

CHAPTER 4

FOOD RESOURCES AND DIET

4.1 INTRODUCTION

Feeding ecology is a fundamental aspect of ecological energetics, influencing both energy intake and energy expenditure. For an animal to meet its energy requirements, energy gained from individual food items must be balanced against the energetic costs of obtaining those items and extracting the available energy. Thus, the nutritional quality of food items and their availability are important determinants of feeding strategies. Wombats live in seasonal environments which affect food quality and availability, and it is probable that these herbivores use strategies to cope with seasonal fluctuations in food quality. As outlined in Chapter 1, strategies that wombats might use to maintain a level of energy intake during poor seasons similar to that of good seasons are to increase feeding selectivity for higher quality food items or to select feeding areas that contain a higher proportion of higher quality food items (or some combination of both). Another strategy might be to increase the rate of food intake (at the expense of selectivity) and attempt to digest the more easily digested components and simply shunt the poorer quality material through the digestive tract. Alternatively, wombats might be forced to accept declining levels of energy intake as food quality/availability decline and compensate for the energy deficit by reducing energy expenditure. Lastly, they might mobilise stored metabolites.

In this chapter I examine a number of core aspects of the feeding ecology of common wombats at Riamukka State Forest. I determine the diet of common wombats and compare this to the availability of potential food items in the field to investigate feeding selectivity. I also determine the nutritional quality of potential food items to examine the influence of nutritional quality on dietary proportions and feeding selectivity. The information on food quality, diets and feeding selectivity presented in this chapter is combined with the results of home-range analysis (Chapter 5) and field energetics (Chapter 7) to examine feeding strategies used by common wombats (Chapter 8).

4.2 FOOD AVAILABILITY

4.2.1 Classification of food resources

Previous studies (Wells 1973; Mallett and Cooke 1986) indicate that common wombats are grazers of primarily monocot species of the herb layer, and are not known to eat the leaves of trees and shrubs such as eucalyptus and acacia. At the Riamukka SF site, trees and shrubs were almost exclusively eucalypts and acacias. For the purposes of this study, I have assumed that the diet of wombats is confined to the herb layer.

Plant species in the herb layer were collected during spring and summer '94 when most of these species were reproducing (facilitating their identification) and were placed in a field herbarium for reference. This reference collection was invaluable for aiding in the identification of grasses during winter when seedheads were not present. I was able to identify the vast majority of plants in the herb layer to the level of species during all seasons. Some species could not be reliably separated in the field and so were placed into groups. Plants that could not be identified to species were usually in the younger growth stages or did not have reproductive parts. In most cases, these plants (particularly grasses) could usually be identified to genus. Species that could not be identified to genus were placed into groups; for example, Sedges, Rosette Forbs or Other Forbs.

Lomandra longifolia and ferns (excluding bracken) were not sampled for biomass. These species grew almost exclusively in a large contiguous area (some of

which was included in the study site) whereas other species in the herb layer were dispersed throughout the site. The biomass of *Lomandra* and ferns relative to the biomass of other species at the study site was therefore highly dependant on the size and location of the study area, which to some extent was arbitrary. Moreover, the relative availability of *Lomandra* to common wombats was likely to depend on the extent of overlap of individual wombat home-ranges with the *Lomandra*/fern areas and the proportion of time spent in these areas, rather than on the abundance of other plant species at the site.

4.2.2 Preliminary trials

I initially trialed clipped quadrats to determine the yield of each herbaceous species at the Riamukka SF study site. This method involved clipping and hand-sorting plant species from randomly located 0.25 m² quadrats. Each plant species was separated during clipping and stored in paper bags for subsequent drying and weighing. Although this technique accurately measures the yield of each species in a quadrat, it was found to be extremely time consuming. The number of quadrats required to adequately sample sites with any degree of precision would have taken far in excess of the time available for this component of the study, and so this method was discontinued.

4.2.3 Species composition and biomass of the herb layer

A more rapid method than clipped quadrats for determining biomass and species composition of the herb layer is to combine the dry weight rank ('t Mannetje and Haydock 1963) and comparative yield (Haydock and Shaw 1975) methods. These methods largely rely on visual estimation of quadrats and therefore the estimation of each quadrat is not as accurate as clipping. However, the rapidity of these methods enables a far greater sampling intensity and therefore they have the advantage of providing a more precise estimate for the time spent.

The dry weight rank method is an empirically derived model used to estimate pasture species composition. This method involved assigning the ranks of first, second and third to species in randomly located 0.25 m² quadrats, on the basis of a visual estimation of their dry weight, with the rank of first being given to the species with the

greatest dry weight. The ranked scores of species from the total number of quadrats were then converted to percentage species composition of the pasture through multiplication by a set of conversion factors. The conversion factors were derived by Tothill *et al.* 1978 from the empirical relation between the actual and ranked dry weight composition of pasture, which these researchers have found to hold for a wide range of pasture types. A disadvantage of the method is that it does not appear to provide a means for measuring error unless repeated sampling is undertaken to determine the estimate (which is beyond the resources of this and most other studies requiring a rapid pasture biomass estimation technique).

Initially, estimating the dry weight ranks of species in quadrats was difficult, particularly when comparing species with different growth forms such as tussock and non-tussock species, or between monocot and dicot species. With practice, and clipping, drying and weighing some species a number of times, the dry weight ranks could be estimated reasonably well.

I derived the field biomass of plant species by estimating the total biomass of the herb layer and then apportioning this to each species according to its percentage composition of the herb layer (as estimated by the dry weight rank method). The biomass of the herb layer was estimated using the comparative yield method. This method involves estimating the biomass (yield) of vegetation in quadrats by visual comparison to a series of reference quadrats of known biomass. Five reference quadrats were subjectively chosen to cover the range of quadrat yields that were likely to be encountered throughout the sampling period at the site. In addition, the reference quadrats were chosen so that the vegetation biomass they contained provided a 1 to 5 (smallest to greatest biomass) linear scale over this biomass range. Quadrat 3 was therefore estimated to be halfway in biomass between quadrat 1 and quadrat 5. This scale of 1 to 5 was subdivided into tenths to enable intermediate values (for example, 4.1) to be selected. The five reference quadrats were left in place for the duration of the sampling period within a season (usually 3 or 4 days). The biomass of each of the randomly located 0.25 m² sampling quadrats was given a place on the scale by visual comparison to the reference quadrats. A polaroid camera was used to take photographs of the five reference quadrats at the beginning of each sampling period. This enabled

accurate comparisons to be made between the sampling quadrats and the reference quadrats when the randomly placed sampling quadrats (which were located throughout each vegetation area) were not in the vicinity of the reference quadrats. At the end of each field sampling period vegetation in the five reference quadrats was clipped, dried and weighed, and an equation relating quadrat scale to actual weight of each reference quadrat was determined by fitting a linear or quadratic regression line through a plot of their weights. The scale values of the randomly placed sampling quadrats could then be converted to estimated biomass.

I used the program BOTANAL (Tothill *et al.* 1978) to compute the yield and percentage composition of each plant species (or species group) in the herb layer from the raw quadrat data. For convenience, the same randomly located quadrats that were used to estimate the biomass of the pasture were also used to estimate the dry weight rank of species.

The dry weight rank and comparative yield methods of estimating pasture biomass and species composition have been found to be adequate for regular sampling of a wide range of pasture types both in Australia (Tothill *et al.* 1978; Bryan and Evans 1973; Rees *et al.* 1976) and overseas (eg. Bedell 1973; Walker 1976). Friedel *et al.* (1988) evaluated these techniques for the monitoring of arid rangelands and concluded that although they were not as accurate as some other techniques, when used in combination they were time-efficient for providing a given level of precision in estimates, particularly in heterogeneous pastures. A number of studies on macropods have apparently successfully used these techniques to investigate fluctuations in pasture biomass and availability (eg. Short 1986; Coulson *et al.* 1989).

4.2.4 Sampling Regime

I assessed the availability and quality of food resources for one species of wombat only, the common wombat. Food resources were being investigated for the northern hairy-nosed wombat at the Epping Forest study site as part of another study. Aspects of the nutritional quality of food resources for the southern hairy-nosed wombat on Brookfield CP have been examined by Wells (1973). Time constraints did not permit me

to assess other aspects of food resources for southern hairy-nosed wombats (such as seasonal abundance and species composition).

I examined the availability (herb layer biomass and species composition) of food resources for common wombats at the Riamukka SF study site. The Riamukka SF site was stratified into Forest, Woodland and Cleared (open grazed pasture) (refer to Chapter 3). Tothill *et al.* (1978) suggest that 50 to 100 quadrats per plot (or stratified sampling area) should be an adequate sampling intensity for most pastures when using the Dry weight rank and comparative yield methods. Time constraints during this study did not permit more than 60 quadrats per stratified area, thus a total of 180 quadrats were used to sample the 3 stratified areas at the site during each season. Time constraints did not permit me to assess the abundance of plant parts (which cannot be done using the dry weight rank and comparative yield methods).

I began pilot sampling of the herb layer during autumn '94 to become familiar with the plant species and practise estimating dry weight ranks. Data used in this study were collected from each season between winter '94 and autumn '96 (ie. 2 years or 8 seasons). Samples for nutrient analyses were collected during 1995.

4.2.5 Nutrient Analyses

Protein and carbohydrate are the main sources of energy from food for mammalian herbivores and therefore are generally assumed to be important determinants of food quality (Van Soest 1964; Owen-Smith 1982; Raojevic *et al.* 1994; Tixier *et al.* 1997). The crude protein content of plant tissues is often determined from the nitrogen content, since almost all of the nitrogen in tissues is incorporated as protein. Carbohydrate can be present as simple sugars (usually in the cell contents) or as more complex forms (usually as part of the cell wall structure). Structural carbohydrates can be difficult for herbivores to digest, requiring prolonged fermentation periods. Plants also have a number of other compounds in their cell walls that are difficult or impossible for mammalian herbivores to digest, including cellulose, hemicellulose and lignin, and together with insoluble structural carbohydrates are usually referred to as 'fibre'. Because fibre is difficult to digest, and the proportion that remains undigested has no

nutritive value, fibre content is generally thought to be an important determinant of food quality (Demment and Van Soest 1985; Owen-Smith 1992).

In addition, plant defences to herbivory, such as chemical compounds (toxins or compounds that impede digestion) and physical structures (eg. hairs and spines) can affect palatability of plants. Grasses have bodies of mineral silica in their tissue, which increase the abrasiveness of their tissues to teeth (McNaughton *et al.* 1985). Mammalian grazing herbivores such as the Macropodidae and Vombatidae have molar progression or rootless continuously growing teeth to counter the consequences of abrasive material in their diets (Sanson 1989).

The digestive efficiency (or assimilation coefficient) of herbivores has been estimated by comparing the concentration of naturally occurring indigestible elements in the diet (such as manganese) to their concentration in faeces. The concentration of indigestible material in the diet increases as digestible material is absorbed by the body and hence removed from the digestive tract. If digestive efficiency and either the rate of food intake or rate of faecal excretion (ie. the rate of throughput of digesta) are known, an absolute value for material assimilated into the body (and hence total energy extracted from the diet) can be derived. In this study, measurement in the field of the rate of food intake or rate of defecation was not practicable, and hence a value for absolute assimilation of material was not determined using this method. Absolute values for rate of food intake and energy extracted from food were calculated by other methods (Chapters 6 and 7).

The values given for nutrient parameters in the following sections are the means of two or three replicates for each sample. Due to time constraints, samples were not replicated more than three times and consequently interspecific differences in nutrient parameters were not tested statistically.

Water content and Gross Energy

The water content of the main plant species in the diet (section 4.3.5) was determined for both the dryer winter and wetter summer by clipping, weighing, and drying in an oven at 60°C until weight stabilised. The gross energy content (kJ.g⁻¹) of dried plant samples was determined by bomb calorimetry.

Nitrogen

Nitrogen analyses were determined in a Technicon AutoAnalyser (Technicon Instruments, N. Y.). The Kjeldahl method was used to digest the samples. Briefly, this method involves heating .5g of finely ground plant sample with 10 ml. of digestion mix (1000ml sulphuric acid, 300g. potassium sulphate and 1g. selenium) to 370 degrees C. and digesting for approx. 2 hours. This digest was then added to a buffered alkaline solution containing sodium salicylate, sodium nitroprusside and sodium hypochlorite. The nitrogen content was determined colorimetrically (at 660 nm) from the degree of colour saturation of the liquid (Anon. 1977).

Neutral-detergent fibre

Almost all of the fibre in plants is contained within the structural compounds of the cell walls (though certain non-structural carbohydrates are sometimes defined as fibre). This fibre can be extracted using a neutral-detergent solution. Neutral-detergent fibre (NDF) was determined using the method of Goering and Van Soest (1970). In this method, neutral-detergent is used to remove soluble protein and carbohydrate, leaving insoluble fibre. Briefly, finely ground plant sample was added to a neutral-detergent solution containing sodium lauryl sulphate, disodium ethylene-diaminetetrace (EDTA), sodium borate decahydrate, disodium hydrogen phosphate, 2-ethoxyethanol, decahydronaphthalene and sodium sulfite, heated in a reflux apparatus, vacuum filtered and washed with acetone. The filtered residual (neutral-detergent fibre) was dried and weighed.

Lignin, Cellulose, Hemicellulose and Silica

Cell-wall fibre contains cellulose, lignin and hemicellulose. The proportion of cellulose and lignin can be determined by the acid-detergent procedure. Calculating the difference between acid-detergent fibre (cellulose and lignin only) and neutral-detergent fibre (total cell-wall fibre) gives the hemicellulose content. The acid-detergent fibre (ADF) content was determined using the method of Goering and Van Soest (1970). Briefly, finely ground plant sample was added to an acid-detergent solution containing Sulfuric acid, cetyl trimethylammonium bromide (CTAB) and decahydronaphthalene,

heated in a reflux apparatus, vacuum filtered and washed with acetone. The filtered residual (ADF) was dried and weighed.

Lignin was removed from the ADF by adding saturated Potassium permanganate solution and lignin buffer solution (containing Ferric nitrate, Silver nitrate, Acetic acid, Potassium acetate and Tertiary butyl alcohol), and vacuum filtering. A demineralising solution (containing oxalic acid, 95% ethanol, and concentrated hydrochloric acid) was then added to the filtered residue. The residue was washed, firstly with distilled water and then ethanol, and then dried and weighed. Lignin was calculated from the weight loss of the acid-detergent material. The residual material was then ashed in a muffle furnace. Cellulose was calculated as the weight loss upon ashing. Silica was extracted from the ashed material by adding 48% Hydrobromic acid and washing with acetone, then re-ashing. Silica was determined from the weight loss of the ashed material.

4.2.6 Results

Biomass of the herb layer

Seasonal biomass (kg/ha) of the herb layer averaged over the three vegetation areas at the Riamukka SF study site is shown in Figure 4.1. Also shown on Figure 4.1 are monthly rainfall totals recorded during the sampling period and the long-term mean monthly maximum temperatures (also see Chapter 3). Seasonal biomass levels ranged from 5260 kg/ha during summer '96 down to 2140 kg/ha during winter '95. Rainfall varied markedly between months, peaking during summer. Biomass of the herb layer showed a similar pattern to rainfall, with higher biomass occurring during summer.

