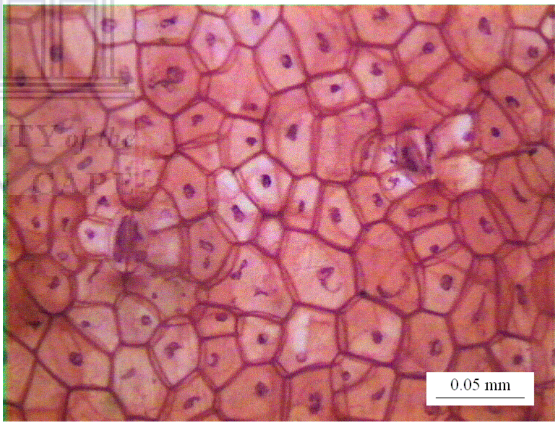

	

Plate 94: *Hermannia scabra* leaf surface (200x): Stain crystallisation obscures some features but the straight to curved anticlinal walls of a few unspecialised epidermal cells are partially visible.	Plate 95: *Urtica urens* abaxial surface (400x): Numerous epidermal cells with thin, sinuous anticlinal walls. Epidermal cells stained very lightly possibly because of the thin walls.

Family: Urticaceae	Family: Zygophyllaceae
	
Plate 96: *Urtica urens* abaxial surface (400x): A stinging emergence is clearly visible on the epidermis.	Plate 97: *Zygophyllum morgsana* adaxial surface (400x): Anomocytic stomatal complexes visible on the epidermal surface.

Family: Zygophyllaceae - continued

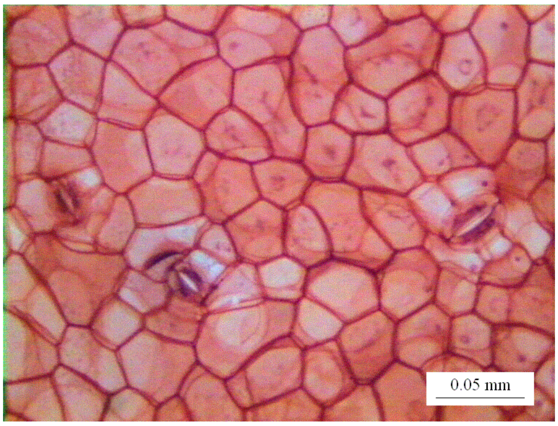


Plate 98: *Zygophyllum morgsana* abaxial surface (400x): Elliptical shaped stomata visible on the epidermal surface.