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COMPARATIVE EVALUATION OF DIET SELECTION, HERBAGE INTAKE AND PERFORMANCE OF LAMBS GRAZING YORKSHIRE FOG (*Holcus lanatus* L.), PERENNIAL RYEGRASS (*Lolium perenne* L.) AND TALL FESCUE (*Festuca arundinacea* Schreb.) AND ASSESSMENT OF EFFECTS OF CONDENSED TANNINS (CT) IN THE GRASSES ON LAMB PERFORMANCE

A thesis presented in partial fulfilment of the requirements for the degree of Doctor of Philosophy at Plant Science Department of Massey University, Palmerston North, New Zealand.

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ABSTRACT

A series of grazing experiments was carried out at the Pasture and Crop Research Unit, Massey University, Palmerston North, New Zealand, to compare Yorkshire fog (*Holcus lanatus* cv. Massey Basyn)/white clover (*Trifolium repens* cv. Grasslands Tahora) with perennial ryegrass (*Lolium perenne* cv. Grasslands Nui)/white clover cv. Grasslands Tahora and tall fescue (*Festuca arundinacea* cv. Grassland Roa)/white clover cv. Grasslands Tahora pastures with reference to grazing behaviour, diet selection, herbage intake and performance of lambs, and to specifically assess the effects of low concentrations of condensed tannins (CT) in grasses on body growth and wool growth of animals. Half of the lambs were drenched with polyethylene glycol (PEG) (CT inactivated) and the remainder were drenched with water as a control (CT acting) in each experiment. PEG is assumed to specifically bind and inactivate CT without influencing the digestion of other nutrients.

In the first experiment, a comparative study of grazing behaviour, diet selection, herbage intake and performance of lambs grazing Yorkshire fog/white clover and

ryegrass/white clover swards was made from late May to late June, 1993. Thirty-six lambs, balanced in sets of six based on initial fasted weight continuously grazed paddocks with three replicates of the two pasture treatments for 7 weeks. Yorkshire fog had greater sward bulk density and intake per bite (68 vs 51 \pm 7.1 mg OM/bite) than ryegrass. Perennial ryegrass had a consistent superiority over Yorkshire fog in organic matter digestibility (OMD) (80 vs 77 \pm 0.3 %, $P \leq 0.05$) and herbage OM intake (1117 vs 930 \pm 31.5 g/day, $P \leq 0.1$), resulting in faster liveweight gain (174 vs 144 \pm 9.7 g/day), significantly higher carcass weight (17.7 vs 16.3 \pm 0.1 kg, $P \leq 0.05$) and dressing out % (49 vs 48 \pm 0.2, $P \leq 0.05$). Low CT concentrations (1.7 - 2.2 g/kg DM) were found in the diets selected from both the grasses; these low CT concentrations had no effect on grazing behaviour, diet selection and herbage intake. Small responses to PEG administration were observed in initial liveweight gain, but PEG had no effects on overall liveweight gain, carcass weight, carcass weight gain and GR (depth of total soft tissue over the 12th rib at a point 11 cm from the mid carcass).

The next two experiments were designed to compare Yorkshire fog cv. Massey Basyn/white clover cv. Grassland Tahora with tall fescue cv. Grassland Roa/white clover cv. Grassland Tahora pastures in terms of grazing behaviour, diet selection, herbage intake and performance of lambs, and to further quantify the effects of low CT concentrations in the grasses on lamb performance, especially on initial liveweight gain of lambs, under rotational grazing management in late spring, summer and early autumn, 1993/1994. The comparisons between Yorkshire fog and tall fescue pastures were made under similar sward conditions. Previous grazing experience on the appropriate pasture and sex were designed as treatments as well as pasture species and PEG supplementation. Forty-eight lambs balanced for previous grazing experience and sex in sets of sixteen were used in each experiment. One group of 16 was slaughtered as the initial group at the start of each experiment to measure the carcass weight. The other two groups of lambs grazed six paddocks of each pasture treatment in a 30-day rotation.

Tall fescue had higher total N than Yorkshire fog in early December (3.56 vs 3.43 ± 0.018 % DM, $P \leq 0.05$) and late February (3.24 vs 2.91 ± 0.022 % DM, $P \leq 0.0001$), and had higher OMD in early December (81 vs 78 ± 0.6 %, $P \leq 0.01$) and late February (72 vs 68 ± 1.1 %, $P \leq 0.05$), but lower OMD in early February (71 vs 74 ± 1.1 %, $P \leq 0.05$). Yorkshire fog produced faster liveweight gain (99 vs 76 ± 6.7 g/day, $P \leq 0.1$), greater carcass weight (14.7 vs 13.9 ± 0.2 kg, $P \leq 0.05$) and faster carcass weight gain (32 vs 20 ± 3.1 g/day, $P \leq 0.05$) than tall fescue in late spring and summer (Experiment 2), but not in late summer and early autumn (Experiment 3). Male lambs had faster liveweight gain than female lambs in Experiment 2 (95 vs 80 ± 3.3 g/day, $P \leq 0.05$) and in Experiment 3 (80 vs 72 ± 2.3 g/day, $P \leq 0.05$). Previous grazing experience had no effects on final liveweight gain, carcass weight, carcass weight gain. There was no significant effect of interaction between previous pasture and current pasture on these parameters.

The results of the experiments further confirmed the low CT concentrations (1 - 2.1 g/kg DM) present in Yorkshire fog in Experiment 1 and small responses of lambs to PEG supplementation in initial liveweight gain only in Yorkshire fog (101 vs 92 ± 4.1 g/day, $P \leq 0.1$) in Experiment 2. There were no significant effects on carcass weight, dressing out, GR and wool growth rate. Lower faecal egg counts in lambs in Yorkshire fog than in tall fescue suggested some potential of Yorkshire fog for parasite control. The low CT concentrations in the Yorkshire fog reduced to some extent rumen ammonia concentration, but were not enough to effectively promote animal performance. The relatively low CT concentrations detected in tall fescue were probably an artifact, because there was no PEG effect on rumen ammonia concentration for tall fescue.

The final grazing experiment was conducted to evaluate grazing behaviour, herbage intake and performance of lambs as affected by grazing selection opportunity and low condensed tannin (CT) concentrations in Yorkshire fog/white clover pasture under rotational grazing management from late November, 1994 to early February, 1995. Twelve lambs were slaughtered as the initial group at

the start of the experiment to measure the preliminary carcass weight. Forty-eight lambs were allocated to two groups in sets of twenty-four and rotationally grazed eight paddocks each of 0.1 ha, in which a "leader" group of 24 lambs grazed each paddock for four days, followed by a similar "follower" group of 24 lambs grazing for four days.

The leader/follower grazing regime created the desired contrasts in herbage quality and quantity. The superiority in sward allowance, selection opportunity, diet quality and reduced possibility of infection by worm parasites resulted, as expected, in faster body growth and wool growth rate in the 'leader' lambs than in the 'follower' lambs. The results of the experiment further confirmed the findings of the influence of low CT concentrations in Yorkshire fog on rumen ammonia concentration. The effect of low CT concentrations on animal performance was not different for generous and restricted grazing.

The following general conclusions can be drawn from this series of experiments:

1) The diets selected by sheep comprised more green material and less dead material than the swards offered to the animals, while diet composition was determined largely by the structure and distribution of sward components rather than by deliberate selection by the animals.

2) Herbage OM intake was influenced to a greater extent by nutritional factors than by behavioral limitations, there being substantially higher herbage OMD and OM intake on ryegrass than on Yorkshire fog in winter.

3) Perennial ryegrass/white clover pasture tended to have higher animal production than Yorkshire fog/white clover pasture under continuous grazing management in winter, and Yorkshire fog pasture produced slightly higher animal performance than tall fescue in rotational grazing management in late spring and early summer.

4) The results of the trials confirmed that low CT concentrations (0.18 - 0.32 % on a DM basis) were present in Yorkshire fog, and provided evidence that perennial ryegrass contained relatively low CT concentrations, but the low CT concentrations detected in tall fescue were probably an artifact of the current procedures of analysing CT.

5) The low CT concentrations in the grasses had no effect on grazing behaviour, diet selection or herbage intake. The low CT concentrations in Yorkshire fog to some extent reduced rumen ammonia concentration, but were not enough to effectively improve animal production.

Keywords: Yorkshire fog (*Holcus lanatus*), white clover (*Trifolium repens*), perennial ryegrass (*Lolium perenne*), tall fescue (*Festuca arundinacea*), condensed tannins (CT), polyethylene glycol (PEG), grazing behaviour, diet selection, herbage intake, animal performance.

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LIST OF ABBREVIATIONS

AA	Amino acid
BTRT	The rate of biting
CCS	Carcass weight
cm	Centimetre
CP	Crude protein
Cr	Chromium
CWL	Corrected wool weight (g/100 cm ²)
CT	Condensed tannins
CTRL	Control
DOM	Digestible organic matter
DOMI	Digestible organic matter intake
EAA	Essential amino acids
FEC	Faecal egg count
FSW	Fasted weight
g	Gram
GR	A measurement of total soft tissue depth over the 12th rib at a point 11 cm from the carcass midline
GRNM	Green material
GT	Grazing time
IB	Intake per bite
INTK	Herbage intake (g/day)
kg	Kilograms
k _g	Efficiency of utilisation of ME for growth
k _l	Efficiency of utilisation of ME for lactation
k _m	Efficiency of utilisation of ME for maintenance

Cont.

Ltd	Limited
LW	Live weight
LWG	Liveweight gain
ME	Metabolisable energy
mg	Milligram
min	Minute
MW	Molecular weight
MTTK	Herbage Intake (g/kg $W^{0.75}$)
N	Nitrogen
NAN	Non-ammonia nitrogen
NH ₃	Ammonia
OMD	Organic matter digestibility
OMI	Organic matter intake
PEG	Polyethylene glycol
PER	Period
PRVSP	Previous species
RUT	Ruminating time
RST	Resting time
SEM	Standard error of mean
Sig	Significance
SPP	Species
WLGTH	Wool growth rate

CHAPTER 1

GENERAL INTRODUCTION AND OBJECTIVES

Effective grazing management systems are based on the comprehensive understanding of plant-animal relationships, especially of responses of animals to different sward characteristics in grazing behaviour, diet selection, herbage intake and performance and the influence of defoliation by animals on pasture composition, growth and utilization. Traditional pastures in New Zealand agricultural systems mostly comprise perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*). 'Massey Basyn' Yorkshire fog (*Holcus lanatus*) has been evaluated by some researchers as a potential species for pasture production, especially in low soil fertility where perennial ryegrass has limited production (Jacques, 1962; Vartha and Clifford, 1971; Clements and Easton, 1974; Dunbar, 1974; Scott and Hardacre, 1974; Watkin and Robinson, 1974; Hagggar, 1976; Harvey *et al.*, 1984; Watt, 1987; Morton *et al.*, 1992). Grassland Roa tall fescue (*Festuca arundinacea*) has been reported as superior to ryegrass cultivars in terms of pasture and animal production in areas prone to moisture stress (Watkin, 1975; Wilson, 1975; Kain *et al.*, 1979; Goold and Van der Elst, 1979; Anderson, 1982; Wright *et al.*, 1985; Brock, 1983; Thomson *et al.*, 1988;). However, there is limited information on comparative evaluation of Yorkshire fog with tall fescue and ryegrass pastures in terms of grazing behaviour, diet selection, herbage intake and animal performance (Hagggar, 1976; Goold and Van der Elst, 1979; Wright *et al.*, 1985; Thomson *et al.*, 1988; Morton *et al.*, 1992).

The performance of animals is mainly dependent on nutrient intake and the efficiency of utilization of ingested nutrients (Hodgson, 1990). Nutrient intake is the product of the amount of herbage and the concentration of nutrients in the herbage (Hodgson, 1990) and is restricted by herbage intake, digestibility and metabolizability (Mitchell *et al.*, 1991). Herbage intake is influenced by nutritional factors such as *in vitro* digestibility of herbage and non-nutritional factors such as

sward characteristics (height, mass, bulk density, botanical composition, structure of sward canopy), grazing behaviour and diet selection of animals (Poppi *et al.*, 1987). Under grazing conditions, the effect of sward characteristics on ingestive behaviour and the physical ability of animals to harvest herbage may be major factors controlling herbage intake (Hodgson, 1985b; 1986; 1990; Poppi *et al.*, 1987).

Dietary protein and energy are the most important factors for ruminant production. The availability of amino acids, especially sulphur-containing amino acids, is often limiting for wool growth and for protein synthesis in young ruminants (Wang, 1995). When ruminants are fed on high quality temperate fresh forages containing a high content of protein, about 70% of the forage protein is degraded in the rumen and only 30% escapes to the small intestine for absorption (Ulyatt *et al.*, 1975). The excessive degradation of protein in the rumen often produces a degree of inefficient nitrogen digestion and deficient amino acid absorption, especially for high producing animals, such as lactating ewes, dairy cows and young animals (Barry, 1981). Therefore, there has been interest in the effects of condensed tannins (CT) in forages in protecting plant protein from degradation in the rumen and improving the efficiency of dietary N utilization in ruminants fed high quality fresh forages. Low to moderate CT content (20 - 40 g/kg DM) in forages has been thought to have beneficial effects in increasing the quantity of protein passing out of the rumen for digestion in the intestine and hence improving efficiency of protein utilization (Reid *et al.*, 1974; Barry, 1985; Barry *et al.*, 1986; Barry, 1989; Chiquette *et al.*, 1989; Waghorn and Jones, 1989; Waghorn *et al.*, 1990; McNabb *et al.*, 1993a; 1993b; Wang *et al.*, 1994). High CT concentrations (> 50 g/kg DM) have been reported to depress voluntary intake, rumen fibre digestion and animal production (Barry and Duncan, 1984; Barry and Manley, 1984; Pritchard *et al.*, 1992). Much information on the effects of CT on the nutritional status of forages is available for legumes. More recently, the low CT concentrations in grasses have aroused great interest (Terrill *et al.*, 1992b). However, there is limited information on the effects of these relatively low CT

concentrations (< 10 g/kg DM) on the performance of grazing animals, or on the CT status of alternative grass species.

This thesis reports the results of four field studies in which particular attention has been paid to:

- 1) comparative studies of Yorkshire fog with ryegrass and tall fescue pastures in terms of grazing behaviour, diet selection, herbage intake and performance of animals and animal production from pastures;
- 2) assessment of the effects of low CT concentrations in grasses on performance of growing lambs, including incidental observations on the control of worm parasites.
- 3) The series of studies was planned to cover a range of seasonal and sward conditions, and to offer contrasts in grazing management and opportunity for selective grazing.

CHAPTER 2

LITERATURE REVIEW

2.1. GENERAL INTRODUCTION

The output of milk, meat or wool of ruminants is the reliable expression of the feeding value of forages. The feeding value of a forage depends upon voluntary feed intake (VFI), the proportion of nutrients digested, and the efficiency of utilization of digested nutrients for productive processes. The nutritional value of the organic components is influenced by the ease with which they can be digested and incorporated into microbial tissue, and the site of digestion and absorption in the alimentary tract (Hodgson, 1990).

Grazing management systems can operate efficiently on the basis of an understanding of the plant-animal system. We need to appreciate the various contributions made by sward characteristics such as surface height, mass, bulk density, the ratio of leaf:stem, the proportion of green leaves and the spatial-temporal arrangement of all these parts in influencing ingestive behaviour, herbage intake, diet selection and performance of grazing ruminants, to comprehensively understand the plant-animal interaction and to make practical decisions about management in grazing systems.

Alternative plant species may influence any or all of the above aspects of animal nutrition and performance. In addition, attention has focused recently on the potential benefits of the condensed tannins (CT) in pasture plants on animal health and performance (liveweight gain, carcass weight, GR and wool growth rate).

The objectives of this research programme (see Chapter 1) were to compare three alternative grass species (perennial ryegrass (*Lolium perenne*), Yorkshire

fog (*Holcus lanatus*) and tall fescue (*Festuca arundinacea*) as components of simple grass/clover mixtures, on the ingestive behaviour, herbage intake and performance of grazing lambs, including an investigation of the CT contents in the grasses and implications for animal performance.

The purposes of this review are: (i) to discuss the supply of nutrients in forages and factors affecting the nutritional value of forages; (ii) to review the effects of sward characteristics and animal characteristics on grazing behaviour, herbage intake and diet selection to develop a general principle for the relationship between plants and animals in grazing systems; (iii) to define the influence of condensed tannins on the nutritional value of forages, herbage intake and performance of grazing ruminants.

These factors will be considered in general terms, drawing information from a range of forages. The chapter will conclude with a brief outline of the specific characteristics of Yorkshire fog and tall fescue as alternatives to perennial ryegrass in pastoral systems.

2.2. NUTRITIONAL VALUE OF FORAGES

Maximum production of pasture is not always associated with the largest amount of nutrients available for animals. Variations in pasture composition, structure and maturity, and differences in digestion and metabolism of absorbed nutrients by animals largely affect the performance of grazing animals. *Nutritive value of forages* is defined in the classic sense as the concentration of nutrients in a feed, or animal response per unit of intake. *Feeding value of forages* is defined as animal growth and production (meat, wool and milk) from a forage (Ulyatt, 1973) and depends on the nutrient intake, nutrient digestibility and the efficiency of conversion of digested nutrients into body tissue or milk (Hodgson, 1990). Nutrient intake itself is the product of the amount of herbage eaten and the concentration of nutrient in the herbage (Hodgson, 1990). Nutritive value can

also be defined as the product of digestibility and the efficiency of utilization of digested nutrients, so feeding value can be defined as a function of herbage intake and nutritive value. The feeding values of many forages have commonly been evaluated in terms of liveweight gain or milk production of animals. This section will focus on the ability of forage to supply nutrients for ruminants and factors affecting the nutritional value of forages, and briefly discuss animal factors affecting the digestion and utilization of nutrients in forages. Herbage intake, another important factor controlling animal production, will be discussed in Section 2.3 and Section 2.4.

2.2.1. Variations in Nutritional Value of Forages

The ability of forage to supply nutrients for animals and responses of animals to the nutrients are often assessed by nutritional value of forage. The nutritional value of herbage varies with: (i) anatomical structure and chemical composition of forages; (ii) species and the components within a species; (iii) different seasons and the stage of growth; (iv) variation within a sward such as top and bottom parts.

Anatomical structure and chemical composition of pasture plants vary widely between species and their component parts, and contribute to the differences in nutritional value of forage. The anatomical arrangement of forage tissues and the chemical composition and structure of cell walls largely determine the digestibility of forages (Ehlke and Casler, 1985). Cell types with thickened secondary walls are the main contributors to poor quality of herbage. The proportions of thick- and thin-walled cell types in leaf and stem generally account for the differences in cell wall content and digestibility between organs and species (Wilson, 1994). The proportion of the main thick-walled tissues (vascular and sclerenchyma) from lowest to highest is in the order of legume lamina, midrib and petiole < grass lamina < grass leaf sheath, grass leaf midrib, grass and legume stem (Akin, 1989; Wilson, 1990; 1993).

Cell walls consist principally of hemicellulose, cellulose and lignin. Cellulose can be effectively degraded within the rumen, and provided the associated lignin content is low, the overall digestibility of cellulose may exceed 80% in young vegetative forage. Lignin is not extensively digested in the rumen and increasing concentration of it causes overall forage digestibility to decline, as the spatial distribution of lignin within the species reduces the accessibility of the other nutrients, and in particular cellulose, to ruminal processes of digestion (Beever, 1993a). Leaves contain considerably less total cell wall material, particularly lignin, than stem from the same plant and this is compensated for by greater proportions of other carbohydrates, protein and lipid (Black, 1990). However, the effect of the progressive increases in the ratio of cell wall to cell contents and in the degree of lignification of the cell walls is that the digestibility of leaf tissue falls from a level of 80-90 per cent in young, expanding leaves to less than 70 per cent in mature leaves (Hodgson, 1990). It is these differences in structure and composition that cause forages to have a wide range of digestibility.

Legumes have generally higher nutritional value than grasses. The mean DM digestibility coefficient of temperate grasses is higher than that of tropical grasses. The lower digestibility of tropical grasses is caused by higher proportion of thick-walled tissues, such as vascular bundles and sclerenchyma than in temperate pasture grasses and legumes (Minson and McLeod, 1970; Wilson, 1994). The DM digestibility of temperate and tropical legumes is similar (Wilson, 1994).

Digestibility is clearly related to herbage maturity because the structure and composition of plants and the components within a species change markedly as the plants mature. During rapid spring growth, forage normally contains high nutrient concentrations and promotes animal growth, weight gain and milk production. Increases in reproductive stem and dead material with maturity actually reduce amount of nutrients eaten by grazing animals. White clover maintains a higher digestibility than the grasses because the amount of structural

tissue in the plant is lower, and probably because dead tissue tends to disappear more quickly than from a grass sward (Hodgson, 1990). Clovers tend to have less cell wall constituents than grasses at the same stage of maturity (Hodgson, 1990), but they have greater proportions of storage and soluble carbohydrate, protein and lipid (Wilson, 1994). White clovers maintain a higher digestibility as they mature than red clover and lucerne, because of a continual turnover of the leaves and petioles (Ulyatt, 1981). The DM digestibility of all plant parts for temperate grasses is similarly high at an immature stage of growth, but at maturity there are large differences in DM digestibility between the different fractions and large decreases occur in DM digestibility of stem. A similar pattern of differences exists in digestibility of temperate legumes such as *Medicago sativa* (Tilley and Terry, 1969; Minson, 1990). Thus the decline in digestibility with maturity is often caused by increasing proportions of stem and by changes in the chemical composition of plants. Generally, increased structural carbohydrates (cellulose and hemicellulose) and lignin, and decreased readily fermentable carbohydrates (soluble sugars and pectin) and crude protein as a plant matures contribute to the decline of digestibility of forages (Ulyatt, 1981; Vallentine, 1990). The rate of decline in digestibility varies with species, especially differences in chemical composition between species (Ulyatt, 1981). Total nitrogen content of grasses varies widely in different seasons and that of clovers has a much narrower range (Beever *et al.*, 1986).

The arrangement of plant components within a sward canopy means that the digestibility of successive layers of herbage within the sward is likely to decline with increasing proximity to ground level (Hodgson, 1990). There is a difference between the top and bottom parts of a sward in digestibility. Armstrong *et al.* (1993a) showed that rape (*Brassica napus*) had higher OM digestibility in the upper stems than in lower stems. This is consistent with results reported by other authors (Pritchard *et al.*, 1963; Hendricksen and Minson, 1985; Minson, 1990).

These points suggest that the nutritional value of forages can be improved by:

(i) restricting the reproductive growth of grasses to reduce the accumulation of low quality stem in pasture; (ii) choosing to use vegetative forage; (iii) Increasing the proportion of legume in the sward; (iv) grazing the top horizon of the sward.

In vitro digestibility is widely considered to be the most useful and accurate single laboratory measure of forage nutritive value (Walker, 1959; Minson, 1981; Goldman *et al.*, 1987). It provides a reliable estimate of *in vivo* digestibility and provides an approximate measure of available energy (Ayres, 1991). Ayres (1991) stated that *in vitro* digestibility is an important practical measure of nutritional value for: (i) plant improvement - as a primary screening characteristic; (ii) pasture development - as a criterion for choosing superior species and monitoring the impact of management practices; (iii) livestock feeding - as a diagnostic tool for predicting animal requirements for supplementary feeding.

2.2.2. Animal Factors Affecting Digestion & Utilization of Nutrients in Forages

Sward characteristics associated with the nutritional value of forages have been emphasised in the preceding section. This section will simply discuss the animal aspects related to the processes of digestion and utilization of nutrients ingested by ruminants.

The teeth of ruminants are especially adapted for biting and tearing pasture plants during grazing and can efficiently comminute the plant particles by chewing and rumination to a small size that can pass through the rumen quickly.

Plant materials grazed by ruminants are subjected to breakdown by rumen contractions and chewing following regurgitation during periods of rumination and microbial digestion. About 60% of digestible DM is digested in the rumen, including a degradability of approximately 70% for plant protein, and most of the digestible fibre (Waghorn *et al.* 1990). Approximately 25% of the OM digested

in the rumen is lost to the animal as methane, ammonia and heat of fermentation (Ulyatt, 1981). Rumen digestion provides about 70% of the available energy (metabolizable energy) to the animal, primarily as volatile fatty acids (VFA) which are by-products of bacterial metabolism and are absorbed from the rumen into the bloodstream (Waghom *et al.*, 1990).

The rate of digestion of forages and their potential degradability within the rumen can have a large variation. Animal species vary widely in rumen digestion. Goats have greater apparent DM digestibility, a larger rumen pool of DM and liquid (relative to $W^{0.75}$), greater apparent digestibility of fibre, especially of lignin, and greater rumen fractional degradation rates (FDR) of cellulose, hemicellulose and lignin than sheep (Domingue *et al.*, 1991). The more efficient fibre digestion of goats has been attributed in part to slower fractional outflow rate (FOR) of particulate dry matter from the rumen, and hence to a longer exposure of plant cell wall to microbial attack in the rumen (Watson and Norton, 1982; Doyle *et al.*, 1984; Domingue *et al.*, 1991). Goats sustain higher rumen ammonia concentrations than sheep when fed in low-quality forages (Watson and Norton, 1982). This is supported by Domingue *et al.* (1991), who reported a higher rumen ammonia concentration and lower rumen pH in goats than sheep when fed a low-quality roughage.

The rate of digestion of forages is also affected by the composition of the components eaten by the animals and is positively related to the soluble dry matter content of the plant (Smith *et al.*, 1972). Soluble carbohydrates are degraded by rumen microorganisms about 150 times faster and storage carbohydrate about five times faster than structural carbohydrate (Maeng and Baldwin, 1976). The potential degradability of structural carbohydrate in leaves is higher than that in stem with similar fibre concentration (Poppi *et al.*, 1981a; 1981b). White clover has higher soluble fractions of organic matter and crude protein, resulting in higher degradation rates of OM and CP and lower rumen-undegradable OM and CP. As a consequence of higher protein content and

differences in degradation, both rumen-degradable protein and rumen escape protein contents were higher in white clover than in ryegrass (Steg *et al.*, 1994). There was little difference between many temperate grasses and legumes in potential protein degradability (0.73 vs 0.73 g/g) (Black, 1990).

The rate of passage of digesta from the rumen is related to cell wall characteristics, which influence the ease of physical comminution of forage by chewing and digestion, and the size and shape of the resultant particles (Wilson, 1994). There is more difficulty in breaking down the leaves of tropical grasses than temperate grasses to small particles. For most higher quality temperate grasses and legumes, in contrast, leaves can be easily disrupted by chewing and disintegrated into isolated vascular bundles which quickly reduces particle size (Winson, 1994). However, loss of the epidermis and digestion of walls probably plays little part in breakdown of grass stems (Wilson, 1994). Physical destruction of stems largely depends on chewing, and the effort needed is greater than for leaves (McLeod *et al.* 1990).

All animals require nutrients in order to maintain body processes and for reproduction. Nutrients absorbed from the digestive tract include volatile fatty acids, amino acids, long chain fatty acids, glucose, minerals and vitamins, which are used in the synthesis of the many different compounds found in meat, milk, and wool, and to replace nutrients used for maintaining life processes including reproduction. If one of these nutrients is deficient and cannot be synthesized by the animal, then production will be limited by the deficient nutrient and the metabolizable energy (ME) in the forage will be inefficiently utilized by the animal (Minson, 1990).

Energy is required for the muscular work of circulation and respiration and in mammals for maintaining body temperature (Minson, 1990). The digestible energy (DE) of forage is closely correlated with the proportion of dry matter and organic matter (OM) digested. In most circumstances the major determinant of

animal performance is likely to be intake of metabolizable energy (Hodgson, 1990). Hodgson (1990) stated that the metabolizable energy content of forage is closely related to the digestibility of organic matter. The net energy is the quantity of energy that can be retained in a product or used to spare the catabolism of the body reserves for maintenance purposes. Forages with a high ME value generally have a high NE value. Although ruminant production from forage usually depends on voluntary intake, concentration of digestible energy, or a combination of both, and variations in the efficiency of utilization of the digestible or metabolizable energy for fattening or growth can cause the differences in production (Minson, 1990). The OM apparently digested in the gastro-intestinal tract is not all of equal nutritive value to the animal because of differences in the quality of end-products formed at various sites of digestion (Ulyatt, 1973). The extent of energy retention in growing cattle is largely a function of total ME intake, the estimated ME requirement of the animal for maintenance and the estimated efficiency with which the ME available above maintenance is used for production (Beever *et al.*, 1993a).

Ruminants utilize the major dietary nutrients with different efficiencies. The efficiency of utilization can be expressed with increasing precision from a food conversion ratio (e.g. feed consumed per unit of liveweight gain) through to the true efficiency of utilization of metabolizable energy (ME) for various functions such as: maintenance (k_m), growth (k_g), fattening (k_f) or lactation (k_l) (Ulyatt, 1973). Efficiency of utilization of digested nutrients is largely influenced by: (i) forage species and the chemical composition within a species; (ii) species of animal; (iii) sites of digestion

Differences in forage species and composition within a species should lead to differences in the efficiencies of utilization of nutrients by ruminants. The nutritive value of a herbage is closely associated with the efficiency of utilization of its ME for maintenance, fattening and lactation, and all the partial efficiencies change with increasing nutritive value (Ulyatt, 1973).

The efficiency of utilization varies with species of animals. Cattle digest the dry matter in forage more efficiently than do sheep when fed diets of similar chemical composition (Cipolloni *et al.*, 1951). The lower digestive efficiency of sheep is associated with the reduced fibre digestion caused by the shorter time of forage retention in the reticulorumen (Rees and Little, 1980; Poppi *et al.* 1981a). There is no difference between sheep and cattle in crude protein digestibility (Minson, 1990).

The efficiency of utilization of metabolizable energy is related to species and seasons. The usable energy in range grasses on a dry matter basis is relatively stable while plants are green and growing, but drops somewhat nearing maturity and following maturity (Vallentine, 1990). Givens *et al.* (1993a) reported that ME concentration in herbage was higher in spring than in summer and ME content fell with increasing maturity in spring growths, and this decline was 3-4 times faster than for autumn-harvested materials from observation of the energy value and chemical compositions of 70 herbages harvested over two years. This is consistent with the reports by Corbett *et al.* (1966) and Rattray and Joyce (1974). Higher efficiency of utilization of ME in spring herbage may be related to extra glycogenic amino acids being absorbed from the small intestine per unit of ME intake, thus enhancing the utilization of acetate (MacRae *et al.*, 1985; MacRae, 1987).

Animal performance can be limited because of insufficient essential amino acids absorbed relative to the energy available and can be improved with increased absorption of protein or amino acids in young animals (Barry, 1981; Black and Mulholland, 1983; Barry and Manley, 1986; Poppi *et al.*, 1988). One alternative to protect dietary protein is to exploit the potential of condensed tannin (CT) in forages. Detailed information about CT will be discussed in Section 2.6.

One of the major weaknesses of the current systems used in the UK for meeting the energy and protein requirements of ruminants is that they are largely

independent of each other (Beever, 1993a). Mathematical models, which integrate the utilization of protein and energy at the level of the whole animal, would be important components of rationing systems (Gill, 1991). However, no model yet exists which can accurately simulate animal metabolism in all circumstances and in relation to improving the predicting of nutrient supply there remain certain issues which will require further research before an adequate understanding can be provided, as stated by Gill *et al.* (1989).

Vallentine (1990) showed that information on a grazing animal's nutritive status has typically been determined by monitoring (i) the chemical composition of the standing crop available to the grazing animal; (ii) the intake and nutrient composition of the diet; (iii) the grazing animal's physical measurements and performance; (iv) level of nutrients stored in the animal's body. Combinations of the above approaches may be required to make optimal grazing management decisions that affect the nutritional status of grazing animals (Vallentine, 1990). This suggests that nutrient intake is an important factor affecting animal production under grazing conditions.

