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Selection by Grazing Sheep of Pasture Plants at Low Herbage Availability and Responses of the Plants to Grazing

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Abstract

Merino sheep grazing annual pasture at the beginning of the growing season when the amount of herbage on offer was small, preferred to graze Wimmera ryegrass *Lolium rigidum* or subterranean clover *Trifolium subterraneum* rather than capeweed *Arctotheca calendula*, and *Erodium botrys* was avoided completely. Behaviour observations showed that capeweed plants were usually avoided. When the plants were grasped they were sometimes pulled up by the roots and then dropped so that the number of capeweed plants in the pasture declined. Supplementation with oats reduced grass intake. Harvesting behaviour changed with pasture conditions: as grass height declined in the pasture, the rates of biting, stepping and head swinging increased.

Pasture measurements showed that, whilst capeweed plants continued to increase in height during grazing, as did ungrazed controls, ryegrass and clover plants decreased or remained short. Herbage dry matter increased in all species, owing especially to basal growth. The proportion of shoots and petioles which were erect increased in ungrazed plants, but the proportion which were prostrate was much greater in grazed plants. Individual plants adapted their growth form in a way which counteracted the depredations of grazers.

The ecological implications of these findings are important. Firstly, the sheep were not foraging optimally in terms of maximising rate of intake, since two abundant species were largely ignored even though food availability was low. Secondly, because of their selectivity the sheep were giving the capeweed and *Erodium* a competitive advantage which, in these pastures, will persist through the growing season.

Introduction

Like other large grazers, a sheep is able to modify various aspects of its grazing behaviour according to the characteristics of the pasture which it is grazing. A series of decisions must be taken about which plant, or part of plant, to eat, how large a bite to take, how fast to bite, how soon to move on, etc. (Broom 1981, p. 150). Since rate of processing in the gut often limits intake, large generalist hervibores should be selective in feeding so that the optimal nutrient mix within a given total bulk of food can be obtained (Westoby 1974). Hence, as Watkin and Clements (1978) point out, given the opportunity all grazing animals are selective in their diet. Such statements do, however, raise the question of what the animal will do at low levels of herbage availability when rate of processing may not limit intake. Will it be selective and hence energetically less efficient? In this study, food selection by Merino sheep was assessed at the beginning of the growing season on annual pasture in Western Australia, at which time it is generally considered that sheep are unselective. It is well known that, in the study area, pastures seeded with ryegrass *Lolium rigidum* and subterranean clover *Trifolium subterraneum* and

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grazed, include increasing proportions of capeweed *Arctotheca calendula* and sometimes *Erodium botrys* as they age. The question of whether such changes are attributable in part to differential grazing of the species by sheep was investigated by measuring behaviour, monitoring pasture composition and taking fistula samples during the first 6 weeks after introduction to the pasture.

The regular monitoring of plants in grazed and ungrazed pasture also made possible a study of some of the responses of the pasture plants to grazing. Phenotypic changes in pasture plants as a consequence of grazing include changes in growth form (Hickey 1961; Jameson 1963; Kydd 1966) or reproductive season (van Dijk 1955; Brougham and Harris 1967; Charles 1972), the production of chemical defences (Arnold and Hill 1972; Harborne 1982; Crawley 1983), the development of physical defences such as thorns (Abrahamson 1975) and mechanical changes which make the plant tougher (Vincent 1982). Individual plants may also be able to respond to grazing by changing growth rate (Vickery 1972; McNaughton 1983). The growth form was recorded during this study by assessing the extent to which growth was upright or prostrate.