Seasonal biomass of the herb layer for each of the three vegetation areas (Cleared, Woodland and Forest; see Chapter 3) are shown in Figure 4.2. Within each season the Cleared area had the lowest biomass and the Woodland had the highest biomass. The biomass of each of these areas varied between seasons and between years within the same season. Each area followed the same inter-seasonal trend in biomass. The biomass of the Cleared area varied more between seasons (Coefficient of Variation = 0.61) than did the other two areas (Woodland, CV = 0.24; Forest, CV = 0.35).

Species composition of the herb layer

The herb layer at the Riamukka study site was dominated by monocots year-round (Figure 4.3). The proportion of monocots was greatest in winter and least in summer. During winter the greatest proportion of monocots occurred in the Woodland, whereas during summer the greatest proportion of monocots occurred in the Forest. In the majority (5/8) of sampling periods, the Cleared area had the lowest proportion of monocots of the three areas (including the lowest recorded value of 72% during summer '96). The Cleared area was the most variable between seasons in the proportion of monocots (CV = 0.09), and the Forest was the least variable (CV = 0.03).

Seasonal biomass of individual plant species recorded in the three areas are given in Appendices 4a, 4b and 4c. Seasonal biomass of the ten most abundant species in each area are shown in Figures 4.4, 4.5 and 4.6. During winter the Cleared area was dominated by tussock snowgrasses (*Poa labillardieri* and to a lesser extent *P. sieberiana*), *Dactylis glomerata* (cocksfoot grass), *Lolium rigidum* (rye grass) and clover (*Trifolium repens*). Also common were *Pteridium esculentum* (bracken), rosette forbs, *Microlaena stipoides*, *Holcus lanatus* (fog grass), sedges and *Scleranthus bifloris*. The herb layer of the Woodland during winter was dominated by snowgrass (*P. sieberiana* and *P. labillardieri*), *Themeda australis* (kangaroo grass) and *H. lanatus*. Also common were various forbs (mostly rosette forbs and *S. bifloris*), *Microlaena*, sedges and bracken. The Forest during winter was dominated by snowgrass (almost exclusively *P. sieberiana* with some *P. labillardieri*). Other common monocots were *Lomandra longifolia*, *Microlaena*, *D. glomerata*, *H. lanatus*, *Dichelachne rara*, *Danthonia racemosa* (wallaby grass), *Cynodon dactylon* (couch), *L. rigidum*, *Bromus hordeaceus* (soft brome) and sedges. Common forbs were *Dichondria repens*, *Geranium dissectum*, *S. bifloris*, clover and various forbs in the 'other forbs' class.

During summer '95 the Cleared area was dominated by snowgrass, but to a lesser extent than in winter. Other dominant species were *D. glomerata*, *Microlaena stipoides*, *L. rigidum* and clover. *Microlaena stipoides* and *D. glomerata* became the dominant species during the following summer ('96). Clover, bracken and rosette forbs were also common during summer.

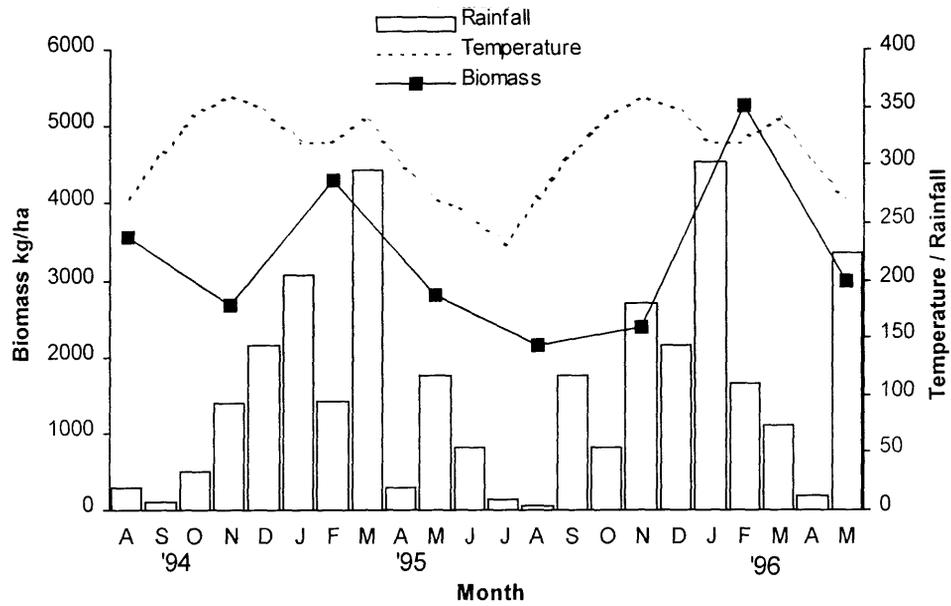


Figure 4.1 Seasonal biomass (kg/ha) of the herb layer averaged across the three vegetation types at Riamukka State Forest. Also shown are rainfall (mm) and temperature (°C x 10: temperature has been multiplied by 10 as a visual aid).

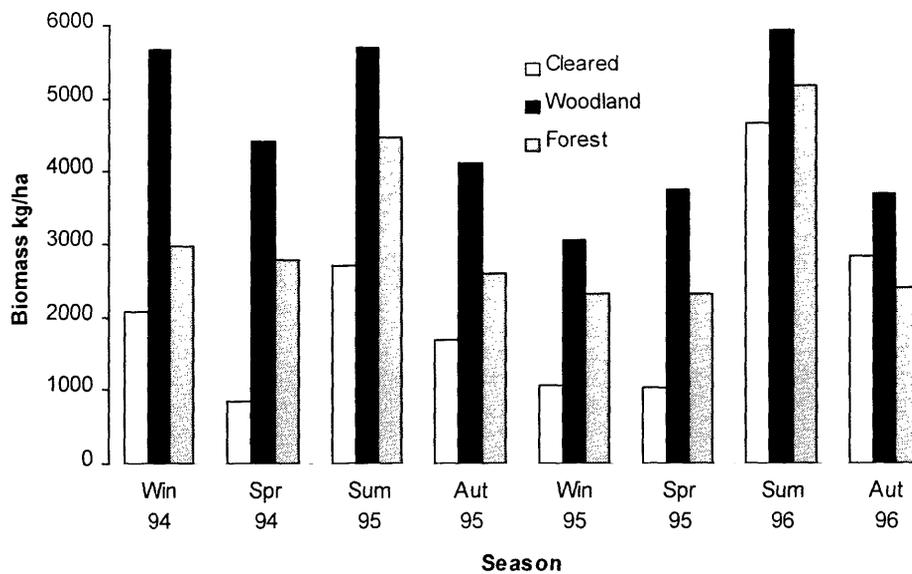


Figure 4.2 Seasonal biomass (kg/ha) of the herb layer for the three vegetation types (Cleared, Woodland, Forest) at Riamukka State Forest.

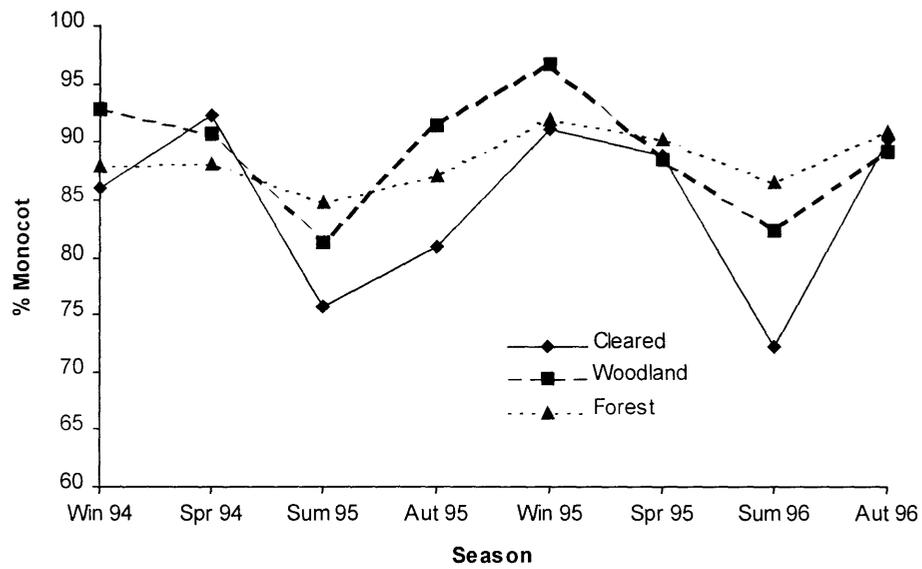


Figure 4.3 The proportion of biomass of the herb layer represented by monocotyledons during each season for the three vegetation types (Cleared, Woodland, Forest) at Riamukka State Forest.

The herb layer in the Woodland during summer was dominated by snowgrass (mostly *P. sieberiana*). Other common species were bracken, *Sorghum halepense* (Johnson grass), *D. glomerata*, *H. lanatus*, *Anthoxanthum odoratum* (sweet vernal grass) and *Microlaena stipoides*. The Forest herb layer during summer was dominated by *P. sieberiana*. Other species, mainly *Microlaena stipoides*, *D. repens*, 'other forbs' and *P. labillardieri*, were present but at a much lower abundance. From qualitative observations, grass seedhead (mostly *Microlaena stipoides* and *Poa* spp.) was abundantly available during summer.

Abundances of individual plant species during spring and autumn in the three areas tended to be intermediate to the abundances of winter and summer. Exceptions were the higher abundance of *S. halepense* in the Woodland and the higher abundance of *Microlaena* in the Cleared area, both during autumn.

Water Content

The water content of the main plant species in the diet (section 4.3.6) averaged 71 ± 6% (n=6) during the dryer winter and 60 ± 8% (n=6) during the wetter summer (a non-significant difference).

Gross Energy

The mean gross energy content of parts for the main grass species in the diet during summer was 16.6 ± 0.8 kJ.g⁻¹ (SE) (n=5) for grass seedhead, 16.3 ± 0.4 kJ.g⁻¹ (n=6) for grass leaf and 14.8 ± 0.4 kJ.g⁻¹ (n=5) for grass sheath/stem. The mean gross energy values for leaves of the main grass species in the diets during winter and spring averaged 16.0 ± 0.6 kJ.g⁻¹ (n = 5) and 16.0 ± 0.5 kJ.g⁻¹ (n = 6) respectively. The gross energy of plants was not sampled during Autumn. Differences between the means for gross energy in the above 5 categories were tested by one-way ANOVA and were found to differ insignificantly ($F_{4,26} = 1.52$, $P = 0.23$). Interestingly, *Poa labillardieri* seedhead was higher in gross energy (19.6 kJ.g⁻¹) than all other plant items sampled and markedly higher than the seedheads of other grasses abundant at the site such as *Microlaena stipoides* (15.3 kJ.g⁻¹), *Holcus lanatus* (15.7 kJ.g⁻¹), *Dactylis glomerata* (16.5 kJ.g⁻¹) and *Danthonia racemosa* (16.2 kJ.g⁻¹) (interspecific differences were not tested statistically due to the small number of replicates for each food item).

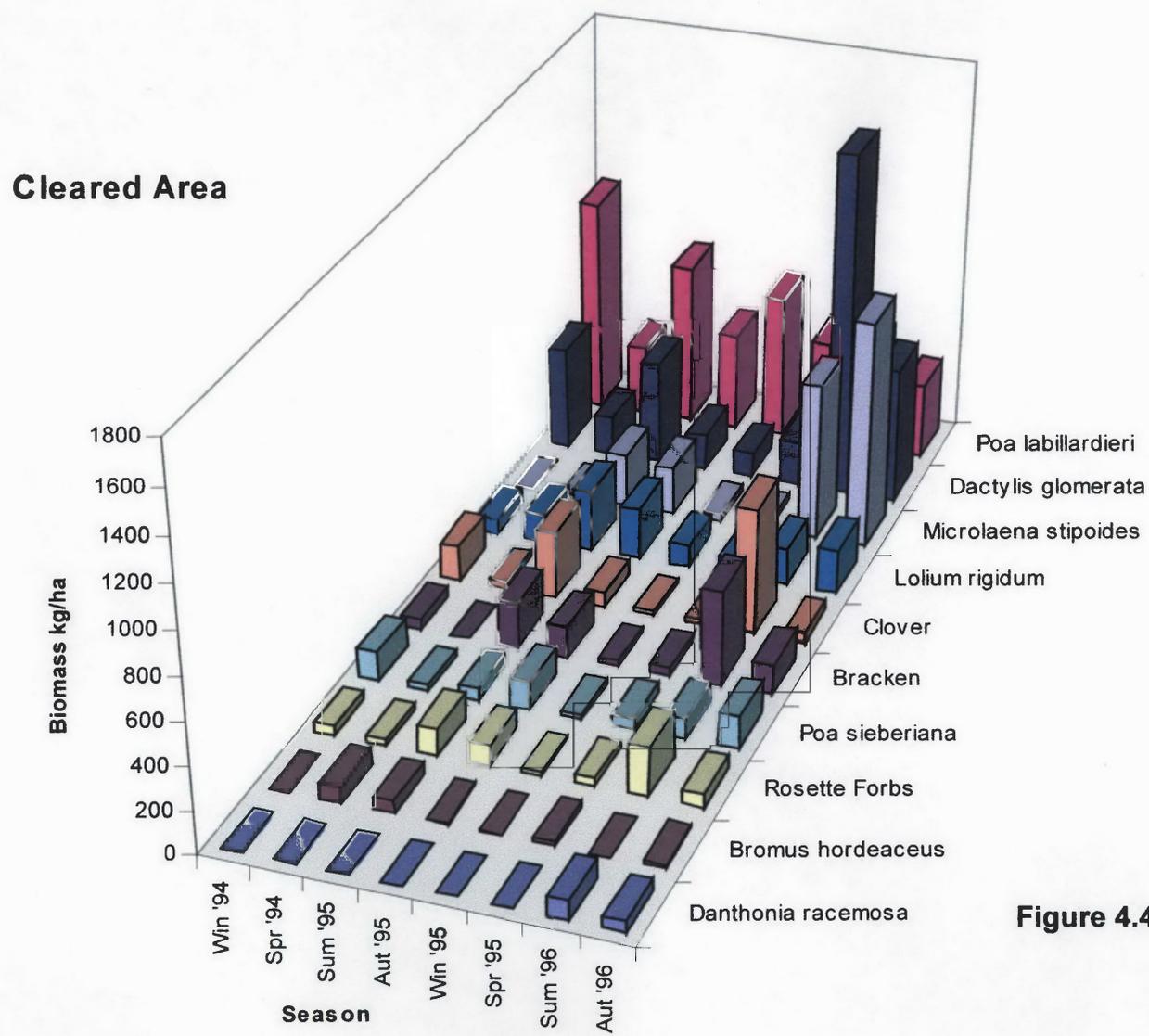


Figure 4.4 Seasonal biomass of the most abundant plant species in the herb layer of the Cleared area.