2.3. CONTROL OF HERBAGE INTAKE

The rate of growth in a growing animal and the milk yield of a lactating animal depend first upon the intake of nutrients, and second upon the efficiency of conversion of ingested nutrients into body tissue or milk (Hodgson, 1990). Nutrient intake itself is the product of the amount of herbage eaten and the concentration of nutrients in that herbage (Hodgson, 1990). Nutrient intake is restricted by three factors: diet digestibility and metabolizability and herbage intake (Mitchell *et al.*, 1991). The amount of feed consumed by grazing ruminants has been estimated by Ulyatt (1984) to account for 50 to 70% of the variation between pastures in their capacity to sustain animal productivity. It is very important to understand theories developed for behavioral limitations in intake control of grazing animals (Hodgson, 1986).

Herbage intake of grazing animals can be considered in terms of the balance between the effects of metabolic, physical and behavioral controls (Hodgson, 1985a). The physical ability of animals to harvest herbage and the effect of structure of the sward on ingestive behaviour, in some cases, may be major controlling factors under grazing conditions (Hodgson, 1986).

Factors influencing herbage intake have been summarized and classified in different ways by different authors. Poppi *et al.* (1987) suggested that the factors influencing pasture intake could be broadly classified as nutritional and non-nutritional. The non-nutritional factors such as pasture structure, pasture height, pasture mass, pasture allowance and post-grazing pasture mass are probably the most important in limiting pasture intake by grazing ruminants. Minson and Wilson (1994) concentrated attention on nutritional factors, as Poppi (1987) indicated, and suggested that the factors affecting voluntary intake by ruminants might be divided into two groups: (i) nutrients essential for maximal microbial activity in the rumen and the maintenance of metabolic function of the animal, and (ii) components of the diet which slow down the passage of forage through the rumen.

Black (1990) stated that the voluntary intake of a grazing ruminant might be limited by: (i) the potential of the animal to use nutrients; (ii) the amount of digesta that can accumulate in the reticulo-rumen; (iii) the rate of the removal of digesta from the rumen through digestion and outflow to the lower gut; and (iv) the time available for eating and ruminating activities.

Hodgson (1990) stated that herbage intake was influenced by three main groups of factors: (i) Those affecting herbage digestion, relating mainly to the maturity and nutrient concentration of the herbage eaten; (ii) Those affecting herbage ingestion, relating mainly to the physical structure of the sward canopy; (iii) Those affecting the demand for nutrients and the digestive capacity and eating capability of the animals concerned, reflecting largely their maturity and

productive state. The three groups of factors may interact with one another to control herbage intake under grazing conditions.

The regulation of intake involves hunger and satiety signals that operate through various hormonal and neural mechanisms to control both short and long term voluntary intake (Mertens, 1994). Eating and digestion cause a number of 'short-term' stimuli to increase in magnitude during a meal and when one, or some integrated combination, of these signals reaches a threshold value for satiety, eating ceases until the satiety signals have decayed sufficiently (Freer, 1981). The feed intake required to satisfy total energy demand of grazing ruminants may commonly not be reached because of limitations to gastro-intestinal tract capacity (Black, 1990).

Though it appears clear that intake is controlled over the long term by energy balance of the animal, short-term intake of meals probably is controlled by a combination of plant structural factors that influence rate of ingestion, the effect of the masticated forage on gut fill, and social behaviour and environmental factors affecting the appetite-satiety complex (Forbes, 1988a; 1988b). Several different factors can cause the rate of forage intake to be so low that neither the animal's potential to utilise nutrients nor its rumen capacity are satisfied (Black, 1990).

Hodgson (1990) suggested that the level of herbage intake achieved in any particular circumstances would be determined by the balance struck between the sensation of physical satiety, behavioral constraints and feeding drive, rather than by any one limiting variable. The sensation of *physical satiety* is function of the degree of distension of the alimentary tract, or of the abdomen, caused by the volume of digesta in the rumen. *Behavioral constraints* limit the potential rate of herbage consumption, and may relate to both sward and animal characteristics and their impacts on intake per bite and bite rate. The *feeding drive* reflects the animal's current demand for nutrients, principally energy, and

in particular the degree to which energy intake falls short of energy expenditure.

Mertens (1994) reviewed the mechanisms of intake and indicated that long term intake in animals was controlled by physiological regulation, physical regulation and psychogenic modulation. Mertens (1994) also stated the dominant roles of physiological regulation and physical limitation on intake were modified by psychogenic stimuli related to palatability, social interaction, disease, and feeding management.

Mertens (1994) showed that when high quality diets were fed, animals ate to meet their energy demand, and intake was limited by the animal's genetic potential to utilise absorbed energy; when low quality diets were fed, the animal consumed feed to the level that matches the capacity of the gastrointestinal tract to handle digesta. An upper limit to voluntary intake is set by the animal's potential energy demand, which includes basal metabolism, the energy required to graze and chew herbage and the capacity for either storing energy as body tissue or secreting it as milk (Freer, 1981).

Dynamic models are well suited to the study of intake regulation because they offer the opportunity to evaluate concepts rigorously as they change over time (Mertens, 1994). It is clear that models of intake control need to make allowance for the trade-off between facilitatory and inhibitory factors ascribable to the physical, structural and nutritional characteristics of herbage and their combined effects on physical, chemostatic, and behavioural controls (Hodgson, 1985a). However, nutritionists and behavioral ecologists have not so far pooled resources in order to provide comparative information on the relative importance of and ranges of sensitivity to the groups of plant characteristics involved in influencing behavioral and nutritional constraints (Hodgson *et al.*, 1994). Hodgson *et al.* (1994) suggested that nutritionists and ecologists should develop common programs to investigate one of the most interesting interface areas in animal science.

A general conceptual model of herbage intake regulation with a 'forage consumption constraint' (FCC) has been developed by Weston (Weston, 1982; 1996; Weston and Davis, 1991), in which voluntary food consumption is regulated by an interplay of the rate of clearance of DM from the rumen and the amount of energy available to the animal relative to its capacity to use energy. The FCC is then the difference between the quantity of forage actually achieved at any given herbage digestibility and the quantity required to meet the capacity to use energy when constraints are absent. For mature wethers, this capacity can be taken on average to be 60 g DOM/kg^{0.75}, while the equivalent value for 30 kg weaners is 90 g DOM/kg^{0.75} (Weston and Davis, 1991). Maximum theoretical intakes are thus the quotient of these values and OM digestibility. The concept is a useful approach to the modelling of intake, to the extent that it permits forage characteristics, rumen load and animal demand to exert their effects on intake (Dove, 1996). However, Dove (1996) suggested that the concept would need to be linked to at least three other components in order to predict intake accurately under grazing conditions: 1) the effects of herbage mass and sward structural characteristics (Freer *et al.*, 1985; 1988); 2) the effects of low protein content of herbage on rumen-degradable protein supply and microbial digestion of cell walls (Freer *et al.*, 1988), and on the ultimate supply of animal of amino acids in relation to the demands of the animal; 3) the substitution between herbage and supplement (Freer *et al.*, 1988).

2.4. GRAZING BEHAVIOUR AND HERBAGE INTAKE OF RUMINANTS

Allden and Whittaker (1970) defined herbage intake by an animal as the product of the rate of intake and the time spent grazing and stated that the rate of intake could be further divided into two components, size of bite and rate of biting. This simple concept provides the basis for active research on the interrelationships between behavioural variables and the sward and animal characteristics influencing them (Hodgson *et al.*, 1994).

Understanding the cause-effect relationships between sward characteristics and herbage intake requires a greater knowledge of the components of sward structure and their influence on the mechanics of the grazing process (Hodgson, 1985b). Three components of ingestive behaviour of grazing ruminants (intake per bite, rate of biting and grazing time) can be used to determine daily herbage intake (Hodgson, 1982; 1985a; Hodgson *et al.*, 1994). This section will concentrate attention upon the effects of sward characteristics on the components of grazing behaviour and herbage intake, the effects of animal characteristics on herbage intake, and the compensatory relationships between variables involved in grazing behaviour and herbage intake.

2.4.1. Herbage Intake and its Variations

Herbage intake can be defined as the product of intake per bite, biting rate and grazing time. The variables are typically influenced by sward structure variables such as height, mass, bulk density, and the ratio of leaf:stem. The structure and the botanical composition of the sward canopy can exert a direct effect upon the herbage intake of grazing animal (Hodgson, 1990).

Much information has been provided on the effects upon ingestive behaviour of sward conditions such as species, height, structure, mass and allowance, and animal characteristics such as species, genotype, and physiological state (Allden and Whittaker, 1970; Jamieson and Hodgson, 1979; 1981; Hodgson, 1977; 1981a; 1981b; 1982; Penning *et al.*, 1984; 1988; 1991a; 1991b; Forbes and Hodgson, 1985; Penning 1986; Poppi *et al.*, 1987; Hughes *et al.*, 1991). Development of techniques for the control and manipulation of both swards and animals under close constraint (Burlison *et al.*, 1991; Mitchell *et al.*, 1991; 1993; Laca *et al.*, 1992), mainly concentrating on estimates of the rate of herbage intake in the short term, has made it possible to investigate ingestive responses in some detail, with particular reference to the dimensions of individual mouthfuls of herbage and factors influencing these dimensions (Hodgson *et al.*, 1994).

Intake per bite is the primary animal response to variation in the physical characteristics of the sward canopy (Hodgson *et al.*, 1994) and is basic to the study of herbage intake by grazing animals because it is the most important determinant of intake rate (Stobbs, 1973a; 1973b; Chacon and Stobbs, 1976; Black and Kenney, 1984; Laca, *et al.*, 1992). Intake per bite is the product of the volume of canopy space occupied by the foliage encompassed at a bite and the bulk density of the foliage in that space (Hodgson, 1985a).

Intake per Bite (IB) = Bite Volume X Bulk Density of Herbage in Grazed Strata

Bite volume can itself be usefully considered as the product of bite depth and the vertical projection of the area encompassed at a bite.

Bite Volume (BV) = Bite Depth (BD) X Bite Area (BA)

Bite depth and bite area are basic units in studying the effect of grazing on vegetation and the influence of sward characteristics on the bite dimensions taken by grazers in grazing systems, and in explaining the dynamics of herbivore-plant interaction at a community level (Lundberg and Astrom, 1990; Burlison *et al.*, 1991; Mitchell *et al.*, 1991; 1993; Laca *et al.*, 1992). Bite depth is the vertical distance between the sward surface and the severed ends of leaves or stems, and thus it is an indicator of the average length of tiller removed (Hodgson, 1986). Bite depth is much more responsive than bite area to variation in sward conditions and, in most circumstances, it is the major determinant of both volume and intake per bite (Hodgson *et al.*, 1994).

Effective bite area of a grazing animal is a result of the interaction of the height of the sward and stiffness of plant units with the harvesting behaviour of the animal (Laca, *et al.*, 1992). Laca *et al.* (1992) stated that animals appeared to respond to sward density by adjusting the number and amplitude of tongue movements to gather, as effectively as possible, the largest feasible bite cross-

section. Bite area appears to be less sensitive to sward variation than does bite depth (Hodgson, 1986). Bite area generally remains relatively constant or shows a tendency to decrease as height increases, in particular in dense swards (Burlison, 1987; Mursan *et al.*, 1989; Mitchell *et al.*, 1991; Laca, *et al.* 1992). On tall swards, bite area may be limited by the maximum extension of tongue sweeps (Laca *et al.*, 1992) and decline with increasing bulk density (Burlison *et al.*, 1991; Laca *et al.*, 1992; Hodgson *et al.*, 1994). On short grass swards, bite area is likely to be limited directly by the difficulty of clamping plants between incisors and dental pad (Laca *et al.*, 1993; Hodgson *et al.*, 1994). In some circumstances, bite area is not significantly correlated with sward variables such as surface height or grazed stratum bulk density (Burlison *et al.*, 1991; Mitchell *et al.*, 1991). For example, surface height, mouth dimensions and limits to the harvesting force are likely to assume less importance than the distance between adjacent leaves or tillers in sparse swards in determining the area effectively encompassed by a bite, because animals may harvest as few as one leaf at a bite (Black and Kenney, 1984; Burlison *et al.*, 1991). In a few cases, bite area by sheep grazing grass swards exhibits positive correlation with sward height (Burlison, 1987). A better understanding of the implications of the interaction between sward variables and bite area will require further investigation of the biting forces involved in grazing swards of differing structure and maturity (Hughes *et al.*, 1991).

Sward height largely determines bite volume for low to moderate bulk density swards. Laca *et al.* (1992) showed that sward height was the most important factor determining bite depth; sward height also had exhibited a positive effect on bite volume, which increased linearly with height on low density swards. This provides new evidence for observations by Mitchell *et al.* (1991) and Milne *et al.* (1982), who reported that bite depth of sheep grazing ryegrass/white clover swards was linearly related to sward height and increased with increasing sward height. However, bite depth is not always linearly increased with increasing height: in some circumstances, the relationship may be asymptotic (Hodgson *et*

al., 1994), as suggested by Mitchell *et al.* (1991) and Laca *et al.* (1992).

An asymptotic relationship may exist between bite dimensions and bulk density. Laca *et al.* (1992) also stated that on tall lucerne swards of high bulk density (more than 2200 g/m³) the increments in bite depth caused by increasing sward height were almost counteracted by reductions in bite area. Black and Kenney (1984) showed a decline in three bite dimensions (bite depth, bite area and bite volume) as mean sward bulk density increased. However, the corresponding relationships with grazed stratum bulk density in the experiment of Burlison *et al.* (1991) were negligible, despite a broadly similar range in bulk density.

Hughes *et al.* (1991) reported that intake per bite at low pasture heights was not constrained by peak bite force, but rather the animal's ability to gather and prehend pasture and to increase bite depth. This is consistent with results found by Illius and Gordon (1987).

Laca *et al.* (1992) indicated that intake per bite was affected independently by sward height and bulk density. This evidence is also provided by Burlison *et al.* (1991). However, more recent studies have showed a strong interaction between sward height and bulk density on intake per bite (Hodgson *et al.*, 1994).

Intake per bite is more sensitive to sward height than to bulk density in temperate sward (Hodgson, 1981b). Laca *et al.* (1992) stated that steers obtained heavier bites on tall sparse swards than on short dense ones with the same herbage mass per unit area. Black and Kenney (1984) showed that steers not only obtained a proportionally equivalent bite depth, but also achieved larger bite areas which resulted in heavier bites in tall sparse swards. Allden and Whittaker (1970) reported that intake per bite increased almost linearly with changing tiller length. However, inconsistent evidence was provided by Burlison *et al.* (1991), who stated that there was no significance in the correlation between intake per bite and height, while intake per bite was significantly related

to grazed stratum bulk density. An asymptotic relationship may exist between intake per bite and grazed stratum bulk density (Stobbs, 1973b; 1975; Black and Kenney, 1984; Burlison *et al.*, 1991). In tropical swards, intake per bite is more sensitive to variation in herbage bulk density than to variation in sward height (Stobbs, 1973a).

Illius *et al.* (1992) showed that intake per bite was increased with clover content in mixed swards. The result indicates that intake per bite is influenced by the differences in the clover content of the grazed sward, and that a higher density of material in the grazed stratum of high clover swards can compensate for reduced bite depth.

The effects of morphological characteristics of plants on bite dimensions by animals lack consistent evidence. The positive examples include evidence that pseudostem acts as a barrier on very short vegetative swards (Barthram and Grant, 1984), that animals adjust their bite depth in relation to the depth of the leafy and pseudostem-free zone of the sward (Barthram, 1981), and that cattle restrict bite depth to the upper surface of the pseudostem layer of tall fescue (*Festuca arundinacea*) (Dougherty *et al.*, 1992). However, Burlison *et al.* (1991) showed that sheep generally grazed only approximately half of the mean leaf depth on grass swards, and that bite depth did not appear to be constrained primarily by the presence of pseudostem. Burlison (1987) also observed that the presence of stem was unlikely to have inhibited bite depth on oats swards as sheep appeared to select stem rather than leaf from the surface stratum. This is supported by Milne *et al.* (1982) and Laca *et al.* (1992). As Hodgson *et al.* (1994) suggested, there has been less success in identifying the morphological characteristics of plants which might control the relationship between sward height and bite depth.

2.4.2. Sward Effects on Herbage Intake

Herbage intake and animal performance are sensitive to a range of sward characteristics (Hodgson, 1977; 1990). Sward height largely influences herbage intake, hence animal performance. Herbage intake increases with increasing sward surface height, before a maximum value is reached. Further increase in sward height may have no effect on herbage intake or may result in a reduction in grazing efficiency because of changes of sward characteristics with increasing height (Hodgson, 1990). This indicates that an asymptotic relationship exists between herbage intake and sward height. This is supported by Penning *et al.* (1991a). Hodgson (1990) suggested that herbage intake and animal performance may start to decline when sward surface height falls below 8-10 cm for grazing cattle and 6-7 cm for sheep.

Variations in the effects of sward height on herbage intake relate to herbage digestibility (Hodgson, 1986; 1990). The relationship between diet digestibility and intake is not necessarily a simple one, because different plant species or components can differ in their rate of digestion at similar levels of digestibility (Hodgson, 1990). The relationship between intake and digestibility is not consistent for all pasture species. Intake increases as digestibility increases and the responses of intake to increasing digestibility may be enhanced to some extent by the effects of parallel changes in sward structure upon behavioral limits (Hodgson, 1986). This indicates that a large difference may exist in intake between forages and their components even when pasture allowance or digestibility are similar.

Herbage allowance is one of the most important pasture factors affecting intake by livestock grazing temperate pastures and is the component of grazing ecosystems that lends itself most readily to manipulation by grazing management (Hodgson, 1984). There is usually a curvilinear relationship between herbage intake and pasture allowance (Hodgson, 1975; Minson and Wilson, 1994), and

the intake of herbage increases as more herbage is offered (Penning, 1986). Combellas and Hodgson (1979) stated that herbage intake was near maximal when grazing efficiency was about 0.50, i.e. when the allowance was equivalent to twice intake. This is supported by Le Du *et al.* (1979). At lower herbage allowance, the relationship may be linear (Baker *et al.*, 1981). Other sward variables may be important in determining herbage intake. Examples include sward dry matter density in determining herbage DM intake rates at lower herbage allowances (Dougherty *et al.*, 1992) and responses of calves and cows to post-grazing sward height as well as allowance (Baker *et al.*, 1981).

Intake is closely correlated with pasture species. Rattray and Clark (1984) reported that the intake of clover by grazing lambs was almost twice that of perennial ryegrass at the same allowance. Davies *et al.* (1991b) also reported that digestible organic matter intake (DOMI) of lambs was higher on grass/clover than on grass-only sward under continuous stocking conditions during the post-weaning period. These results can be explained by the fact that the legumes have a lower ratio of cell wall to cell content and higher rate of digestion than the grasses at any given level of digestibility (Hodgson, 1990).

Herbage intake often has a negative correlation with maturity of forage, partly because of strong development of structural tissues in leaves and stems. At a reproductive stage of forage growth, the relative proportions of leaves and stems become important in influencing the ingestive behaviour because of the effects upon selective grazing behaviour (Hodgson, 1990). Proportions of leaf and stem tissues and living and dead material may also be important in the determination of herbage intake (Dougherty *et al.*, 1992). Dougherty *et al.* (1992) showed that cows might cease grazing when the grazing horizon of vegetative tall fescue swards approached a plane represented by the tops of pseudostems. Increasing structural tissues give rise to large fibre particles in the rumen which are resistant to reduction in size by chewing and digestion, so prolonged retention in the rumen often results in a low intake.

Herbage intake may be affected by the palatability of the material on offer (Hodgson, 1990). Black (1990) stated that the intake of a forage was little affected by palatability *per se* when only one feed was available but, when there is a choice between forage components with equal accessibility, sheep eat a greater proportion of the more palatable material. Hodgson (1990) suggested that the term 'preference' would be used to describe choice between the different components of a sward because of the difficulty in description and measurement of palatability. However, 'preferred' plants will not necessarily be eaten in greater quantity than 'non-preferred' plants where each is offered in isolation (Hodgson, 1990). This indicates that herbage intake by ruminants depends on not only 'preference' of herbage on offer but also other sward characteristics, animal characteristics and the processes of digestion and metabolism in the animal.

2.4.3. Animal Effects on Herbage Intake

The intake potential of an animal depends on its species, sex, physiological state, size, body shape and health (Mertens 1994). Animals differing in production potential eat different amounts of the same herbage and animals with a greater performance generally have a higher herbage intake (Hodgson, 1990). Generally, lactating cows have higher herbage intake than non-lactating animals (Hodgson and Jamieson, 1981; Hodgson, 1990) and rapidly growing animals eat more, relative to body size, than mature animals with little growth potential (Hodgson, 1990). However, the variations in herbage intake may be greater in calves than in adult cattle in some circumstances because of inexperience and the poorer ability of calves to increase herbage intake in response to changing sward conditions (Hodgson and Jamieson, 1981). Milk-fed calves appear to be less sensitive in herbage intake to variations in daily herbage allowance than do other cattle (Combellas and Hodgson, 1979; Le Du *et al.*, 1979; Jamieson and Hodgson, 1979), whereas weaned calves and lactating cows respond similarly in herbage intake to variations in daily herbage allowance (Jamieson and Hodgson, 1979). Alden and Whittaker (1970) provided evidence that young

sheep were better able to maintain intake on very short swards than were older sheep with larger mouths. This indicates that animals differing in age or physiological state may differ in respect of the level of herbage intake established in specified conditions, or of the rate of change in either variable across a range of sward conditions (Hodgson and Jamieson, 1981).

Herbage intake from a sward increases roughly in proportion to the nutrient requirement of animals, except in cases where intake is limited by a deficiency of a specific nutrient (Hodgson, 1990). Deficiencies of essential nutrients including amino acids, minerals and vitamins in the diet are consistently associated with sub-optimal feed intake because they reduce the rate at which the body can use energy (Black, 1984).

2.4.4. Compensatory Relationship Between Variables in Grazing Behaviour and Herbage Intake

Grazing is a complex activity and involves searching for and selecting suitable forage, after which it is prehended and taken into the mouth (Vallentine, 1990). The amount of time spent on each phase of activity is very variable. Grazing time is generally lowest when forage is abundant and of good quality and highest when forage is of low quality or availability is limited (Vallentine, 1990).

To some extent animals can maintain a constant herbage intake with changing sward conditions. Hodgson (1985a) showed that sheep adjusted intake per bite, rate of biting and grazing time in relation to the amount of green leaf on offer. Biting rate usually tends to decline as sward height or herbage mass increase, and as intake per bite increases, principally because the ratio of manipulative to biting jaw movements increases as intake per bite and the size of individual plant components prehended increase (Chambers *et al.*, 1981; Hodgson, 1986).

Intake per bite varies less than bite dimensions, because of compensatory

effects between bite area, bite depth and density (Laca *et al.*, 1992). Laca *et al.* (1992) reported that the compensation of bite depth and bite area among animals resulted in no significant differences in bite volume, hence in intake per bite in dallisgrass (*Paspalum dilatatum* Poir.), and that compensation of bite volume and bulk density of the grazed horizons resulted in no significant differences in intake per bite in the lucerne.

Sward height and structure can have a major influence on the rate of pasture consumption (Hodgson, 1985b; Forbes, 1988a; Black, 1990). Black and Kenney (1984) showed that the rate of intake by sheep grazing a series of artificial pastures increased with both the height and density of the pastures. However, Kenney and Black (1986) reported that both intake rate and pasture availability at maximum intake rate depended greatly on the distribution of plant material within the pasture horizons. When sheep grazed artificial pasture of vegetative subterranean clover where most plant material was in the lamina at the top of the sward, intake rate was less affected by pasture height than for grass, and maximum intake rate approached 27 g/min dry matter when pasture availability was between 2 and 3 t/ha dry matter (Kenney and Black, 1986).

Penning *et al.* (1991a) stated that intake rate reached a maximum apparently because the rate of total jaw movements (prehension bites and mastications) during grazing was constant across all treatments, and that a greater proportion of jaw movements was required to masticate and manipulate the herbage ingested as bite mass increased, and therefore biting rate fell and intake rate remained constant. Similar evidence for maximum intake rates was reported by Black and Kenney (1984) and Alden and Whittaker (1970).

Penning *et al.* (1991b) showed that ewes increased their intake rate over time on a short sward (30 mm) by increasing their rate of prehension biting, while decreasing total grazing time compared with those on a taller sward (90-120 mm). This indicates that animals grazing short swards, in some circumstances,

are able to increase grazing efficiency after they become adapted to the sward conditions.

Reciprocal changes in intake per bite and biting rate may balance to maintain a roughly constant rate of intake on relatively tall swards, but on shorter swards any increase in biting rate is inadequate to balance the decline in intake per bite and rate of intake declines (Hodgson, 1986). Allden and Whittaker (1970) showed that on shorter swards (less than 7.7 cm) animals were unable to compensate for a reduced size of bite by increasing the rate of biting, and the rate of intake declined sharply. A constant rate of intake was maintained by reducing the rate of biting when the mean tiller length was greater than 7.7 cm (Allden and Whittaker, 1970). There was initially a rapid change in rate of intake with increasing tiller length (up to about 15 cm), thereafter there was little change in the rate of intake with increase in tiller length.

Increasing grazing time results in more energy being used for activity and less for production, thus the minimum grazing time to achieve an adequate intake is considered to reflect optimal behaviour. Increase in grazing time does appear to be a compensating response on the part of the animal to a decline in the short-term rate of intake. The intake of pasture may be limited by the time available for eating and ruminating when the rate of the dry matter intake is low (Black, 1990).

When intake per bite is limited herbage intake can be maintained for a short time by compensating increase in grazing time and rate of biting (Vallentine, 1990). However, this compensation is seldom adequate to prevent a fall in daily intake once the short-term rate of intake starts to decline (Hodgson, 1986; 1990). Le Du *et al.* (1979) stated that under rotational management cows did not compensate for restrictions in available herbage by grazing longer. On extremely short swards intake per bite, rate of biting and grazing time may all decline together (Hodgson, 1990). Grazing and ruminating time may be interchangeable to some degree.

Penning *et al.* (1991b) showed that there was a concomitant decrease in time spent ruminating, and time spent idling remained relatively constant, as grazing time increased.

2.5. DIET SELECTION

Animals are faced with a variety of forages in nature or with complex vegetation structure and components which have big variability in nutrient content during their grazing. The animals do not eat all the foods in equivalent amounts, diet selection is a problem that animals have to solve. As forages differ in their nutritive values, the diet that animals attain will vary with selection from the herbage on offer. The ability of animals to recognize and select diets from the herbage available to them is influenced by sward characteristics and animal factors. Emmans (1991) stated that the relevant variables to be considered in the theory of diet selection are animals, the environment within which the animal is kept, and the characteristics of the feeds on offer. Theories of diet selection have been greatly developed and some conceptual models have been made in recent years. This section will not summarize all the theories in detail, but attention will be concentrated on the influence of temperate sward characteristics and animal factors upon diet selection.

2.5.1. General Explanation of Diet Selection and Selection Strategies

Although much research has been done on diet selection of ruminants, it is hard to have a general principle to explain diet selection for grazing ruminants in detail because of its complexity (Arnold, 1966a; 1966b; Arnold and Hill, 1972; Arnold and Maller, 1977; Provenza and Balph, 1987; Bazeley, 1989; 1990; Hodgson *et al.*, 1994). Diet selection has been explained in different ways by different authors. Newman *et al.* (1992) proposed three different categories of explanations for diet selection in sheep: (i) functional explanations which concern why animals behave the way that they do; (ii) mechanistic explanations which

concern how animals behave the way that they do, emphasising the physical and physiological constraints determining the composition of the diet of animals; and (iii) descriptive explanations.

Rogers and Blundell (1991) suggested that it is worth considering the function of diet selection as a starting point for investigating the mechanisms of diet selection: (i) the animal must select a diet which can satisfy its nutritional requirements from the available foods; (ii) in doing this it must avoid ingesting harmful substances; (iii) it must exploit resources efficiently: for many animals food supplies are distributed unevenly in the environment, they may vary with seasons and the acquisition of food competes with other essential activities.

Gordon and Lascano (1993) stated that the suite of decision-making processes involved in selective grazing is termed foraging strategy. Foraging strategy of animals is simply a concept that facilitates description and understanding of plant-animal interactions (Taylor, 1993). Hodgson *et al.* (1994) concluded that visual and olfactory/gustatory cues, mediated by the effects of physical and structural characteristics of vegetation influencing ease and rate of intake, were likely to be important at all levels of scale in the spectrum of choice available to the animal.

Clark and Harris (1985) suggested that for grazing ruminants the most likely strategies are: (i) prey switching where selection is positively correlated with relative abundance; (ii) energy optimisation where selection is constant as relative abundance increases; and (iii) nutritional constraint where selection is negatively correlated with relative abundance. Rogers and Blundell (1991) stated that animals appear to very efficient in their foraging strategies, for example, trading off the quality of a resource against the cost of its procurement.

Black (1990) summarized that the factors influencing diet selection at least involved: (i) ease of eating, measured as potential intake rate when a forage is

offered alone to trained animals for short periods; (ii) sensory factors relating to taste, odour and tactile stimulation; (iii) water content of forage; and (iv) the quantity and spacial distribution of components. These factors are largely related to sward characteristics and involve animal responses to them under grazing conditions, so both sward factors and animal factors will be emphasized in this section.

2.5.2. Sward Characteristics and Diet Selection

Sward characteristics influencing diet selection are mainly considered for: (i) forage species, their components and maturity of all parts; (ii) sward surface height and mass; (iii) sward structure, in particular spatial arrangement of components of sward; (iv) content of clovers in sward; and (v) other factors such as climate, topography and aspect.

Broom and Arnold (1986) showed grazing sheep were highly selective when grazing mixed pastures with a very low biomass. Arnold (1987) showed that selectivity occurred when different species were contained in each patch, even when biomass was low, and preference of sheep changed from month to month. Kenney and Black (1984) showed that when two pastures were offered together, sheep generally preferred the pasture they could eat faster.

The preference for a species within a sward is generally not static but varies with the proportion of the species in the sward, its vertical and horizontal distribution, and varies with seasons and with the animals's prior experience (Marten, 1978; Newman *et al.*, 1992; Gordon and Lascano, 1993). For example, selection for clover is not a static phenomenon, and varies with the proportions of clover in the grazed horizon (Gordon and Lascano, 1993). Actually it is unlikely to observe constant dietary preference because sward conditions change dynamically.

Cattle, sheep and goats favoured differing horizons during their progressive

defoliation of a ryegrass/white clover sward (Nicol and Collins, 1990). Sheep frequently penetrated to about half the depth of the leafy zone of natural grass swards (Burlison, 1987). The response of deer to the wide range of height and density variation was very similar to that of sheep in bite depth, and a difference between them existed in bite area and intake per bite but not bite depth (Mitchell *et al.*, 1991).

Assessment of diet selection may be influenced by the measurement techniques used. There often appears to have been selection for clover if the relationship between the proportion of clover in sward and the proportion of clover in the diet is considered (Clark and Harris, 1985; Vallentine, 1990; Milne, 1991; Ridout and Robson, 1991). When taking into account the relationship between bite depth and sward surface height and examining the actual horizon grazed by sheep, less selection has been found because the proportion of white clover in the grazed horizon of the sward can explain most of the variations in proportion of clover in diet (Milne *et al.*, 1982; Hodgson, 1990). This is supported by some authors (L'Huillier *et al.*, 1984; 1986; Arnold, 1987). Clark *et al.* (1982) found only small differences between the proportions of white clover in the sward and the diet on North Island hill country pastures.