Methods

The pasture studied at the CSIRO Yalanbee Experimental Station, Bakers Hill, W.A., was seeded with a mixture of Wimmera ryegrass *Lolium rigidum* and subterranean clover *Trifolium subterraneum* (cv. Daliak) in May 1983. Two pairs of 0·45 ha paddocks were used, 1 and 2 being 50 m away from 3 and 4, but only paddock 1 was studied in detail. They reached a level of herbage availability at which grazing was possible on 12 July. Two weeks before grazing commenced 12 square wooden frames enclosing 0·25 m^2 of pasture were sunk into the ground in paddock 1 so that the top of the frame was at ground level. This was carried out with minimal disturbance to the herbage, and it allowed the precise identification of small areas. These frames were distributed around the paddock in a regular way such that their contents would be representative of the whole paddock. Two frames were protected from grazing by a wire cover which prevented sheep from touching the plants within the frame but did not affect rain or sunlight falling on the herbage. One of these covers was dislodged by sheep after one week, so data from only one ungrazed frame are presented. Each paddock was stocked with four Merino ewes with a mean weight of 51·2 kg on 12 July, a stocking density of 8·8 ewes ha^{-1}. The ewes remained in the paddock until after the final observations on 27 August.

Pasture Measurements

Pasture changes monitored in paddock 1 were: plant numbers, extended plant height, herbage dry matter (h.d.m.) per unit area and plant growth form. Plant numbers were counted on the day before grazing commenced and at weekly intervals for 5 weeks, whilst plant height and h.d.m. were measured on these days and for one additional week. Two 1 dm^2 areas in each frame were found by measurement from points on the frame in exactly the same way each week, and the area to be counted delineated by a 1 dm^2 three-sided wire frame which could be inserted under vegetation at ground level. All plants whose stem, rosette centre or tiller base was within the 1 dm^2 area were counted. The species present were Wimmera ryegrass *Lolium rigidum*, subterranean clover *Trifolium subterraneum*, capeweed *Arctotheca calendula*, and silvergrass *Vulpia myuras*. The decision as to what to count as one plant was always easy for the clover and capeweed but, for the grasses, adjacent tillers were counted as one plant if movement of one tiller resulted in the other being moved. Extended plant height measurements were taken in 25 by 3 cm strips measured within each of the frames. One strip per frame was measured, except in the ungrazed frame where three strips were measured in the last 2 weeks. The longest leaf of each plant rooted within that strip was measured by holding it perpendicular and marking its tip position on graph paper attached to a board. Those leaves which grew vertically but whose upper regions were bent over towards the ground would usually have been readily available to the grazing sheep, but prostrate tillers would have been harder for sheep to take. Hence the figure for mean extended plant height is an overestimate of actual height above ground where many tillers were prostrate.

Herbage production in paddock 1 was assessed by sampling 3 dm^2 at two sites selected by throwing a marker in a random way before grazing commenced and in weeks 1–4. In week 5 four sites were chosen in this way, and on week 6 the two 1 dm^2 study areas in each frame were cut, together with an additional 4 dm^2 in the ungrazed frame. Each 1 dm^2 sample was marked out using the three-sided wire frame and cut with scissors along the wire so as to include all material which lay within the frame. Each plant was then cut at ground level and all plant material was transferred to a plastic bag. The 1 dm^2 area on either side was cut and kept in the same way. All samples were separated according to plant species and dried overnight at 80°C.

The extent to which plant growth was prostrate or erect was assessed before grazing in two 0·5 dm^2 areas in the covered frame, in the same two areas 5 weeks later and in eight 0·5 dm^2 areas in four of the grazed frames. The four grazed frames were selected because two were at one end of the field and the other two were at the other, whilst in each case the 0·5 dm^2 areas were the right halves of the two regularly counted 1 dm^2 areas. For all tillers or petioles more than 1 cm long on each plant, the angle made to the ground was assessed to within 10°. The angle assessed was that made by the shoot up to the first ligule in ryegrass, that made by the petiole in subterranean clover, and that made by the petiole and base of the midrib in capeweed.

Behaviour Measurements

The behaviour of the ewes in paddock 1 and in paddock 2 adjacent to it was observed from a 4 m high, partially enclosed platform situated just outside one of the common corners of the two paddocks. The observer used binoculars and recorded behaviour by speaking quietly into a tape recorder. No observations were recorded within the first 10 min after ascending to the platform, by which time the ewes had resumed undisturbed activities. Each bite taken, each step and head-swing could be detected and recorded. Sheep were observed in turn, and recording was initiated when the head was lowered to take a bite and terminated if the head was raised so that the back of the neck was horizontal or if more than six successive steps were taken. This allowed the calculation of rates of biting, stepping and head swinging. These rates were calculated on the first and second days of grazing, 10 days later and 15 days later for each of the eight ewes.