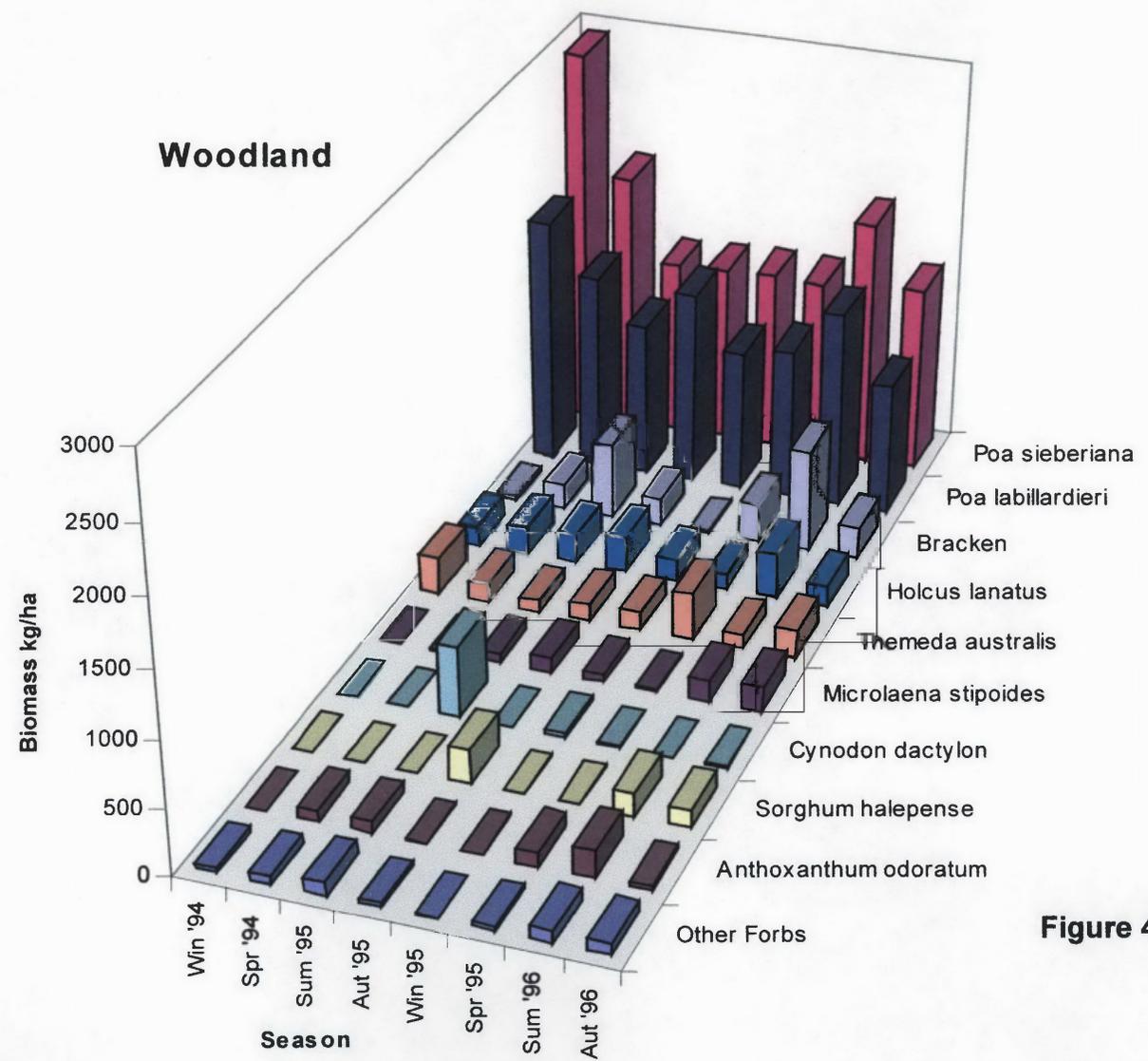


Figure 4.5 Seasonal biomass of the most abundant plant species in the herb layer of the Woodland.

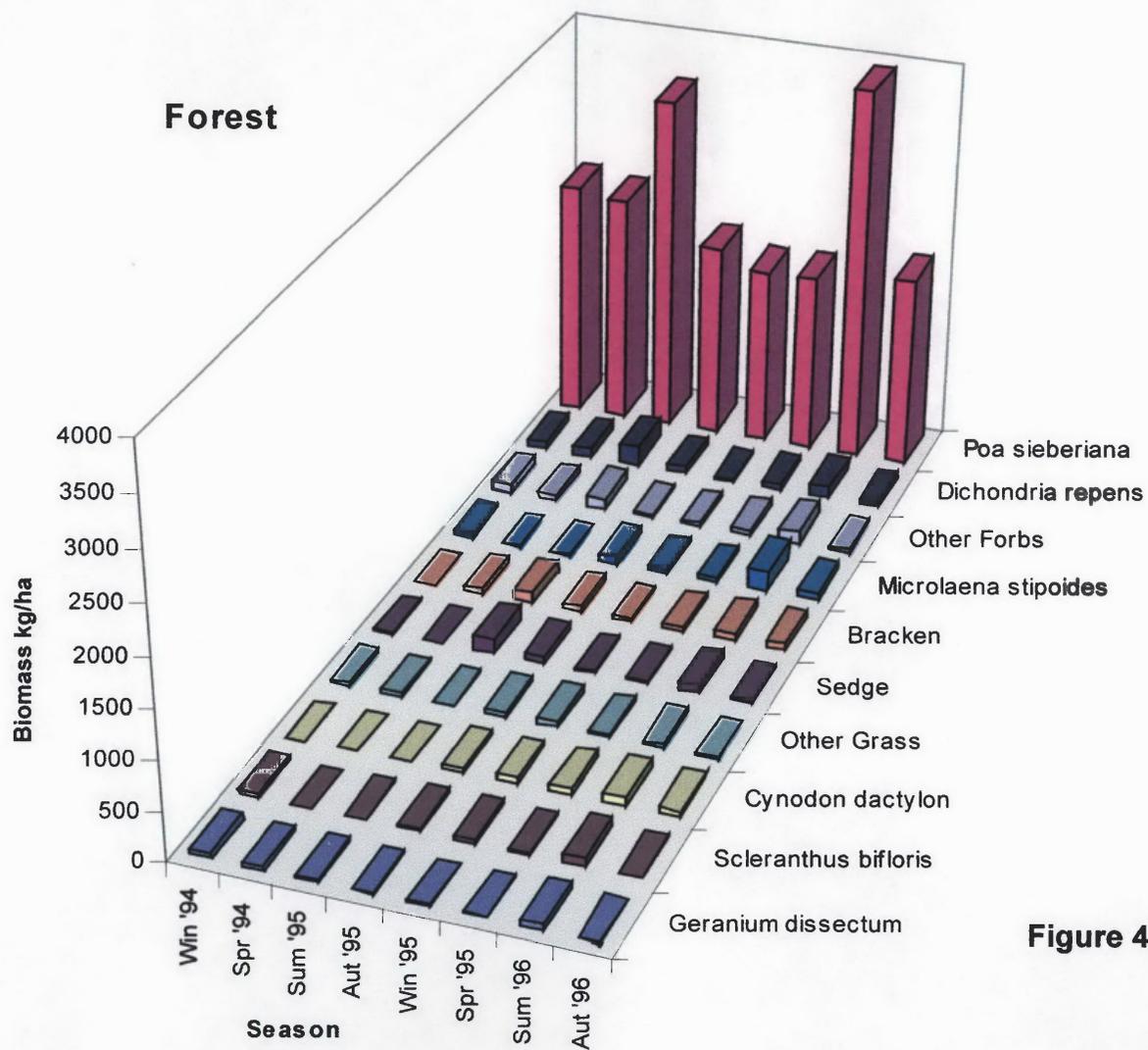


Figure 4.6 Seasonal biomass of the most abundant plant species in the herb layer for the Forest.

Nitrogen

The nitrogen content of plants in the herb layer at the Riamukka site varied markedly between species. Figure 4.7 shows the total nitrogen content of the leaves of species which were most abundant in the herb layer. To facilitate direct comparison the leaves of these species were sampled during summer, the season when all species were present in the herb layer. Plant species whose leaves were relatively high in nitrogen at this time of year included clover (*Trifolium repens*), *Lolium rigidum*, *Cynodon dactylon*, *Dactylis glomerata*, *Microlaena stipoides* and *Bromus hordeaceus*. Species whose leaves were relatively poor in nitrogen included *Poa labillardieri*, *Themeda australis*, *Poa sieberiana*, and the forb *Scleranthus bifloris*. Apart from *Scleranthus bifloris* and clover, the nitrogen content of the other forbs sampled (Rosette forbs, bracken and *Dichondria repens*) fell within the mid-range of all species sampled.

Figure 4.8 shows the total nitrogen content of leaf, sheath/stem and seedhead for the ten most abundant grass species in the herb layer. Plant parts were sampled during summer, the season when grass species were reproducing. For most species, the nitrogen content of sheath/stem was less than that of leaf or seedhead. Leaf was higher in nitrogen than seedhead (which included all the floral parts such as bracts, glumes and seed) in over half of these grass species. Species that were generally poor in nitrogen such as the *Poa* spp. had relatively high seedhead nitrogen values compared to that of the leaf. The variation in nitrogen content of seedhead (C.V. = 26.4) between these ten species was less than for either sheath/stem (C.V. = 67.6) or leaf (C.V. = 49.8).

Appendix 5a shows the seasonal nitrogen content of leaves for species that were abundant in the herb layer during all seasons. For most of these species leaf nitrogen was lower in winter than in other seasons. The most noticeable exception to this trend was clover, in which nitrogen levels dropped markedly during autumn. The nitrogen content of the leaves of the two *Poa* spp. were low year-round, reaching a maximum in summer and a minimum in winter.

Neutral-detergent fibre

The proportion of the leaf made up of neutral-detergent fibre (structural carbohydrates and other compounds) for the main species in the herb layer are shown in Figure 4.9. To facilitate direct comparison, the leaves of these species were sampled during summer, the season when all species were present. The forbs *T. repens*, *D. repens* and the Rosette Forb category had the lowest proportion of NDF in their leaves. The proportion of NDF in the leaves of grass species ranged from 49% to 73%. Grass species with a relatively low proportion of NDF were *Lolium rigidum*, *Danthonia racemosa*, *Anthoxanthum odoratum* and *Bromus hordeaceus*. Grass species with a relatively high proportion of NDF were the *Poa* spp. The monocot *Lomandra longifolia* was also relatively high in the proportion of NDF (72%).

The proportion of NDF for grass parts sampled in summer are shown in Figure 4.10. Sheath/stem contained a higher proportion of NDF than leaf or seedhead. Seedhead was higher in NDF than was leaf in 60% of the species. Leaf was higher in NDF than was seedhead in 30% of species, with the remaining 10% (one species) showing no difference between seedhead and leaf.

The seasonal proportions of NDF in leaves of the main herb layer species are shown in appendix 5b. The seasonal trend was variable between species, with species such as *T. repens*, *B. hordeaceus* and *M. stipoides* showing the lowest proportion of NDF during spring, whereas species such as *L. rigidum*, *A. odoratum*, *H. lanatus*, *P. labillardieri* and *T. australis* showed the converse.

Hemicellulose

The proportion of hemicellulose in leaves of the main species in the herb layer is shown in Figure 4.11. To facilitate direct comparison all leaves were sampled during summer. The proportion of hemicellulose in leaves was highly variable, ranging from 3% to 35%. Bracken and *Scleranthus bifloris* were markedly lower in hemicellulose than the other species, whereas *Cynodon dactylon* was markedly higher than all other species. Amongst grass species, the proportion of hemicellulose in leaves ranged from 14% to 35%. Grass species with a relatively low proportion of hemicellulose in their leaves were *Bromus hordeaceus* and *Danthonia racemosa*. Grass species with a

relatively high proportion of hemicellulose were *Cynodon dactylon* and *Microlaena stipoides*.

The proportion of hemicellulose in grass parts sampled in summer are shown in Figure 4.12. Seedhead tended to contain the highest proportion of hemicellulose and leaf the lowest. The seasonal proportions of hemicellulose in leaves of the main herb layer species are shown in appendix 5c. There does not appear to be a clear seasonal pattern in hemicellulose content across all of the species.

Cellulose

The cellulose content of leaves of the main species in the herb layer during summer are shown in Figure 4.13. Species whose leaves were relatively high in cellulose at this time of year included the *Poa* spp., *Lomandra longifolia* and bracken. Apart from bracken, the leaves of dicot species were lower in cellulose than those of monocot species. Grass species relatively low in cellulose were *Lolium rigidum* and *Cynodon dactylon*.

The proportion of cellulose in leaf, sheath/stem and seedhead for the ten most abundant grass species in the herb layer is shown in Figure 4.14. Plant parts were sampled during summer, the season when grass species were reproducing. Sheath/stem was higher in cellulose than either leaf or seedhead for all species sampled. The *Poa* species showed less difference between sheath/stem and leaf in the content of cellulose than did the other grass species. Seedhead contained a higher proportion of cellulose than leaf in some species but not others.

Appendix 5d shows the seasonal proportions of cellulose in leaves for species that were abundant in the herb layer during each season. The seasonal trend varied between species; generally, the proportion of cellulose reached a maximum in summer for some species and winter for other species.

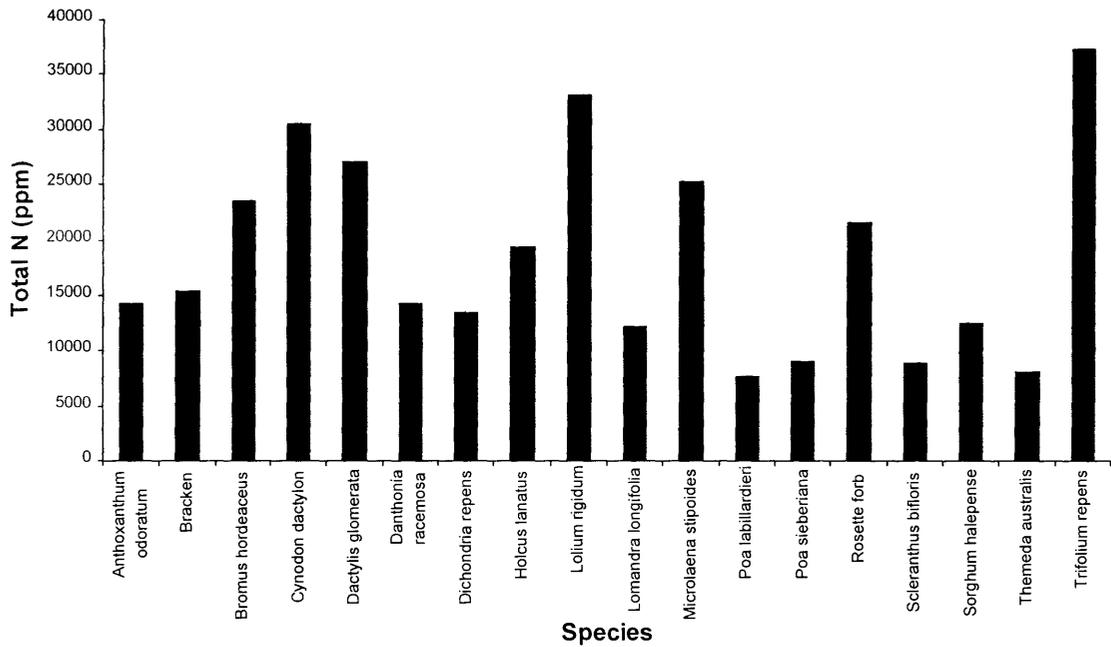


Figure 4.7 Leaf nitrogen content of species that were abundant in the herb layer. Leaves were sampled during summer.