Selection for white clover may be related to the proportion of clover in the sward. Armstrong *et al.* (1993) showed that dietary clover percentage was positively related to the percentage of clover in the plots and was greater than the percentage of clover in the sward, especially in plots with lower proportions of clover. Illius *et al.* (1992) showed that sheep preferred swards with intermediate levels of clover, avoiding those with low or high levels. Milne (1991) found that at low levels of clover in the grazed horizon, there was selection for clover, and at high levels of clover in the grazed horizon there was selection against clover. This has led to development of hypotheses that in foraging circumstances where partial consumption of feeds is taking place, for example, as in most grazing circumstances, animals need to sample food by consumption because other cues

of diet selection are either short-lived or inadequate (Milne, 1991). Newman *et al.* (1992) reported that sheep preferred the opposite species to the one they had previously grazed, rather than a preference of clover over grass.

The height and biomass of vegetation patches have been shown to influence long-term selection (Arnold, 1987). Height differences gave an initial visual cue provided that they were sufficiently large (Illius *et al.*, 1992). In higher herbage masses, animals have the opportunity to graze selectively. Tall patches are preferred, and intermediate contents of clover are selected in preference to low or high contents (Illius *et al.*, 1992; Illius and Gordon, 1993). Gordon and Lascano (1993) showed that taller swards were generally preferred by all species, with sheep showing the least sensitivity to sward height and lowest intake rate differences, and goats being the most sensitive. Black and Kenney (1984) stated that if potential intake rates of the long and short herbage were similar when both were freely accessible, animals would select the long material whenever accessibility of the short material was such that it reduced intake rate below the potential. However, selection is reduced and ingestion of dead material increases as grazing progresses to lower masses.

Adequate green herbage needs to be supplied to grazing animals in order to meet their nutrient requirements. Green leaves and stems are generally preferred and dead material is often rejected by animals unless pasture allowance is low or high proportions of dead material exist within the grazing horizon. The top horizon of natural swards usually has the greater proportion of green leaf, and a higher concentration of nutrients. The herbage eaten by grazing animals has usually a high proportion of green leaf (Arnold, 1981). Selection for leaf by animals can be explained by the fact that leaf requires less chewing than stem, and exhibits faster rates of ingestion, digestion and passage (McLeod *et al.*, 1990). Barthram and Grant (1984) observed that sheep selectively grazed the leaf horizon at the top of a vegetative ryegrass sward and rarely penetrated to the lower levels containing pseudostems and dead material. By removing the top

half of a sward, animals may maximize nutrient intake by increasing bite rate rather than intake per bite (Laca *et al.*, 1992). L'Huillier *et al.* (1984) showed that animals appeared to penetrate the surface canopy to obtain green grass leaf in summer ryegrass pasture, resulting in low apparent intake. L'Huillier *et al.* (1986) found that sheep grazing a ryegrass-white clover pasture during summer in New Zealand largely bypassed the surface horizon containing predominantly dead reproductive stem to graze green material near the base of the sward. These results indicate the ability of animals to discriminate strongly between leaf and mature stem or between live leaf and standing dead material, if necessary by penetrating through the upper strata of the sward canopy to graze preferred material at the base of the canopy.

The degree of selection exerted by grazing animals between alternative sward components (plant species or morphological units) increases as within sward contrasts in plant maturity or physical and biochemical characteristics increase (Hodgson, 1986; Hodgson *et al.*, 1989). An appreciation of the distribution of plant components within the sward canopy is of particular importance to any attempt to interpret differences between the composition of the sward and the diet of grazing animals in terms of the deliberate exercise of choice between alternative plant species or morphological units (Milne *et al.*, 1982; Bircham and Hodgson, 1983; Hodgson, 1985a; Hodgson, 1993). The spatial arrangement of herbage gives herbivores a wide range of opportunities for diet selection (Milne, 1991). In mixed grass-legume swards the spatial dispersion of forage components may influence the diet composition of grazing sheep (Gordon and Lascano, 1993). Milne (1991) stated that even in a simple grass-clover sward, there were choices in the horizontal plane between areas of herbage which differed in species composition, nutritional value and height (Milne, 1991). Grazing animals can select within the vertical plane of a sward between different plant parts of the same species or different species (Milne, 1991). Milne (1991) described the selection by animals within the vertical plane in grass-clover swards, which have considerable variation in grass leaf and stem and clover leaf

and petiole in the vertical plane although they appear relatively homogeneous sward in horizontal plane, as '**bite selection**'. It is clear that the spatial-temporal variability in species distribution should be emphasized to define the proportions of the species on offer.

There are also a number of factors associated with the vegetation as well as factors such as climate, topography and aspect which influence site selection through effects on the energy expenditure of ruminants (Milne, 1991).

2.5.3. Animal Characteristics and Diet Selection

Animal factors influencing diet selection mainly include: (i) animal species, body size or rumen volume; (ii) size and shape of mouthparts for ruminants; (iii) previous experience of ruminants; (iv) social learning. (v) nutrient requirements.

There are different grazing strategies between animal species. Sheep and cattle grazing pastures often select a diet that bears little resemblance to the overall composition of the feed available (Leigh and Mulham, 1966; Dudzinski and Arnold, 1973; L'Huillier *et al.*, 1986; Lascano and Thomas, 1988; Black, 1990). In general, sheep tend to select a diet containing a higher proportion of green leaf and less stem and dead material than is in the pasture (Rattray and Clark, 1984). Clark and Harris (1985) showed that sheep showed a strong preference to graze on clover patches and appeared to discriminate in favour of clover within such patches. Deer exerted greater selection pressure for white clover than for the ryegrass component of a mixed sward (Bootsma *et al.*, 1990). Cattle are generally less severe and/ or less selective than sheep (Grant *et al.*, 1987). Goats have been found to have a different grazing style from sheep or cattle, taking shallower bites from the sward surface (Nicol *et al.*, 1987; Gordon and Lascano, 1993). Goats when given the choice, avoid grazing down into the pasture and may actively discriminate against eating white clover (Gong, 1994).

The degree of selection and diet selected by animals can be related to the body size, especially to rumen volume. Ruminants with a large body size digest fibrous foods better because of relatively larger rumens and longer retention times, whilst small ruminants digest fibrous feeds less well because of shorter retention times and rely on foraging strategies which allow them to ingest a diet with a high cell content (Milne, 1991).

The size and shape of ruminants' mouthparts affect the ability of animals to select discrete food items (Gordon and Illius, 1988). The wide and flat muzzle of ruminants like cattle is often associated with a low degree of selectivity while feeding, whilst a narrower and more pointed dental arcade like that of the goat is usually related to a high degree of selectivity (Milne, 1991). Taste is likely to be more important than sight, smell or touch in influencing bite selection (Milne, 1991).

Experience may be important in influencing the foraging behaviour of sheep, cattle and goats (Hodgson, 1971; Arnold and Maller, 1977; Provenza and Malechek, 1986) with more time being spent foraging and with less food being ingested by inexperienced animals (Milne, 1991). Foraging decisions are influenced not only by incident prey conditions, but also by expectations or techniques which reflect past experience (Illius *et al.*, 1992).

Information gained from each bite is accumulated over successive bites and switching decisions appear to be based on short periods of grazing rather than on individual bites (Illius *et al.*, 1992). Further evidence that grazing animals need to consume vegetation to assess its profitability is that the extent of partial consumption (bite depth) varies with sward characteristics. Sheep make limited use of pre-consumption cues, depending on circumstances, and rely more on information gained during short periods of grazing. However, decisions based on prior recognition of patch types can only have had a limited effect on diet selection, because after making an initial choice, animals switch frequently

between patches, indicating that some form of decision-making occurs during grazing (Illius *et al.*, 1992).

Social learning can be important in the development of food preference in lambs (Lynch *et al.*, 1983; Thorhallsdottir, *et al.* 1987; 1990a; 1990b; 1990c; Provenza and Burrit, 1991), but its effect on diet selection by grazing ruminants has not been studied (Milne, 1991).

The problems of satisfying nutritional requirements differ enormously according to the natural history of the species (Rogers and Blundell, 1991). Evidence that herbivores select nutrients to balance their diet is weak, and particular dietary or anti-nutritional factors can be incorporated into rate-maximizing models by specifying constraints (Stephens and Krebs, 1986). Another possible reason why herbivores may not show intake-maximizing behaviour is that they may face an inherently difficult task in discriminating between the profitability of alternative food sources (Illius *et al.*, 1992). Illius *et al.* (1992) showed that the complexity of vegetation structure and composition lies at the centre of the problem, with variability in nutrient content hypothetically imposing the need for mixed diets in order to balance nutrient intake. The continuous nature of grazing as a food-gathering process and the complexity of the food source combine to obscure the information on which the animal must act to maximize the short term intake rate (Illius *et al.*, 1992).

There are many reports describing the diet selected by animals in different environments, but most provide little basis for understanding why particular plant components are selected. Research on aspects of the biochemistry of dietary preference is particularly active. The role of tannins in plants in terms of their potentially multifaceted role in influencing diet selection is a fascinating one which is currently being actively studied (Milne, 1991). This will be discussed in Selection 2.6.

2.6. CONDENSED TANNINS IN PLANTS AND THEIR EFFECTS UPON NUTRITIONAL VALUE OF FORAGES

Much attention has been concentrated on N and carbohydrate fractions in forages in relation to efficiency of utilization of nutrients. Much research on the secondary compounds in forages has been focused on 'antiquality' components which have defense mechanisms against grazing by herbivores. However, the role of tannins, in particular condensed tannins in forage plants has been reported in recent years. This section will concentrate on the definition and ecological role of condensed tannins (CT) in forage plants, and then nutritional effects in agricultural systems. Emphasis will be put on the effects of CT on ruminant herbage intake, rumen digestion and performance (e.g. body growth, wool growth and carcass fatness).

2.6.1. Ecological Significance and Types of Tannins

Tannins are considered secondary metabolites and are irregularly distributed substances that have no specific metabolic function (Mehansho *et al.*, 1987). Tannins are complex polymers conveniently divided into two classes, hydrolysable and condensed tannins, based on their chemical structure. Condensed tannins should not be confused with hydrolysable tannins, which have different protein-binding characteristics (Barry and Manley, 1986).

Tannins are phenolic compounds which are derived from the shikimic acid pathway, and are found in all classes of vascular plants (Barry and Blaney, 1987). The role of plant tannins at the ecological level is almost certainly a mixed function (Zucker, 1983). Some plants first evolved CT production as a defence against attack by pathogenic bacteria and fungi (Swain, 1979); and with time this further evolved as a defence against attack by insects and finally against being eaten by herbivores (Barry, 1989).

Tannins are effective as defence against herbivores because they can affect both the nutritional availability of soluble plant proteins and polysaccharides and the activity of the digestive enzymes and symbiotic microorganisms of the herbivore's own gut (Robbins *et al.*, 1978a; Swain, 1979). Tannins are not only capable of sequestering the nucleic acids, protein, and polysaccharides of plant tissues themselves, hence preventing the breakdown of the polymers by fungal and bacterial extracellular hydrolase, but many other essential enzymes of the attacking organisms may be inhibited, thus affecting their overall metabolism (Swain, 1979). By complexing with protein, nucleic acids, and polysaccharides in fallen leaves, tannins also affect the rate of metabolism of these polymers by soil organisms (Swain, 1979).

2.6.2. Biological Significance of Condensed Tannins

CT are recognised as being antinutritional in the diet of monogastric animals, because high concentrations can reduce the absorption of protein from the small intestine (Wiseman and Cole, 1988). Although optimal CT concentrations for ruminants have not yet been accurately defined, high CT concentrations (>50 g/kg DM) in *Lotus* sp. are recognised as being detrimental (Barry, 1985; Barry and Duncan, 1984; Terrill *et al.*, 1992b; Waghorn *et al.*, 1990). Low CT concentrations in forage plants are thought to be of nutritional advantage to grazing ruminants (Barry and Duncan, 1984; Barry and Manley, 1984; Barry, 1985; 1989; Waghorn *et al.*, 1987a; 1987b; Waghorn *et al.*, 1990; Terrill *et al.*, 1992b; Waghorn *et al.*, 1994a; 1994b). From the results of much research, the beneficial effects of low dietary condensed tannin concentrations on ruminants are summarised as: (i) binding plant proteins, reducing their solubility and degradation in the rumen by microorganisms (Barry and Duncan, 1984; Barry, 1985; Barry *et al.*, 1986; Waghorn *et al.*, 1987a); (ii) increasing plant proteins passing out of the rumen to the intestine for digestion and increasing the availability and absorption of essential amino acids (Waghorn *et al.*, 1987b; Waghorn *et al.*, 1990; McNabb *et al.*, 1993b; Waghorn *et al.*, 1994a; 1994b);

(iii) preventing animal bloat (Reid *et al.*, 1974; Waghorn and Jones, 1989; Chiquette *et al.*, 1989; Waghorn *et al.* 1990). (iv) increasing rates of body and wool growth in growing sheep (Terrill *et al.*, 1992b; Wang *et al.*, 1994).

Much research has been done by spraying forages (Barry and Duncan, 1984; Barry, 1985) or drenching animals with polyethylene glycol (PEG; MW 3,350) (Waghorn *et al.*, 1987; 1994a; 1994b; Wang *et al.*, 1994) to study the CT in the forages and their effects on ruminants. PEG can bind with CT and form much stronger chemical bonds than do plant proteins, and thus prevent CT reacting with protein or displace CT from a pre-formed CT:protein complex. Barry and Duncan (1984) reduced the total reactive condensed-tannin content of lotus through spraying the forage with PEG, with the tannin-PEG complex being excreted in the faeces. This is supported by other results (Jones and Mangan, 1977; Barry and Manley, 1986). The effectiveness of PEG is dependent on the amount of tannin in the complex and the age of the complex at the time of addition of PEG (Jones and Mangan, 1977).

2.6.3. Concentrations of CT in Plants

Condensed tannins (CT) are present in many plant species such as sainfoin (*Onobrychis viciifolia*), haresfoot trefoil (*Trifolium arvense* L.), birdsfoot trefoil (*Lotus corniculatus*), Grasslands Maku lotus (*Lotus pedunculatus*), crown vetch (*Coronilla varia*) and dock (*Rumex obtusifolius*) (Jones *et al.*, 1976; Waghorn and Jones, 1989; Waghorn *et al.*, 1990). CT concentrations in the legumes range from 1.5 to 187 g/kg DM, but in herbs and grasses are relatively low (<2.5 g/kg DM) (Terrill *et al.*, 1992a).

Condensed tannins (CT) occur in specialised cells which are distributed at random throughout the leaves and stems of *Lotus* sp. and of sainfoin (Barry and Manley, 1986). When tissue of these species is disintegrated, CT react with and precipitate soluble leaf protein by hydrogen bonding under the appropriate

conditions to form insoluble complexes. The bonding between CT and protein is reversible with pH.

2.6.3.1. Separations of CT Fractions

Analysis of CT in plant material is complicated by their reactivity with other compounds (Terrill *et al.*, 1992a). Techniques have been developed for measuring extractable CT in forages (Jones and Mangan, 1977), neutral detergent fibre residue (Reed *et al.* 1982) and separation of total CT in forages (Terrill *et al.*, 1992a). The new technique by Terrill *et al.* (1992a) can separate total CT in forages into extractable, protein-bound and fibre-bound fractions. A low proportion of CT was extractable (33-35%) when total CT concentration was low (6 - 30 g/kg DM) in freeze-dried legumes, but a high proportion of total CT was extractable in grasses containing small CT concentrations (1.1-1.4 g/kg DM) (Terrill *et al.*, 1992a). The proportion of extractable CT increases with increment of total CT and is normally about 70% of total CT in legumes.

2.6.3.2. Factors Affecting CT Concentration in Plants

Concentrations of CT in plants vary with: (i) plant species; (ii) plant genotype within a species (Lowther *et al.*, 1987; Barry and Blaney, 1987). (iii) components of plants (Jones *et al.*, 1973; Barry, 1989); (iv) stage of plant growth; (v) growing conditions such as soil fertility and temperature conditions (Barry and Forss, 1983; Barry and Blaney, 1986).

Concentrations of CT in *Lotus corniculatus* were much lower than in *Lotus pedunculatus* cv. Grasslands Maku when grown under low soil-fertility (pH 5.2) conditions (Barry, 1985; Lowther *et al.*, 1987). When grown under warm conditions in high-fertility soils, *Lotus pedunculatus* contained lower CT concentrations (20 g/kg DM) (John and Lancashire, 1981) than sainfoin (28 - 30 g/kg DM) (Barry and Manley, 1986). Within *Lotus corniculatus*, CT concentrations

were lower for semi-erect (1-8 g/kg DM) than for erect types (12-39 g/kg DM) (Lowther *et al.*, 1987).

Concentrations of CT were low and ranged from 1-2 g/kg DM in grasses such as perennial ryegrass, Yorkshire fog (*Holcus lanatus*) (Terrill *et al.*, 1992a; Montossi *et al.*, 1994; Iason *et al.*, 1995). Chicory (*Chichorium intybus*) also had a low CT concentration (4.2 g/kg DM) (Terrill *et al.*, 1992a).

Concentrations of CT also vary with plant components. The concentrations of CT in dock were 2-3 times as high in leaf as in stem, and were highest in the inflorescence (Waghorn and Jones, 1989). Concentrations of condensed tannins in forages increase with maturity (Bums, 1978; Chiquette *et al.*, 1989; Waghorn and Jones, 1989).

Lotus pedunculatus grown under low soil fertility conditions contained more than twice as much total condensed tannins as *Lotus* grown under high soil-fertility conditions. *Lotus pedunculatus* (cv. Grasslands Maku) contained 20-30 g CT/kg DM when grown under warm conditions in high-fertility soils (John and Lancashire, 1981) and 70-80 g CT/kg DM when grown in acid, low-fertility soils (Barry and Forss, 1983; Barry, 1985). Application of phosphorus and sulphur fertiliser stimulated DM yield and reduced forage CT concentration in *Lotus pedunculatus* (cv. Grasslands Maku) grown under cold conditions in acid, low-fertility soils. These results indicate that improved growing conditions may reduce CT concentrations of *Lotus pedunculatus* (Barry and Forss, 1983).

2.6.4. Effects of CT on the Nutritional Value of Forages

Tannin sometimes acts as a toxin rather than a digestion inhibitor (Mehansho *et al.*, 1987; Hagerman *et al.*, 1992). CT are recognised as being antinutritional in the diet of monogastric animals, because high concentrations can reduce the absorption of protein from the small intestine (Wiseman and Cole, 1988). High

condensed tannins in some plants are recognised as being detrimental to ruminants (McLeod, 1974; Barry and Duncan, 1984; Zucker, 1983; Pritchard *et al.*, 1988; Terrill *et al.*, 1989; Windham *et al.*, 1990; Waghom *et al.*, 1990; 1994a;). Typical detrimental effects of CT include a marked depression in DM and nitrogen digestibility, inhibited microbial activity (Waghom *et al.*, 1990), low rumen fibre digestion, a low voluntary feed intake (Waghom *et al.*, 1990), and poor animal performance (Barry and Manley, 1984; Barry, 1985; Barry *et al.*, 1986; Waghom *et al.*, 1994a). However, attention is paid here on effects of low-moderate CT concentrations on the nutritional value of forages and ruminant digestion and metabolism in this section.

2.6.4.1. Effects of Condensed Tannins on Digestion

Condensed tannins bind with plant protein during mastication to form a stable complex (Barry and Manley, 1984). Stability of the CT-protein complex is strongly pH-dependent, being stable and insoluble in the pH range 3.5-7.0, but unstable at pH < 3.0 and at pH 8.0 (Jones and Mangan, 1977). This indicates that condensed tannins in fresh forages can theoretically reduce plant protein degradation rates in the rumen (pH 5.8-6.8), yet allow their solubilization and release in the abomasum (pH 2.5-3.5) and small intestine (pH 7.5-8.5). Barry and Manley (1984) observed a strong positive correlation between the tannin content of plants and the flow of protein out of the rumen. Reducing ruminal degradation of plant protein and increasing crude protein flow to the intestine improved the nutritive value of plants for ruminants (Barry and Manley, 1984; Waghom *et al.*, 1987; Mangan, 1988).

2.6.4.1.1. Effects of CT on N Digestion and Absorption

Leaf protein is largely concentrated in the chloroplast and consists of the soluble stromal protein and the particulate lamella protein. The cells and chloroplast are ruptured during mastication of herbage by ruminants and large quantities of

soluble protein are released. Most soluble proteins are rapidly degraded in the rumen and fermented to ammonia (Jones and Mangan, 1977). Therefore, inefficient nitrogen digestion often occurs when animals are fed with fresh forages or graze in high quality temperate grass pasture, especially in the normal ryegrass-white clover pasture in New Zealand (Barry, 1982; Barry and Duncan, 1984; Waghorn and Barry, 1987; Barry, 1989; Waghorn *et al.*, 1990). However, ruminants have more non-ammonia nitrogen flowing out of the rumen into the abomasum when fresh forages containing CT are fed compared with those fed fresh forages not containing CT. The presence of low CT concentrations in forage plants can increase the quantity of protein available for absorption (Waghorn *et al.* 1990). CT reduce rumen degradation of soluble proteins and increase the quantity of protein passing out of the rumen for digestion in the intestines by reversible hydrogen bonding. Evidence for the protection of plant protein from degradation in the rumen by CT can be certified by: (i) the rise in rumen ammonia concentration in PEG-treated animals fed *Lotus pedunculatus* (Waghorn *et al.*, 1990); (ii) the much lower concentrations of ammonia in rumen digesta than normal when diets containing sainfoin, lotus or dock are fed to ruminants (Waghorn, 1994b).

The potential benefits of CT to ruminant nutrition are associated with the effects on N digestion (Waghorn *et al.*, 1994b). CT increased the flow of feed nitrogen (N) to the abomasum (Barry and Duncan, 1984; Waghorn *et al.*, 1987a) and improved N retention, or flux of amino acids to the intestine, but CT reduced N digestibility (0.67 vs. 0.81 for Tannin and PEG-groups) (Waghorn *et al.*, 1994b). More feed protein was thus potentially available for absorption from the small intestine. CT did not affect microbial N flux to the abomasum (Barry and Manley, 1984; Waghorn *et al.*, 1994a). Due to their reactivity with protein, increasing dietary reactive CT concentration in the range 0-110 g/kg DM linearly increases the duodenal flow of non-ammonia nitrogen (NAN) per unit of total N consumed in sheep fed fresh *Lotus* diet (Barry and Blaney, 1987). However, apparent digestibility of crude protein was found to be decreased slightly by CT (Barry and

Manley, 1984; Waghorn *et al.*, 1987a; Waghorn *et al.*, 1994a). Examples involved: (i) 70% and 78% CP digestibility observed by Waghorn *et al.* (1987) when sheep fed *Lotus corniculatus* containing 22 g CT/kg DM vs. the same forage treated with PEG; (ii) 56% and 71% digestibility reported by Barry and Manley (1984) when feeding *Lotus pedunculatus* containing 106 g CT/kg DM and 46 g CT/kg DM; (iii) 70% and 76% digestibility found by Waghorn *et al.* (1994a) when sheep were fed *Lotus pedunculatus* containing 55 g CT/kg DM compared with those fed the same forage with PEG.

Absorption of one or more essential amino acids from the small intestine was below the requirements of growing lambs fed on fresh ryegrass (*Lolium perenne*)-based herbage (Barry, 1981). Similar deficiencies in the absorption of essential amino acids, relative to the requirements for optimum production at the level of voluntary ME intake achieved, occurred in lactating ewes and dairy cows consuming fresh pasture *ad libitum* of high metabolizable energy (11.3 MJ ME/kg DM) and total nitrogen (33 g/kg DM) content (Barry, 1982). The presence of CT in forage plants often increases absorption of amino acids in the intestine (Barry and Forss, 1983; Barry and Duncan, 1984; Barry and Reid, 1984; Waghorn *et al.*, 1987b; 1990; Terrill *et al.*, 1992b; McNabb *et al.*, 1993b). Lee *et al.* (1992) observed that *Lotus pedunculatus* significantly improved the supply and utilization of cysteine, which is the first-limiting amino acid for both skin growth and wool production (Black and Reis, 1979), at a whole level. The CT therefore appears to overcome one of the major constraints to improved ruminant production from high-quality forages, namely the wastage of plant protein through microbial degradation in the rumen (Waghorn *et al.*, 1994b).

Waghorn *et al.* (1987b) showed that protection from degradation appeared to favour essential amino acid (EAA) supply to sheep, so that in the presence of 22 g CT/kg DM, 50% more EAA and 14% more non-essential amino acids (NEAA) reached the abomasum. Apparent absorption of EAA from the small intestine was 62% higher, and for NEAA 9% lower than in sheep fed the same diet where

CT was made ineffective by rumen infusion of polyethylene glycol. From the observations of effects of CT (55 g/kg DM) in *Lotus pedunculatus* on nitrogenous aspects of digestion, Waghom *et al.* (1994a) showed the beneficial effects of CT in reducing rumen degradation of feed protein were negated in part by a reduction of fractional absorption of amino acids (AA) from the small intestine. Fractional absorption of essential AA was 0.79 and 0.66 respectively in sheep with and without PEG infusion; values for non-essential AA were 0.73 and 0.59 respectively. The reduction in fractional absorption of amino acids was compensated for by the increased nitrogen flowing to the intestine with CT, and hence net absorption was not affected.

2.6.4.1.2. Effects of CT on DM, OM and Fibre Digestion

Effects of CT on fibre digestion partially depend on the content of CT in the forages fed to animals. Low CT (22 g/kg DM) in *Lotus corniculatus* did not affect digestion of neutral detergent fibre (NDF) in the rumen or in the whole digestive tract (Waghom *et al.*, 1987a). Low-medium CT (55 g/kg DM) in *Lotus pedunculatus* did not affect the digestion of cellulose or hemicellulose (Waghom *et al.*, 1994a). However, high dietary CT concentration (106 g/kg DM) in *Lotus pedunculatus* reduced rumen digestion of hemicellulose by 52% compared with low-medium CT (46 g/kg DM) (Barry and Manley 1984). This is consistent with reports by Barry *et al.* (1986) who showed that high dietary CT concentration linearly reduced rumen digestion of hemicellulose.

Effects of CT on digestibility of fibre had been found to be variable with plant species and content of CT. Digestibility of cellulose and hemicellulose was lower in sheep fed sainfoin containing CT compared with ryegrass or white clover (Ulyatt and Egan, 1979). Barry and Manley (1984) showed an 19% reduction in cellulose digestibility and a 23% reduction in hemicellulose digestibility when sheep were fed material with 106 g CT/kg DM compared with lotus containing 46 g CT/kg DM. However, the digestibility of fibre was not affected by medium

CT in *Lotus pedunculatus* (Waghorn *et al.*, 1994a).

DM digestibility, the proportion of DM digested in the rumen and rate of digestion in the rumen were enhanced by administering PEG to sheep eating *Lotus pedunculatus* (Waghorn *et al.*, 1994b). Barry and Manley (1984) reported that CT depressed OM digestibility when sheep were fed *Lotus pedunculatus* containing 106 g CT/kg DM. However, Chiquette *et al.* (1989) showed OM digestibility of forages was not affected by tannin levels of 32 g/ kg DM and below. The latter observation was consistent with reports of John and Lancashire (1981) and Barry *et al.* (1986).

Limited information showed CT in *Lotus corniculatus* to have no (or little) effect on VFA concentration, but markedly change the molar proportions of individual VFA (Terrill *et al.*, 1992a; Wang *et al.*, 1994). This evidence is supported by Chiquette *et al.* (1989). Waghorn *et al.* (1994a) reported CT in *Lotus pedunculatus* resulted in a lower concentration of VFA in rumen liquor, especially in acetate concentration, and the CT reduced the molar proportion of acetate but increased the molar proportions of propionate, butyrate and isovalerate on day 9 of experiment, and had little effect on the molar proportions of VFA by day 21. The lower VFA concentrations indicate a slower rate of fermentation by CT in sheep fed on *Lotus pedunculatus*. These results were obtained from sheep having a high nitrogen intake. When diets have either a low nitrogen content or restricted intake, nutrients available to animals would be reduced from a reduction in fractional absorption of amino acid, and in that case amino acid absorption may have limited production.

2.6.4.2. Effects of CT on DM Intake, Diet Selection and Performance of Animals

Effects of CT on DM intake and ruminant performance have been reported to be variable. High CT concentrations have been blamed for low palatability, reduced

voluntary intake and poor digestibility of herbage. Low-medium CT concentrations have been reported to have a beneficial effect in protecting plant protein from degradation by rumen bacteria, in increasing absorption of essential amino acids from the intestine, and hence in increasing rates of body and wool growth in growing sheep (Terrill *et al.*, 1992b).

Free and bound CT contents are recognised to be indices of the detrimental and beneficial effects produced by forage CT (Barry and Reid, 1985). Free CT content in *Lotus* is strongly and positively correlated with the total CT content (Barry and Forss, 1983). Free CT are highly reactive, have an affinity for forming hydrogen-bonded complexes with proteins, and are known to react with and precipitate microbial and digestive enzymes (McLeod, 1974). When sheep are fed on high CT forages, especially if the tannin-protein complex formed during disintegration of such plants releases high proportions of free tannin, both increased intakes of free CT into the rumen and large quantities of free CT released into the small intestine during protein digestion affect microbial and digestive enzymes. Free tannin in the rumen and in the intestine was probably responsible for the large depression of cellulose and hemicellulose digestion and a slower rate of microbial fermentation in the rumen observed by Barry and Manley (1984), and is thus a cause of depressed voluntary intake (Barry and Duncan, 1984). This is indicated by the larger rumen pool size, slower turnover, and lower concentration of volatile fatty acids (Waghorn *et al.*, 1994b).

High levels of protein protection were associated with reduced feed intakes (Waghorn *et al.*, 1990). Very high CT concentrations (76-90 g/kg DM) have been proved to be nutritionally detrimental (Barry, 1985), as found by Van Hoven (1984) for game animals forced to eat browse plants under drought conditions in South Africa. Although the limited information available has not indicated a clear relationship between CT content and DM intake, reduced DM intake of sheep by high CT (60-110 g/kg DM) in *Lotus pedunculatus* has been reported by Barry and Duncan (1984). The high level of CT reduced apparent digestibility

of both DM and nitrogen (Barry and Duncan, 1984; Barry and Manley, 1984). The depression in both the voluntary intake and digestion of organic matter by high concentrations of CT depressed ME intake. The stimulation of hemicellulose and cellulose digestion by PEG administration to sheep fed forage with high CT concentration suggests that the CT was depressing rumen digestion (Barry and Duncan, 1984). Pritchard *et al.* (1988) reported that the CT in *Acacia aneura* (mulga) (20-110 g/kg DM) depressed intakes by 40-50%, to submaintenance levels, compared with sheep given mulga with 24 g PEG/day. Also, Waghorn *et al.* (1994a) showed that sheep fed *Lotus pedunculatus* containing 55 g CT/kg DM ate 12% less feed than those receiving PEG during the digestion period. This is consistent with the findings of Waghorn *et al.* (1990). The reduction in intake due to CT in *Lotus pedunculatus* is nevertheless substantially less than that with some other forages. The sheep with the lower intakes had larger rumen volumes and a slower rate of clearance than when PEG was infused. In contrast, DM intakes of sheep fed *Lotus* containing 22 g CT/kg DM did not decline after 24 days of feeding (Waghorn *et al.*, 1990).