Ewes grazing within 20 m of the observer could be observed through binoculars in sufficient detail to allow the recognition of the plants within reach of the animal and the plants which were being ingested. A total of 77 min of such detailed observation, involving all eight animals, was possible during 9 h of behaviour observation on 12, 13, 22 and 27 July 1983.

Fistula Sampling Experiment

In order to monitor directly the plant species grazed on the pasture and to assess the effects of supplementation on food preferences, two wethers, each of which had been fitted with a rumen fistula some months earlier, were used. The animals were put into paddock 3 whose nearest corner was 50 m away from paddock 1 and which was similar to it except that it included *Erodium* as well as the other pasture species. A 250 ml fistula sample was collected 2 h later. The wethers were kept in this paddock until dusk and then housed in a small pen overnight with oats provided in a trough. The procedure of keeping the animals in one of the four paddocks during the daytime and in the small pen with oats supplement at night was repeated for 10 days, 15–25 August 1983. On days 3 and 10 of supplementation each animal grazed in paddock 3 and a 250 ml fistula sample was taken after 2 h. The fistula samples were thoroughly mixed by hand, a subsample taken and all green material separated into plant species under a microscope. Each plant species from the green material in the sample was dried overnight at 80°C and weighed. On the day after the second sample was taken a total of 100 samples of pasture were taken from paddock 3, separated into species, dried overnight at 80°C and weighed.

Results

Behaviour observations showed that the ewes grazed across the frames with no hesitation and there was no sign of differential plant growth inside and outside the frames. Thus data from the frames are presented as typical for the paddock.

Plant Growth

The number of grass plants present in the regularly monitored areas did not change during the experimental period, but there was a small increase in the number of subterranean clover plants due to germination in the first two weeks

(Fig. 1). The number of capeweed plants declined by 35·1% during the study, a result which the behaviour observations help to explain. Entire plants were found lying on the pasture on 11 occasions; on eight of these they were capeweed and on three ryegrass.

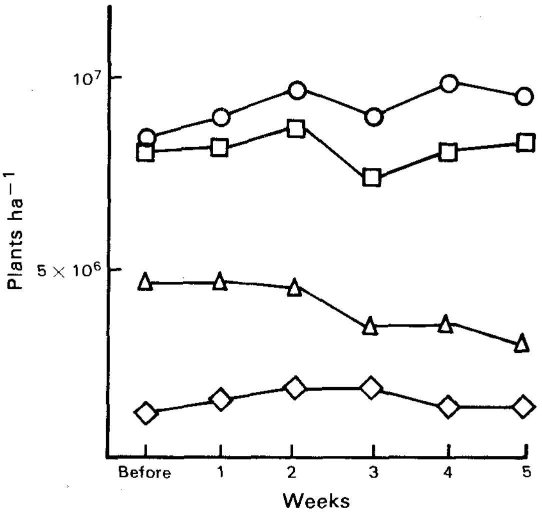

Fig. 1. Densities of plants present in the same 20 areas of pasture before grazing and in successive weeks of grazing. Significant changes before grazing *v.* week 5 (paired *t* test on differences) were: increase in subterranean clover, $P = 0{\cdot}04$; decrease in capeweed, $P = 0{\cdot}009$. ○ Sub. clover; □ ryegrass; △ capeweed; ◇ silvergrass.