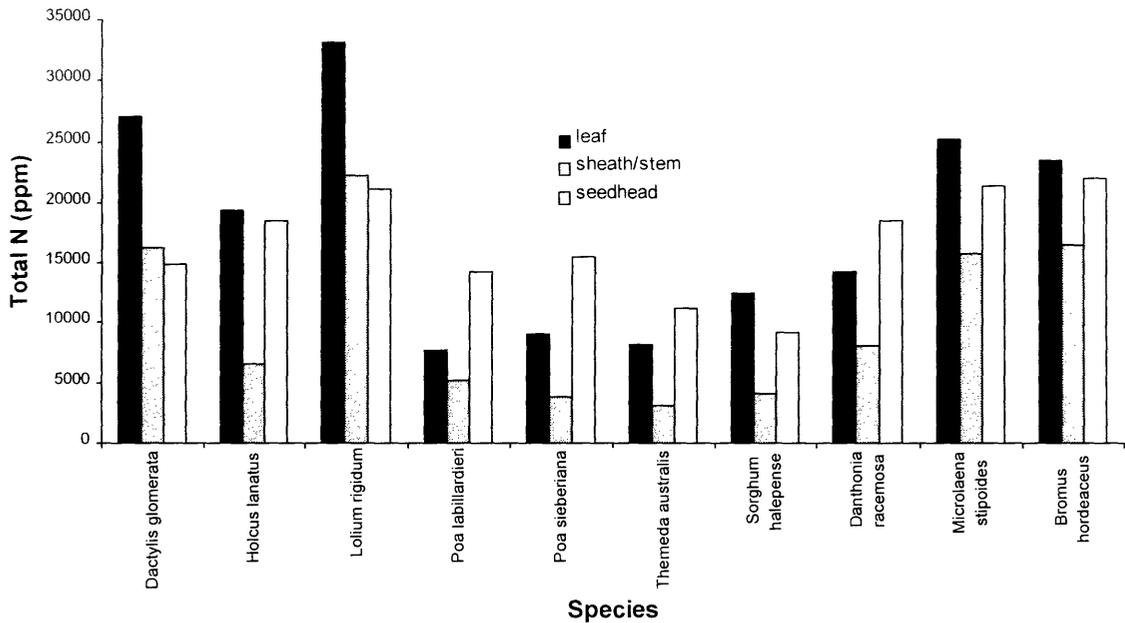


Figure 4.8 Nitrogen content of leaf, sheath/stem and seedhead for grass species that were abundant in the herb layer. Plant parts were sampled during summer.

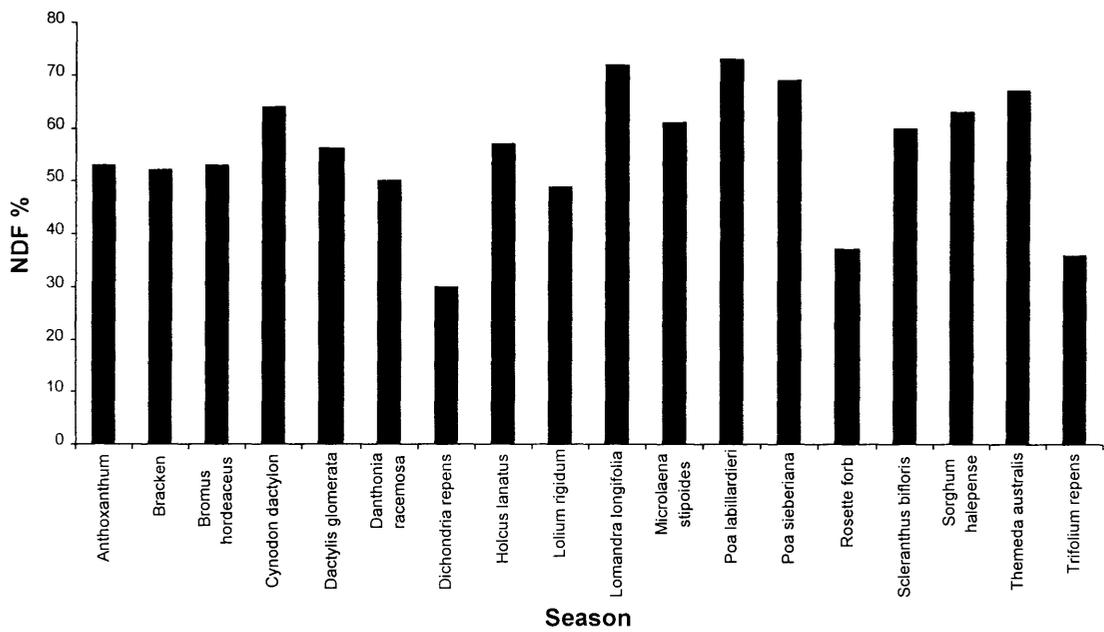


Figure 4.9 Proportion of neutral-detergent fibre (NDF) of species that were abundant in the herb layer. Leaves were sampled during summer.

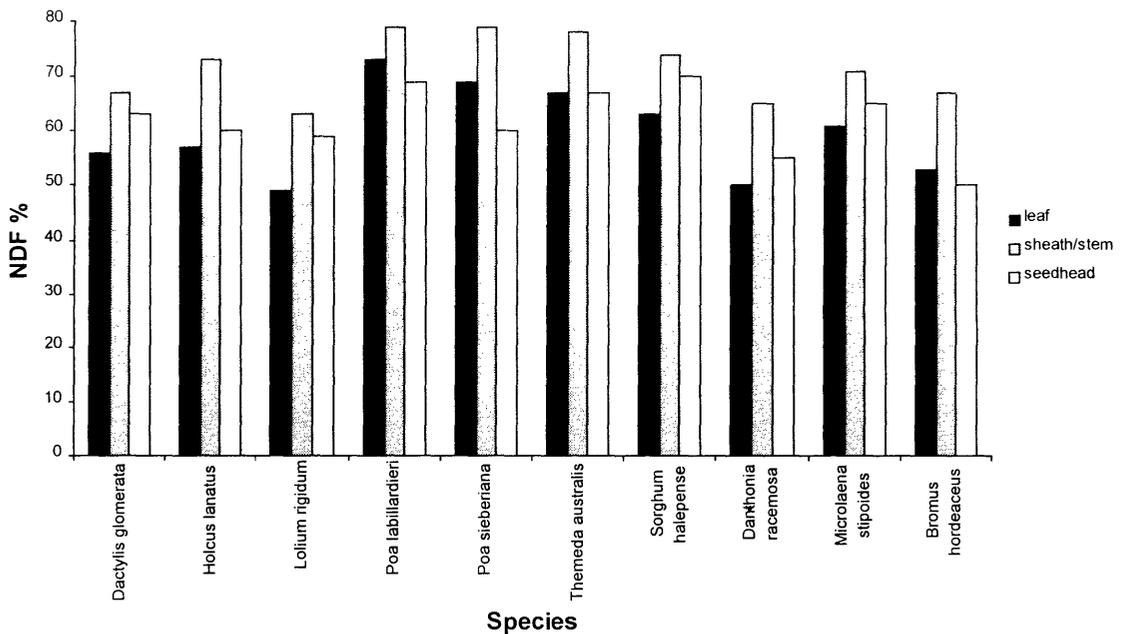


Figure 4.10 The proportion of neutral-detergent fibre (NDF) in leaf, sheath/stem and seedhead of species that were abundant in the herb layer. Plant parts were sampled during summer.

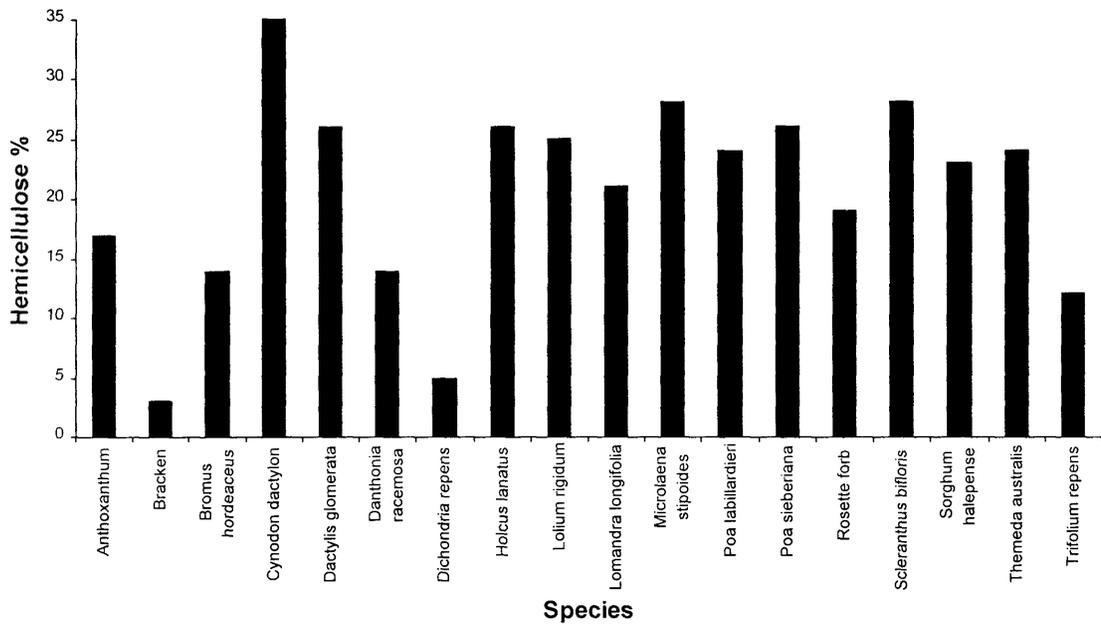


Figure 4.11 The proportion of hemicellulose in the leaves of species that were abundant in the herb layer. Leaves were sampled during summer.

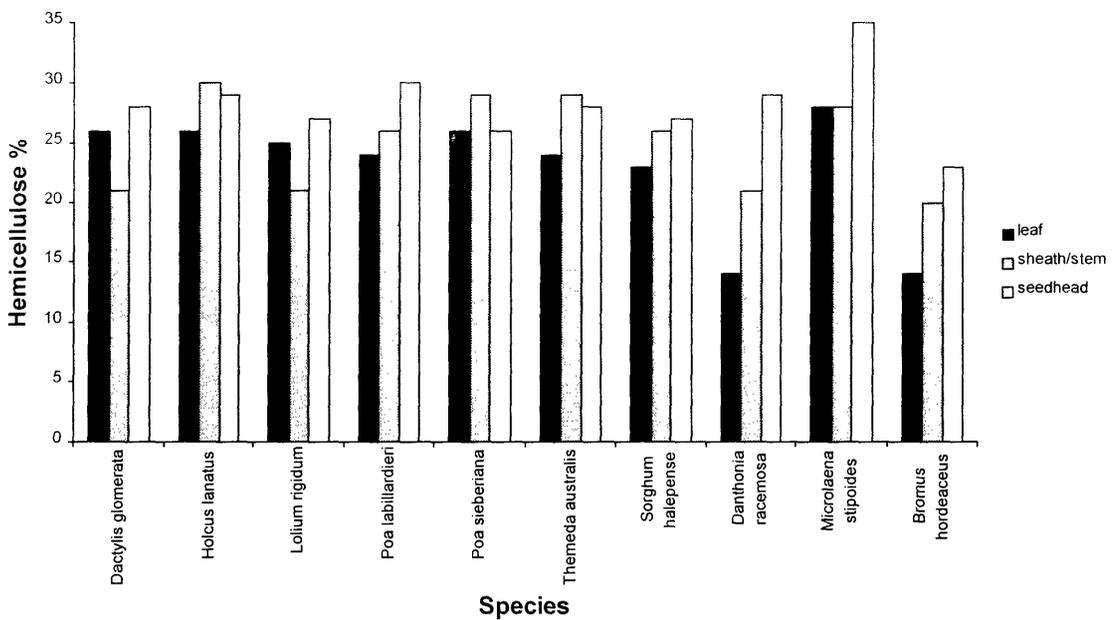


Figure 4.12 The proportion of hemicellulose in leaf, sheath/stem and seedhead for grass species that were abundant in the herb layer. Plant parts were sampled during summer.

Lignin

The lignin content of leaves of the main species in the herb layer during summer are shown in Figure 4.15. The lignin content of leaves ranged from 4% to 16%. *Lomandra longifolia* and bracken were markedly different to the other species, having almost twice as much lignin in their leaves as any other species. The lowest lignin value recorded was for the Rosette Forb group.

The proportion of lignin in leaf, sheath/stem and seedhead for the ten most abundant grass species in the herb layer is shown in Figure 4.16. Plant parts were sampled during summer, the season when grass species were reproducing. In 7 species, the proportion of lignin was higher in sheath/stem than in leaf or seedhead, and in the remaining 3 species seedhead highest in lignin. Lignin in sheath/stem of *Poa* spp. was markedly higher than in other plant parts, compared to the other species.

Appendix 5e shows the seasonal proportions of lignin in leaves for species that were abundant in the herb layer during each season. The seasonal trend varied between species. *Themeda australis* was markedly higher in lignin than other species, particularly during spring. The lowest lignin values for any of these species (*Lolium rigidum*) were also recorded in spring.

Silica

The silica content of leaves of the main species in the herb layer in summer at Riamukka are shown in Figure 4.17. The silica content in leaves varied markedly between species. Plant species whose leaves were relatively high in silica at this time of year included *Themeda australis* and *Sorghum halepense*. Species whose leaves were relatively low in silica included forbs, bracken, clover and *Lomandra longifolia*. Grass species relatively low in silica were *Lolium rigidum* and *Cynodon dactylon*.

Figure 4.18 shows the silica content of leaf, sheath/stem and seedhead for the ten most abundant grass species in the herb layer. Plant parts were sampled during summer, the season when grass species were reproducing. Sheath/stem was lower in silica than

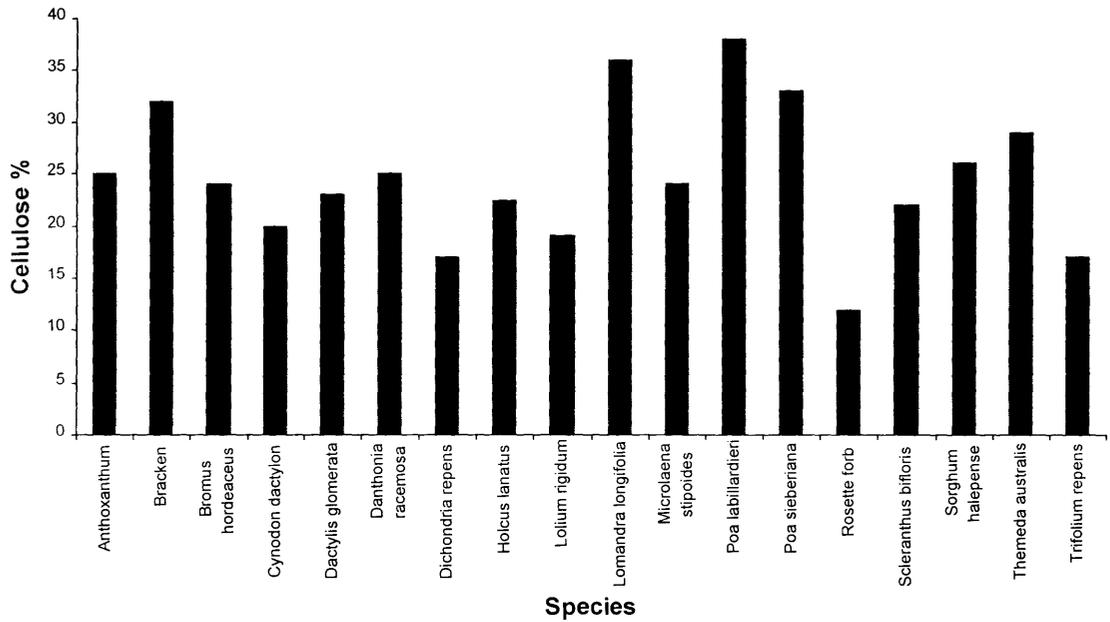


Figure 4.13 The cellulose content of the leaves of species that were abundant in the herb layer. Leaves were sampled during summer.