Although diet selection by some mammalian herbivores is inversely correlated with tannins (Provenza *et al.*, 1990), very little information has been found on the effect of CT on the diet selection of ruminants. Selection by cows against dock was minimal, and was confined to an occasional rejection of mature stems and sometimes seed heads (Waghorn and Jones, 1989). The low intakes of sheep eating high-CT forage appear to be a consequence of rumen function rather than of palatability (Waghorn *et al.*, 1994a). Palatability is unlikely to mediate the effect of CT on intake (Waghorn *et al.*, 1990). The authors reported that the stem fraction containing 2.2% CT in the DM was rejected when sheep were fed *Lotus pedunculatus*, but the leaflets containing 8.5% CT were nipped off the stems and eaten. Further, Jones and Mangan (1977) showed CT from sainfoin was unable to form insoluble complexes with submaxillary mucoprotein, so that the lubricating properties of the salivary mucoprotein, and this aspect of palatability, were unaffected. The rumen DM pool size was not reduced despite

a lower ME intake.

An alternative procedure for reducing the impact of CT on intake (and digestibility) might be drying the forages for hay (Waghom *et al.*, 1994a). Terrill *et al.* (1989) found intake and digestibility of sheep fed *Sericea lespedeza* to be less affected by CT from field-dried than from fresh frozen forage, and Kraiem *et al.* (1990) did not detect any CT effects when *Lotus corniculatus* hay was fed to steers.

Partial adaptation of grazing ruminants to the high dietary concentration of CT in *Lotus pedunculatus* has been recorded (Barry, 1985). Lowther and Barry (1985) found that liveweight gain (LWG) of lambs grazing areas oversown with lotus (9.0% CT) were initially low (60-100 g/d) and then increased (120-140 g/d), whereas LWG of lambs grazing areas oversown with white clover were consistently high (120-130 g/d).

Concentrations of CT in forage plants greatly affect the performance of grazing ruminants. High concentrations of CT prevent maximum expression of liveweight gain and wool growth in grazing sheep. Poor performance of animals has been observed when fed forages high in CT concentration. High concentrations of *Lotus* CT (6.0-9.0% DM) depress cell wall digestion, voluntary intake and liveweight gain (LWG). Barry (1985) showed that high concentrations of CT prevented maximum expression of liveweight gain and wool growth when young sheep grazed on *Lotus pedunculatus* (7.6-9.0% CT).

Both sainfoin and Maku *Lotus* are about 60% better than perennial ryegrass for promoting lamb growth when fed *ad libitum* (Ulyatt, 1981). Purchas and Keogh (1984) found that carcass fat content was consistently lower in lambs grazing a CT-containing legume (*Lotus pedunculatus*) than a non CT-containing legume (*Trifolium repens*). The high nutritive value of sainfoin and *Lotus* cannot be attributed simply to the digestible components of the plants, their digestibility or

to level of intake (Ulyatt and Egan 1979; Egan and Ulyatt, 1980; Waghorn *et al.*, 1987a; 1990; Mangan, 1988), but must relate to the effect of digestion on products available for absorption and utilization for growth (Waghorn *et al.*, 1990). N retention or apparent absorption from the intestine was always substantially higher in sheep fed on low CT lotus than those fed on the equivalent CT-free herbage at similar levels of intake (Waghorn *et al.*, 1990).

The production of milk, meat and wool could be increased if grazed pasture contained low CT content in the DM. CT concentrations up to about 2-3% of dietary DM are probably optimising nutritive value (Waghorn *et al.*, 1990). Wang *et al.* (1994) showed action of CT in *Lotus comiculatus* increased wool production and slightly increased live weight. Waghorn *et al.* (1990) also showed evidence for an improved performance of sheep by CT in *Lotus comiculatus* or sainfoin in a summary of eight reports. Wool growth has long been known to be sensitive to protein absorption (Kempton, 1979), as the presence of CT in lotus and sainfoin increased both amino acid absorption and nitrogen retention (Ulyatt and Egan, 1979; John and Lancashire, 1981; Barry and Manley, 1984).

Barry (1985) showed PEG supplement increased wool growth in sheep fed on *Lotus pedunculatus* containing high CT concentration. Part of the increase in wool growth following administration of PEG to sheep fed high CT *Lotus* PEG may be attributed to the increase in forage intake which occurs when dietary reactive CT concentration is reduced following PEG application to high-tannin lotus (Barry and Duncan, 1984).

Terrill *et al.* (1992b) showed rates of wool growth were consistently higher for lambs grazing sulla (*Hedysarum coronarium*; 4.0-5.0% CT) than those grazing pasture, with the CT concentration in sulla being neither stimulatory nor inhibitory to body growth or voluntary feed intake (VFI). During spring and early summer, when wool growth rates were highest, CT present in both pasture and sulla increased wool growth rate; when wool growth rates were low during winter, CT

had no effect upon the wool growth of grazing sheep. Purchas and Keogh (1984) found carcass fat content to be consistently lower in lambs grazing a CT-containing legume (*Lotus pedunculatus*) than a non CT-containing legume (*Trifolium repens*). However, Waghorn *et al.* (1994a) showed that live weights and yields of greasy wool from mid-side patches in sheep fed *Lotus pedunculatus* containing low-medium CT, grown under conditions of medium-high fertility, were similar for PEG and Tannin groups.

2.6.4.3. Condensed Tannins and Bloat

Bloat, a serious disorder in cattle or sheep, is a familiar hazard when cattle are fed certain common legumes - white clover, red clover, subterranean clover and lucerne (Reid *et al.*, 1974). It is caused by a stable and persistent foam generated in the rumen, which interferes with eructation of gases arising from digestion (Clarke and Reid, 1974). Foam stabilisation appears in part to be a consequence of fraction 1 (F1) plant leaf protein (E.C.4.1.1.39) released into rumen liquor (Jones *et al.*, 1978). The soluble proteins present in rumen contents of cattle grazing lush pastures such as white clover (*Trifolium repens* L.), red clover (*Trifolium pratense* L.) or lucerne (*Medicago sativa* L.), have been implicated as the surfactant responsible for the persistent foams that develop in the rumen of animals suffering from bloat.

In contrast to most pasture legumes, the species containing condensed tannins are known not to induce bloat. Bloat has not been recorded in cattle grazing lotus, sainfoin and other species containing CT (Jones and Lyttleton, 1971; Jones *et al.*, 1973; Reid *et al.*, 1974). The absence of bloat with these species is often attributed to the presence of CT. The CT can bind and precipitate F1 protein to form insoluble tannin complexes, and thus reduce the F1 protein concentration in rumen liquor (Jones and Mangan, 1977; Waghorn and Jones, 1989). Waghorn and Jones (1989) demonstrated both *in vitro* and *in vivo* that CT from dock was able to precipitate F1 protein from lucerne. Cows did not bloat

when the diet contained 0.13 - 0.23 % CT of DM (Waghorn and Jones, 1989) and only 0.17% CT in the DM precipitated 50% of the F1 protein in the macerate (Waghorn *et al.*, 1990). Reid *et al.* (1974) also showed that no froth was seen in ruminal or duodenal contents of sheep fed sainfoin. This contrasts markedly with the situation in sheep fed white clover (*Trifolium repens*), when the ruminal contents are characteristically very frothy, and froth commonly occurs in the duodenal contents (Reid *et al.*, 1974). These results suggest that the presence of CT uniformly distributed throughout leaf and stem tissue in forage plants would reduce rumen degradation of soluble proteins, and such reduction in plant protein solubility in the rumen would also eliminate the disorder 'frothy bloat'.

2.6.5. Potential Part of CT in Grazing System

Many of the beneficial effects of CT on ruminants, including leaner lambs grazing *Lotus pedunculatus* than white clover (Purchas and Keogh, 1984), increased wool growth in sheep fed sulla than sulla with PEG (Terrill *et al.*, 1992b), the absence of bloat in cattle (Jones and Lyttleton, 1971) and reduced effects of gastrointestinal nematodes in sheep (Niezen *et al.*, 1993b), are associated with a greater availability and absorption of N or amino acids (Waghorn *et al.*, 1987b; 1994a).

A net benefit only occurs with ruminants given fresh-forage diets when the tannins react with forage proteins and reduce their solubility. Concentration of CT in forages used in pasture production should be in the range expected to increase protein utilization by ruminants whilst minimising any effects of tannins in depressing voluntary intake and digestibility of DM. The ideal dietary CT concentration would therefore seem to be the minimum amount of CT necessary to render the plant protein insoluble (Barry, 1985). Barry *et al.* (1986) stated that choice of an optimum concentration of CT in Lotus depends on a balance between its positive effect in increasing duodenal NAN flow and its negative effect in depressing apparent digestibility of energy and OM and rumen digestion

of hemicellulose and of pectin. They suggested a suitable compromise for both secondary and primary growth would appear to be about 3.0-4.0% CT. Waghorn *et al.* (1994b) also recommended a similar concentration of CT in *Lotus*, which represents a balance between the positive effect of CT in improving the efficiency of N digestion and the effect in depressing rumen carbohydrate digestion. Waghorn *et al.* (1990) stated that the concentration of CT in herbage eaten should not exceed 4%, and upper limit should probably be 2-3% of DM.

Incorporating low concentrations of CT into pasture DM would improve pasture quality and ruminant productivity (Waghorn *et al.*, 1990). However, the backbone of New Zealand farming - ryegrass and white clover contains little CT except for the flower petal of white clover (Jones *et al.*, 1976). Unfortunately, no evidence has been found for the expression of CT in white clover foliage (Waghorn *et al.*, 1990). This provides a very strong challenge for plant breeders and plant molecular biologists to enable CT to be expressed in the foliage. Waghorn *et al.* (1990) optimistically estimate that productivity would likely be increased 10-15% and bloat would be eliminated if white clover with 8% CT in its foliage accounted for 20-30% of pasture DM consumed.

2.7. PASTURE SPECIES

Traditional pastures mostly comprise ryegrass and white clover in New Zealand agricultural systems. Perennial ryegrass swards have generally greater herbage production than Yorkshire fog under fertile conditions (Haggar, 1976; Watt, 1987; Frame, 1992; Morton *et al.*, 1992), hence produce better animal performance either under continuous or rational grazing managements (Morton *et al.*, 1992; Niezen *et al.*, 1993a; Montossi, 1995; Niezen *et al.*, 1995; Hodgson *et al.*, 1996). However, the limitation of these pastures, associated with sensitivity to drought, grass grub, stem weevil, ryegrass staggers and low pasture production in poorer environments, have prompted the evaluation of alternative species.

Yorkshire fog (*Holcus lanatus* L.) is a constituent of many North Island hill country swards, and is productive in all seasons of the year and the main contributor to yield of some pastures in autumn and winter (Watkin and Robinson, 1974; Scott and Hardacre, 1974). It has some advantages compared with other grasses: (i) an ability to compete with other grass species under both low and high fertility conditions (Scott and Hardacre, 1974); (ii) very vigorous growth and complete ground cover on exposed hill subsoils (Dunbar, 1974); (iii) a higher mean N concentration when swards are irrigated, fertilized and cut monthly (Haggar, 1976); (iv) similar pasture production (herbage dry matter) and (v) similar liveweight gain to ryegrass (Watkin and Robinson 1974; Haggar, 1976; Morton *et al.*, 1992). These results indicate that the agronomic value of Yorkshire fog may have been underestimated (Jacques, 1962; Smith *et al.*, 1972; Harvey, *et al.*, 1984; Watt, 1978), and that this grass may have potential in pasture production in New Zealand (Jacques, 1962; Vartha and Clifford, 1971; Clements and Easton, 1974; Dunbar, 1974; Watkin and Robinson, 1974; Cameron, 1979). Of increasing interest is the fact that Yorkshire fog contains small amounts of condensed tannins (CT), so the effects of low CT concentrations on the nutritional value of the grass have been emphasised in recent years. Little is known about CT concentrations in other grasses and their effects on the performance of grazing animals.

Tall fescue (*Festuca arundinacea*), widely used in the U.S.A. as a forage, was introduced to New Zealand from various European sources over 100 years ago. Wild tall fescue plants are generally coarse and unpalatable to stock. However, tall fescue has many potential advantages such as adaptation to a wide range of soil and climate conditions, high productivity, persistence, responsiveness to fertilizer, ease of management, withstanding abusive grazing management and greater tolerance to grass grub than perennial ryegrass. The cultivars Aberystwyth S170 and Grasslands Roa have superiority over ryegrass cultivars in terms of pasture production over summer-autumn, especially in areas prone to long periods of moisture stress (Watkin, 1975; Wilson, 1975; Kain *et al.*, 1979;

Goold and Van der Elst, 1979; Anderson, 1982; Brock, 1983; Thomson *et al.*, 1988), so best use of tall fescue would be made in areas where perennial ryegrass does not persist because of lack of summer moisture. A major problem for tall fescue is its very slow seedling growth, so it has considerable competitive disadvantage in mixed swards. No evidence of toxicity in improved cultivars such as Grasslands Roa has been recorded in New Zealand (Brock, 1983; Wright *et al.*, 1985; Kearns, 1986). Tall fescue Grasslands Roa can produce similar liveweight gains and carcass weights in weaned lambs to perennial ryegrass (Wright *et al.*, 1985; Brock, 1983).

2.8. CONCLUSIONS

Herbage digestibility is a major nutritional factor influencing herbage intake of grazing ruminants. The potential influence of non-nutritional characteristics of swards on herbage intake under grazing conditions should be emphasized, in particular the importance of behavioural limitations in the control of herbage intake.

Although the controlled techniques have the problem of not being able to determine behavioral activities in the long term or herbage intake per day, they have made it possible to investigate separate effects of sward characteristics on grazing behaviour, herbage intake and diet selection of animals. A precise prediction for herbage intake under grazing conditions is still very difficult because of complex interactions among the factors concerned, but factors affecting herbage intake are becoming better understood. Increasing qualitative knowledge enables it to be possible to develop quantitative approaches to improve understanding of the plant-animal system.

Much research on effects of CT on nutritional value of forages has been done in recent years, and this provides a knowledge base of the mechanisms of ruminant digestion and absorption affected by CT in forages. However, the basic

research has mostly been done with legumes such as *Lotus corniculatus* and *Lotus pedunculatus*. Further observations on other plant species containing CT are required to have a better understanding of effects of CT on proteolysis and absorption. The beneficial effects of CT in forages should be enhanced and the antinutritional effects, especially in many tropical forages, should be reduced.

The potential of Yorkshire fog and tall fescue as alternative species in New Zealand agricultural systems needs to be further investigated.

CHAPTER 3

EXPERIMENT 1: HERBAGE INTAKE AND PERFORMANCE OF LAMBS GRAZING YORKSHIRE FOG AND PERENNIAL RYEGRASS PASTURES IN WINTER.

ABSTRACT

A comparative trial was carried out to assess the grazing behaviour, diet selection, herbage intake and performance of lambs grazing Yorkshire fog (*Holcus lanatus* cv. Massey Basyn)/white clover (*Trifolium repens* cv. Grasslands Tahora) and perennial ryegrass (*Lolium perenne* cv. Grasslands Nui)/white clover (*Trifolium repens* cv. Grasslands Tahora) pastures and to evaluate the effects of small amounts of condensed tannins (CT) in the grasses on body growth and wool growth of the grazing lambs under a continuous grazing management in winter, 1993.

36 lambs with mean initial weight 29 ± 2.3 kg were allocated to balanced groups in sets of six, with three replicates of the two pasture treatments. Individual paddocks were grazed continuously for 7 weeks. Half of the lambs were drenched with 10 g polyethylene glycol (PEG: MW 4000) twice daily at 0830 and 1700 hrs and the remaining lambs were drenched with water as a control.

Sward surface height declined from 16 cm to 6 cm on both swards over the experiment. Yorkshire fog tended to have a greater herbage mass, sward bulk density, lower proportions of live leaf and white clover and higher proportion of dead material than perennial ryegrass.

The times spent in grazing, ruminating and resting did not differ on the two

pastures. The rate of biting was lower on Yorkshire fog than on ryegrass in late June when the sward bulk density was substantially higher on Yorkshire fog. Although there was no significant difference between the two pastures, intake per bite was slightly higher on Yorkshire fog than on perennial ryegrass during a 5-day period in late June (68 vs. 51 ± 7.1 mg OM/bite).

The organic matter digestibility (OMD) of the diets declined with time for both the swards but ryegrass had a consistently superior digestibility (80 vs. 77 ± 0.3 , $P \leq 0.05$). There were low concentrations of CT in the diets for both the grasses, while ryegrass had higher CT content than Yorkshire fog (2.1 vs. 1.8 ± 0.07 g/kg DM, $P \leq 0.05$).

There was higher herbage OM intake in lambs on ryegrass than on Yorkshire fog, especially in early June (1181 vs. 917 ± 45.2 g/day, $P \leq 0.05$). The greater herbage intake on perennial ryegrass was probably associated with higher proportion of leaf and higher OM digestibility in the diet.

Liveweight gain was slightly higher on ryegrass than on fog (174 vs. 144 ± 9.7 g/day) but not significantly different, and was not influenced by PEG administration. Carcass weight of lambs at slaughter was significantly higher on ryegrass than on Yorkshire fog (17.1 vs. 16.3 ± 0.1 , $P < 0.05$). A higher dressing out % was recorded on ryegrass than on Yorkshire fog (49 vs. 48 ± 0.2 %, $P \leq 0.1$). Wool growth of lambs was similar between the two pastures. PEG administration did not significantly influence liveweight gain, carcass weight, dressing out or GR. PEG administration improved the rate of wool growth in lambs on ryegrass and slightly decreased it in lambs grazing Yorkshire fog.

From this winter experiment, it is concluded that: (i) ryegrass pasture had slightly higher animal production than Yorkshire fog; (ii) small amounts of CT in these grasses were not enough to affect body growth; (iii) effects of CT on wool growth of lambs grazing perennial ryegrass/white clover and Yorkshire fog/white clover

pastures lacked consistency. The action of PEG in lambs grazing grasses containing low CT concentrations needs to be further evaluated.

Keywords: Yorkshire fog (*Holcus lanatus*); perennial ryegrass (*Lolium perenne*); white clover (*Trifolium repens*); condensed tannins (CT); polyethylene glycol (PEG); grazing behaviour; diet selection; herbage intake; animal performance.

3.1. INTRODUCTION

In agricultural systems, low contents of CT in forage plants are thought to be beneficial to grazing ruminants (McLeod, 1974; Barry and Duncan, 1984; Barry and Manley, 1984; Barry, 1985; Waghorn *et al.*, 1987a; Waghorn *et al.*, 1990; Terrill *et al.*, 1992b). Although optimal CT concentrations in the DM have not yet been accurately defined, a value of 20 g CT/kg DM has been suggested (Barry, 1989). Small CT concentrations (20 g/kg DM) in forages may reduce rumen protein degradation and increase protein supply and absorption of essential amino acids, and hence promote animal performance (Barry, 1985; Barry and Duncan, 1984; Barry *et al.*, 1986; Waghorn *et al.*, 1987b; 1990; Terrill *et al.*, 1992b; McNabb *et al.*, 1993b). CT concentrations vary widely with plant species, components and maturity (Burns, 1978; Chiquette *et al.*, 1989; Waghorn and Jones, 1989; Iason *et al.*, 1995). Therefore, effects of CT in forages may be influenced by grazing selection and intake.

Limited information is available on the grazing behaviour, diet selection, herbage intake and performance of animals grazing Yorkshire fog pasture. This experiment was designed to compare these parameters in lambs grazing Yorkshire fog with those on perennial ryegrass and to assess the effects of low CT concentrations in these grasses on body growth and wool growth.

3.2. MATERIALS AND METHODS

3.2.1. Experimental Site

The experiment was carried out at the Pasture and Crop Research Unit, Massey University from 30 May to 15 July, 1993. The experimental plots were sited on a Tokomaru silt loam soil, classified as an Aeric Fragiaqualf (gleyed, yellow-grey earth). Average annual precipitation is approximately 1000 mm and ambient temperature on the experimental site ranges from 7°C (July) to 18°C (January). The monthly rainfall and mean soil temperature (10 cm depth) in 1993 compared with 10-year average values at the site are presented in Appendix 3.1.

3.2.2. Swards

Two pastures, one of perennial ryegrass (*Lolium perenne* cv. 'Grasslands Nui') and white clover (*Trifolium repens* L. cv. 'Grasslands Tahora') sown at the rate of 18 and 2 kg/ha, and one of Yorkshire fog (*Holcus lanatus* cv. 'Massey Basyn') and white clover (*Trifolium repens* L. cv. 'Grasslands Tahora') sown at 3 and 2 kg/ha respectively in March, 1988, were used in three replicates of 0.2 ha paddocks for each forage. The paddocks were under continuous stocking management with sheep and were cleared from grazing after application of fertilizer in April 1993, and thus allowed to accumulate herbage before the experiment started. Additional paddocks of Yorkshire fog and perennial ryegrass were used as supplementary grazing.

Nitrogen and phosphate fertilizers were applied at 50 kg of urea and 300 kg of superphosphate ha⁻¹ in April 1993. Additional application of urea was made twice at the rate of 50 kg/ha in November, 1992 and in January, 1993.

Dock (*Rumex obtusifolius*) in the experiment plots was cleared away by hoeing before the experiment started.

3.2.3. Animals and Treatments

Forty-six Suffolk x Romney female lambs, spring-born with mean initial weights 29.3 kg (SD: 2.3), were used for the experiment. All the lambs grazed both perennial ryegrass and Yorkshire fog pastures for two weeks before the experiment started.

Ten lambs drawn at random were slaughtered at the beginning of the experiment to measure carcass weight. The remaining 36 lambs were divided into 6 groups balanced for liveweight and randomly allocated to graze continuously the six paddocks for 7 weeks. The lambs were drenched with Levamisol (Nilverm, Coopers-Pitman-Moore, New Zealand Ltd.) to remove any internal parasites prior to the experiment and at the mid-point of experiment.

Half of the lambs grazing each paddock were drenched with polyethylene glycol (PEG; MW 4000) at 10g PEG twice daily at 0830 and 1630 hrs to bind and inactivate CT in the rumen. PEG was administered as 50% w/v solution in water. The dose of PEG was calculated on the basis of daily herbage intake and the expected CT content in the grasses (Barry and Forss, 1983). The remaining lambs were drenched with water at 20 ml at the same times. All the lambs were slaughtered at the end of the experiment.

3.3. Measurements

3.3.1. Sward Measurements

Sward surface height was measured weekly using a sward stick (Barthram, 1986). Fifty measurements of the undisturbed foliage were made at random in each paddock. *Herbage mass* was estimated at intervals of two weeks by cutting ten 0.1 m² rectangular quadrats in each paddock to ground level with an electric shearing head. Five sward height measurements were made in each quadrat

before the herbage was cut. The herbage samples were dried in an oven at 80°C for 48-72 hours and weighed individually. *Herbage bulk density* was calculated by dividing herbage mass by sward surface height per paddock.

Botanical composition was determined from bulked samples cut to ground level at two-week intervals. In the laboratory the samples were separated into species, and then into leaf, pseudostem and dead material within each species, and the relative contributions of plant parts were calculated. The vertical distribution of plant parts within the sward canopy was measured fortnightly by using an inclined point quadrat set at 32.5° to the horizontal (Warren Wilson, 1963). At least 100 contacts were recorded per paddock and each contact was identified in terms of species, morphology (leaf or stem for grasses; leaf or petiole for clover), state (live or dead) and height above ground level.

3.3.2. Grazing Behaviour and Herbage Intake

All measurements of grazing behaviour, diet selection and herbage intake were made in two 5-day periods, respectively in early June and in late June.

Observations of 24-hour grazing behaviour were made from a caravan parked near the paddocks. Grazing activities were recorded for each lamb by the method of Jamieson and Hodgson (1979) at intervals of 15 minutes during one continuous period of 24 hours. During darkness an infra-red nightscope was used to aid identification of animals' activities.

Rates of biting was measured using the 20 bite-method of Forbes and Hodgson (1985) by means of a stopwatch during periods of peak grazing activity at dawn, midmorning, early afternoon and in the evening. Recording continued if the animals walked with the head down selecting herbage, and also continued if the head was lifted while a large mouthful of herbage was being chewed in between bouts of biting.

Observations on diet composition were made using two pairs of wethers fistulated at the oesophagus (OF) which were kept in supplementary paddocks for 4-5 days and then cycled round experimental paddocks in pairs in a balanced design staying 2 days in each paddock before sampling. The two pairs of wethers were rotated between six paddocks and moved every day so that one oesophageal extrusa sample was collected from each sheep from each paddock during each 5-day period. Extrusa samples were collected in the afternoon after the sheep were penned for 4-5 hours, and were immediately removed to avoid contamination with rumen material. Extrusa samples were sealed in polythene bags, taken back to the laboratory in an ice box, weighed, frozen and stored at -20°C until analysis. The samples were divided into two portions.

One portion of the extrusa was used to determine botanical composition of the diet by suspending duplicate samples in water in a shallow tray and identifying the material at reference points over a grid with 100 points (Clark and Hodgson, 1986). The extrusa samples were classified as green grasses, green legume (white clover) and dead material. The other portion was freeze-dried for estimating DM and further laboratory analyses. Total N was determined by using the Kjeldahl method; *In vitro* digestibility was determined by the enzymatic method of Roughan and Holland (1977); CT (extractable CT, protein-bound CT and fibre-bound CT) were determined by the method of Terrill *et al.* (1992a).

Estimates of herbage intake were made using the techniques described by Hodgson and Rodriguez (1971):

$$\text{Herbage intake} = F/(100-D) \times 100$$

where F is faecal OM output of the grazing animals, estimated indirectly using intraruminal chromium controlled-release capsules (CRC) (Captec NZ Ltd, Auckland) and the procedures described by Parker *et al.*, (1989), and D is the *in vitro* OM digestibility (OMD %) obtained from oesophageal extrusa samples.

CRCs were administered orally to sheep at the start of the experiment for the measurement of faecal OM output and hence herbage intake. A second CRC was administered to each lamb three weeks before the end of the experiment for the measurement of release rate of CRCs in the rumen. Faecal sampling from the rectum for each lamb commenced 7 or 8 days after chromium capsules had been administered and continued for five days. Faecal samples were bulked for individual lambs on a dry weight basis over two periods of five days and chromium in faeces was determined by the method of Costigan and Ellis (1987). The release rate of chromium was estimated from CRCs collected from all lambs at slaughter, three weeks after the second capsule was administered.

PEG is indigestible and specifically binds and inactivates CT without affecting other nutrients (Wang, 1995). PEG administered (20 g/day) was deducted from faecal output of the lambs with PEG supplement before herbage intake was estimated.

3.3.3. Liveweight Gain, Carcass Gain, Dressing out and Carcass Fatness.

Lamb live weight was recorded at weekly intervals and the fasted weight recorded at the beginning and at the end of the experiment. All the lambs were slaughtered when the experiment ended to measure carcass weight, carcass composition, dressing out percentage and GR, a measurement of total soft tissue depth over the 12th rib at a point 11 cm from the midline of the carcass (Kirton, 1989). Initial carcass weight of the experimental lambs was predicted from the regression established with the 10 slaughter samples at the beginning of the experiment. Carcass gain was estimated using the initial estimated carcass weight and final carcass weight.

3.3.4. The Rate of Wool Growth

A single wool sample was clipped from 10 X 10 cm² patches (the final area clipped was determined from calliper measurements of the four sides and the diagonal) to skin level on the right mid-side of all the lambs at the beginning and end of the experiment. Greasy wool samples were conditioned at 20°C and 65% relative humidity for 48 hours, weighed and scoured using the method described by Morris (1992). The weight of clean wool was measured on each wool sample, and subsequently the rate of wool growth per unit area was calculated. The comparisons between treatments were conducted based on corrected wool weight (mg/100 cm² patches) on the right mid-side of the lambs.

3.4. Statistical Analysis

The experimental data were processed and analyzed using the SAS package (SAS Institute Inc., 1990). Swards were analyzed using a point quadrat package (Butler, 1991). Analyses of variance were used to compare sward measurements such as surface height, mass and bulk density, and components (green grasses, green white clover and dead material) and chemical composition (N, CT and *in vitro* digestibility) of diets selected by sheep on the two pastures. Analyses of covariance were used to assess effects of sward species, PEG administration and their interactions on animal data such as liveweight gain, carcass gain, dressing out, GR and wool growth based on a Split-plot design. Swards (Yorkshire fog and ryegrass) were used as a main plot and PEG administration or not (CT inactivated or operating) in each group as the sub-plot. The initial live weight of lambs was used as a co-variate to analyze live weight gain of lambs. Repeated measures analysis of variance was performed for live weights at the different times over the experiment. Carcass weight was used as a co-variate to analyze carcass GR data. Initial wool samples from the mid-side area of each lamb at the beginning of experiment were used as co-variates for analysis to estimate wool growth.

3.5. RESULTS

Attention is focused on the main effects of pasture species and their repeated measurements in different periods. Most interactions between effects of species and PEG administration were not significant, and are not presented here.

3.5.1. Sward Characteristics

3.5.1.1. Sward Surface Height

Sward surface height showed a similar trend in both ryegrass and Yorkshire fog pastures (Figure 3.1), decreasing from 15-16 cm at the beginning to 5-6 cm at the end of experiment. There was no significant difference in sward height between the two pastures at any time.

3.5.1.2. Herbage Mass and Bulk Density

The herbage masses of the two swards are shown in Table 3.1. Herbage mass decreased for the two pastures over the experiment and Yorkshire fog had a consistent advantage in herbage mass over perennial ryegrass. The difference in herbage mass between the two pastures was significant ($P < 0.05$) on three dates of measurement but not significant on 16 June, whilst the largest difference was found on 14 July.

Yorkshire fog had consistently higher bulk density than ryegrass (Table 3.1), the largest differences between the two swards in bulk density also occurring at the end of experiment.

3.5.1.3. Botanical Composition of Swards

The botanical composition of ryegrass and fog pastures by hand separation is

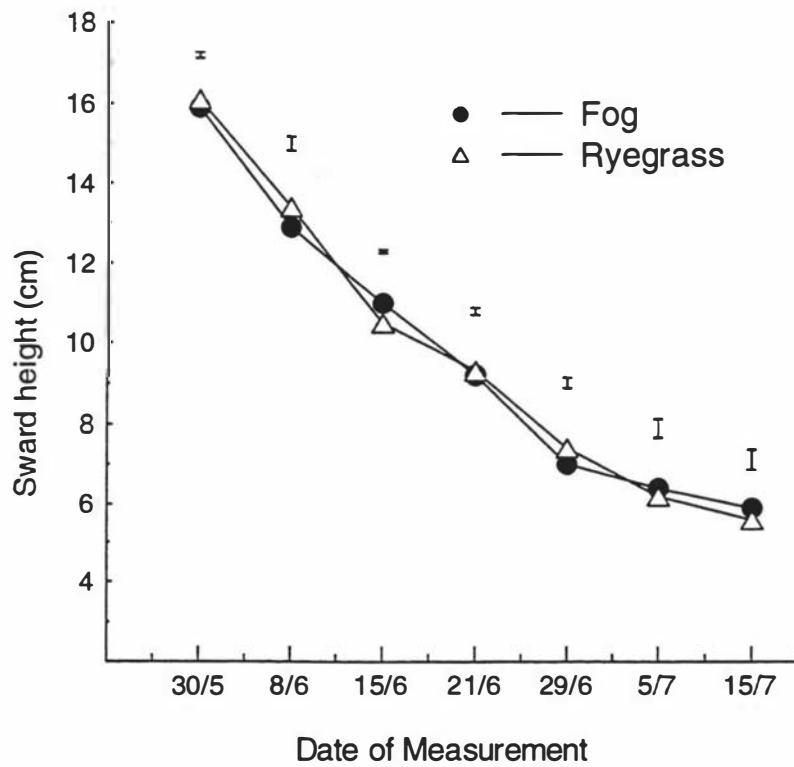


Figure 3.1 Sward surface height (cm) of ryegrass/clover and Yorkshire fog/clover pastures under continuous grazing management in winter

Table 3.1. Sward characteristics of ryegrass/clover and Yorkshire fog/clover pastures under a continuous grazing management in winter, 1993.