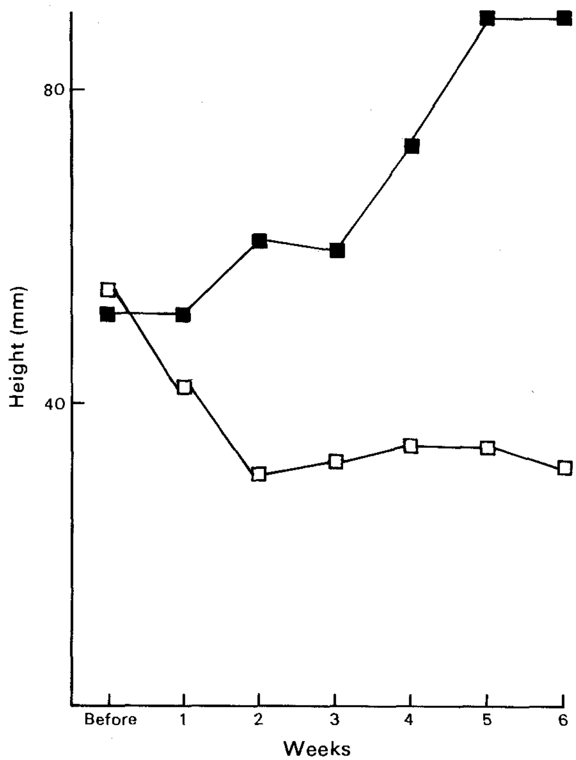

Fig. 2. Mean extended heights of Wimmera ryegrass plants in the same 25 by 3 cm strips of pasture before grazing, in successive weeks of grazing (□) and in ungrazed (■) pasture.

The mean extended height of the three main pasture plants increased in the ungrazed frame and that of capeweed also increased in the grazed areas (Figs 2 and 3). The mean extended height of Wimmera ryegrass declined during the first 2 weeks of grazing and then remained at 30–34 mm, whilst that of grazed subterranean clover remained at 13–20 mm throughout the experiment (comparisons of slopes of linear regressions, grazed *v.* ungrazed: ryegrass $P < 0 \cdot 001$, clover $P < 0 \cdot 001$, capeweed $P > 0 \cdot 05$). The significant differences between the grazed and ungrazed areas in the extended heights of ryegrass and clover, but not that of capeweed, show that the sheep were refraining from eating available capeweed. Many large capeweed plants but no tall grass or clover plants were present in the paddock at the end of week 6.

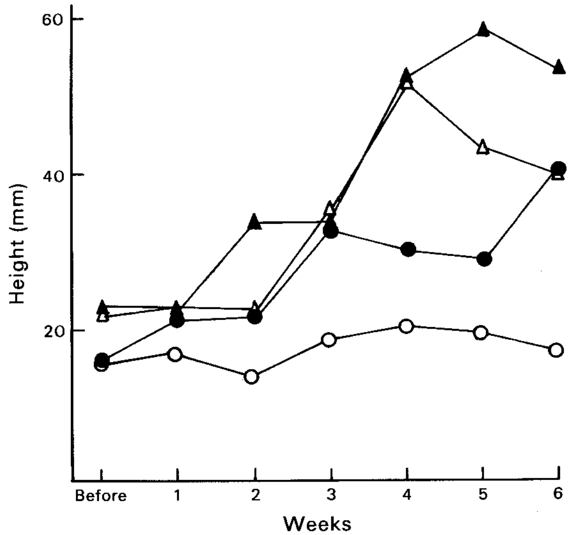

Fig. 3. Mean extended heights of subterranean clover (circles) and capeweed (triangles) plants in the same 25 by 3 cm strips of pasture before grazing, in successive weeks of grazing (open symbols) and in ungrazed (closed symbols) pasture.

Herbage dry matter of all species showed an exponential increase over the 6 weeks (Fig. 4). The slope for capeweed appears steeper, but this is not significant. Silvergrass plants were small but grow at the same rate as ryegrass. These results provide less information about the food preferences of the sheep because much of the weight increase was due to growth at the base of the plants and the majority of the plant material present was less than 20 mm from the ground and hence not normally consumed by the sheep. The mean total herbage dry matter on 11 July, before grazing, was 310 kg ha^{-1}. After 6 weeks of grazing it was 1460 kg ha^{-1} on the grazed areas and 2360 kg ha^{-1} on the ungrazed areas.