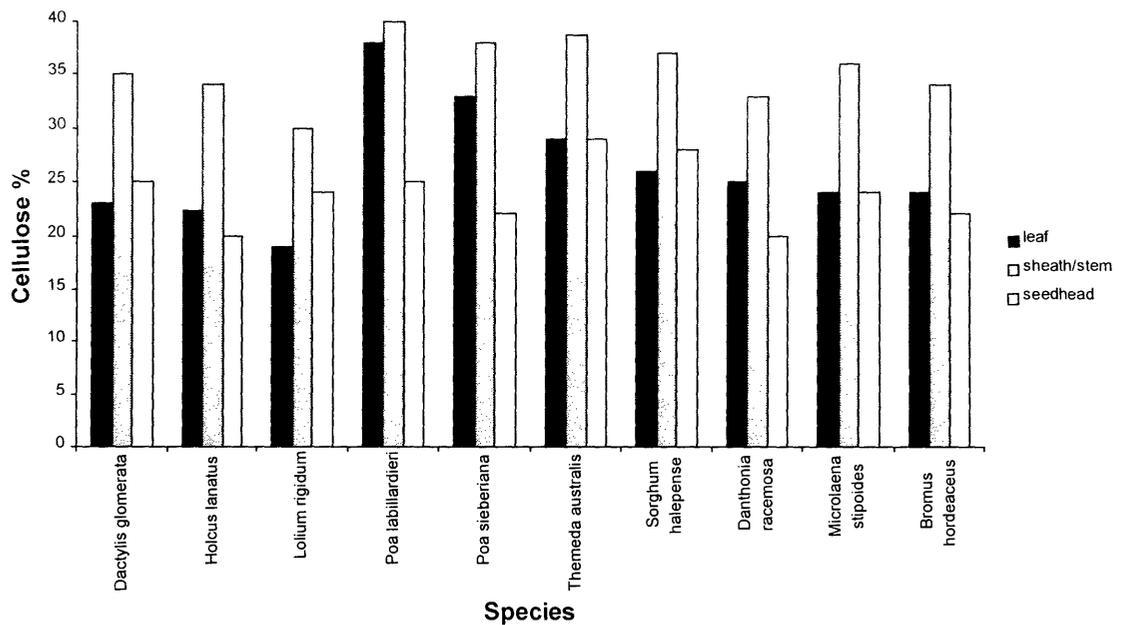


Figure 4.14 The cellulose content of leaf, sheath/stem and seedhead for grass species that were abundant in the herb layer. Plant parts were sampled during summer.

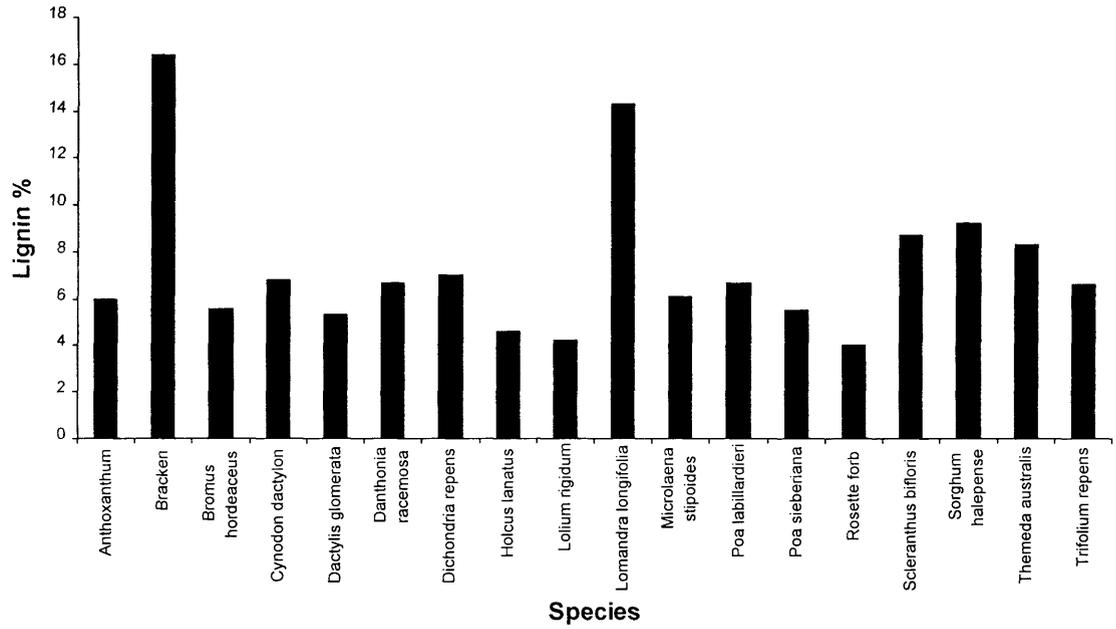


Figure 4.15 The lignin content of the leaves of species that were abundant in the herb layer. Leaves were sampled during summer.

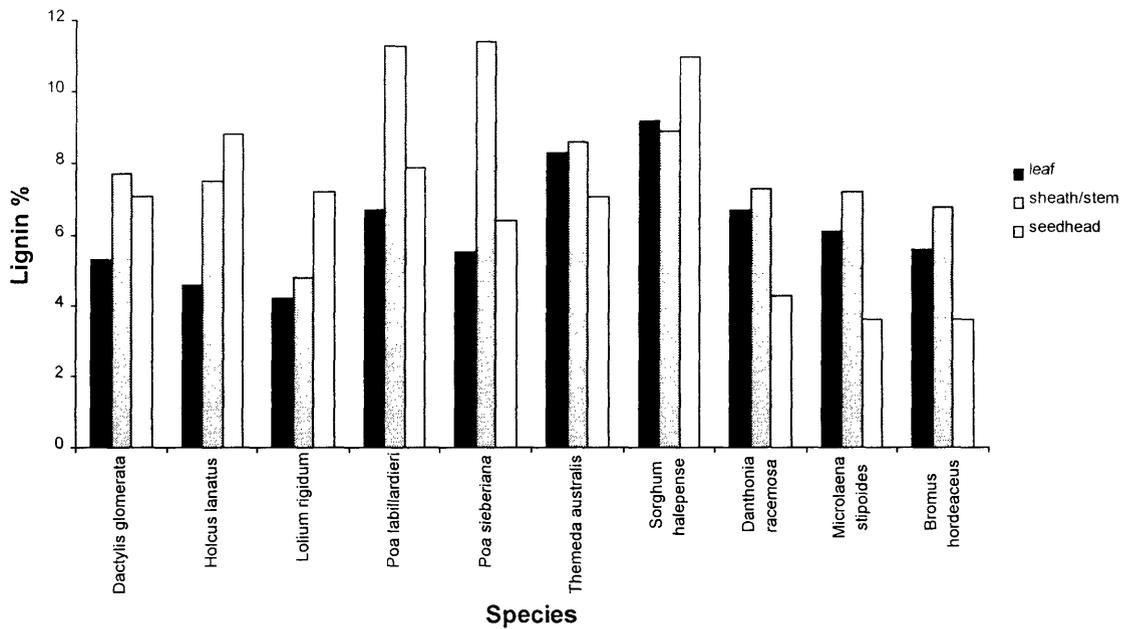


Figure 4.16 The lignin content of leaf, sheath/stem and seedhead for grass species that were abundant in the herb layer. Plant parts were sampled during summer.

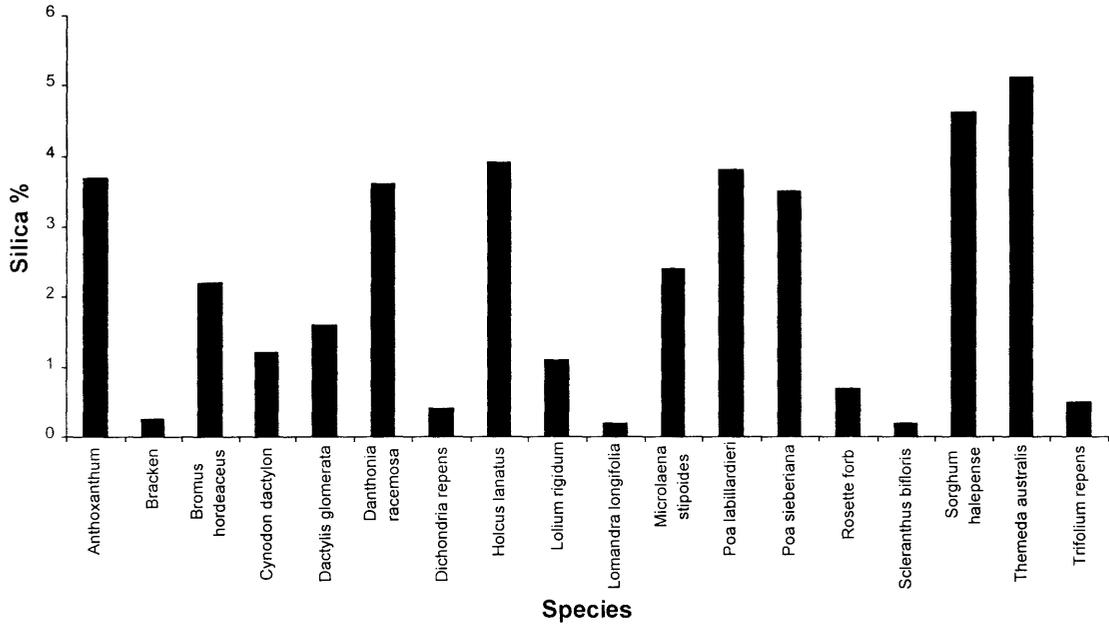


Figure 4.17 The silica content of the leaves of species that were abundant in the herb layer. Leaves were sampled during summer.

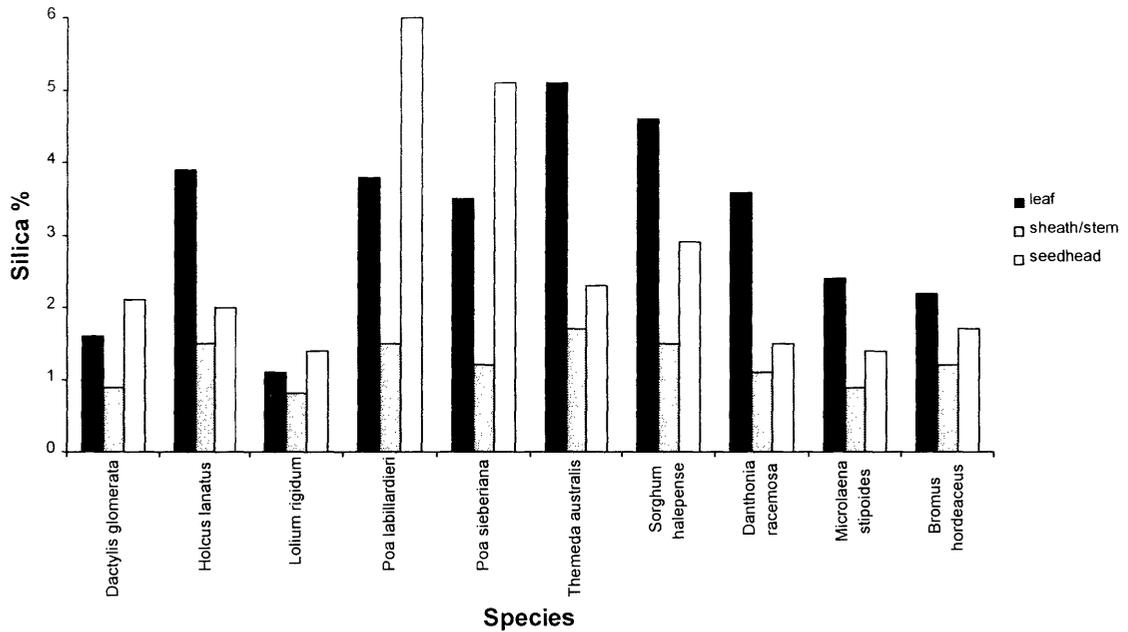


Figure 4.18 The silica content of leaf, sheath/stem and seedhead for grass species that were abundant in the herb layer. Plant parts were sampled during summer.

either leaf or seedhead. For most species, the highest silica levels were found in the leaves; the exceptions were *Poa* spp. which had the highest silica levels in the seedhead.

Appendix 5f shows the seasonal proportions of silica in leaves for species that were abundant in the herb layer during each season. The seasonal trend varied between species, though for many species the proportion of silica was higher in winter and spring than in summer and autumn. Seasonal silica levels varied markedly in *Poa* spp. and *Themeda australis*.

4.2.7 Overview of Food resources

Riamukka has a moderately seasonal environment; it experiences short mild summers and long cool to cold winters with occasional snow. Rain falls throughout the year, but is weakly summer dominated. Temperature rather than rainfall probably exerts the strongest influence on growth and reproduction of pasture species. Herb layer biomass during the summer months can be twice that of the winter months. Plant species that are able to tolerate and still grow in cold temperatures (cool season species) are abundant in the herb layer during winter and spring. Warmer summer temperatures stimulate growth and reproduction in a wide range of grasses and forbs, including the 'cool season' species. However, species that respond to warm temperatures with rapid growth soon become abundant, increasing the species diversity and biomass of the pasture.

Pastures at the Riamukka site were dominated year round by snow grasses (*Poa* spp.), common tussock species in alpine or sub-alpine areas. Snow grasses were lower in nutritional quality, being higher in fibre, cellulose and silica, and lower in nitrogen, than almost all of the other species present at Riamukka,. During winter the cool season grasses (rye grass *Lolium rigidum* and cocksfoot *Dactylis glomerata*) comprised a greater proportion of the pasture than in the warmer months. These cool season species contrasted strongly to the snow grasses in being of relatively higher nutritional value. During summer the proportions of other species, such as *Microlaena stipoides*, clover, bracken and various forbs, become relatively greater. These species are also relatively

more nutritious than the dominant snow grasses. Grass seedhead was abundant during summer.

4.3 DIET

4.3.1 Introduction

Methods of examining herbivore diets include direct observation of feeding, examination of plants for signs of being eaten, samples of food obtained from the mouths or gut, and analysis of faeces. Ideally, the method should not cause stress to the animal and should be accurate. Because the aim of this study was to investigate the ecological energetics of a wild population of common wombats under natural field conditions, the method used to examine the diets must not interfere with the normal habits of the animals, and must not cause stress or mortality. Direct observation of feeding was not possible, and examination of plants for grazing was not practicable; faecal analysis was therefore the obvious choice.