	Herbage mass (kg DM/ha)				Bulk density (mg DM/cm ³)			
	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig.
30 May, 1993	2710	3210	145	*	1.9	2.4	0.07	**
16 June, 1993	2200	2510	137	NS	2.6	2.9	0.11	*
29 June, 1993	1590	2010	115	*	2.4	3.0	0.15	***
14 July, 1993	1020	1520	93	***	1.9	2.8	0.12	***

In this and other tables:

+: Significant at P<0.1; *: Significant at P< 0.05; **: Significant at P<0.01;

***: Significant at P<0.001; NS: Not significant.

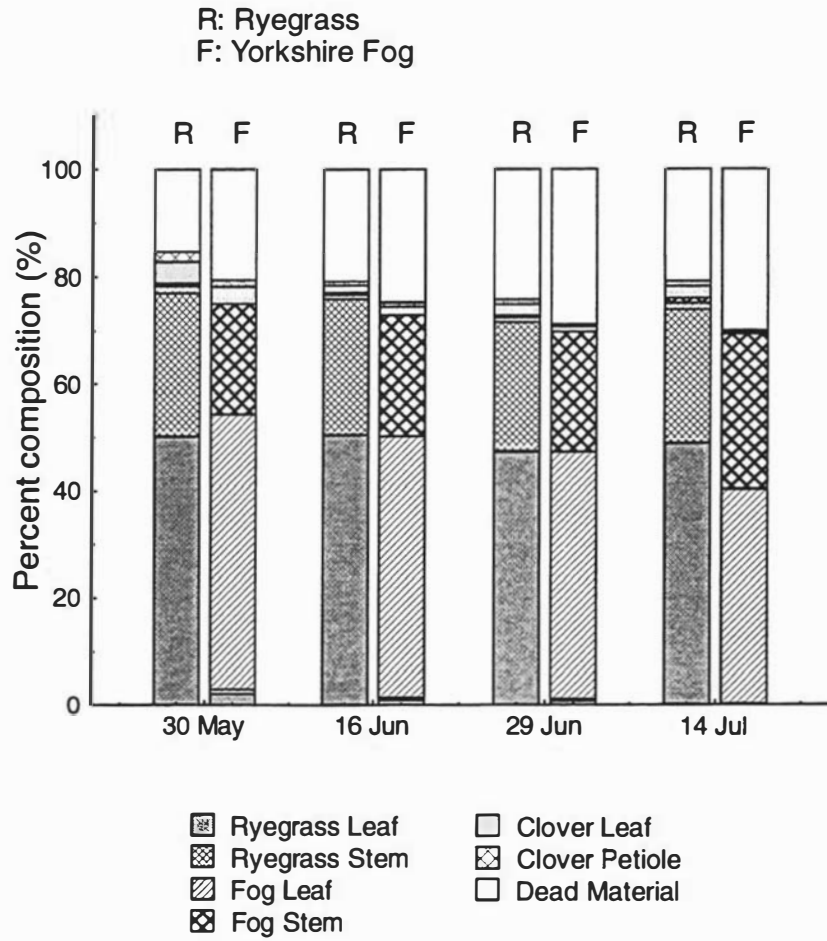


Figure 3.2 Botanical composition (%) of ryegrass/clover and Yorkshire fog/clover pastures under continuous grazing management in winter.

Table 3.2. Botanical composition (%) of ryegrass/clover and Yorkshire fog/clover pastures under continuous grazing management in winter, 1993.

	30 May, 1993				16 June, 1993				29 June, 1993				14 July, 1993			
	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig.
Main grass leaf	50	51	1.0	NS	51	49	1.0	NS	47	46	0.9	NS	49	40	1.8	**
Main grass stem	27	21	1.4	*	25	23	0.4	**	24	23	0.8	NS	25	29	1.8	NS
Other grass leaf	1	2	0.3	NS	1	1	0.2	NS	1	1	0.3	NS	1	<1	0.3	NS
Other grass stem	1	1	0.1	NS	<1	1	0.1	NS	<1	<1	0.1	NS	1	<1	0.3	*
Grass leaf	52	53	1.0	NS	51	50	1.1	NS	48	47	0.8	NS	50	40	1.6	**
Grass stem	27	22	1.3	*	26	23	0.5	NS	25	23	0.8	NS	26	29	1.8	NS
Total grass	79	75	1.3	NS	77	73	1.0	*	73	70	0.6	*	76	69	2.0	*
Clover leaf	4	3	0.5	NS	1	2	0.2	NS	2	1.	0.2	**	2	1	0.1	***
Clover petiole	2	1	0.4	NS	1	1	0.1	NS	1	<1	0.1	**	1	<1	0.1	***
Total clover	6	4	0.9	NS	2	2	0.3	NS	3	1	0.2	**	3	1	0.2	***
Dead Material	15	21	0.9	**	21	25	1.0	*	24	29	0.5	***	21	30	2.0	*

shown in Figure 3.2 and Table 3.2. Green grass was the main contributor to both pastures. Both the swards were dominated by main species although there were other grass species in each sward. There were no significant differences between pastures in the proportion of main grass leaf on 30 May, 16 June and 29 June, but a highly significant difference ($P < 0.01$) was found on 14 July. The ryegrass sward had a higher proportion of main grass stem than Yorkshire fog on 30 May and 16 June, but there was a lower proportion of main grass stem in ryegrass than in Yorkshire fog on 14 July. Total grass leaf and stem tended to have similar trends to main grass leaf and stem on the two swards.

There were no significant differences in the proportion of white clover between the swards on 30 May and 16 June, and the proportion of white clover decreased with grazing. However, the proportion of clover declined more rapidly on Yorkshire fog than on ryegrass and was significantly lower at the end of the experiment. The proportion of total green herbage decreased on both the swards. Yorkshire fog had a 50% higher proportion of dead material than ryegrass when the experiment ended.

3.5.1.4. Canopy Structure within the Sward

The point quadrat data from the two swards is summarized in Figures 3.3 and 3.4. The structures and distributions of plant parts were similar in the two swards. Grass leaf was the main contributor to the two pastures based on the number of contacts for all parts. There was a decrease in contacts with green components (leaf and stem) and increase with dead material in both swards over the experiment. The Yorkshire fog sward was observed to have lower proportions of main grass leaf and total green grasses, and higher proportions of dead material in the different strata, than the ryegrass sward.

The main grass leaf was distributed in the medium-upper strata in the range of 4 - 8 cm, while main grass stem was distributed in the medium-bottom strata in

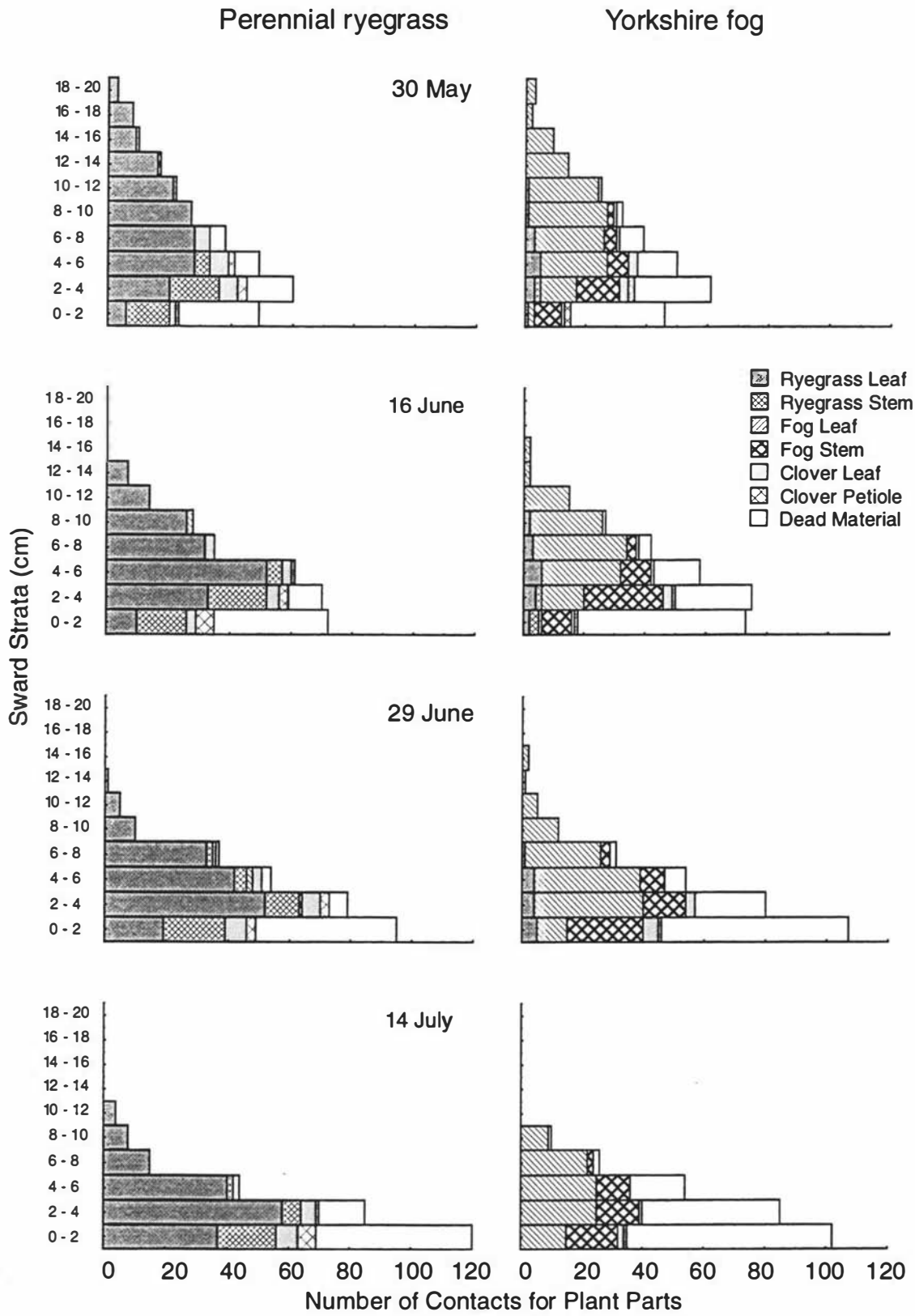


Figure 3.3. The stratum structure of plant parts within the sward canopy of ryegrass/clover and Yorkshire fog/clover pastures under continuous grazing management in winter

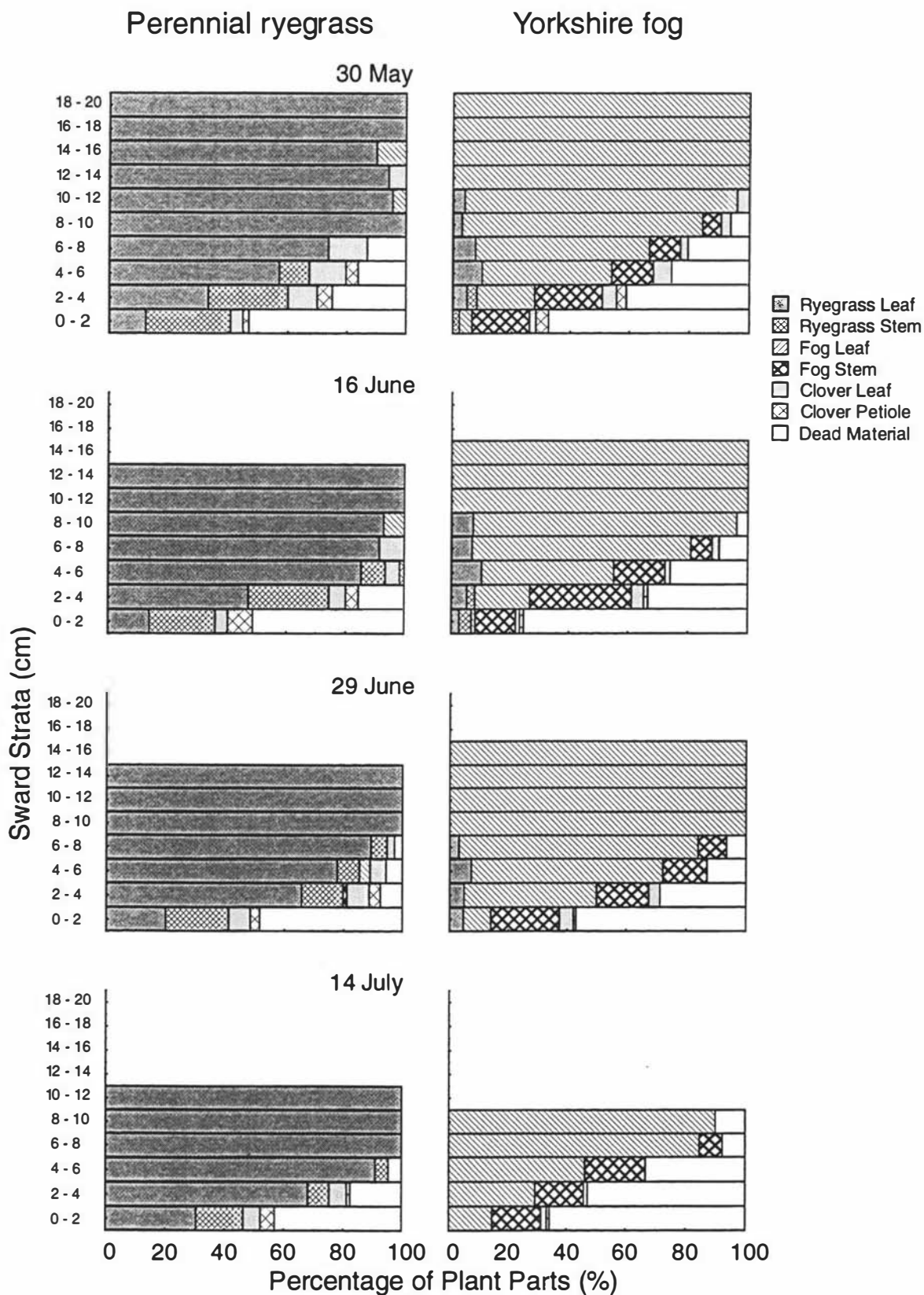


Figure 3.4. The percentage of plant parts in the different strata of ryegrass/clover and Yorkshire fog/clover pastures under continuous grazing management in winter

the range of 0 - 6 cm. White clover was mainly concentrated in the medium stratum (2 - 8 cm) in both swards at the start of the experiment, and concentrated at the bottom of the sward at the end. The dead material was commonly distributed at the bottom of swards where the ranges of distribution were 0 - 4 cm in the ryegrass sward and 0 - 6 cm in the Yorkshire fog sward.

3.5.2. Diet Composition - Botanical and Chemical

The botanical composition of the samples selected by OF sheep is shown in Table 3.3. The oesophageal extrusa samples were classified into grass, legume and dead material because there were some difficulties in identifying main grass and other grass when the extrusa samples were suspended in water. The green grasses made main contributions to the diets selected by OF sheep for both swards in the two periods. There were small proportions of white clover and dead material in the diets for both swards, the proportion of dead material being slightly increased in Period 2 compared with that in Period 1, but no period or sward effects were significant.

The chemical composition of the samples selected in both pastures is shown in Table 3.4. There was higher organic matter digestibility (OMD) and slightly lower concentration of N for the diet selected by OF sheep grazing on ryegrass than those on Yorkshire fog in the two periods. Although the difference between swards did not change much, there was a decline in OMD for the diet selected in Period 2 compared with Period 1.

Small amounts of CT were detected in the diet samples for Yorkshire fog and ryegrass. Total CT concentration for the diet selected was higher on ryegrass than on Yorkshire fog (2.1 vs 1.8 \pm 0.1 g/kg DM).

Table 3.3. The botanical composition of the samples selected by OF sheep grazing ryegrass/clover and Yorkshire fog/clover in winter, 1993.

	Period 1		Period 2		SEM	F value for		
	Ryegrass	Fog	Ryegrass	Fog		Per‡	SPP	Per x SPP
Grasses (%)	95	96	92	93	2.0	NS	NS	NS
Clover (%)	3	1	1	2	1.2	NS	NS	NS
Dead material (%)	2	3	7	5	1.5	NS	NS	NS

‡: Two periods of sampling and observation were made in early (Period 1) and late June (Period 2) in 1993.

Table 3.4. Chemical composition of the samples selected by OF sheep grazing ryegrass/clover and Yorkshire fog/clover pastures in winter, 1993.

	Period 1		Period 2		SEM	F value for		
	Ryegrass	Fog	Ryegrass	Fog		Per	SPP	PER*SPP
Total N (% DM)	4.5	5.0	4.2	4.5	-	-	-	-
OMD	80	77	79	77	0.5	+	*	NS
Condensed tannins (CT:g/kg DM)								
Extractable	1.16	1.08	1.01	1.18	0.112	NS	NS	NS
Protein-bound	0.67	0.49	0.85	0.39	0.153	NS	+	NS
Fibre-bound	0.32	0.17	0.16	0.22	0.058	NS	NS	NS
Total	2.15	1.74	2.02	1.78	0.105	NS	*	NS

3.5.3. Grazing Behaviour

There were no significant differences between forage species in the times spent grazing, ruminating and resting (Table 3.5). There were significant interaction effects between pasture species and period on the rate of biting ($P < 0.05$). The rate of biting was higher on ryegrass pasture than on Yorkshire fog ($P < 0.05$) in Period 2. Although there were no treatment effects and interaction effects between pasture and periods, intake per bite increased more quickly with time on Yorkshire fog than on ryegrass. Therefore, intake per bite was higher on Yorkshire fog than on ryegrass in Period 2 (68 vs 51 ± 7.1 mg OM/bite) although the difference was not significant (Table 3.5).

3.5.4. Herbage Intake

Mean release rates of Cr_2O_3 , estimated from CRCs collected from experimental lambs at slaughter were not influenced by species or PEG administration. Therefore, a standard release rate of Cr_2O_3 (215.4 ± 8.11 mg/day) was used to determine the faecal output in lambs on the two pastures.

Lambs had greater herbage OM and DOM intake on ryegrass pasture than on Yorkshire fog pasture ($P \leq 0.1$) (Table 3.6). There was an interaction effect between species and period on herbage OM intake ($P < 0.05$). Herbage OM intake showed a large decline for lambs on ryegrass, but not on Yorkshire fog in Period 2. Herbage OM intake was not influenced by PEG and the interaction between species and PEG administration was not significant.

3.5.5. Liveweight Gain, Carcass Weight, Dressing Out and GR

The time trends of liveweight and liveweight gain on both swards are shown in Figures 3.5 and 3.6. There was a general decline in liveweight gain of lambs as

Table 3.5. Grazing behaviour of lambs grazing ryegrass/clover and Yorkshire fog/clover in the two periods of winter, 1993.

	Period 1		Period 2		SEM	F value for		
	Ryegrass	Fog	Ryegrass	Fog		Per	SPP	PER*SPP
Grazing time (min 24 h ⁻¹)	580	560	580	600	18	NS	NS	NS
Ruminating time (min 24 h ⁻¹)	380	370	360	360	9	NS	NS	NS
Resting time (min 24 h ⁻¹)	440	470	460	440	21	NS	NS	NS
The rate of biting (bites/min)	55	56	67	59	1.0	***	*	**
Intake per bite (mg OM/bite)	48	50	51	68	7.1	NS	NS	NS

Table 3.6. Effects of species and PEG administration on herbage OM and DOM intakes of lambs grazing ryegrass/clover and Yorkshire fog/clover pastures in winter, 1993.

	Ryegrass		Fog		SEM	F value for		
	Ctrl	PEG	Ctrl	PEG		SPP	PEG	SPP*PEG
OM intake (g/day)	1138	1096	895	966	71.3	+	NS	NS
OM intake (g/kg W ^{0.75} /day)	83	79	66	72	5.4	+	NS	NS
DOM intake (g/day)	905	871	689	744	56.3	*	NS	NS
DOM intake (g/kg W ^{0.75} /day)	66	63	51	55	4.3	+	NS	NS

	Period 1		Period 2		SEM	F value for		
	Ryegrass	Fog	Ryegrass	Fog		SPP	PER	SPP*PER
OM intake (g/day)	1181	917	1053	943	45.2	+	*	NS
OM intake (g/kg W ^{0.75} /day)	88	73	70	68	3.4	+	NS	NS
DOM intake (g/day)	945	706	832	726	35.5	*	NS	+
DOM intake (g/kg W ^{0.75} /day)	70	54	58	52	2.7	+	*	+

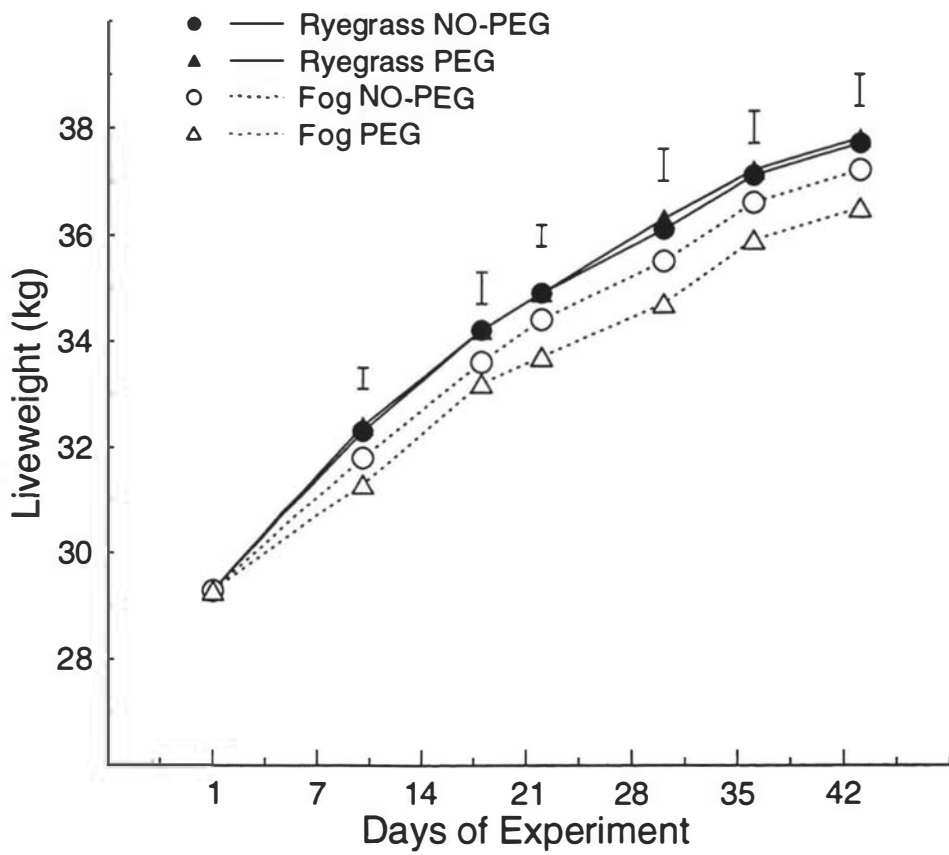


Figure 3.5. Liveweight (kg) of lambs grazing ryegrass/white clover and Yorkshire fog/white clover pastures in winter

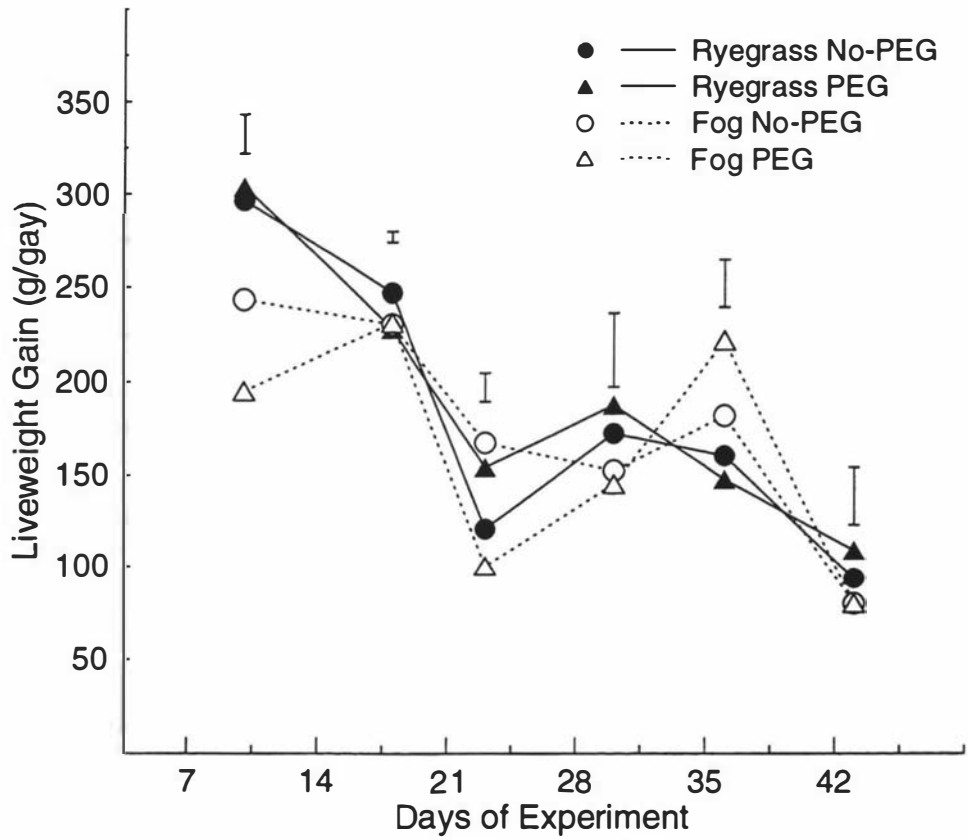


Figure 3.6. Liveweight gain (g/day) of lambs grazing ryegrass/white clover and Yorkshire fog/white clover pastures between two measurements in winter

Table 3.7. Effects of pasture species and PEG administration on liveweight gain, carcass weight, carcass weight gain, dressing out % and wool growth of lambs grazing ryegrass/clover and Yorkshire fog/clover in winter, 1993.

	Species effect			Interaction of species x PEG					F Value for		
				Ryegrass		Fog		SEM			
	Ryegrass	Fog	SEM	Ctrl	PEG	Ctrl	PEG		SEM	SPP	PEG
Liveweight gain (g/day)	174	144	9.7	173	174	145	142	9.6	NS	NS	NS
Carcass weight (kg)	17.1	16.3	0.1	17.0	17.1	16.3	16.2	0.2	*	NS	NS
Carcass weight gain (g/day)	89	70	2.7	87	90	71	69	4.3	*	NS	NS
Dressing out %	49	48	0.2	48	49	48	49	0.5	+	NS	NS
GR (cm) Left	9	9	1.3	9	9	10	9	0.4	NS	NS	NS
Right	10	9	1.0	10	9	10	9	0.4	NS	NS	NS
Rate of wool growth (mg/100 cm ² per day)	84	81	2.0	78	91	87	74	3.4	NS	NS	**

the experiment progressed (Figure 3.6). Initial weight gains were slower for lambs on Yorkshire fog than on perennial ryegrass, and slower for PEG than control lambs on Yorkshire fog but not on ryegrass (Figure 3.6). These initial differences persisted until the end of trial, but neither the species effect nor the species and PEG interaction were significant overall (Table 3.7). Differences in carcass weight and carcass weight gain between the two pastures were significant ($P < 0.05$). Dressing out % was slightly higher in lambs on ryegrass pasture than that on Yorkshire fog pasture. No significant difference was observed in GR. PEG administration had no effects on liveweight gain, carcass weight, dressing out or GR.

3.5.6. The Rate of Wool Growth

Effects of species and PEG administration on wool growth are also shown in Table 3.7. There was no significant difference in the rate of wool growth in lambs between the two pastures. There was a significant interaction between the effects of species and PEG administration on the rate of wool growth. The rate of wool growth of lambs was slightly increased on ryegrass and decreased on Yorkshire fog pasture by use of PEG.

3.6. DISCUSSION

Animals may differ in respect of the diet selected, the activities for grazing behaviour, the level of herbage intake, and the rate of body growth and wool growth obtained under a set of sward conditions. In these studies the comparisons of the responses of grazing lambs to two pastures, Yorkshire fog and ryegrass, were made under continuous grazing management in winter. Particular attention was paid to the assessment of the effects of low CT concentrations in the grasses on the liveweight gain and wool growth of grazing lambs. Throughout the thesis attention is focused on relatively small treatment effects, some of which may only be assessed by evaluation over several

experiments.

3.6.1. Sward Characteristics

Sward surface height on both swards was approximately 16 cm at the start of the experiment, decreasing over the experiment, and finally became close to 5 cm when the experiment ended (Figure 3.1). The sward surface height should not have a large effect on herbage intake based on the recommended sward surface height of 6-7 cm for nonrestricted herbage intake of lambs (Hodgson, 1990). Herbage mass of both swards was set initially to more than 2500 kg DM/ha in order to maintain forage supply over the experiment. The difference in herbage mass between pastures in favour of Yorkshire fog was found over the experiment (Table 3.1). This result was similar to observation by Hu (1993) on perennial ryegrass and Yorkshire fog swards in winter in a previous trial. Yorkshire fog had higher bulk density than ryegrass, especially in mid July. The higher herbage mass and sward bulk density on Yorkshire fog than on ryegrass were partly associated with the higher tiller population and longer and heavier pseudostems on Yorkshire fog (Hu, 1993). These results suggest that Yorkshire fog had a more vigorous growth in winter than perennial ryegrass (Dunbar, 1974; Haggard, 1976), though the lower intake of Yorkshire fog (Table 3.6) must be taken into account.

The botanical analyses of swards by hand separation showed that the proportion of total green herbage decreased with grazing, while the proportion of dead material increased on both the swards, particularly Yorkshire fog (Figure 3.2 and Table 3.2). The increased proportion of dead material was partially because the rate of forage growth was low in winter, and largely because green herbage in the upper strata of swards was grazed by animals and a relative high proportion of dead material accumulated at the bottom of the swards, particularly Yorkshire fog (Figure 3.3). The higher proportion of dead material on Yorkshire fog has been reported in summer (Niezen, 1993a) and in autumn (Hu, 1993). Similar

trends were observed from the point quadrat data (Figures 3.3 and 3.4).

The proportion of white clover was not high; it was similar between the two pastures at the start of experiment, and decreased as the experiment progressed (Table 3.2). The ryegrass sward had a significantly higher proportion of clover in late June and mid July (Table 3.2). This may be explained by the structure and distribution of clover within the sward canopy on both pastures. White clover was concentrated in the bottom and mid-bottom strata within the sward canopy much more on ryegrass than on Yorkshire fog (Figure 3.4), so was more susceptible to defoliation in the Yorkshire fog sward.

3.6.2. Botanical and Chemical Composition of the Diet Selected

There was a higher proportion of green grass in the diets than in both swards on offer (Tables 3.2 and 3.3). Green grasses were main contributors to the diets, and dead material was a minor component of the diets on both swards. These results indicated that sheep grazed the leaf horizon at the top of vegetative ryegrass and Yorkshire fog swards (Figures 3.3 and 3.4) and rarely penetrated to the lower levels containing pseudostems and dead material. This is in agreement with the observations by other researchers (Arnold, 1981; Rattray and Clark, 1984; Montossi, 1995).

Selection for clover is related to the proportion of clover in swards, especially the proportion in the actual grazed horizon, and spatial variability in species distribution. Most of the variation in proportion of clover in the diets of grazing animals can be explained by the proportion of white clover in the grazed horizon of the sward, when taking into account the relationship between bite depth and sward surface height and examining the actual horizon grazed by sheep (Milne *et al.*, 1982; Hodgson, 1990). There was selection for clover at low levels of clover in the grazed horizon in some reports (Clark and Harris, 1985; Milne, 1991; Ridout and Robson, 1991; Armstrong *et al.*, 1993). In the current

experiment, clover comprised a small proportion of the diets selected by OF sheep from both swards, and no selection for clover was observed based on the proportion of white clover in sward and diet. This is closely associated with the distribution of clover on both swards. The importance of distribution of clover within the sward canopy has been emphasized by other researchers (Bircham and Hodgson, 1983; Hodgson, 1985; Milne, 1991; Gordon and Lascano, 1993).