Plant Responses to Grazing

The angles to the ground made by shoots up to the first ligule of Wimmera ryegrass and by petioles of subterranean clover and capeweed are shown in Figs 5, 6 and 7. Ryegrass plants were already largely erect in mid July (median angle 80°), but both subterranean clover and capeweed became more erect by week 6 in the ungrazed area. The median angle increased from 35° to 70° in subterranean clover and from 20° to 50° in capeweed. Grazing for 6 weeks resulted in the presence of considerably more horizontal growth in all three species, with median angles of 0–10° for subterranean clover and capeweed and 25° for ryegrass. Since many new

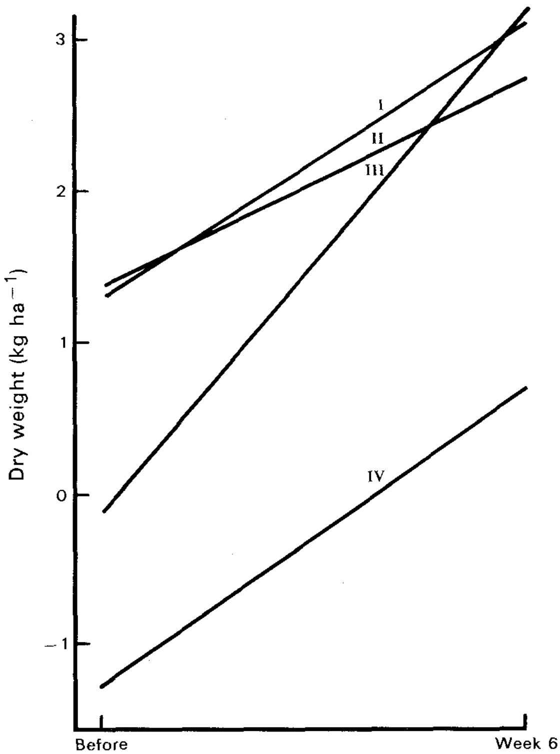

Fig. 4. Regression lines for the logarithm of the dry weight of herbage of each species before grazing and in the six weeks of grazing. The intercept of the regression for silvergrass differed from those for the other species (all $P < 0.01$).
I, subterranean clover; II, ryegrass; III, capeweed; IV, silvergrass.

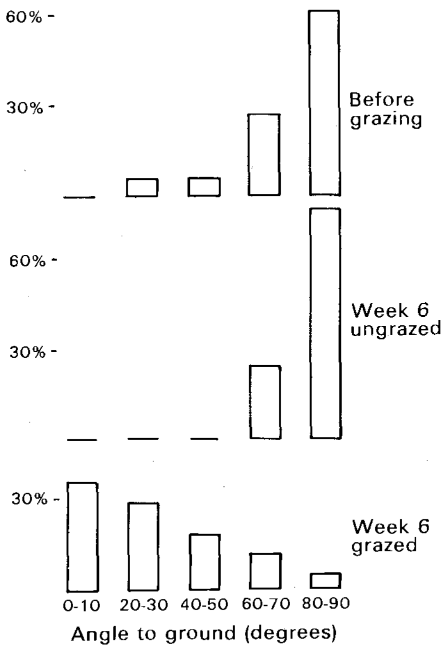

Fig. 5. The extent to which Wimmera ryegrass plants were prostrate or erect is shown as the percentage of tillers whose angles to the ground up to the first ligule were 0–10°, 10–20° etc.
Comparisons using chi-squared test:
before grazing *v.* week 6 grazed, $P < 0.001$;
week 6 ungrazed *v.* week 6 grazed, $P < 0.001$.

tillers and leaves were produced during this time, these must have been more likely to grow horizontally if the plants were being grazed. The change in growth form was especially pronounced in the Wimmera ryegrass in which there was a reversal from largely erect to largely prostrate tillers.