Previous studies (Dunnet *et al.* 1973; Westoby *et al.* 1976; Norbury and Sanson 1992) have shown that faecal analysis may not accurately reflect proportions of food items digested because of errors in epidermis identification and bias associated with differential digestion and differences in the ratio of volume to surface area (epidermis) between food items. Dawson and Ellis (1979) concluded that the method may not give as precise an estimate of the diet as may be obtained from gut samples, but it gives a good relative index for comparing intakes between animals and between the same species at different periods. Pearson (1983) studying the diets of *Lagorchestes hirsutus* noted no significant differences between the assessment of the diet using gut or faecal samples. Cid and Brizuela (1990) believed that the relative proportions of grass leaf and sheath ingested could be determined from epidermal proportions in the diet.

It would appear that, despite potential problems of bias, faecal analysis is a useful technique for herbivore dietary analysis and the only practicable method in some situations. Differences could be expected between ingested and faecal proportions of some plant types and hence comparisons between these types (for example, soft-leaved

forbs and tougher grass species) within a diet should be treated with caution. The method should provide a good relative index for comparing the proportions of food items in the diets of wombats between seasons.

4.3.2 Collection of Faecal Pellets

The large 'blocky' faecal pellets produced by wombats at Riamukka were often deposited on prominent objects, such as rocks, logs or even the dung of much larger herbivores such as horses. These characteristics enabled pellets to be easily distinguished from those of sympatric herbivores such as macropods, domestic stock and wild pigs. Fresh wombat pellets (ie. pellets up to about three days old) were also able to be differentiated from older pellets by their smooth texture, dark wet appearance and presence of a mucous coating; older pellets tend to have a pale bleached appearance with a rough weathered texture. Wombat pellets were abundant at the field site during all seasons except summer, at which time high dung beetle activity during the night meant that few pellets remained intact by dawn.

Ten samples of fresh pellets were collected at the Riamukka site during each of the four seasons over a two year period, totalling 80 samples (10 x 4 x 2). A sample is defined as one pellet collected from a single defecation (a defecation consists of many pellets). Collections were made at approximately the same time as the availability of food resources was being assessed. Approximately equal numbers of samples were collected from each of the three vegetation areas.

4.3.3 Preparation of Plant Epidermis

Reference epidermis

Plant species found in the herb layer were collected, pressed and dried, and species identifications verified by the Division of Botany, University of New England. Most samples of plant parts for the epidermis reference collection were placed in 70% ethanol whilst still fresh. Epidermis was prepared from these samples by a variety of methods, since no single method was found to be successful for all types of plant species and plant parts.

The first method is outlined in Berman and Jarman (1988) and is briefly described here. Samples of plant parts were cut into 5 mm lengths and heated until just simmering in a conical flask containing a solution of 10% chromic/nitric acid. Heating was done by holding the flask over a bunsen flame or placing the flask on a hotplate, during which time the flask was regularly swirled. Once the epidermis began separating from the underlying mesophyll tissue (usually within 5 minutes, but sometimes up to 10 minutes), the flask was removed from the heat and the solution diluted with water to reduce further degradation of the epidermis tissue. The contents of the flask were then transferred to a beaker and a fine brush used to pick up the epidermis fragments. This technique did not work for species whose epidermis was weak and firmly attached to relatively stronger underlying (and often lignified) cells. For these species, the epidermis disintegrated when the underlying cell structure broke up in the acid.

A number of other techniques were used when the epidermis did not separate in the acid solution. Before the sample disintegrated completely, it was removed from the solution (as described above) and placed on a microscope slide. A number '00' or '03' brush was used to lift the edge of the epidermis and roll it off the underlying cells. Alternatively, the brush was used to gently scrape, using repetitive brush strokes, all cellular material away except for the lower epidermis (which usually adhered to the microscope slide). This scraping technique also worked for some fresh samples (particularly grasses) with a scalpel blade used instead of a brush.

A few drops of safranin or gentian violet stain were added to the tissue, which was then left for a few minutes before being rinsed and mounted in glycerol jelly on a microscope slide with a cover slip placed on top.

Faecal Epidermis

A subsample from a pellet randomly chosen from each sample was soaked in a solution of 20% bleach (Sno-White 35g/l sodium hypochlorite) overnight or 50% bleach for 2 - 4 hours. This cleared the epidermal fragments and broke down the mucous in the sample which enabled the fragments to disperse. The bleach was diluted and most of the solution was carefully decanted. The sample was then stained with safranin and left (for an hour or several days) until it was analysed microscopically. During this period the

epidermal particles absorbed the stain and settled to the bottom of the beaker. Prior to the microscopic analysis, the stain solution was diluted and most carefully decanted. A subsample of the stained material was spread across a microscope slide with glycerol and a large (40 x 22 mm) cover slip placed on top. Fragments were spread on the slide so that they did not overlap, since overlap lowers the chance of identification. At all times during the preparation process, care was taken to preserve fragment size, since larger fragments are generally more readily identified than smaller fragments.

4.3.4 Microscopic Analysis

Epidermal fragments were scanned at a magnification of 100x using an Olympus BH-2 microscope. All epidermal fragments were recorded along randomly located parallel strip transects running the length of the slide. Transect width was the diameter of a field of view at 100x and transects were selected so that they did not overlap. Each fragment on the transect was identified to species and plant part, or if this was not possible, categorised to some extent. The area of the fragment contained within the transect was also recorded. Areas of fragments were determined with the aid of an eyepiece graticule. To maintain even sampling intensity between pellet samples (microscope slides) each slide was scanned until the area of 50 fragments had been determined. Tissue that was clearly not of epidermal origin (such as the underlying mesophyll cells) was not included in the analysis.

4.3.5 Statistical Analyses

Parametric tests were conducted on measured total epidermis area for each species in each sample, not on the calculated proportions. The total fragment area recorded from each sample (ie. the area summed from the 50 scanned fragments) varied between samples due to variations in the size of individual fragments. To avoid statistical bias from any sample, the area of epidermis for each species in individual samples was proportionately adjusted so that the total fragment area recorded (ie. sampling intensity) from a sample was even across all samples. Further details of statistical analyses can be found in section 3.10.

4.3.6 Diet Results

Over 35 plant species were identified in the diets of common wombats at Riamukka SF from faecal pellets. Grass species comprised by far the largest proportion (95%) of epidermal fragment area in pellets, with at least 20 species being identified. Sedges contributed 4% of epidermis fragment area, with the remaining 1% of fragment area comprising forbs, *Lomandra* (Xanthorrhoeaceae), and fragments which could not be identified to any category.

Seasonal proportions of grass, sedge, forbs, *Lomandra* and unidentified fragments in the diet are shown in Figure 4.19. Grass dominated the diet during all seasons, ranging from 91% during spring '96 to 97% during winter and summer of '96. The proportion of sedge in the diet varied from 1% during summer '96 to 8% during spring '96 (Figure 4.20). Each of the broad dietary categories of grass, sedge, forb and *Lomandra* were tested separately for differences across the eight seasons (ie 2 yrs). No significant differences were found for any category across the seasons (Grass, Kruskal-Wallis $H_{7,72} = 6.57$, $P = 0.47$; Sedge, Kruskal-Wallis $H_{7,72} = 8.45$, $P = 0.29$; Forb, Kruskal-Wallis $H_{7,72} = 4.07$, $P = 0.77$; *Lomandra*, Kruskal-Wallis $H_{7,72} = 5.13$, $P = 0.64$).

Seasonal proportions of species or species groups in the diet are shown in Table 4.1. Snow grasses *Poa sieberiana* and *P. labillardieri* formed the largest proportion of the grass diet, together comprising 42% of all fragment area. Other grass species important in the diet were *Microlaena stipoides* (17%), *Danthonia racemosa* (7%), *Lolium rigidum* (5%), *Dactylis glomerata* (4%), and *Holcus lanatus* (4%). Epidermal fragments from grasses that could not be identified to species or genus formed 12 % of all epidermis. *Poa* spp. dominated the diet in '95 during all seasons except summer, and dominated in '96 during winter and spring. Conversely, *Microlaena stipoides* was eaten mostly during the summer and autumn months in both years, and was at times the most abundant species in the diet. The highest proportion of *Danthonia racemosa* in the diet was during both summers ('95 and '96) and during autumn '96. *Lolium rigidum* was eaten relatively more during summer '95 and spring '96, and *Dactylis glomerata* was eaten relatively more during autumn of both years. *Lomandra longifolia* was recorded in the diet as just traces during autumn, winter and spring of '95.

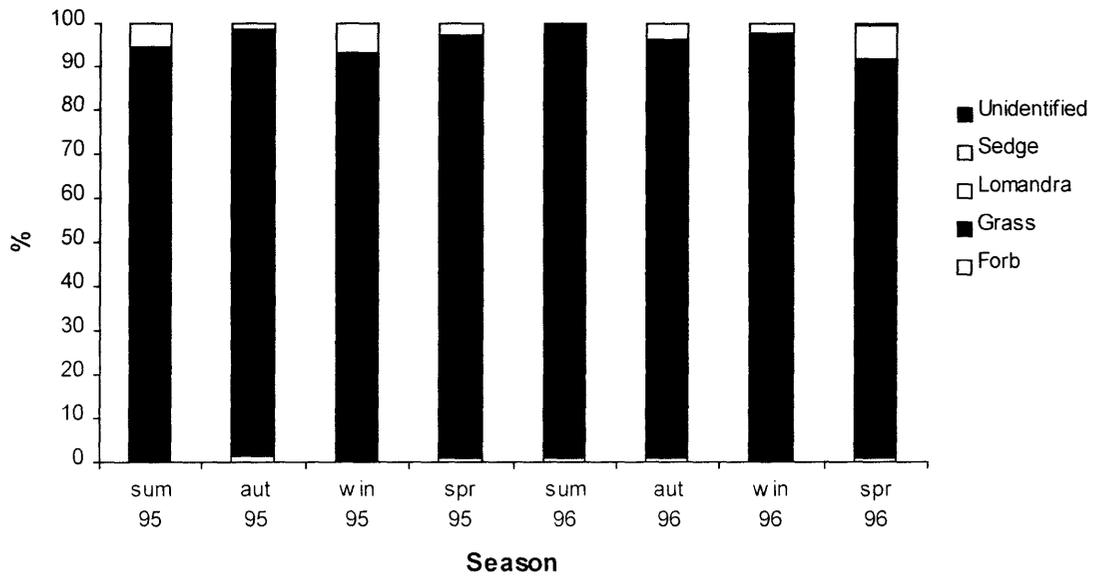


Figure 4.19 Seasonal proportions (%) of major plant groups identified in the diet of common wombats at Riamukka State Forest. The diet for each season was determined by pooling the results from 10 pellet samples.

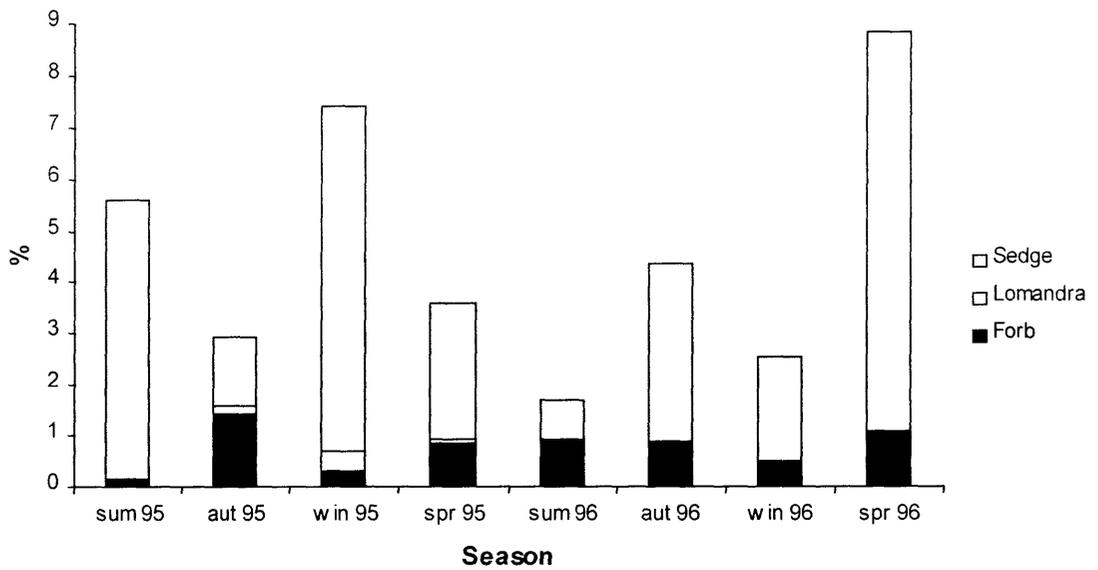


Figure 4.20 Seasonal proportions (%) of Sedge, *Lomandra longifolia* and Forb identified in the diet of common wombats at Riamukka State Forest. The diet for each season was determined by pooling the results from 10 pellet samples.

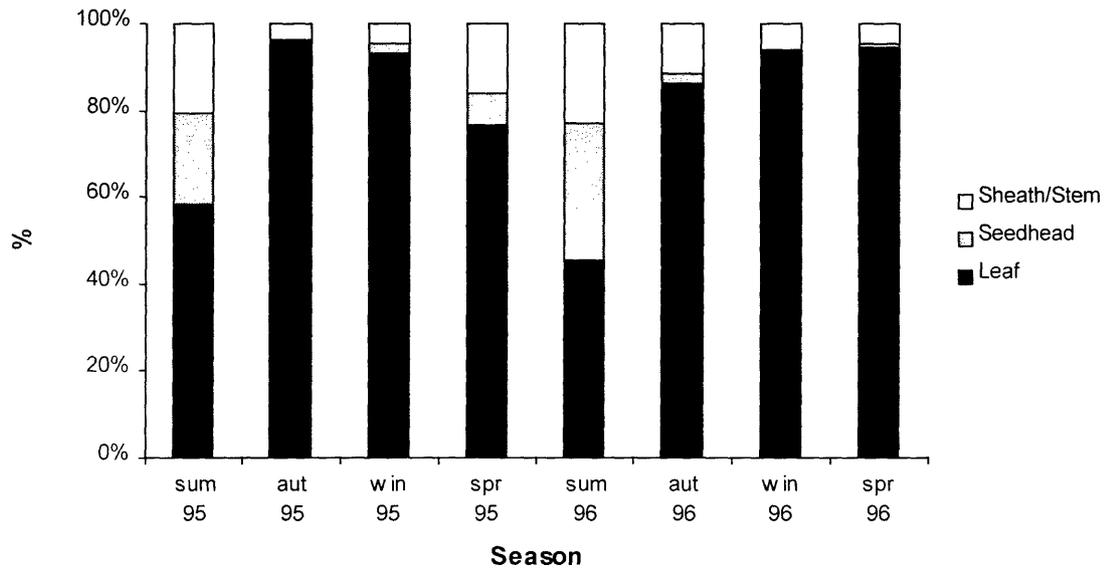


Figure 4.21 Seasonal proportions (%) of grass parts identified in the diet of common wombats at Riamukka State Forest. The diet for each season was determined by pooling the results from 10 pellet samples.