There were differences in the OMD and N concentrations in the diet selected by OF sheep from two pastures, and lower values for both swards in Period 2 compared with in Period 1 (Table 3.4). These differences were closely related to the differences in green leaf and total green herbage between swards (Table 3.2). Ryegrass had higher proportions of total green herbage and green leaf than Yorkshire fog and kept this advantage at each measurement. There was lower OMD in both swards in late June than in early June. The decline was closely related to the lower proportion of green leaf and higher proportion of dead matter of swards on offer in late June.

CT concentrations in the diets were low for both grasses in the trial, similar to evidence from other researchers (Terrill *et al.*, 1992b; Iason *et al.*, 1995; Montossi, 1995). Terrill *et al.* (1992b) emphasized the contribution of Yorkshire fog to low CT concentrations in a ryegrass/white clover/fog pastures and did not allow for the possibility that ryegrass also contains small amounts of CT. In the current study, ryegrass had a significantly higher total CT concentration than Yorkshire fog (Table 3.4). Docks were removed from the swards in order to avoid the confusing effects of their low CT concentration (Waghorn and Jones, 1989) on treatment comparisons. White clover contains little CT except for the flower petals (Jones *et al.*, 1976), but no evidence has been found for the expression of CT in white clover foliage (Waghorn *et al.*, 1990).

3.6.3. Grazing Behaviour and Herbage Intake

No evidence was found for the effects of PEG on the grazing behaviour of lambs. Similar patterns of grazing behaviour were observed on both swards, with the exception of Period 2 when the rate of biting was significantly higher on ryegrass than on Yorkshire fog (Table 3.5). This was the consequence of interaction between decreased sward surface height and slightly lower sward bulk density. A relatively high sward bulk density resulted in little increase in the rate of biting in spite of decreased sward surface height of Yorkshire fog.

There was no significant difference in intake per bite between pastures in the two periods of measurement (Table 3.5), though Yorkshire fog had a 25% greater intake per bite than ryegrass at the estimate in Period 2 (68 vs 51 \pm 7.1 OM mg/bite). However, the rate of biting was slower on Yorkshire fog than on ryegrass in Period 2 (59 vs 67 \pm 1 bites/min). Intake per bite increased on Yorkshire fog in Period 2 but did not change much on ryegrass. The greater intake per bite in sheep from Yorkshire fog in Period 2 was mainly because of an increased sward bulk density. Generally, there is a strong interaction between the effects of sward height and bulk density on intake per bite (Hodgson, 1994). In the trial, sward bulk density may have had a more important part in affecting intake per bite.

The intakes calculated from the arithmetic product of grazing behaviour components (grazing time, biting rate and intake per bite) were 91 and 96 g DOM/kg $W^{0.75}$ /day for ryegrass and Yorkshire fog respectively in Period 1 and 104 and 134 g DOM/kg $W^{0.75}$ /day for the same species in Period 2. These values are above the maximum likely intake of lambs of this size suggested by other researchers (Weston, 1982; Weston and Davis, 1991; Dove, 1996; Weston, 1996). By contrast, the intakes estimated from faecal output and *in vitro* digestibility were 70 and 54 g DOM/kg $W^{0.75}$ /day for ryegrass and Yorkshire fog respectively in Period 1 and 58 and 52 g DOM/kg $W^{0.75}$ /day for the same species

in Period 2, well within the limits of likely intake in such animals. Hence, the estimates of intake are considered to be more realistic than those from the arithmetic product of grazing behaviour data. Therefore, the herbage intakes calculated by this product are not reported in the text.

Higher herbage OM intake in lambs on ryegrass than on Yorkshire fog (Table 3.6) was correlated with high OMD for ryegrass (Table 3.4). In Period 2, the difference in herbage intake between two pastures became smaller compared with in Period 1, though OMD was consistently higher in the diets for ryegrass than for Yorkshire fog, probably because of the compensatory responses to high bulk density of Yorkshire fog. These results indicate that sward structure characteristics may be as important as nutritional value of forages in determining herbage intake.

There were no overall effects of CT on herbage intake. However, PEG administration slightly increased herbage OM intake in lambs grazing Yorkshire fog and slightly decreased herbage OM intake in lambs grazing ryegrass (Table 3.6).

3.6.4. Animal Performance

Lambs had 17% greater liveweight gain, significantly higher carcass weight ($P \leq 0.05$), carcass weight gain ($P \leq 0.05$) and carcass dressing out percentage ($P \leq 0.01$) on ryegrass than on Yorkshire fog (Table 3.7). Although the differences in liveweight gain were not significant, these effects were linked to higher DOM intake for lambs on ryegrass (Table 3.6). There was no significant difference in GR between pastures. A similar result has been reported by Niezen *et al.* (1993a).

High CT concentration reduces body growth and wool growth rates of sheep (Barry and Manley, 1984; Barry, 1985; Barry *et al.*, 1986; Pritchard *et al.*, 1988,

1992; Waghorn *et al.*, 1994a), and low or moderate CT concentrations (2 - 4 % DM) in forage plants can improve performance of grazing ruminants (Ulyatt, 1981; Purchas and Keogh, 1984; Barry, 1985, 1989; Waghorn *et al.*, 1990; Terrill *et al.*, 1992b; Wang *et al.* 1994). There was a small response of liveweight gain in lambs on Yorkshire fog to PEG administration over the initial period, where lambs had a faster liveweight gain in the control group than in PEG-group, but the response did not persist (Figures 3.5 and 3.6). Thus, there was no significant difference in liveweight gain, carcass weight and carcass weight gain between the PEG and control groups on Yorkshire fog. Terrill *et al.* (1992b) suggested that once daily PEG administration may not completely eliminate binding of plant proteins to CT in the rumen and that animal responses to PEG administration in their trial may not have been the maximum values. In the current experiment, the lambs were drenched twice daily with PEG, but the liveweight gain, carcass weight and carcass weight gain of lambs were not influenced by PEG administration. Subject to reservations about the initial effects on Yorkshire fog, this suggests that the low CT concentration in the grasses was not high enough to affect the body growth of lambs. Estimates of the effects of PEG on rumen fermentation can be provided by measurements of rumen ammonia concentrations. These measurements were not made in the current study, but were in later experiments.

Terrill *et al.* (1992b) reported that CT present in ryegrass/clover/Yorkshire fog pasture increased wool growth, when wool growth rate was high during spring and early summer, but CT had no effect upon the wool growth of grazing sheep when wool growth rates were low during winter. The interaction between pasture species and PEG administration on the rate of wool growth was significant in the current experiment (Table 3.7). PEG slightly decreased the rate of wool growth in lambs on Yorkshire fog, and increased the rate of wool growth in lambs on ryegrass. The increased rate of wool growth in lambs grazing ryegrass pasture by PEG administration was unexpected. Improvement of liveweight gain in lambs grazing ryegrass by PEG has been reported by other researchers (Terrill *et al.*,

1992b; Niezen *et al.*, 1993b). This effect is hard to explain, and requires further investigation.

3.7. CONCLUSIONS

There was a higher herbage mass, greater sward bulk density and lower proportion of green leaf and green herbage on Yorkshire fog than on ryegrass. Ryegrass had superior herbage OMD and OM intake to Yorkshire fog in winter.

Grazing behaviour did not differ between two pastures, with the exception of measurements in late June. The greater intake per bite and lower biting rate on Yorkshire fog at the time appeared attributable to increased sward bulk density and the greater proportion of dead material on the sward.

Lambs had a slower liveweight gain and lower carcass weight on Yorkshire fog pasture than on ryegrass. The evidence suggests that lower OMD and higher proportion of dead material on Yorkshire fog were important factors limiting herbage intake and animal production.

Low CT concentrations were detected in the diets for both the grasses, and ryegrass had slightly higher total CT content than Yorkshire fog. Since grasses comprised more than 90+% of intake, this provides new evidence that low CT concentrations exist in the ryegrass. PEG did not influence liveweight gain and carcass weight in lambs on either pasture or the rate of wool growth in lambs on Yorkshire fog overall, but did increase wool growth in lambs on ryegrass. More research is required to quantify the minimal effective CT concentrations in forage to increase animal production.

CHAPTER 4

EXPERIMENTS 2 & 3: COMPARATIVE STUDIES OF HERBAGE INTAKE AND ANIMAL PERFORMANCE OF LAMBS GRAZING YORKSHIRE FOG (*Holcus lanatus*) AND TALL FESCUE (*Festuca arundinacea*) PASTURES UNDER A ROTATIONAL MANAGEMENT

ABSTRACT

Two grazing experiments (Experiment 2 and Experiment 3) were conducted on Yorkshire fog (*Holcus lanatus* cv. Massey Basyn)/white clover (*Trifolium repens* cv. Grassland Tahora) and tall fescue (*Festuca arundinacea* cv. Grassland Roa)/white clover pastures to assess the grazing behaviour, herbage intake and performance of lambs and to evaluate the effects of low condensed tannin (CT) concentrations in the grasses on the performance of lambs under rotational management in late spring, summer and early autumn (from 22 November, 1993 to 29 March, 1994).

In each experiment, forty-eight lambs were allocated to three groups, balanced for previous pasture grazing experience prior to the experiment and for sex, in sets of sixteen. One group was slaughtered at the start of experiment to measure the initial carcass composition of lambs. The other two groups of lambs were put into two pasture treatments and rotationally grazed paddocks within each pasture. Half of the lambs within each pasture were drenched with 10 g polyethylene glycol (PEG: MW 3350) twice daily at 0830 and 1630 hrs and the remaining lambs were drenched with water as a control.

Experiment 2

There were similar sward surface height, herbage mass and bulk density on both swards. Yorkshire fog had higher proportions of sown grass leaf and stem and lower proportions of other grass leaf and stem than tall fescue in December and in January. The proportion of grass leaf decreased and the proportion of grass stem increased after grazing compared with those before grazing.

There were slightly higher total N (3.56 vs 3.43 ± 0.018 % DM, $P \leq 0.05$) and organic matter digestibility (OMD) (81 vs 78 ± 0.6 %, $P \leq 0.01$) on tall fescue than on Yorkshire fog in early December, but no significant differences in late December. There were low CT concentrations in the diets from both grasses, and Yorkshire fog had higher CT concentrations than tall fescue in early December (1.89 vs 1.32 ± 0.081 g/kg DM, $P \leq 0.05$).

There was more time spent grazing, faster rate of biting and greater intake per bite on Yorkshire fog than on tall fescue, but no significant difference in herbage OM intake was found between the two pastures. Sex of lamb did not affect daily grazing activities of lambs, but male lambs had higher herbage OM intake than female (828 vs 741 ± 29.5 g/day, $P \leq 0.1$). PEG administration had no significant effects on grazing behaviour, but had a negative effect on herbage OM intake of lambs (746 vs 823 ± 29.5 g/day, $P \leq 0.1$).

Grazing experience had no significant effects on liveweight gain, carcass weight, carcass weight gain and wool growth. Lambs on Yorkshire fog pasture had faster liveweight gain (99 vs 76 ± 6.7 g/day, $P \leq 0.1$), greater carcass weight (14.7 vs 13.9 ± 0.2 kg, $P \leq 0.05$) at slaughter and faster carcass weight gain (32 vs 20 ± 3.1 g/day, $P < 0.05$), and had faster rate of wool growth than lambs on tall fescue in January (117 vs 100 ± 4.2 mg/100cm² per day, $P \leq 1$). Castrated male lambs had a higher liveweight gain than females (95 vs 80 ± 3.3 g/day, $P \leq 0.05$), but there were no significant effects on carcass weight, carcass weight gain, GR and

wool growth. PEG administration had negative effects on liveweight gain of lambs in the initial period of the experiment (92 vs 101 ± 4.1 g/day, $P \leq 0.1$), but no significant effects on carcass weight, dressing out, GR and the rate of wool growth overall in lambs on both the pastures.

Experiment 3

There were consistently lower sward surface heights before and after grazing on tall fescue than on Yorkshire fog, with the exception of early February and mid March. There were similar herbage masses between the two pastures, but Yorkshire fog had higher residual herbage masses than tall fescue (1930 vs 1720 ± 53 kg DM/ha, $P \leq 0.01$). Yorkshire fog had a higher proportion of sown grass (65 vs 51 ± 2.7 %, $P \leq 0.01$), a lower proportion of other grasses (7 vs 16 ± 1.5 %, $P \leq 0.05$) and a lower proportion of white clover (4 vs 8 ± 1.0 %, $P \leq 0.05$) than tall fescue before grazing. However, the proportion of sown grass leaf after grazing decreased to a greater extent on Yorkshire fog than on tall fescue, with increasing proportions of grass stem and dead material compared with those before grazing. There was no significant difference in total sown grass, but tall fescue had higher proportions of other grasses (13 vs 9 ± 0.6 %, $P \leq 0.001$) and white clover (4 vs 1 ± 0.6 %, $P \leq 0.001$) than Yorkshire fog after grazing.

The diet from Yorkshire fog had higher CT concentrations overall and higher OMD (74 vs 71 ± 1.1 %, $P \leq 0.1$) in early February, while that from tall fescue had higher total N (3.24 vs 2.91 ± 0.022 % DM, $P \leq 0.01$) and OMD (72 vs 68 ± 1.1 %, $P \leq 0.05$) in late February.

There was longer time spent grazing (620 vs 590 ± 6 min, $P \leq 0.05$), faster rate of biting (49 vs 48 ± 0.5 bites/min, $P \leq 0.1$) in lambs and smaller intake per bite of OF sheep (58 vs 65 ± 3.1 mg OM/bite, $P \leq 0.1$) on tall fescue than on Yorkshire fog. Herbage OM intake was higher on tall fescue than on Yorkshire fog in late February (870 vs 639 ± 62.1 g/day, $P \leq 0.05$). Castrated male lambs had greater

herbage OM intake than females (1015 vs 838 ± 53.3 g/day, $P \leq 0.05$). Lambs had faster wool growth rate on Yorkshire fog than on tall fescue (123 vs 112 ± 2.8 g/100cm² per day, $P \leq 0.05$) in March, while castrated male lambs had faster liveweight gain (80 vs 72 ± 2.3 g/day, $P \leq 0.05$), carcass weight (14.4 vs 14.0 ± 0.1 kg, $P \leq 0.05$) and carcass weight gain than females (33 vs 27 ± 1.7 g/day, $P \leq 0.05$).

From the two experiments, it was concluded that: (i) There were similar herbage masses between Yorkshire fog and tall fescue, while tall fescue had an advantage in dietary OMD over Yorkshire fog except for early February, and had consistently lower CT concentrations than Yorkshire fog; (ii) The nutritional characteristics of the swards were more important in determining herbage OM intake than grazing behaviour; (iii) Yorkshire fog had slightly higher animal production than tall fescue in late spring and summer, but tall fescue had an advantage over Yorkshire fog in early autumn; (iv) Animal production was largely influenced by current pastures and sex rather than previous pastures and PEG administration; (v) small amounts of CT in these grasses were not high enough to improve animal performance effectively.

Keywords: Yorkshire fog (*Holcus lanatus*); tall fescue (*Festuca arundinacea*); white clover (*Trifolium repens*); condensed tannins (CT); polyethylene glycol (PEG); grazing behaviour; diet selection; herbage intake, animal performance.

4.1. INTRODUCTION

Information from comparative studies of lambs grazing on Yorkshire fog and tall fescue pastures is limited in terms of grazing behaviour, diet selection, herbage intake and animal performance. The purpose of the experiments reported in this chapter was to compare the grazing behaviour, herbage intake and performance of lambs grazing on Yorkshire fog with those on tall fescue in late spring, summer

and early autumn and to further assess the effects of the small CT concentrations in these grasses on lamb performance.

4.2. MATERIALS AND METHODS

The standard procedures in the present experiments were similar to those used in Chapter 3 (Experiment 1). Only new procedures in experiments 2 and 3 are described here.

4.2.1. Experimental Site and Duration

Two grazing experiments were carried out at the Pasture and Crop Research Unit, Massey University. Experiment 2 was conducted from 21 November, 1993 to 26 January, 1994 and Experiment 3 was conducted from 25 January to 30 March, 1994. The experimental site was located on a Tokomaru silt loam soil classified as an Aeric Fragiaqualf (gleyed, yellow-grey earth) with Olsen P values in the range of 20-30 $\mu\text{g/g}$. The monthly rainfall, mean soil temperature (10 cm depth) in late 1993 and early 1994 compared with 10-year average values for the site are presented in Appendix 4.1.

4.2.2. Swards

Two pastures, Yorkshire fog/clover and tall fescue/clover, were used in the two experiments which were conducted in sequence with identical procedures. The two swards were established by spraying with Roundup (Monsanto, NZ Ltd) at 3 litre per hectare in April, 1993 and then direct drilled with Yorkshire fog, tall fescue and white clover at 6 kg/ha, 30 kg/ha and 3 kg/ha. A fertiliser containing N 12%, P 10% and K 10% was applied at 90 kg/ha. Each pasture was divided into six paddocks of approximately 0.1 ha each in area to be grazed by the lambs rotationally. Additional areas of Yorkshire fog and perennial ryegrass were used as supplementary paddocks.

4.2.3. Animals and Treatments

Two flocks of lambs grazed Yorkshire fog and perennial ryegrass pastures for four weeks, then forty-eight Suffolk x Romney lambs were selected in each of two grazing experiments. The pre-experimental four week period of grazing Yorkshire fog and ryegrass pastures was used as a treatment of preliminary grazing experience. The lambs were allocated to three groups balanced for previous grazing experience and sex in sets of sixteen. One group was slaughtered as the initial group at the start of experiment to measure the carcass composition of lambs. The other two groups of lambs were allocated to the two pasture treatments and grazed the six paddocks within each treatment in rotation, remaining for 5 days in each paddock.

All the lambs were drenched with Levamisol (Nilverm, Coopers-Pitman-Moore, New Zealand Ltd.) to remove internal parasites prior to the experiment and subsequently at monthly intervals. The lambs had free access to water over the experiment.

Half of the lambs, balanced for previous grazing experience and for sex, were drenched with polyethylene glycol (PEG; MW 3350) at 10g PEG twice daily at 0830 and 1630 hours to bind and inactivate CT in the rumen. PEG was administered as 50% w/v solution. The dose of PEG was calculated on the basis of daily herbage intake and the expected CT content in the grasses (Barry and Forss, 1983). The remainder of the lambs were drenched with the same amount of water as a control. All the lambs were slaughtered at the end of experiment to determine the carcass weight, dressing out percentage (carcass weight/fasted weight) and carcass GR measurement.

4.3. MEASUREMENTS

4.3.1. Sward Measurements

Sward surface height was measured before and after grazing each paddock using a sward stick (Barthram, 1986). *Herbage mass* was estimated in each paddock before and after grazing. *Herbage bulk density* was calculated by dividing herbage mass by sward surface height per paddock. *Botanical composition* was determined from bulked samples taken to ground level before and after grazing each paddock. The vertical and horizontal structure of swards was measured using an inclined point quadrat set at 32.5° to the horizontal (Warren Wilson, 1963). At least 200 contacts were recorded per paddock. The procedures of the measurements above were same as described in Chapter 3.

4.3.2. Ingestive Behaviour and Herbage Intake

Two observations of 24-hour grazing behaviour were made from a caravan parked near the paddocks for Experiment 2 in December, 1993; four observations were made for Experiment 3 in February and March, 1994.

Observations of diet composition were made using two pairs of wethers fistulated at the oesophagus (OF). The two pairs of wethers grazed the two experimental pastures for a week before sampling and were switched between pastures every day. During two 5-day periods, 20 oesophageal extrusa samples were collected from each pasture respectively in December 1993 (Experiment 2), February and March 1994 (Experiment 3).

Herbage OM intake measurement was undertaken according to procedures described in Chapter 3. Chromium release rates for treatments were measured by dosing second capsules into the lambs three weeks before the experiment ended and estimating chromium disappearance over the period to slaughter.

4.3.3. Faecal Egg Counts (FECs)

All the experimental lambs were drenched with Levamisol (Nilverm, Coopers-Pitman-Moore, New Zealand Ltd) at the start of experiment and subsequently at monthly intervals. Faecal samples were first collected two weeks after drenching and then immediately before the next drenching. Faecal egg counts were estimated using a Modified McMaster technique as described by Williamson *et al.* (1994).

4.3.4. Rumen Ammonia Concentration

12 wethers fistulated in the rumen were used to estimate rumen ammonia concentration in February, 1994. Three selected randomly out of 6 wethers used in each pasture were drenched with PEG twice daily and the remaining 3 wethers were drenched with water as a control. Metal probes covered in a synthetic fibre were suspended in the rumens of the wethers. Twenty ml rumen liquor was collected by syringe every four hours commencing at 0800 hour for a continuous 24 hours two weeks after PEG administration commenced. The rumen fluid collected was immediately deproteinized after sampling (5 ml of 2.5 M H_2SO_4 saturated with MgSO_4 for NH_3 samples), then the deproteinized NH_3 samples were centrifuged at 3000 g for 15 min. The supernatant fluid was stored at -20°C until analysis to determine rumen NH_3 . The wethers were then switched between drenching treatments within pastures, and the same procedures repeated in a second period. Rumen ammonia concentration was determined using the method described by Waghorn *et al.* (1987a).

4.3.5. Liveweight Gain, Carcass Gain, Dressing Out and Carcass Fatness.

Lamb liveweight was recorded at weekly intervals and fasted weight recorded at monthly intervals. The lambs were slaughtered, and hot carcass weight was recorded and carcass GR was measured at the end of each experiment. Initial

carcass weight of the experimental lambs was predicted from the regression established from the 16 slaughter samples at the beginning of experiment. Liveweight gain, carcass gain and dressing out % were calculated. Carcass GR was measured as an indirect fat content assessment in terms of measurement of total soft tissue depth over the 12th rib at a point 11 cm from the mid carcass (Kirton, 1989).

4.3.6. The Rate of Wool Growth

A single wool sample was clipped, using procedures described in Chapter 3, at the beginning, mid-point and end of the experiment. Greasy wool sample was conditioned for 48 hours, weighed and scoured. The weight of clean wool was measured, and subsequently the rate of wool growth was calculated. The comparisons between treatments were conducted based on corrected wool weight (mg)/100 cm² patches on the right mid-side of the lambs.

4.4. STATISTICAL ANALYSIS

The experimental data were processed and analyzed using the SAS package (SAS Institute Inc., 1985 and 1990). Sward structure data were analyzed using a point quadrat package (Butler, 1991). One way analysis of variance was used to compare sward measurements such as surface height, herbage mass, bulk density, botanical components (green grasses, green white clover and dead material) and chemical composition (N, CT and in vitro digestibility) of diets selected by sheep on the two pastures. Analyses of covariance were used to assess the effects of grazing experience (previous pasture), current pasture, sex, PEG administration and the interactions among these variates on animal performance such as liveweight gain, carcass gain, carcass dressing out %, GR and wool growth based on a Split-plot design. Both previous pasture experience (Yorkshire fog and ryegrass) and current pastures (Yorkshire fog and tall fescue) were used as main plots, and then sex and PEG administration were arranged

completely at random as sub-plots. The initial liveweight of lambs was used as a co-variate to analyze liveweight gain of lambs. Repeated measures analysis of variance was performed for live weights at the different times over the experiment. Initial wool samples from the mid-side area of each lamb at the start of experiment were used as a co-variate for analysis to estimate wool growth. Carcass weight was used as a co-variate to analyze carcass GR data in Experiment 3. In experiment 2, some carcass assessments were missed at slaughter (Appendix Data 4.5). Analyses of variance for these variables were based on missing plot routines, but covariance analysis was precluded.

4.5. RESULTS

Experiment 2 and 3 were sequential. The results are reported separately because of differences in sheep and seasons between the two experiments, but are considered together in a combined discussion.

There were limited significant effects of interactions amongst previous pasture, current pasture, sex and PEG administration on grazing behaviour, herbage intake and performance in the two experiments. Therefore, attention is concentrated on the main effects of previous pasture, current pasture, sex and PEG administration and the interaction of previous pasture and current pasture in this section.

4.5.1. EXPERIMENT 2

4.5.1.1. Sward Characteristics

4.5.1.1.1. Sward Surface Height

There was similar sward surface height on both pastures, with the exception of mid-December, where there was a greater surface height on Yorkshire fog than

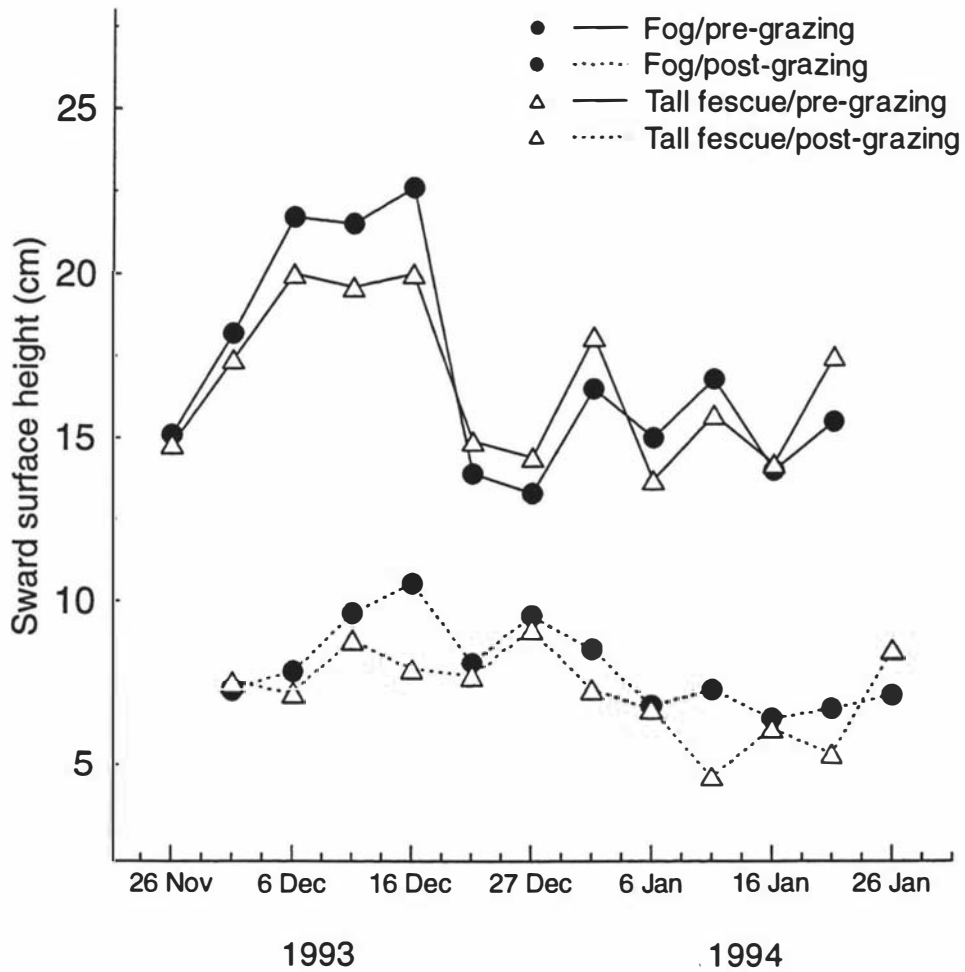


Figure 4.1 Sward surface height (cm) of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in late spring and early summer, 1993/1994.

on tall fescue (Figure 4.1). Sward surface heights were in the range of 13 - 23 cm before grazing and were in the range 6 - 10 cm after grazing on both swards in December. In January, the surface heights decreased when lambs grazed the regrowth of the pastures compared with the initial growth in December, being in the range of 13 - 17 cm before grazing and in the range of 5 - 8 cm after grazing.

4.5.1.1.2. Herbage Mass and Bulk Density

Herbage masses on the two swards are shown in Table 4.1. Herbage mass between the two pastures before grazing was similar, but Yorkshire fog had a slight advantage (6%) in residual herbage mass over tall fescue. Bulk density was very similar between the two swards before and after grazing (Table 4.1).

4.5.1.1.3. Botanical Composition of Swards

The botanical compositions of Yorkshire fog and tall fescue pastures by hand separation are shown in Figure 4.2 and Table 4.2. Green grasses were the main contributors to both pastures, and white clover accounted for less than 10% of total components. Yorkshire fog had a higher proportion of sown grass ($P \leq 0.1$) and lower proportions of other grasses ($P \leq 0.05$) and white clover ($P \leq 0.1$) than tall fescue sward. Yorkshire fog had a higher proportion of sown grass leaf ($P \leq 0.05$) and a lower proportion of other grass leaf ($P \leq 0.05$) than tall fescue before grazing. The proportion of grass leaf decreased and the proportions of grass stem and dead material increased after grazing on both pastures. There were significantly higher proportions of sown grass stem ($P \leq 0.001$) and lower proportions of other grass stem ($P \leq 0.001$) and clover leaf ($P \leq 0.05$) on Yorkshire fog than on tall fescue after grazing. The proportion of dead material tended to have a similar trend of variation on both swards, but Yorkshire fog had a higher proportion of dead material than tall fescue before grazing ($P \leq 0.1$). There was a greater increase in the proportion of dead material on tall fescue sward than Yorkshire fog sward after grazing (Tables 4.2 and Figure 4.2).