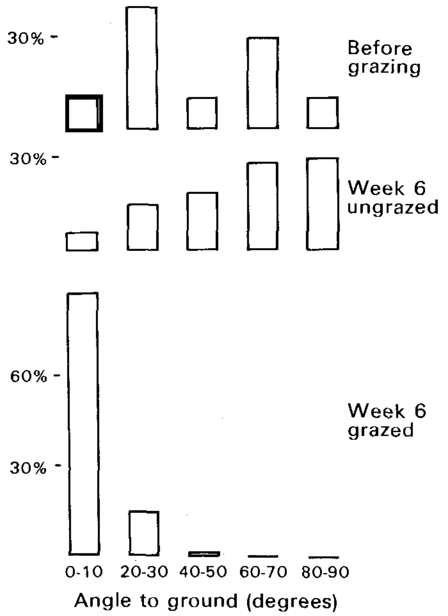

Fig. 6. The extent to which subterranean clover plants were prostrate or erect is shown as the percentage of petioles whose angles to the ground were 0–10°, 10–20° etc. Comparisons using chi-squared test: before grazing *v*. week 6 ungrazed $P < 0{\cdot}05$, before grazing *v*. week 6 grazed $P < 0{\cdot}001$, week 6 ungrazed *v*. week 6 grazed $P < 0{\cdot}001$.

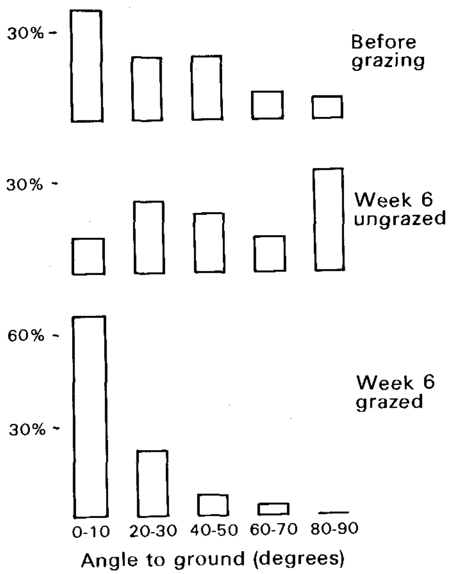

Fig. 7. The extent to which capeweed plants were prostrate or erect is shown as the percentage of petioles and bases of midribs whose angles to the ground were 0–10°, 10–20° etc. Comparisons using chi-squared test: before grazing *v*. week 6 ungrazed $P < 0{\cdot}02$, before grazing *v*. week 6 grazed $P < 0{\cdot}001$, week 6 ungrazed *v*. week 6 grazed $P < 0{\cdot}001$.

Grazing Behaviour

The eight ewes showed an increase in the mean rate of biting, the numbers of steps and the numbers of head swings per 100 bites from the first day of grazing to the end of the second week of grazing (Table 1). There was individual variation in behaviour, so paired t-tests were used on the data. During this period the mean height of clover and capeweed changed little but that of ryegrass declined.

Detailed observations through binoculars of ewes grazing close to the observation platform showed that the animals grazed most frequently in areas of grass and to a lesser extent in areas of clover. It was easy to see grass or capeweed being ingested, but harder to see the ingestion of clover. The faster nibbling movements associated with feeding on clover were normally distinguishable.

Table 1. Grazing behaviour of Merino ewes at two different pasture heights (Mean ± s.d.)

	Day 1 (12.vii)	Day 15 (27.vii)	t test
Length of longest leaf per ryegrass tiller (mm)	54·3 ± 15·1	30·4 ± 12·3	$P < 0{\cdot}0001$
Bites min^{-1}	66·9 ± 5·8	75·6 ± 7·2	$P = 0{\cdot}019$
Steps per 100 bites	9·4 ± 3·6	13·6 ± 3·2	$P = 0{\cdot}019$
Head swings per 100 bites	1·2 ± 1·0	2·7 ± 1·0	$P = 0{\cdot}05$

Almost all of the 77 min of detailed observation was spent taking grass or clover. Capeweed was observed to be taken on only eight occasions; on two of these the plants were very small, and on three other occasions the ewes walked on immediately after taking the capeweed. Capeweed was seen to be taken into the mouth and spat out twice, and capeweed plants were pulled up and dropped twice.