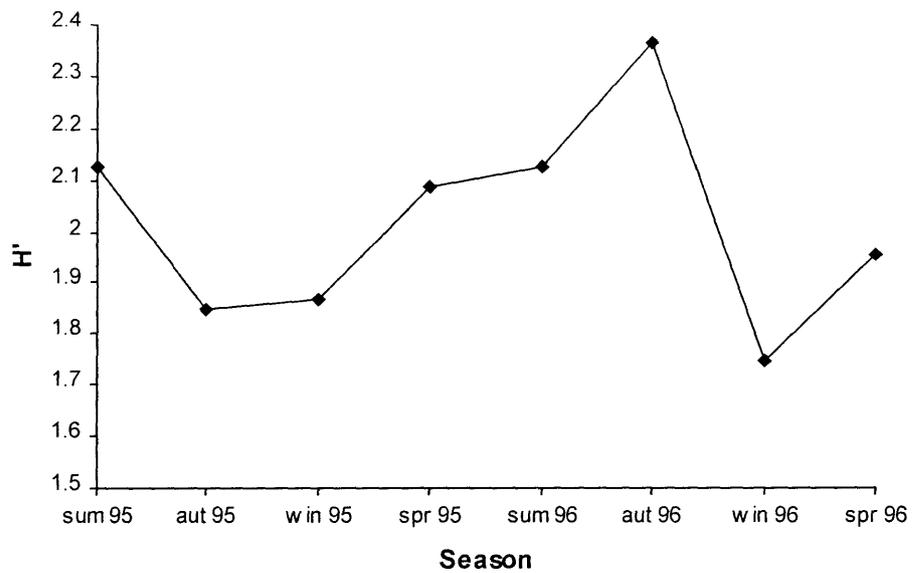


Figure 4.22 Shannon-Wiener diversity index (H') for species in the diet of common wombats over two years at Riamukka State Forest

Ninety-seven percent of epidermis area in faecal pellets could be identified to either leaf, sheath/stem or seedhead. Of the epidermis that could be identified to plant part, leaf comprised the greatest proportion (81%); stem and grass sheath together comprised 11%, and grass seedhead comprised 8%. The seasonal proportions of plant parts in the diet are shown in Figure 4.21. The seasonal proportion of grass seedhead in the diet varied significantly from just traces during autumn '95 and winter '96 to an important component of the diet during summer (21% in summer '95 and 32% in summer '96) (Kruskal-Wallis $H_{7,72} = 54.25$, $P < 0.001$, Kruskal-Wallis comparison of median rank). The proportion of sheath/stem in the diet during summer was significantly greater than that of the other seasons (ANOVA $F_{7,72} = 9.85$, $P = 0.001$, Tukey HSD). The proportion of leaf in the diet was significantly lower during summer than during the other seasons (ANOVA $F_{7,72} = 26.49$, $P = 0.001$, Tukey HSD).

The Shannon-Wiener Index (H') of diversity was calculated for plant species in the diet (Figure 4.22). Dietary diversity was lower in winter than in summer. The greatest diversity occurred during autumn '96, though this appears to be a departure from the seasonal trend.

4.4 DIETARY SELECTIVITY

4.4.1 General

The degree to which common wombats 'selected' food resources from those resources available to them was determined by comparing the proportions of various food classes in their diet to their proportions in the field. Selectivity for food resources was considered at two levels: Firstly, how selective were wombats in their overall feeding? That is, from the range of potential food classes available to wombats (considered in this study to be herbaceous plant species), how did their overall level of utilisation differ from their availability in the field? Secondly, from those food classes eaten, how strongly was each individual food class selected for? In describing the overall selectivity of wombats in feeding, the first level is also describing the (dietary) niche breadth.

Various indices have been proposed to describe a species' overall use of resources relative to their availability (Levins 1968; Colwell and Futuyma 1971; Schoener 1974; Hurlbert 1978; Petraitis 1979). However, these indices either suffer from unrealistic assumptions about the availability or use of resources, or they do not take into account the number of resources available, or the biological meaning of the index is not readily understood.

The simplest way to compare the overall use of resources with their availability is to sum the absolute value of the differences between the proportion of each resource utilised and its proportion in the field. For a wombat's selectivity in feeding the equation is:

$$S = \sum |R_i - P_i|$$

where S is the level of 'selectivity', R_i is the proportion of food class i in the diet and P_i is the proportion of food class i in the field. Note that not all food classes considered have to be eaten, thus R_i also represents food classes potentially eaten. This index ranges from 0 for completely unselective feeding, to values approaching 2 for highly selective feeding. Multiplying by 0.5 gives a more convenient range of 0 to 1:

$$S^* = 0.5 \sum |R_i - P_i|$$

This index simply corresponds to the area of intersection between two frequency distributions, which Feinsinger *et al.* (1981) consider to be the most appropriate measure comparing resource utilisation and resource availability, and hence niche breadth. Their 'Proportional Similarity Index' (PI) of niche breadth:

$$PI = 1 - 0.5 \sum |R_i - P_i|$$

is identical to S^* except that the direction of the index is reversed; it ranges from 0 for the most narrow niche (maximum selectivity) to 1 for the broadest niche (zero selectivity or random feeding). Both indices return a single value corresponding to the overall selectivity or niche breadth, for a particular diet.

Describing the extent to which a wombat has selected for any individual food class is more difficult, and, again, many indices have been proposed since Ivlev's (1961) forage ratio. Lechowicz (1982) provides a review of the main selectivity (or electivity)

indices and concludes that none are perfect. Simply comparing the proportion of a food class in the diet to its proportion of all food classes utilised in the field (Ivlev's forage ratio R_i/P_i , or Ivlev's Electivity index $(R_i-P_i)/(R_i+P_i)$ does not take account of the importance of its contribution to the diet. For example, a selectivity value of 0.5 means that the food class was twice as prevalent in the field as in the diet, yet this could equally apply to a rare plant of which little was eaten or to the most common plant in the field that formed the dietary staple. The simplest solution is to express the difference between the two proportions as a proportion of the relative abundance of that food class in the field, ie.: $(R_i-P_i)/P_i$. However, this results in the undesirable range of -1 (maximum selection against) to +infinity (maximum selection for), rather than the ideal -1 to +1. It appears that no simple equation will satisfy both criteria of accounting for the relative abundance of resources and a symmetric range around 0 (no selectivity) of -1 to +1.

Although intuitively more difficult to understand, the electivity index E^* , proposed by Vanderploeg and Scavia (1979) has the properties of taking into account the relative abundance and number of all food classes in the field, and has the convenient range of -1 to +1 with 0 for random feeding. Their equation is:

$$W_i = (R_i/P_i) / \sum(R_i/P_i)$$

$$E^* = [W_i - (1/n)] / [W_i + (1/n)]$$

where n is the number of food classes. This index is essentially an Ivlev forage ratio normalised so that the sum of all such ratios in a sample equals one (the W_i part of the equation) and then modified to give a range of -1 to +1 (E^*). Lechowicz (1982) considers E^* to be the overall best, but not perfect, electivity index. He states that the index may be thought of as representing the feeder's perception of the value of a food type in relation to its abundance and the other food types available.

All measures of selectivity suffer to some degree from sensitivity to small sample sizes (such as those of rare food items). No matter how intensive the sampling effort, some food classes will tend to be rare in both the diet and the field. Comparing these very small values often results in ridiculously extreme selectivity values. To overcome this problem a subjective "cutoff" level was given to sample size; food classes representing less than 0.5% of both the diet and field proportions were considered to be

insufficient to demonstrate selectivity and so proportions were assigned equal values in the analysis by making the field proportion equal to the dietary proportion. A food class present in the diet but not detected in the field indicated that this food item was rare in the field and so to include it in the analysis it was assigned a small (0.5%) field proportion.

4.4.2 Selectivity and Feeding Areas

As mentioned in the preceding section, determination of feeding selectivity requires knowledge of food resources available and food resources eaten. The presence of three habitat types at the Riamukka study site complicated the assessment of feeding selectivity for wombats. Each of the three vegetation areas differed to some extent in the species composition and abundance of the ground-level vegetation. Therefore, any 'overall' or 'mean' measure of the availability of food resources for the study area will be dependant on the proportions of each of the three areas included in the measure (the proportions of these areas included in the study site was to some extent arbitrary). Moreover, wombats might not be using each area equally for feeding. Home-ranges of common wombats at Riamukka SF (Chapter 5) included each of the three stratified vegetation areas (Cleared, Woodland and Forest). These areas were therefore potential feeding places for wombats, and this was confirmed by opportunistic observations of individuals feeding in these areas. However, I was not able to determine the proportion of time individuals spent feeding in each of the areas by either observation or home-range analysis. Nocturnal observation of behaviour (including feeding) was difficult, and proportions of time spent in each of the three areas as determined from home-range analysis might not reflect feeding times in these areas. In order to examine levels of feeding selectivity and overcome problems of assigning proportions of areas to the analysis, the proportions of food classes in the diet was compared to the proportions of food classes in each of the three potential feeding areas. That is, I compared the diet of common wombats at Riamukka separately to each habitat, though it should be remembered that wombats most likely fed in more than one area.

4.4.3 Selectivity Results

The proportional similarity index (*PI*) comparing plant species in the diet to plant species in each of the three areas is shown in Figure 4.23. The effect of area and season on the feeding selectivity for plant species was assessed by ANOVA. Common wombats exhibited significantly higher levels of overall feeding selectivity (lower *PI*) in summer than in winter ($F_{7,216} = 26.18$, $P < 0.001$, Tukey HSD), though feeding selectivity was not significantly different between areas ($F_{7,216} = 0.72$, $P = 0.49$). The significant area \times season interaction ($F_{14,216} = 1.76$, $P = 0.046$) indicates that the seasonal pattern in the level of feeding selectivity was not the same for all areas. The most noticeable departure in the seasonal trend occurred in the Cleared area during autumn '96 and to a lesser extent during summer '95, when *PI* values were higher (lower selectivity) than for the other areas.

The proportional similarity index (*PI*) comparing plant groups (grass, sedge, forb, *Lomandra*) in the diet to plant groups in each of the three areas is shown in Figure 4.24. The effect of area and season on the feeding selectivity for plant groups was assessed by ANOVA. Wombats exhibited significantly higher levels of feeding selectivity (lower *PI*) in the summer than in the other seasons ($F_{7,216} = 23.16$, $P < 0.001$, Tukey HSD $\alpha = 0.025$) and higher levels of selectivity for the Cleared area than for the Forest ($F_{7,216} = 3.90$, $P = 0.02$, Tukey HSD $\alpha = 0.025$). The strong area \times season interaction ($F_{14,216} = 5.56$, $P < 0.001$) indicates that the seasonal pattern in the levels of *PI* was not the same for all areas. This interaction was most likely due to the relatively strong seasonal effect on *PI* for the Cleared area and the weak seasonal effect on *PI* for the Forest. The relationship between *PI* and Shannon-Wiener Diversity Index (H') for the ground-level plant species in each of the three vegetation areas is shown in Figure 4.25. Least-squares linear regression analyses indicated that dietary niche breadth (*PI*) and plant diversity (H') were not significantly correlated for the Forest ($R^2 < 0.00$; overall significance of regression, $P = 0.82$), but were significantly negatively correlated for the cleared area ($R^2 = 0.64$; overall significance of regression, $P = 0.017$) and for the Woodland ($R^2 = 0.83$; overall significance of regression, $P = 0.002$). The lack of correlation for the Forest area was probably due to the lack of seasonal variation in ground-layer vegetation in this area.

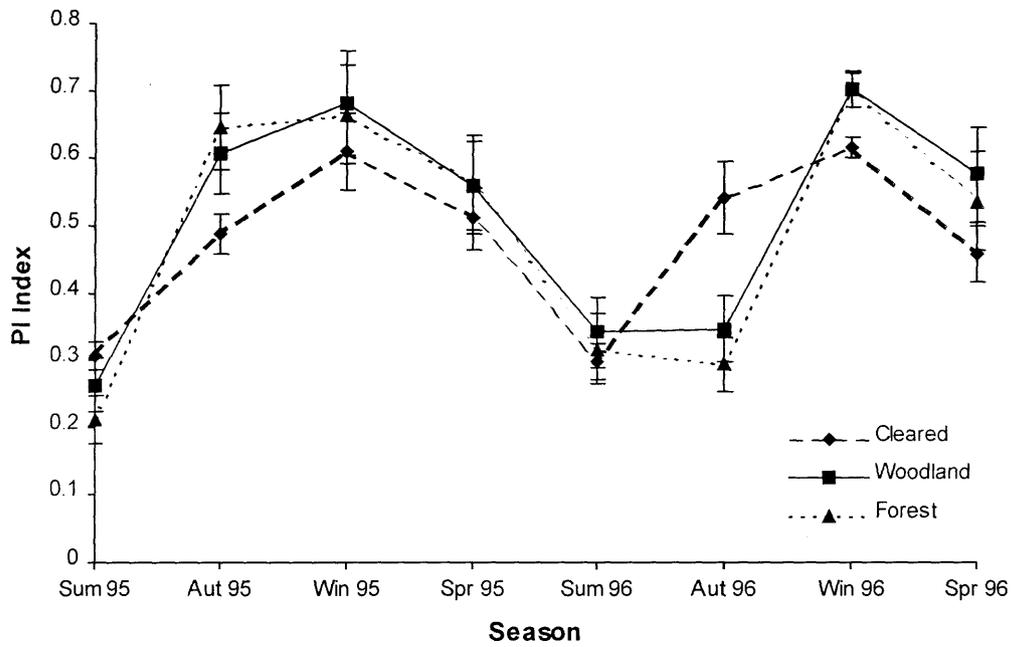


Figure 4.23 The Proportional Similarity Index (PI) for selectivity in overall feeding for plant species by common wombats in the three vegetation areas at Riamukka State Forest.

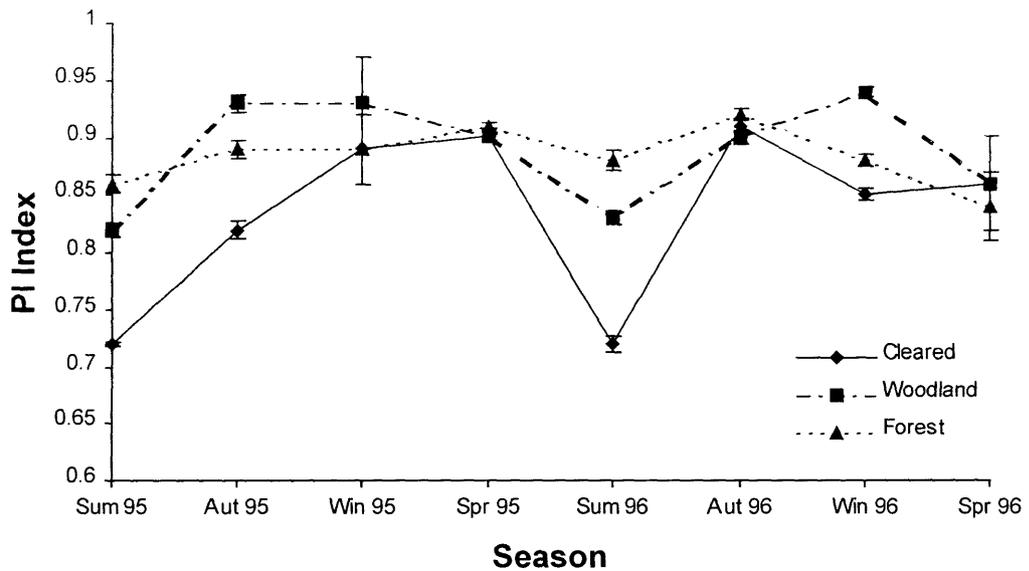


Figure 4.24 The Proportional Similarity Index (PI) for selectivity in overall feeding for the major plant groups by common wombats in the three vegetation areas at Riamukka State Forest.