Table 4.1. Sward characteristics of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in late spring and early summer, 1993/1994

	Fog	Tall fescue	SEM	Sig.
Before grazing				
Herbage mass (kg DM/ha)	3850	3750	102	NS
Bulk density (mg DM/cm ³)	2.3	2.2	0.07	NS
After grazing				
Herbage mass (kg DM/ha)	2820	2650	81	NS
Bulk density (mg DM/cm ³)	3.9	4.3	0.18	NS

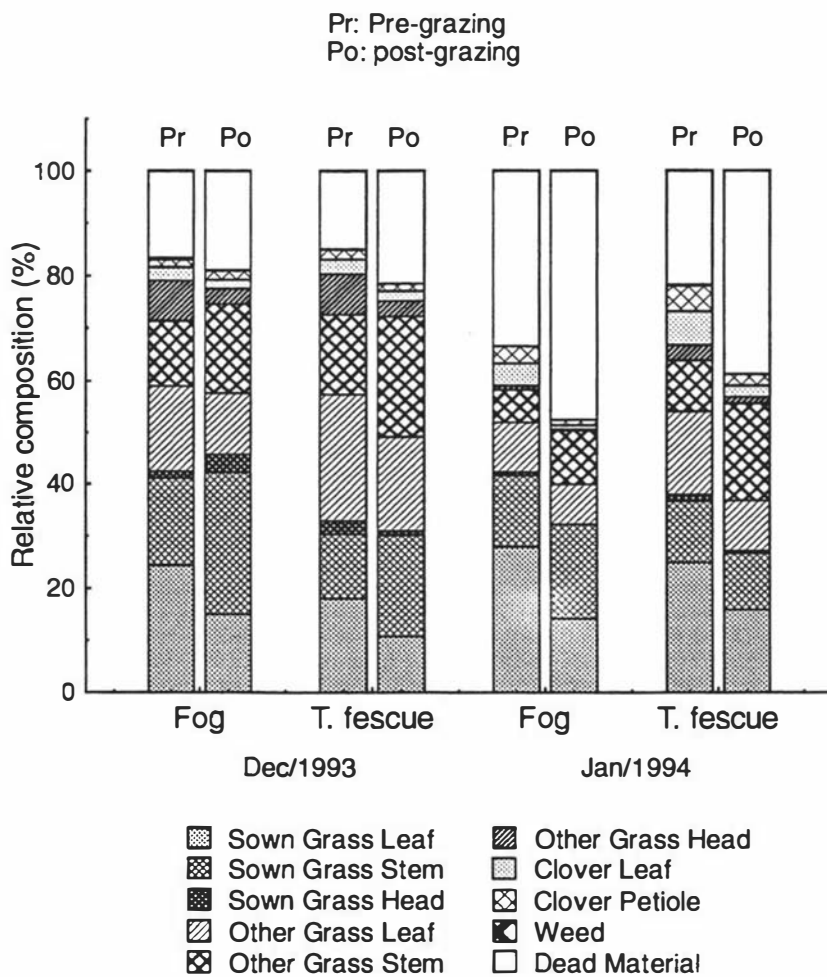


Figure 4.2. Botanical composition (%) of Yorkshire fog/white clover and tall fescue/white clover pastures under a rotational grazing management in late spring and early summer

Table 4.2. The percentage (%) of components of Yorkshire fog/clover and tall fescue/clover swards before and after grazing under rotational grazing management in late spring and early summer, 1993/1994

	Before grazing				After grazing			
	Fog fescue	Tall fescue	SEM	Sig.	Fog fescue	Tall fescue	SEM	Sig.
Sown grass leaf	26	21	1.4	*	15	13	0.7	NS
Sown grass stem	15	12	1.1	+	23	15	1.0	***
Sown grass seed head	1	2	0.7	NS	2	1	0.2	**
Total sown grass	42	35	2.3	+	40	29	1.3	***
Other grass leaf	13	21	1.6	*	10	14	0.5	***
Other grass stem	10	12	1.3	NS	13	21	0.7	***
Other grass seed head	4	5	0.5	NS	2	2	0.4	NS
Total other grasses	27	38	2.4	*	25	37	1.1	***
Clover leaf	4	5	0.5	+	1	2	0.2	*
Clover petiole	2	3	0.5	NS	2	2	0.2	NS
Total clover	6	8	0.8	+	3	4	0.3	*
Weed	<1	<1	0.1	NS	0	0	0.0	NS
Dead Material	25	18	2.2	+	32	30	1.3	NS

4.5.1.1.4. Canopy Structure within the Sward

The point quadrat data from the two swards are summarized in Figures 4.3 and 4.4. Before grazing, the structures and distributions of plant parts were similar in the two swards, and sown and other grass leaves were the main contributors. The sown and other grass leaves were distributed in the medium-upper strata, while grass stems were distributed in the medium-bottom strata of 0 - 8 cm. White clover was mainly concentrated in the medium strata of 2 - 8 cm on both swards and dead material was concentrated in the bottom strata of 0 - 4 cm on both swards before grazing (Figure 4.3). After grazing, there was a decrease in sown grass leaf and an increase in grass stem and dead material on both swards (Figure 4.4). The relative contribution of other grasses increased, especially in tall fescue.

4.5.1.2. Animal Measurements

4.5.1.2.1. Diet Composition - botanical and chemical

The botanical composition of the samples selected by OF sheep is shown at Table 4.3. There was little difference in the proportions of all the plant parts in the diets from the two swards. The green grasses made main contributions to the diets selected by OF sheep for both swards, while white clover and dead material accounted for very small proportions of the total diets. There were more green grasses and less white clover and dead material in the diets than in the whole swards offered to the sheep based on the point quadrat data and on the herbage samples by hand separation.

The chemical composition of the samples selected in both pastures is shown in Table 4.4. There were higher total N ($P \leq 0.05$), and organic matter digestibility (OMD) ($P \leq 0.01$) on tall fescue than on Yorkshire fog in Period 1. There were higher protein-bound ($P \leq 0.001$), fibre-bound ($P \leq 0.1$) and total CT concentrations

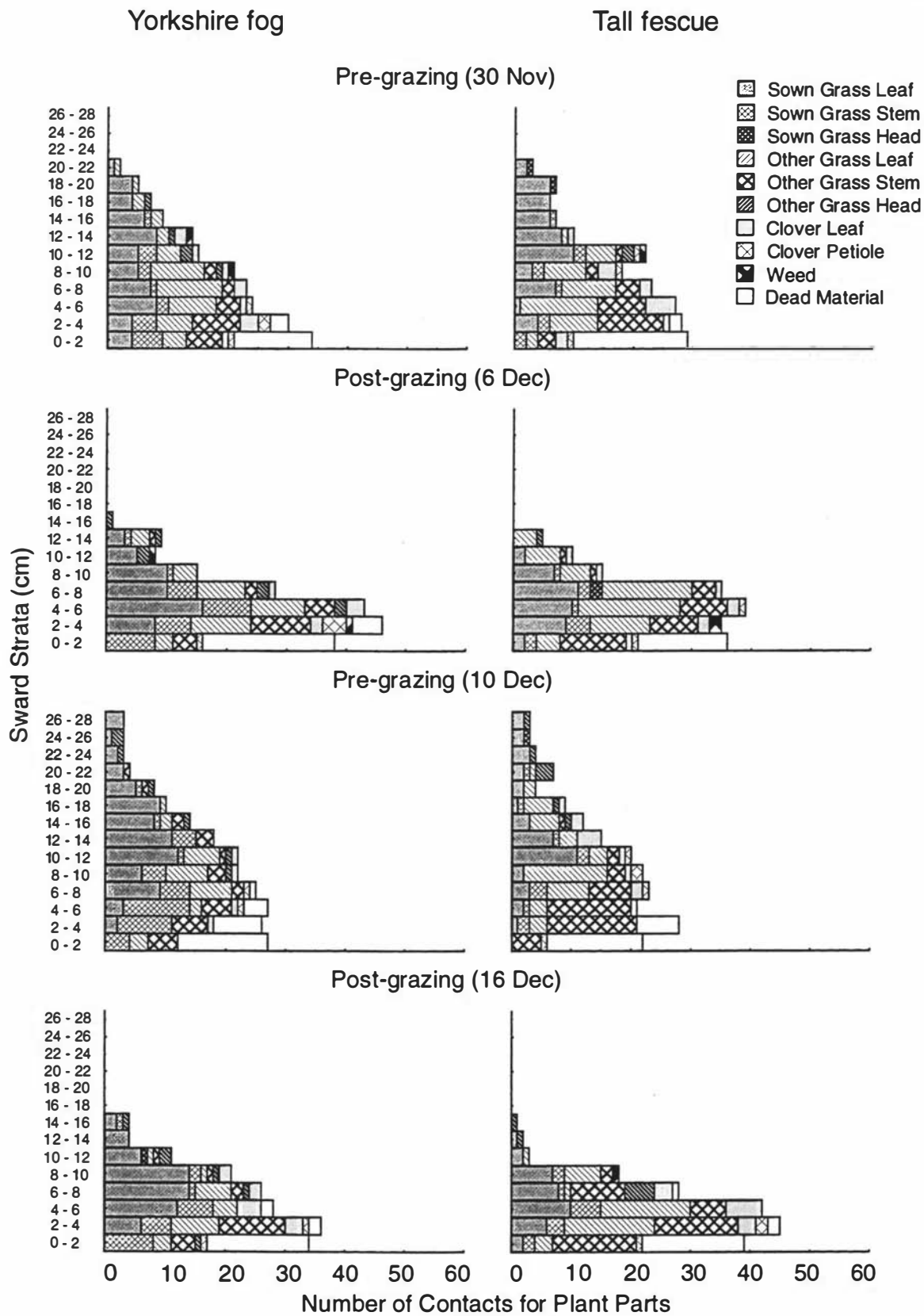


Figure 4.3. The stratum structure of plant parts within the sward canopy of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in late spring and early summer, 1993.

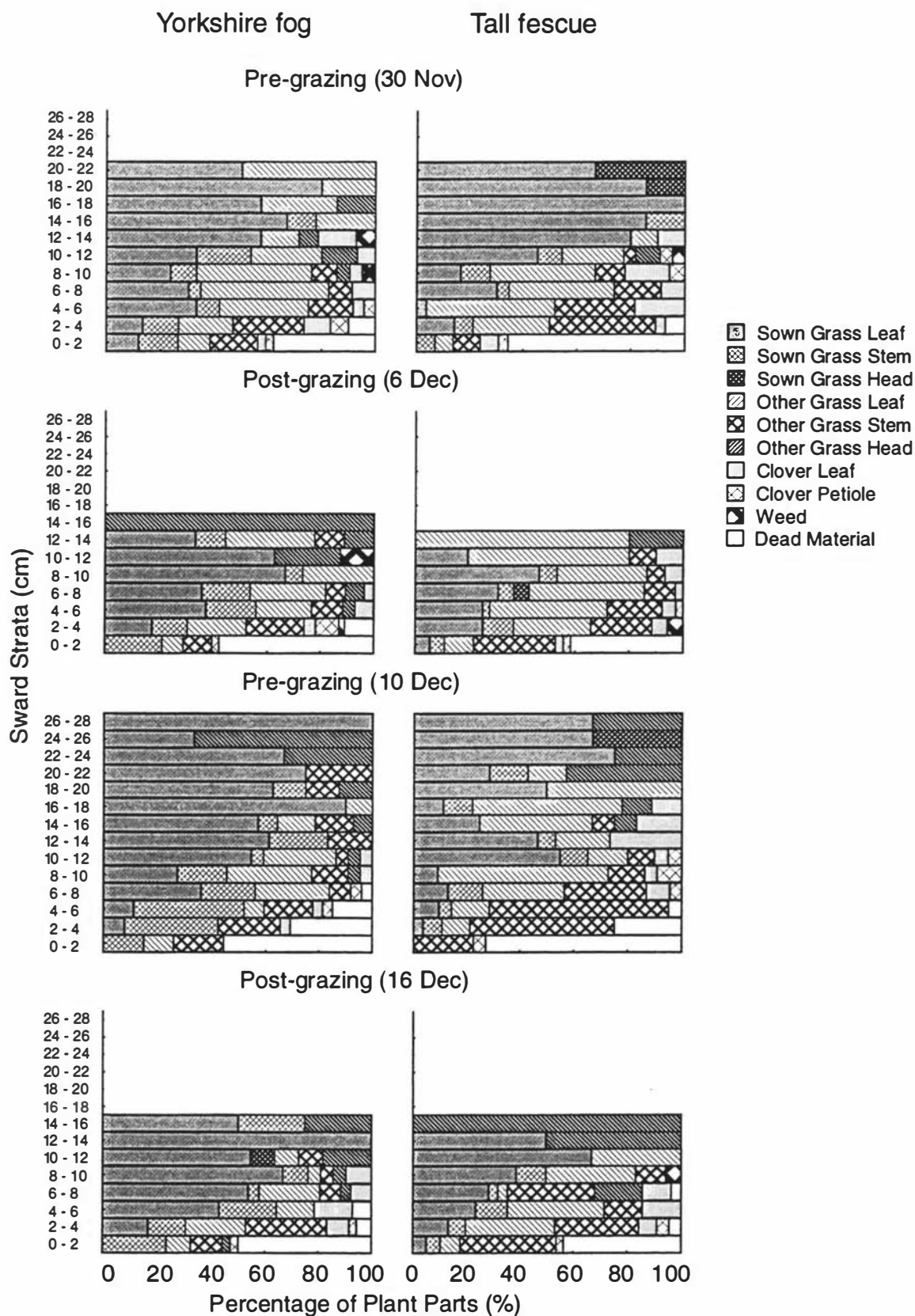


Figure 4.4. The percentage of plant parts in the different strata of Yorkshire fog/clover and tall fescue/clover swards under rotational grazing management in late spring and early summer, 1993/1994.

Table 4.3. The percentage of components in the samples selected by OF sheep grazing Yorkshire fog/clover and tall fescue/clover in spring and early summer, 1993/1994

	Yorkshire fog				Tall fescue				Extrusa samples from			
	Sward samples ¹		Sward canopy ²		Sward ¹		Sward canopy ²		Fog	Tall fescue	SEM	Sig.
	Pre-grazing	Post-grazing	Overall >8cm		Pre-grazing	Post-grazing	Overall >8cm					
Grasses (%)	80	77	82	93	80	74	79	91	96	95	0.2	NS
Clover (%)	3	4	9	7	5	3	9	9	2	2	0.2	NS
Weed (%)	<1	0	0	0	0	0	0	0	0	0	0.0	NS
Dead material (%)	17	19	9	0	15	23	12	0	2	3	0.2	NS

¹: Herbage samples by hand separation;

²: Point quadrat data.

Table 4.4. Chemical composition of the samples selected by OF sheep grazing Yorkshire fog/clover and tall fescue/clover pastures in spring and early summer, 1993/1994.

	Period 1				Period 2				Overall effects			F value for		
	Fog	Tall fescue	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Fog	Tall fescue	SEM	Spp	Per	Spp x Per
Total N (% DM)	3.43	3.56	0.018	*	3.03	2.97	0.131	NS	3.23	3.26	0.066	NS	**	NS
OMD (%)	78	81	0.6	**	80	79	0.9	NS	79	80	0.6	NS	NS	*
CT (g/kg DM)														
Extractable	0.15	0.15	0.046	NS	0.18	0.19	0.025	NS	0.16	0.17	0.026	NS	NS	NS
Protein-bound	1.31	0.79	0.025	**	1.45	0.65	0.100	*	1.38	0.72	0.051	***	NS	NS
Fibre-bound	0.43	0.38	0.013	+	0.38	0.29	0.045	NS	0.40	0.33	0.023	+	+	NS
Total	1.89	1.32	0.081	*	2.00	1.13	0.088	*	1.94	1.22	0.060	**	NS	NS

Extrusa samples were taken in early December (Period 1) and late December (Period 2), 1993.

($P \leq 0.01$) overall in the diets from Yorkshire fog sward than from tall fescue sward. There was little difference in extractable CT between diets on the two swards.

4.5.1.2.2. Grazing Behaviour

The results of the observations of grazing behaviour are shown in Table 4.5. There was more time spent in grazing ($P \leq 0.05$) and ruminating ($P \leq 0.1$) and less time in resting ($P \leq 0.01$) on Yorkshire fog than on tall fescue. There were no effects of previous pasture, current pasture and PEG administration on daily grazing activities of lambs, with the exception of effects of previous pasture on ruminating ($P \leq 0.1$). The rate of biting in lambs was faster on Yorkshire fog than on tall fescue ($P \leq 0.05$). Intake per bite was greater on Yorkshire fog than on tall fescue ($P \leq 0.05$).

4.5.1.2.3. Herbage Intake

Mean release rates of Cr_2O_3 , estimated from the second CRC collected from each lamb at slaughter, were not influenced by treatments in the current experiment. Therefore, a standard release rate of Cr_2O_3 (224.3 ± 10.92 mg/day) was used to determine the faecal output in lambs on the two pastures.

Herbage OM intake was not influenced by previous pasture and current pasture (Table 4.5). Male lambs had significantly greater herbage OM intake than female lambs ($P \leq 0.1$), but there was no significant difference in herbage OM intake in terms of metabolizable weight (g/kg $W^{0.75}$ /day) between male and female. PEG administration had a negative effect on herbage OM intake in lambs ($P \leq 0.1$).

4.5.1.2.4. Faecal Egg Counts

All samples of faecal egg count two weeks after first drenching were zero, so means of the samples of faecal egg counts before second drenching and before

Table 4.5. Grazing behaviour and herbage OM and DOM intakes of lambs grazing Yorkshire fog/clover and tall fescue/clover in late spring and early summer , 1993/1994.

	Main effects (n=16)															
	Previous pasture				Current pasture				SEX				PEG			
	Ryegrass	Fog	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Male	Female	SEM	Sig.	Ctrl	PEG	SEM	Sig.
Grazing time (min)	560	560	5	NS	570	550	5	*	560	560	11	NS	550	570	11	NS
Ruminating time (min)	280	290	4	+	300	280	4	+	280	290	7	NS	290	290	7	NS
Resting time (min)	510	500	6	NS	480	520	6	**	510	490	14	NS	510	500	14	NS
The rate of biting (bites/min)	42	42	0.1	NS	43	42	0.1	*	42	42	0.4	NS	42	42	0.4	NS
Intake per bite (mg OM/ bite)					85	75	3.5	*								
OM intake (g/day)	768	801	19.4	NS	796	773	19.4	NS	828	741	29.5	+	823	746	29.5	+
OM intake (g/kg W ^{0.75})	59	64	1.9	NS	62	61	1.9	NS	64	59	2.5	NS	65	58	2.5	+
DOM intake (g/day)	611	637	15.6	NS	630	618	15.6	NS	659	589	23.6	+	655	593	23.6	+
DOM intake (g/kg W ^{0.75})	47	51	1.5	NS	49	49	1.5	NS	51	47	2.0	NS	52	46	2.0	+

Table 4.6. Faecal egg counts (eggs/g faeces) of lambs grazing Yorkshire fog/clover and tall fescue/clover pastures in late spring and early summer, 1993/1994.

	Main effects (n = 8)											
	Current pasture				SEX				PEG			
	Fog	Tall fescue	SEM	Sig.	Male	Female	SEM	Sig.	Ctrl	PEG	SEM	Sig.
Egg counts (eggs/g faeces)	430	760	101	*	770	430	101	*	620	580	101	NS

the end of the experiment are summarised in Table 4.6. There were significantly higher egg counts for lambs on tall fescue than on Yorkshire fog (Table 4.6). Male lambs had a higher egg count than females. There was no significant effect of PEG administration on egg counts for lambs. These results were not affected by logarithmic or square root transformation.

4.5.1.2.5. Liveweight Gain, Carcass Weight, Dressing Out and GR

The time trends of liveweight and liveweight gain on both swards are shown at Figures 4.5 and 4.6. Initial weight gains were similar for lambs on both pastures, and then there was a general decline in liveweight gain of lambs as the experiment progressed, especially on tall fescue (Figure 4.6).

Lambs had faster liveweight gain on Yorkshire fog than on tall fescue over the experiment ($P \leq 0.1$), especially in the second month (from late December to late January) ($P \leq 0.05$) (Table 4.7). Male lambs had higher liveweight gain than females in the first month (from late November to late December) ($P \leq 0.05$) and over the experiment as a whole ($P \leq 0.05$). Liveweight gain was greater in control than in PEG drenched lambs in the initial month of the experiment ($P \leq 0.1$). Carcass weight and carcass weight gain of lambs at slaughter were higher on Yorkshire fog than on tall fescue ($P < 0.05$), and were not affected by sex or PEG administration.

4.5.1.2.6. The Rate of Wool Growth

Lambs had higher rate of wool growth on Yorkshire fog than on tall fescue in the second month ($P \leq 0.1$) (Table 4.7). There were no significant effects of previous pasture, grazing pasture, sex or PEG administration on the rate of wool growth in the first month.

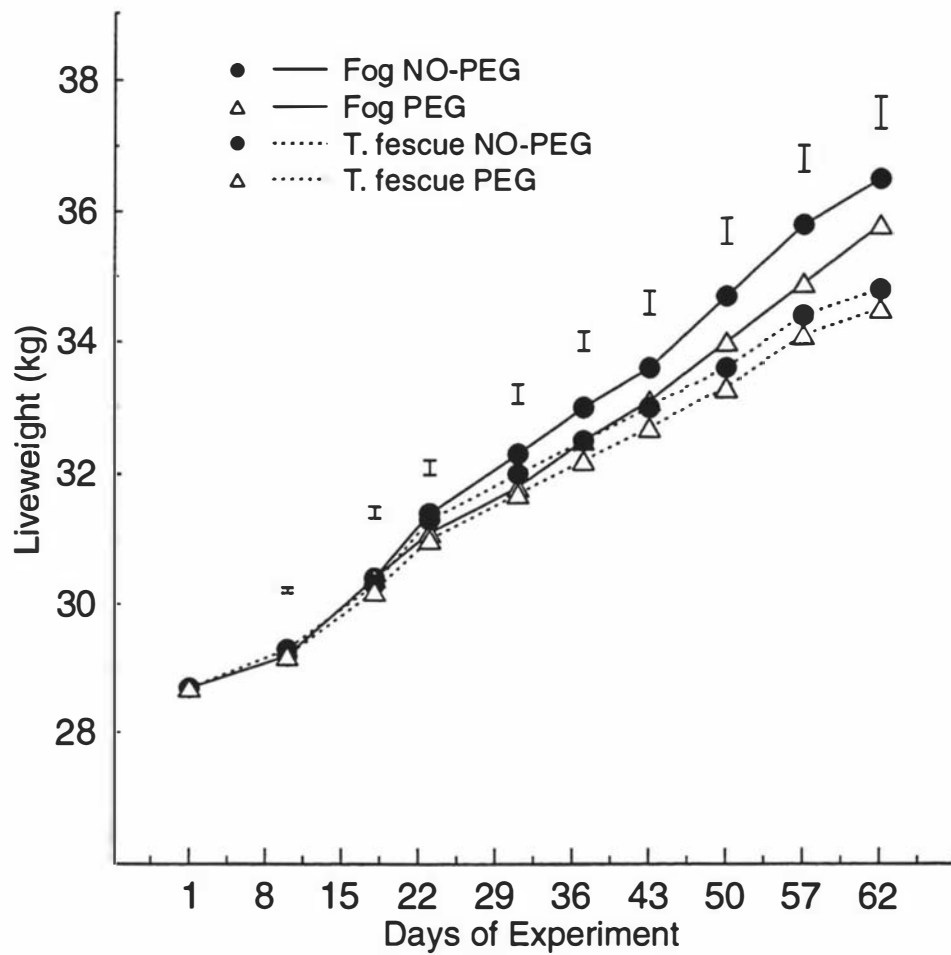


Figure 4.5. Liveweight (kg) of lambs grazing Yorkshire fog/clover and tall fescue/clover pastures under a rotational management in late spring and early summer, 1993/1994.

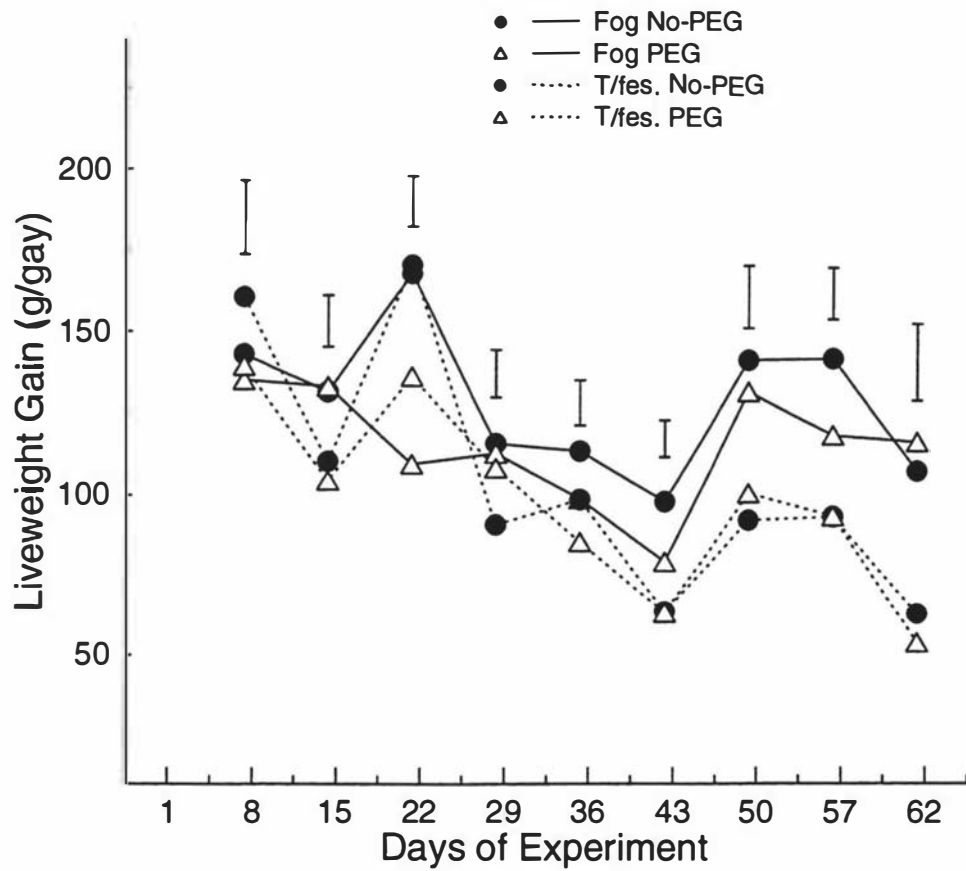


Figure 4.6 Liveweight gain (g/day) of lambs grazing Yorkshire fog/clover and tall fescue/clover pastures under a rotational management in late spring and early summer, 1993/1994

Table 4.7. Effects of previous pasture, current pasture, sex and condensed tannins (CT) on the liveweight gain, carcass weight, carcass weight gain, dressing out %, GR and wool growth rate of lambs grazing Yorkshire fog/clover and tall fescue/clover pasture in late spring and early summer, 1993/1994

	Main effects (n=16)															
	Previous pasture				Current pasture				SEX				PEG			
	Ryegrass	Fog	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Male	Female	SEM	Sig.	Ctrl	PEG	SEM	Sig.
Liveweight gain (g/day)																
22/11/93 - 22/12/93	108	86	10.6	NS	102	92	9.3	NS	107	87	4.4	*	101	92	4.1	+
23/12/93 - 26/01/94	83	76	7.4	NS	98	61	5.7	*	87	72	5.8	NS	81	78	4.6	NS
22/11/93 - 26/01/94	94	81	7.7	NS	99	76	6.7	+	95	80	3.3	*	90	85	3.0	NS
Carcass weight (kg)	-	-	-		14.7	13.9	0.2	*	14.4	14.3	0.2	NS	14.5	14.2	0.2	NS
Carcass weight gain (g/day)	-	-	-		32	20	3.1	*	26	26	3.3	NS	28	24	3.0	NS
Dressing out %	-	-	-		45	44	0.4	NS	44	45	0.4	NS	44	45	0.4	NS
GR (mm) Left	-	-	-		5	5	0.5	NS	5	5	0.5	NS	5	5	0.5	NS
Right	-	-	-		6	5	0.7	NS	5	5	0.7	NS	5	5	0.6	NS
Wool growth rate (mg/100cm ² per day)																
22/11/93 - 22/12/93	117	124	4.3	NS	122	119	3.9	NS	118	123	4.2	NS	119	122	3.7	NS
23/12/93 - 26/01/94	109	108	4.6	NS	117	101	4.2	+	107	110	4.1	NS	109	108	3.7	NS

4.5.2. EXPERIMENT 3

4.5.2.1. Sward Characteristics

4.5.2.1.1. Sward Surface Height

Surface heights were maintained at about 9 - 12 cm pre-grazing and 4-6 cm post-grazing on both pastures over the experiment (Figure 4.7). Yorkshire fog had a slightly higher surface height than tall fescue for pre-grazing and post-grazing swards, with the exception of the initial period, where the surface height was higher on tall fescue than on Yorkshire fog sward, and in early March, where there was a similar surface height on the two pastures before grazing.

4.5.2.1.2. Herbage Mass and Bulk Density

Herbage masses and bulk densities of the two swards are shown in Table 4.8. There was similar herbage mass for pre-grazing swards between the two pastures, but Yorkshire fog sward had significantly higher residual herbage mass than tall fescue ($P \leq 0.01$). Bulk density was not significantly different between the two swards before grazing, but slightly greater in Yorkshire fog sward than in tall fescue sward after grazing ($P \leq 0.1$). Post-grazing bulk density increased compared with that before grazing on both swards.

4.5.2.1.3. Botanical Composition of Swards

The botanical compositions of swards by hand separation are presented in Table 4.9. Sown grass largely contributed to the composition of the swards, although other grasses such as perennial ryegrass and *Poa* spp. made some contributions to the swards. Yorkshire fog had significantly higher proportion of sown grass leaf ($P \leq 0.1$) and total sown grass ($P \leq 0.01$) and smaller proportions of other grass stem ($P \leq 0.01$), total other grasses ($P \leq 0.05$) and white clover ($P \leq 0.05$) than tall

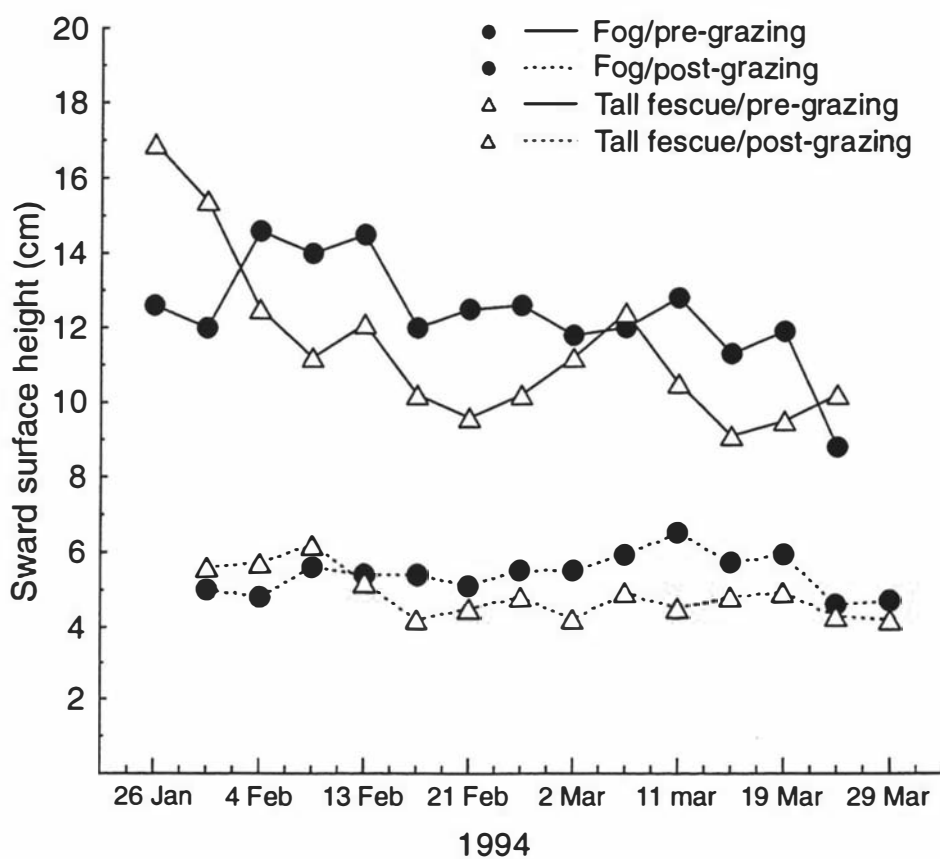


Figure 4.7 Sward surface height (cm) of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in summer and early autumn, 1994.

Table 4.8. Sward characteristics of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in summer and early autumn, 1994.