Table 2. Percentages by dry weight of plant species in pasture and in fistula sample

Species	Rye-grass	Sub. clover	Capeweed	*Erodium*	Silver-grass
In paddock	16·9	44·2	27·9	10·2	0·8
Animal A (unsupplemented)	18·3	78·9	0·6	0	2·2
Animal A (supplemented, took little)	11·4	76·6	11·4	0	0·6
Animal B (unsupplemented)	83·8	8·5	6·6	0	1·1
Animal B (supplemented, took much)	12·8	75·1	11·2	0	0·9

On 30 occasions involving each of the eight ewes, they were observed to avoid eating capeweed which was in the area of pasture which would normally have been grazed immediately in front of the animal. Sometimes the head was swung away from the capeweed, sometimes a step over capeweed was taken, sometimes grass or clover was selected from between capeweed plants, and sometimes capeweed leaves were pushed aside and clover taken from underneath them.

Contents of Fistula Samples

The two wethers used in this experiment grazed a paddock similar to that from which the pasture growth data were collected but which included a fifth plant species, *Erodium botrys*. The proportions by dry weight of the five plant species in the pasture and in rumen fistula samples taken shortly after feeding are shown in Table 2. The data from days 3 and 10 of supplementation were similar so were combined in Table 2. The two wethers differed in their species preferences before supplementation, but neither ever took any *Erodium*, and both took much less capeweed than would be expected from pasture composition. Observation of feeding and of fistula sample content showed differential intake of oats. Animal A ate principally subterranean clover, took little of the oats available to it, and scarcely changed its diet on pasture when the oats were available. Animal B ate principally ryegrass before supplementation, but consumed considerable quantities of oats and then switched the majority of its intake on pasture to clover.

Discussion

There is much evidence for selection amongst plant species whilst grazing by both domestic and wild sheep (e.g. Arnold 1964; Hoefs 1974). Preferences for forage plant species may change during the year (Davies 1964; Arnold *et al.* 1966; Arnold, unpubl.) and may differ according to the previous grazing experience of the animal (Arnold 1964; Arnold and Maller 1977). The first question considered in this study was whether Merino ewes would select amongst pasture plant species known to be edible when relatively little herbage was on offer. All three of the principal plants on this Western Australian annual pasture, Wimmera ryegrass, subterranean clover and capeweed, were initially at low levels of herbage dry matter per unit area of pasture, 310 kg ha^{-1} in total, and it was not until about the sixth week of grazing that the total herbage availability reached the amount necessary for ewes to obtain maximum food intake (1460 kg ha^{-1}, Fig. 4). There were considerable differences in the extended heights of the species after grazing. Both the grass and the clover were restricted to a height which was significantly lower than that in an enclosed, ungrazed area, but there was no such significant difference for capeweed which continued to grow taller throughout 6 weeks of grazing (Figs 1–3). Capeweed plants which were large compared with other species in the pasture were evident at the end of the grazing period. Behaviour observations showed that capeweed was often actively avoided and was sometimes dropped or spat out if taken into the mouth. There were few observations of capeweed being eaten, but very many of clover and grass being eaten. Analysis of the fistula samples confirmed that the amount of capeweed ingested by two wethers was considerably less than that which would be expected from pasture composition (Table 2). A further species, *Erodium*, which formed 10·2% of the herbage dry matter in the pasture grazed by the fistulated animals, was found not to have been ingested at all.