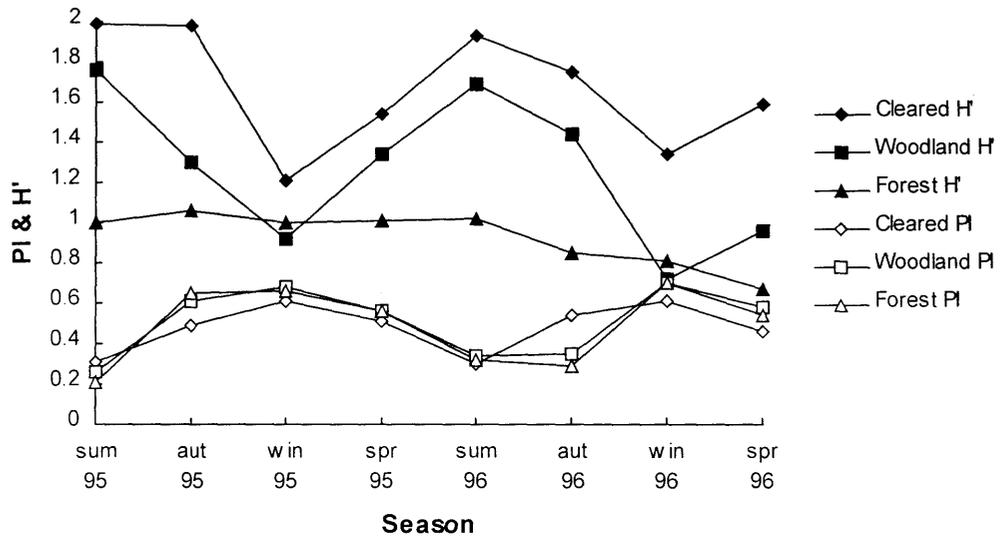


Figure 4.25 The Proportional Similarity Index (PI) for selectivity in overall feeding for plant species by common wombats and Shannon-Wiener Diversity Index (H') for ground level plant species in the three vegetation areas at Riamukka State Forest.

Electivity (E^*) indices for individual species groups are given in Appendix 6. Amongst the grass species, wombats demonstrated positive selection for some species and negative selection (ie. selection against) for other species. Wombats showed positive selection for *Microlaena stipoides* year-round in all three areas. *Poa* species were selected for in all seasons in the Cleared area, and during all seasons except spring '95 and summer '96 in the Woodland and Forest areas. Positive selection was shown for *Holcus lanatus* in all areas and in all seasons except summer '95 and winter '95, when it was selected against in all areas. Positive selection was also shown for *Danthonia racemosa* in all areas and in all seasons except summer '95, when it was selected against in all areas. In all three areas, *Dactylis glomerata* was selected for in summer '96, autumn '96 and winter '96, but not in other seasons. Negative selection was shown for all other grass species, strongly so for *Paspalum dilatatum*, *Bromus hordeaceus* and *Deyeuxia mesathera*. Wombats selected for sedge species in all areas from autumn '95 to summer 96, with the strongest selection shown in all three areas in spring '95. Although the diet of wombats included a small proportion (<1%) of forbs, negative selection was shown for these species during all seasons in all areas.

4.4.4 Food Quality and Dietary Choice

Regression analyses were used to examine the influence of the measured nutrient parameters (nitrogen content, NDF, hemicellulose, cellulose, lignin and silica) on the proportions of plant species in the diet, the proportions of 'food items' (plant parts from each species) in the diet, and the levels of feeding selectivity (E^*) for individual plant species. Only plant species for which nutrient analyses have been conducted were included in the analyses. Due to time constraints, the biomass (and hence availability to wombats) of different plant parts for each species in the pasture was not assessed. Therefore, while the influence of nutrient parameters on plant parts in the diet could be assessed, the influence of nutrient parameters on feeding selectivity for plant parts of plant species could not.

Each of the nutrient parameters were separately regressed on either dietary proportions of plant species, dietary proportions of plant parts, or feeding selectivity for plant species. None of the nutrient parameters by themselves significantly explained the

variation in the dietary proportions or feeding selectivity. Multivariate regression models that included various combinations of the nutrient parameters also did not significantly explain the proportions of different plant species or plant parts in the diet, nor feeding selectivity for plant species.

4.5 DISCUSSION

4.5.1 Food Availability and Quality

Summary of availability

Biomass of the herb layer at Riamukka was greater during summer than winter and, of the three areas stratified on vegetation structure, the woodland had the greatest biomass and the cleared paddock had the lowest. Species composition of the ground level vegetation was dominated by grasses during all seasons, mostly *Poa labillardieri*, *P. sieberiana*, *Microlaena stipoides*, *Dactylis glomerata*, *Lolium rigidum* and *Holcus lanatus*, though the relative proportions of these species varied seasonally.

Water Content and Nutritional Quality

The lack of significant difference in moisture content of plant species in the diet between winter and summer at Riamukka (and in fact a trend for higher moisture content in winter) is contrary to expectations based on rainfall patterns. This lack of difference may be a result of lower evapotranspiration during the cooler season which compensates for the slightly decreased winter rainfall leading to relatively constant soil moisture between seasons.

The gross energy contents of the main plant species in the diets of wombats are consistent with the values recorded by Nagy *et al.* (1990). Nutritional quality (as defined by the content of nitrogen, fibre and silica) varied widely between plant species. For example, clover (*Trifolium repens*) was high in nitrogen, low in fibre (NDF, ADF) and silica, and moderate in lignin and cellulose. Conversely, *Poa* spp. were low in nitrogen, high in cellulose, fibre (NDF, ADF) and silica, and would conventionally be considered to be of lower nutritional quality than clover. Broadly, grasses and other monocots

differed from forbs in their fibre (NDF, ADF) and silica content. Even amongst grasses, values of nutritional parameters varied widely, with species such as *Lolium rigidum* and *Dactylis glomerata* being of (conventionally) higher quality than species such as *Poa* or *Themeda australis*. Seedhead of *Poa* spp., however, appeared to be higher in energy content than that of other grass species. Despite seasonal differences in temperature and to a lesser extent rainfall, there did not appear to be a consistent seasonal trend in the nutrient parameters measured across all plant species sampled.

4.5.2 Previous dietary studies of wombats

There have been few studies of the diets of wombats, and none have evaluated selectivity in detail. Mallett and Cooke (1986) found that the diet of common wombats consisted of mostly monocots (grasses, sedges and *Lomandra*). Grasses formed the bulk of the diet but sedges comprised the greater proportion during some seasons in places where grasses were less abundant. Common wombats also consumed significant proportions of *Lomandra effusa* and clover. McIlroy (1973) observed common wombats feeding and concluded that the diet consisted largely of grasses, mostly *Danthonia* and *Themeda*, with other species such as *Lomandra* and clover being eaten. Rishworth *et al.* (1995) found the dominant food eaten by common wombats in *Pinus radiata* plantations was grasses, but that rushes, bark, roots and pine needles were also eaten in places where grasses were less common. Southern hairy-nosed wombats are also apparently grazers of monocots, eating primarily grasses such as *Stipa* spp. at Brookfield CP (Wells 1973; Lehmann 1979), though the succulent leaves of saltbush (*Maireana* sp.) at this site are also occasionally eaten during the dry summer (pers obs). Mallett and Cooke (1986) concluded that wombats preferred monocots that were 'coarse and fibrous', and state that wombats have been observed to scour (watery faeces) if fed a diet that is too succulent.

4.5.3 Diet

The results of this study indicate that common wombats are grazers, eating almost exclusively monocot species. Grass species dominated the diet during all seasons; forbs comprised less than one percent of faecal material, and tree or shrub species were not detected in the diet. Important food species for common wombats were *Poa*

labillardieri, *Poa sieberiana*, *Microlaena stipoides*, *Danthonia racemosa*, *Lolium rigidum*, *Dactylis glomerata* and *Holcus lanatus*. The slender, wiry-leaved *Poa* tussock grasses provided the dietary staple. Thus, despite tooth-to-tooth plucking, wombats were not taking only short, broad-bladed grasses.

Common wombats ate a range of above-ground plant parts, including monocot sheath/stem and seedhead. Common wombats ate mostly monocot leaf, with proportionately more leaf and less sheath/stem being ingested during the winter months. Monocot seedhead was an important dietary item when available. Forb reproductive parts (flower, seed, fruit) were not detected in the diet, suggesting that these dietary items are eaten only rarely or not at all. It is possible that wombats may have eaten subterranean plant parts (roots, tubers), but that these did not show up in the dietary analysis because of a lack of distinctive epidermal structure. It is likely, however, that large quantities of root tissue would have been detected in the microscopy analysis.

The very high proportion of leaf compared to sheath and stem in the diet of common wombats more closely resembles the diets of the macropodid grazers (Dawson 1989; Evans and Jarman 1999) than the diets of eutherian grazers (bovids and cervids) which include more stem and sheath (Gwynne and Bell 1968; Dunham 1979). The high proportion of leaf in the diet could indicate selection for this plant part, but might also be due to the high proportion of *Poa* spp. in the diet which are 'leafy' grass species.

The intake of seedhead was substantial during both summers, and was unexpected, given that wombats have a wide bite and are usually considered to be predominantly folivorous. A high proportion of plant reproductive parts in the diet is generally associated with smaller herbivores, which tend to have higher metabolic rates and correspondingly higher requirements for food items concentrated in easily-digested carbohydrate (see chapter 1). In this respect, the diet of common wombats would appear to be more closely aligned with species of smaller body weight, and with species of the Macropodidae (kangaroos and wallabies) which have also been shown to consume high proportions of seedhead (Jarman 1994; Evans and Jarman 1999). The seasonally high proportion of monocot seedhead in the diet of wombats is in contrast to that of eutherian grazing herbivores of similar mass to wombats, whose diets tend to be predominantly folivorous (although bovids and cervids do eat fleshy fruits and large seedpods) (Jarman

1994). It is likely that seedhead in the diet was from *Microlaena stipoides* and *Poa* spp. which were the most abundantly available in the pasture. *Poa* seedhead had the highest concentration of gross energy of all plant items sampled, but it was not particularly nitrogen-rich and had the highest proportion of silica of all items sampled. *Microlaena* seedhead was moderate in gross energy, reasonably high in nitrogen (protein) and low in lignin and silica. Ingesting, high proportions of these seedheads would provide a source high in protein and possibly energy, but are also high in silica.

Despite a huge reliance on grasses, the diet showed substantial seasonal variation. Dietary diversity increased as pasture diversity increased, indicating a diet largely reflecting availability. Clover was abundant at the site, but was not detected in the diet. The powerful dental mill of wombats combined with the susceptibility of clover epidermis to digestive breakdown (Slayter and Jones 1971) suggests that if clover was eaten it might not be detected in the faeces (but see section 4.1.4). If clover was ingested in proportion to its abundance in the field, this dietary item could have represented 13% of the diet in some seasons.

The diet of common wombats in this study is broadly similar to that reported in other studies. A contrast to other studies was the absence of clover from the diet and the presence of *Lomandra* as just traces in this study. Site descriptions suggest that the availability of grasses to wombats may have been greater at Riamukka SF than in the other areas studied, and this might account to some extent for dietary differences. However, the absence of clover in the diet of wombats in this study is puzzling given its apparent availability and its presence in diets from other studies. Clover is also not frequent in the diets of kangaroos at this site (Jeffery 1996).

4.5.4 Selectivity

Common wombats ate a wide range of plants in the herb layer at Riamukka, but they are not indiscriminant feeders. Rather, common wombats demonstrated moderate selectivity for food items. Positive selection was shown for monocots and negative selection for forbs. Grass species were eaten in broadly similar proportions to their abundances in the field, but with moderate to strong selection or rejection of a few species. Common wombats potentially fed in all three stratified vegetation areas, as all

areas were included in their home-ranges (Chapter 5). Comparing the diet to each area indicated that if wombats had fed in each area, they maintained a similar level of overall feeding selectivity (Proportional Similarity Index) between areas. In other words, the diet did not reflect the plant species in one area more than in another. This is despite the areas differing to some extent in their plant species composition.

Feeding selectivity (and hence dietary niche breadth) did, however, vary seasonally. Despite an increase in the diversity of species in both the pasture and the diet during summer, the PI fell, indicating that feeding selectivity of wombats also increased (resulting in a narrower dietary niche breadth). Simply looking at dietary proportions to infer which species are being selected for or against (rejected) can be misleading, as selectivity also depends on relative abundances of potential food species in the pasture at the time. The E* Index for feeding selectivity for individual plant species (appendix 4) suggests that the higher summer selectivity was partly due to higher selectivity for *Poa* spp. (despite comprising a lower proportion of the diet at this time), *Microlaena stipoides* and grasses in the 'Other Grasses' category, and greater rejection of Sedges and grasses such as *Themeda australis*, *Holcus lanatus* (despite the higher proportion in the diet at this time), *Dactylis glomerata* and *Dichelachne rara*. The results of this study indicate that feeding selectivity for a particular plant species may change seasonally, and that this seasonal pattern may change between years. In addition, if the diet was obtained from more than one habitat (and there is some evidence that this was the case), their level of selectivity for individual plant species would have varied depending upon habitat. Such variation between seasons, years and areas in feeding selectivity means that identifying 'preferred species' for wombats was not simple, and highlights the importance of the relative abundance of other species at a given time and place.

Common wombats at Riamukka ate a mixture of high and low quality food items. Notably, wombats ate a high proportion of the abundant but low-quality *Poa* spp, and indeed, showed selectivity for this species. This genus appears to be the staple food for wombats at Riamukka SF. These *Poa* tussock spp. are avoided by cattle and sheep (pers obs) and are regarded by Graziers in the region to be poor quality forage. The nutritional analyses conducted as part of this study support this assertion. Common wombats were also selecting for, and eating substantial quantities of, some native species that are

conventionally regarded as being nutritionally good, such as *Microlaena stipoides*. Factors influencing choice of dietary items by herbivores is notoriously complex, though for ruminants such choice is often attributed to the relative proportions of fibre, carbohydrate and protein. The picture is further complicated by the presence of plant defences to herbivory and the need for a herbivore to obtain a nutritionally balanced diet. The nutritional parameters measured in this study did not explain the proportions of different items in the diet, nor feeding selectivity for these items. Although not examined as part of this study, selectivity at the level of individual plant species and plant part might provide a better insight into relationships between dietary choice and nutritional quality. It should be noted that multiple regression analyses combine variables linearly, though it is not known if a linear combination of nutritional parameters is an appropriate model for explaining dietary choice in herbivores. It is clear that wombats are flexible in the food resources able to be utilised, enabling them to vary their diet in response to seasonal pasture composition.

4.5.5 Summary

Riamukka has a seasonal environment, affecting pasture growth and quality. Pastures were dominated year round by snow grasses (*Poa* spp.) which were lower in nutritional quality than almost all of the other species present. Common wombats were found to be grass specialists, with the dominant *Poa* spp. providing the dietary staple. Despite a huge reliance on grasses, the diet showed substantial seasonal variation, with diversity of both diet and pasture being higher during summer than winter. Wombats were moderately selective feeders, and demonstrated higher selectivity (narrower niche breadth) when pasture diversity was highest (summer). The nutritional parameters measured in food items did not significantly explain the variations in the diet or in feeding selectivity.