It has been suggested on the basis of studies using grass tillers protruding through holes in boards that sheep prefer to graze in localised sites where rate of food intake can be fastest (Kenney and Black 1984), and intake is usually greater on taller swards (Jamieson and Hodgson 1979). Taller plants are preferred unless plant density is very high (Black and Kenney 1984). The capeweed plants in our study were not rejected because of their small size, however, since their average height was always greater than subterranean clover plants, and they were taller than the Wimmera ryegrass plants on weeks 3–6. Height of grazing may differ according to species (Gammon and Roberts 1978), but some small capeweed plants were grazed and the larger plants were readily available to sheep. It is not known why capeweed was preferred less than the grass or clover and *Erodium* avoided completely. It was apparent from the behaviour observations that grass and clover were taken first, just as plants in the family Chenopodiaceae were avoided by sheep until grass had been eaten (Leigh and Mulham 1966) and ryegrass pasture treated with high levels of slurry was avoided by cattle until untainted pasture had been eaten (Broom *et al.* 1975). There may well be site-specific factors influencing the taste or smell of capeweed and *Erodium*, for in another site, both species were eaten in proportion to their contribution to the swards except in October (Arnold unpubl.). The plant species in the experimental paddocks were thoroughly mixed, so that most 1 dm^2 areas included all three species, but selection amongst species still occurred. Even amongst preferred plant species there is selection, and grazers may vary individually in this respect. The diets of individual red deer (*Cervus elephas*) varied in grass content from 5% to 80% (van de Veen 1979). One of the fistulated wethers in this study took principally subterranean clover (over 75% d.m. on each day), whilst the other took mainly grass. The second animal consumed oats supplement when it was offered and, after this, took little grass.

The movements involved in harvesting pasture plants change according to the characteristics of the pasture. The rate of biting increases as pasture height declines in cattle (Chacon and Stobbs 1976; Broom 1981, p. 155) and in sheep (Jamieson and Hodgson 1979; Penning *et al.* 1984). In this study, a decline of 44% in extended sward height, due entirely to changes in the grass, resulted in increases in bite rate of 13%, in rate of stepping of 14%, and in rate of head swinging of 22% (Table 1).

Another interesting behaviour observed was the dropping or spitting out of capeweed plants during grazing. This behaviour probably accounted for the records of plants, largely capeweed, found lying on the pasture and perhaps also for much of the decline of 35% in the number of capeweed plants in the regularly monitored areas. The uprooting of this non-preferred plant species will have the effect of improving the pasture by favouring the growth of the preferred species. Other herbivores such as some coral reef fish have been reported to weed their regularly visited areas by removing inedible plants. It is not known whether the sheep sought out the non-preferred species and removed them.

Pasture plants show a wide range of responses to grazing (Jameson 1963; Watkin and Clements 1978). The three major species in the pasture studied increased their dry matter weight above ground despite being grazed (Fig. 4). The amount of material in the basal areas of the plants appeared to have increased, but for Wimmera ryegrass and subterranean clover, there may have been no change in the amount of leaf, since this was harvested at a rate similar to its rate of production. The other change in the grazed plants was in the proportions of erect and prostrate shoots and petioles. As shown in Figs 5–7, grazed plants became more prostrate, whereas ungrazed plants became more erect during the 6-week study. The change in the ungrazed plants must have been due in part to competition between plants for light, but the change in the ryegrass from a median angle to the ground of 80° before grazing to 25° after grazing could only be due to responses of the plants to grazing. Increases in prostrate growth have also been reported by Hickey (1961), who studied cattle-grazed *Agropyron desertorum* in New Mexico, U.S.A., and Kydd (1966) who studied sheep-grazed *Lolium perenne* in Berkshire, U.K. The ability of individual plants to change their growth form when grazed is an important means of countering the depredations of grazers. The genotype must be able to grow upwards rapidly in order to compete effectively with other plants for light but adapt its growth form, and perhaps other characteristics, when grazed.

The results of this study have important implications concerning foraging behaviour in sheep. The biomass of pasture for all but the sixth week was too low for sheep to obtain their food requirements, and yet they were selective against species which would have increased their food intake. Since the energy value of all of the species is very similar in winter, the sheep were certainly not foraging optimally in terms of energy return.

The selective grazing described here also has consequences for pasture composition. The capeweed and *Erodium* would gain a competitive advantage, despite some drop in capeweed plant numbers, and increase their contribution to pasture yield. Many pastures in this area which have been grazed by sheep for several seasons have a large proportion of capeweed in them. In all of these pastures the composition at the end of the growing season is determined by composition in early August, and the higher the biomass at the end of the season the more seed a species is likely to produce to perpetuate its advantage. It is likely that the presence of more large capeweed plants would result in more capeweed seed for the next season.

Acknowledgments

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