	Fog	Tall fescue	SEM	Spp
Before grazing				
Herbage mass (DM kg/ha)	2860	2870	81	NS
Bulk density (DM mg/cm ³)	2.7	2.7	0.07	NS
After grazing				
Herbage mass (DM kg/ha)	1930	1720	53	**
Bulk density (DM mg/cm ³)	3.9	3.7	0.08	+

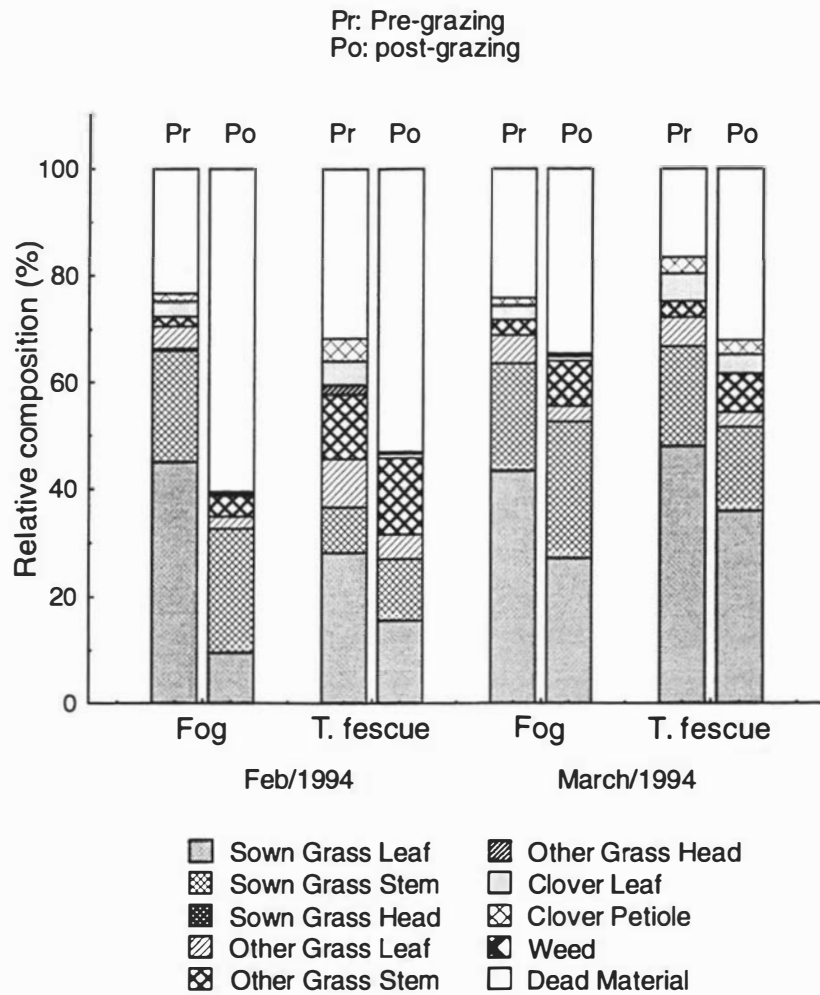


Figure 4.8. Botanical composition (%) of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in summer and early autumn, 1994

Table 4.9. The percentage (%) of components of Yorkshire fog and tall fescue swards before and after grazing under rotational grazing management in summer and early autumn, 1994.

	Before grazing				After grazing			
	Fog	Tall fescue	SEM	Sig.	Fog	Tall fescue	SEM	Sig.
Sown grass leaf	44	38	2.0	+	18	26	0.9	***
Sown grass stem	21	13	1.2	***	24	14	0.8	***
Sown grass seed head	<1	0	0.1	NS	0	0	0.0	NS
Total sown grass	65	51	2.7	**	42	39	1.6	NS
Other grass leaf	5	7	1.0	NS	3	4	0.2	*
Other grass stem	2	8	0.6	**	6	10	0.4	***
Other grass seed head	0	1	0.3	NS	0	0	0.0	NS
Total other grasses	7	16	1.5	*	9	13	0.6	***
Clover leaf	3	5	0.4	*	1	2	0.2	***
Clover petiole	1	4	0.6	*	<1	2	0.4	**
Total clover	4	8	1.0	*	1	4	0.6	***
Weed	0	0	0.0	NS	0	0	0.0	NS
Dead Material	24	25	2.7	NS	48	44	2.2	NS

fescue before grazing. After grazing, the proportions of sown and other grass leaves and white clover decreased, while the proportion of dead material increased on both swards (Figure 4.8). There was no significant difference in the proportions of total sown grass, but Yorkshire fog had significantly lower proportions of sown grass leaf ($P \leq 0.001$), other grass leaf ($P \leq 0.05$), total other grasses ($P \leq 0.001$) and white clover ($P \leq 0.001$), and had higher proportion of sown grass stem ($P \leq 0.001$) than tall fescue. There were no significant differences in the proportions of dead material between the two pastures before and after grazing.

4.5.2.1.4. Canopy Structure within the Sward

The vertical distribution and relative proportions of all the plant parts within the sward canopy are shown in Figures 4.9a, 4.9b, 4.10a and 4.10b. There was a similar distribution of sown grass between tall fescue and Yorkshire fog in February. Before grazing, sown grass leaf was distributed in the medium-upper strata of the swards, while grass stem was distributed in the medium-bottom strata of 0 - 8 cm and dead material was distributed in the bottom 0 - 4 cm. After grazing, sown grass leaf decreased and grass stem increased on Yorkshire fog but there was little change in the proportions for tall fescue, so tall fescue had higher proportion of grass leaf and lower proportion of sown grass stem than Yorkshire fog. The proportion of white clover was higher on tall fescue than on Yorkshire fog, especially for post-grazing sward. The proportion of dead material relatively increased after grazing on Yorkshire fog but to only a small extent on tall fescue.

In March, sown grass leaf was mainly concentrated in the medium-upper strata of 2 - 10 cm, while grass stem was distributed in the medium-bottom strata of 0 - 6 cm on Yorkshire fog sward and in the bottom of 0 - 4 cm on tall fescue sward. There were higher amounts and percentages of grass stem on Yorkshire fog than on tall fescue both pre-grazing and post-grazing. On the contrary, other

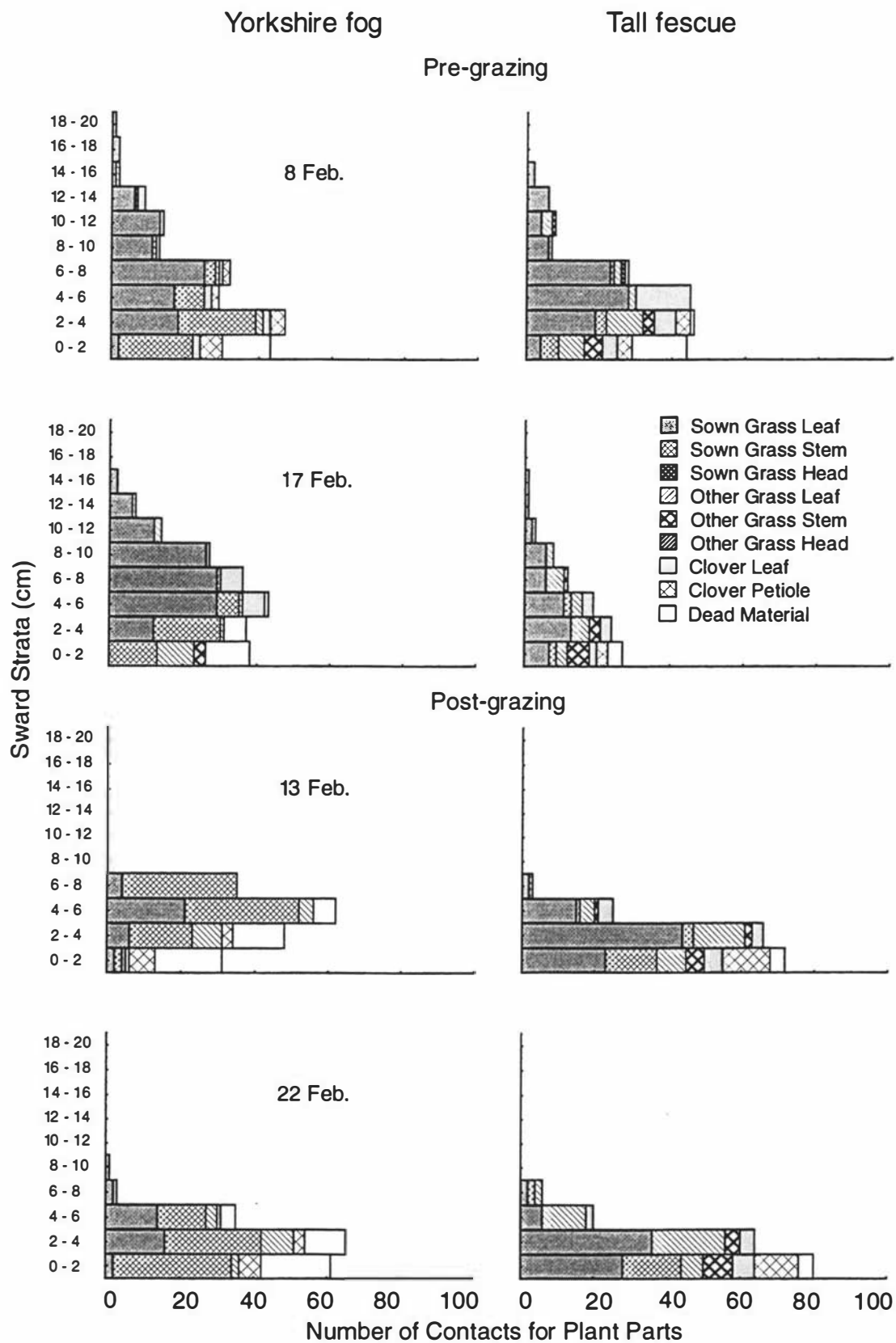


Figure 4.9a. The stratum structure of plant parts within the sward canopy of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in summer (February, 1994).

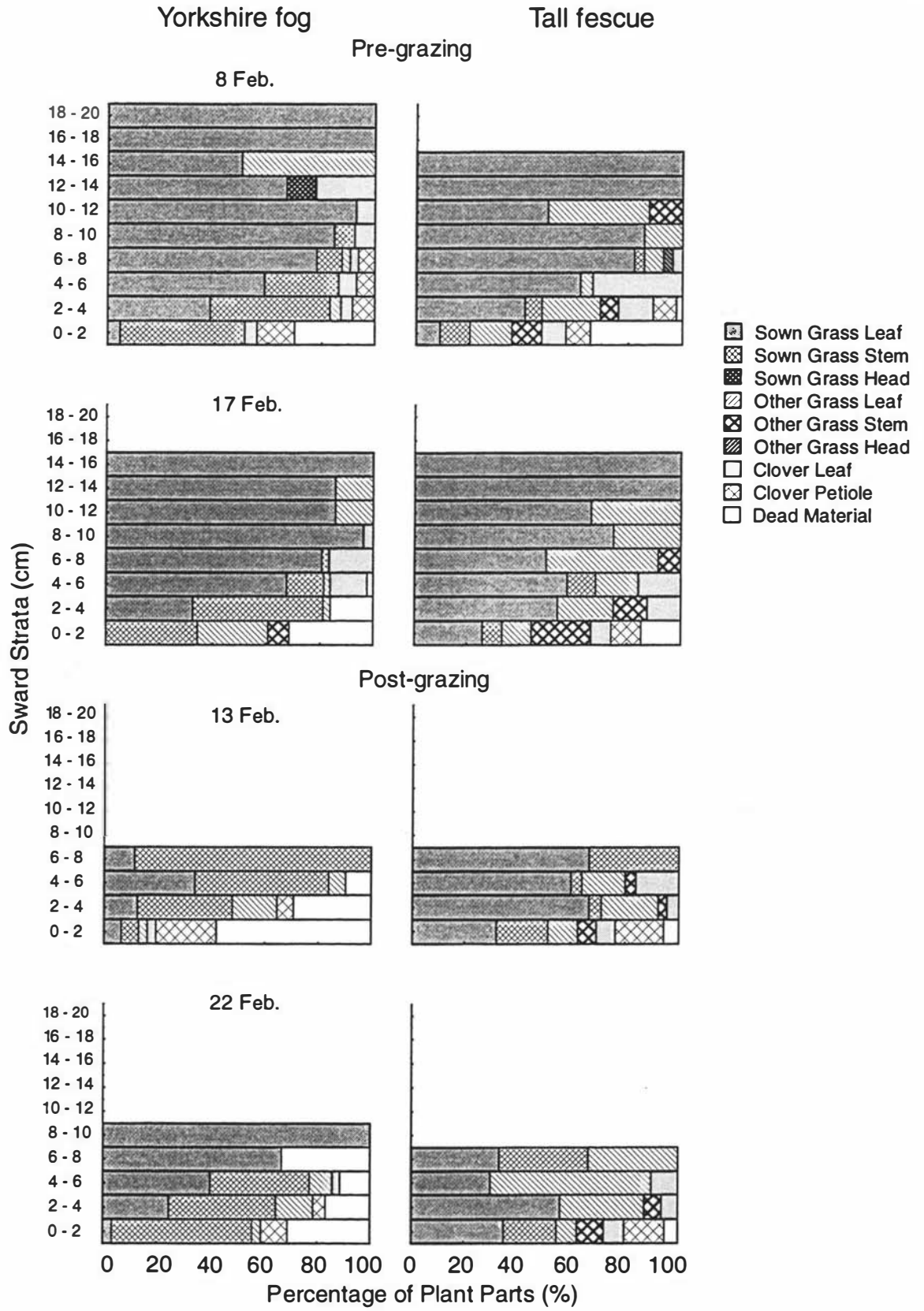


Figure 4.9b. The percentage of plant parts in the different strata of Yorkshire fog/clover and tall fescue/clover swards under rotational grazing management in summer (February, 1994).

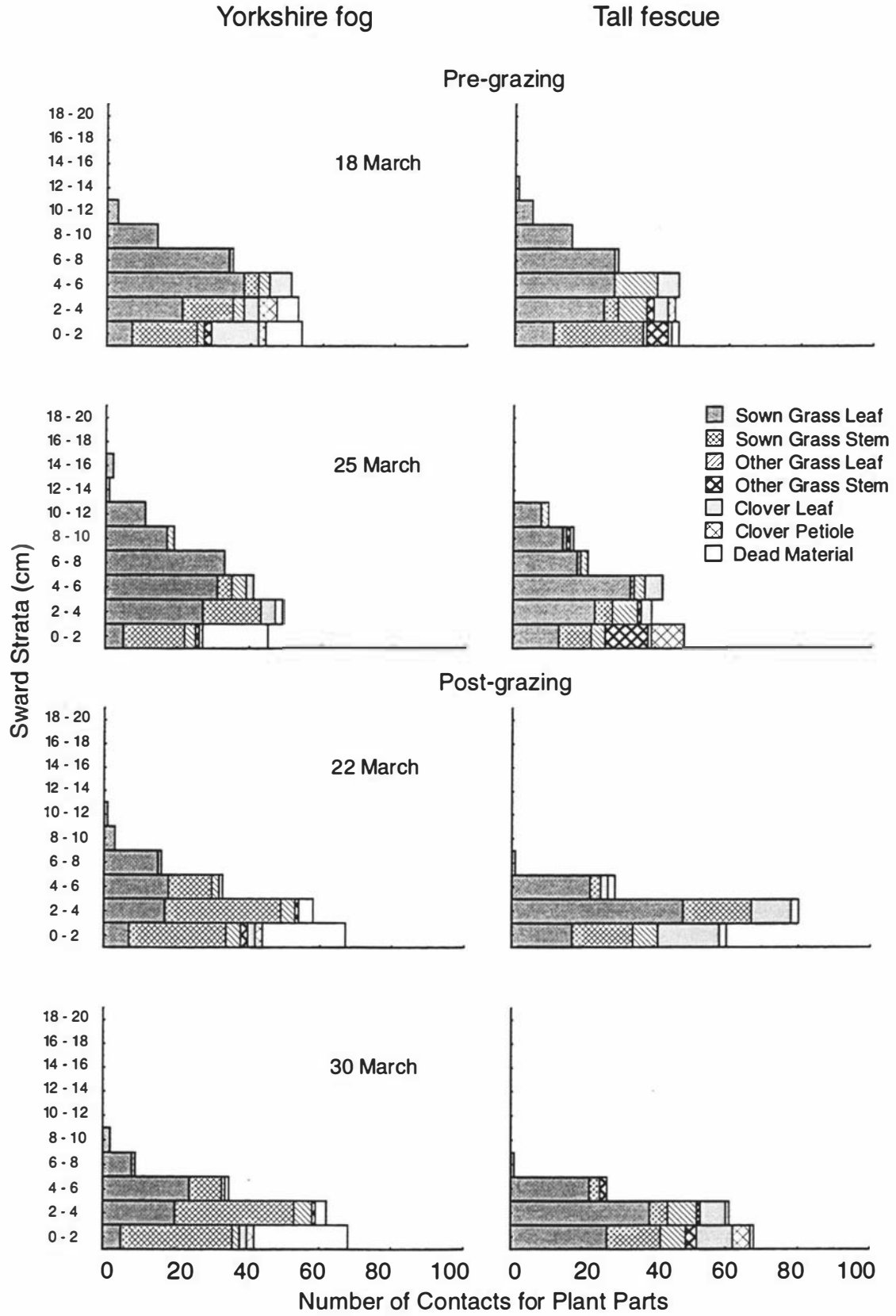


Figure 4.10a. The stratum structure of plant parts within the sward canopy of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in early autumn (March, 1994).

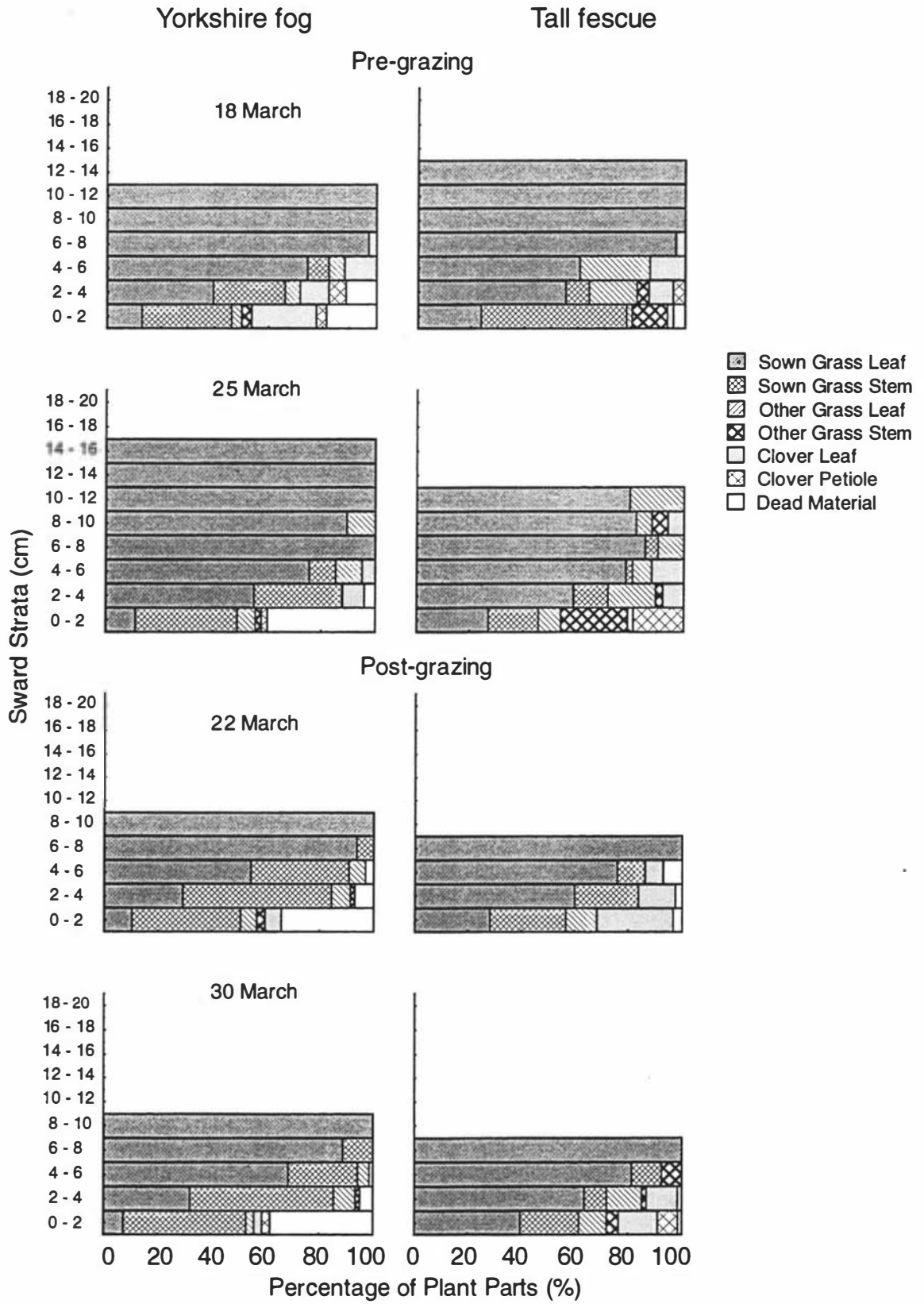


Figure 4.10b. The percentage of plant parts in the different strata of Yorkshire fog/clover and tall fescue/clover swards under rotational grazing management in summer (March, 1994).

grasses such as *Poa* spp and perennial ryegrass, were contacted more on tall fescue than on Yorkshire fog pre-grazing. White clover was distributed in the strata of 0 - 6 cm within the sward canopy and was contacted much more on tall fescue than on Yorkshire fog after grazing (Figures 4.10a and 4.10b). Dead material was commonly distributed in the bottom strata of 0 -4 cm on Yorkshire fog and in the bottom of 0 - 2 cm on tall fescue, with fewer contacts on tall fescue than on Yorkshire fog.

4.5.2.2. Animal Measurements

4.5.2.2.1. Diet Composition - botanical and chemical

The botanical composition of the samples selected by OF sheep is shown in Table 4.10. The oesophageal extrusa samples were dissected into grass, legume and dead material, because weed was not found in the diets. The green grasses made main contributions to the diets selected by OF sheep for both swards, while white clover and dead material accounted for small proportions in the diets for both swards. There were more grasses and less white clover and dead material in the diets than in the swards offered on both pastures.

The chemical composition of the diets selected from both pastures is shown in Table 4.11. There were inconsistent values of total N concentration and OMD in the diets on the two swards in the different periods. Yorkshire fog had a higher OMD than tall fescue ($P \leq 0.1$) in Period 1 in February, but there was significantly lower N concentration and OMD for the diet selected by OF sheep grazing on Yorkshire fog than on tall fescue in Period 2. In March, the difference in OMD in the diets between swards was still significant. There was an increase in OMD for the diets selected in March compared with those in Periods 1 and 2 of February.

There were consistently higher CT concentrations in the diets on Yorkshire fog than on tall fescue. Extractable and total CT concentration for the diet selected

Table 4.10. The percentage (%) of components in the samples selected by OF sheep grazing Yorkshire fog/clover and tall fescue/clover in summer and early autumn, 1994.

	Yorkshire fog				Tall fescue				Extrusa samples from			
	Sward samples ¹		Sward canopy ²		Sward ¹		Sward canopy ²		Fog	Tall fescue	SEM	Sig.
	Pre-grazing	Post-grazing	Overall	>4cm	Pre-grazing	Post-grazing	Overall	>4cm				
Grass (%)	72	52	85	93	67	53	85	90	94	95	0.6	NS
Clover (%)	4	1	10	7	8	3	12	10	2	1	0.4	NS
Weed (%)	0	0	0	0	0	1	0	0	0	0	0	NS
Dead material (%)	24	47	5	0	25	43	3	0	4	4	0.3	NS

¹: Herbage samples by hand separation;

²: Point quadrat data.

Table 4.11. Chemical composition of the samples selected by OF sheep grazing Yorkshire fog/clover and tall fescue/clover pastures in summer and early autumn, 1994¹.

	February				March		SEM	Overall			F value for		
	Period 1		Period 2		Period 4			Fog	Tall fescue	SEM	Spp	Per	Spp x Per
	Fog	Tall fescue	Fog	Tall fescue	Fog	Tall fescue							
Total N	3.13	3.01	2.91	3.24	3.86	3.86	0.022	3.30	3.37	0.013	*	***	***
OMD	74	71	68	72	77	79	1.1	73	74	0.6	NS	***	*
Condensed tannins (CT:g/kg DM/)													
Extractable	0.36	0.05	0.43	0.00	0.52	0.00	0.047	0.43	0.02	0.027	***	NS	NS
Protein-bound	1.26	0.90	1.170	0.79	0.82	0.83	0.043	1.08	0.84	0.024	***	**	**
Fibre-bound	0.52	0.39	0.510	0.37	0.37	0.35	0.024	0.47	0.37	0.014	**	*	NS
Total	2.14	1.34	2.11	1.16	1.71	1.18	0.073	1.98	1.22	0.042	***	*	+

¹: Extrusa samples were taken in early February (Period 1), late February (Period 2) and late March (Period 4).

were higher on Yorkshire fog than on tall fescue although there were similar protein-bound and fibre-bound CT concentrations in March. Protein-bound CT made major contribution to the chemical composition of the diets for both the pastures at all dates of measurements.

4.5.2.2.2. Grazing Behaviour

Observations of grazing behaviour in lambs and intake per bite in OF sheep are shown in Table 4.12. Lambs spent more time in grazing ($P \leq 0.05$) and less time in resting ($P \leq 0.1$) on tall fescue than on Yorkshire fog. The rate of biting in lambs was faster on tall fescue than on Yorkshire fog ($P \leq 0.1$), while intake per bite of OF sheep was smaller on tall fescue than on Yorkshire fog ($P \leq 0.1$). There were no significant effects of previous pasture, sex and PEG administration on grazing behaviour.

4.5.2.2.3. Herbage Intake

Mean release rate of Cr_2O_3 was estimated from CRCs collected from experimental lambs at slaughter in March. There was no significant difference in release rate of chromium from lambs amongst treatments. Therefore, a common release rate of Cr_2O_3 (209.0 ± 9.82 mg/day) was used to determine the faecal output in lambs on the two pastures in all the periods of measurements.

There were no significant effects of previous pasture or current pasture on herbage OM intake overall (Table 4.12), though lambs had higher herbage OM intake on tall fescue than on Yorkshire fog in late February (Appendix 4.11). Male lambs had significantly greater herbage OM intake than females ($P \leq 0.05$). There was higher herbage OM intake in control than in PEG drenched lambs ($P \leq 0.05$).

Table 4.12. Grazing behaviour and herbage OM and DOM intakes of lambs grazing Yorkshire fog/clover and tall fescue/clover in summer and early autumn, 1994.

	Main effects (n=16)															
	Previous pasture				Current pasture				SEX				PEG			
	Ryegrass	Fog	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Male	Female	SEM	Sig.	Ctrl	PEG	SEM	Sig.
Grazing time (min)	600	610	6	NS	590	620	6	*	600	610	9	NS	610	600	9	NS
Ruminating time (min)	270	280	3	NS	280	280	3	NS	280	280	8	NS	280	280	8	NS
Resting time (min)	520	500	8	NS	520	500	8	+	500	520	7	+	500	520	6	NS
The rate of biting (bites/min)	48	48	0.5	NS	48	49	0.4	+	48	49	0.8	NS	49	48	0.8	NS
Intake per bite (mg OM/bite)					65	58	3.1	+								
OM intake (g/day)	963	890	62.7	NS	897	956	67.7	NS	1015	838	53.3	*	1019	834	58.4	*
OM intake (g/kg W ^{0.75})	68	64	4.8	NS	69	64	5.2	NS	72	61	3.9	+	72	61	4.3	+
DOM intake (g/day)	725	671	46.7	NS	669	726	50.4	NS	765	631	39.9	*	765	630	43.8	*
DOM intake (g/kg W ^{0.75})	51	48	3.6	NS	48	52	3.9	NS	54	46	2.9	+	54	46	3.2	+

4.5.2.2.4. Faecal Egg Counts (FECs)

Means of faecal egg counts from the samples taken before second drenching and at the end of the experiment are summarised in Table 4.13. There were no significant differences in FECs amongst current pasture, sex and PEG administration.

4.5.2.2.5. Rumen Ammonia Concentration

Rumen ammonia concentrations were consistently higher in ruminal fistulated wethers (RF) grazing on tall fescue than on Yorkshire fog, with the exception of measurements at 1200 and 2400 hrs (Figure 4.11 and Appendix 4.13). There were no significant effects of interaction between swards and PEG administration on rumen ammonia concentrations at any sampling times, but rumen ammonia concentration was increased by PEG administration on Yorkshire fog swards in the measurement at 1200 hours. The increase happened on Yorkshire fog 4 hrs after PEG administration, but there was no effect of PEG on rumen ammonia concentrations on Yorkshire fog at other times or on tall fescue at any time.

4.5.2.2.6. Liveweight Gain, Carcass Weight, Dressing Out and GR

The trend of liveweight gain showed that lambs grazing Yorkshire fog pasture tended to have faster liveweight gain in the initial period and slower liveweight gain in the later period than lambs grazing tall fescue (Figure 4.13). All lambs showed slow liveweight gain in the initial measurement (February) and fast liveweight gain in March, where liveweight gain was double that in February.

There were no significant effects of previous pasture, current pasture and PEG administration on liveweight gain, carcass weight and carcass weight gain, but male lambs had faster liveweight gain ($P \leq 0.05$), carcass weight and carcass weight gain ($P \leq 0.05$) than females (Table 4.14). There was 9.4% higher

Table 4.13. Faecal egg counts (eggs/g faeces) of lambs grazing Yorkshire fog/clover and tall fescue/clover pastures in summer and early autumn, 1994.

	Main effects (n = 8)											
	Current pasture				SEX				PEG			
	Fog	Tall fescue	SEM	Sig.	Male	Female	SEM	Sig.	Ctrl	PEG	SEM	Sig.
Egg counts (eggs/g faeces)	140	130	36	NS	110	160	36	NS	110	160	36	NS

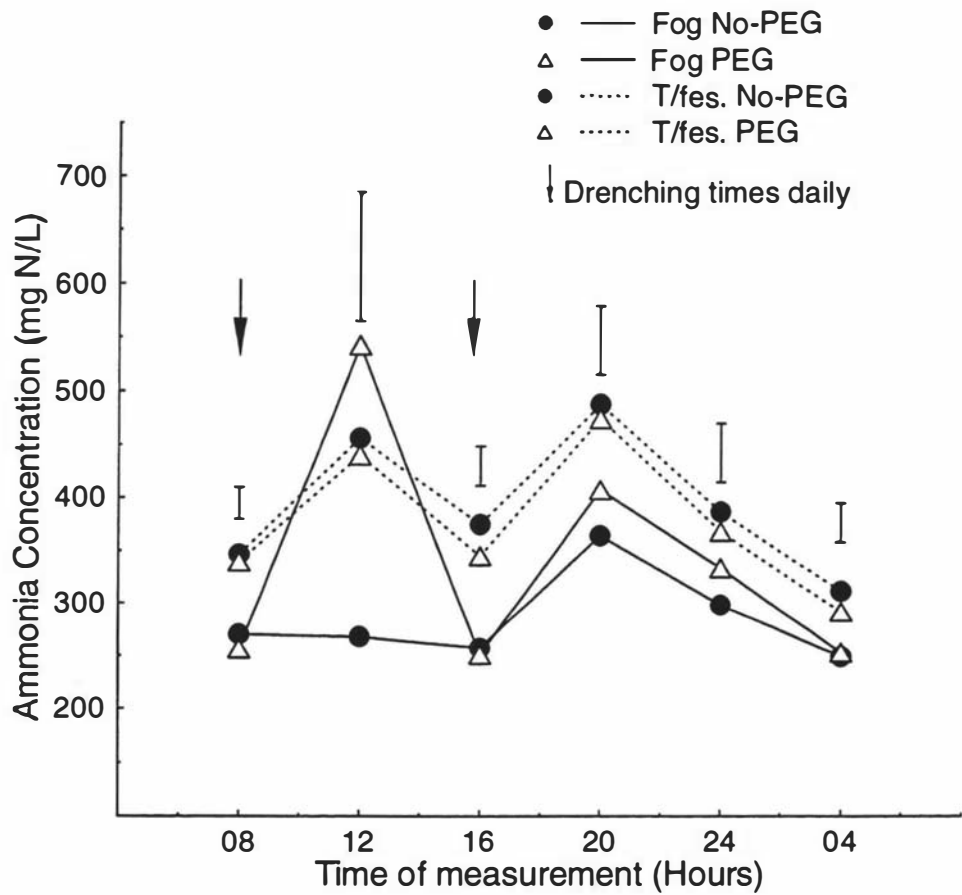


Figure 4.11. Ammonia concentration (mg N/L) of sheep fistulated in the rumen on Yorkshire fog/clover and tall fescue/clover pastures in summer.

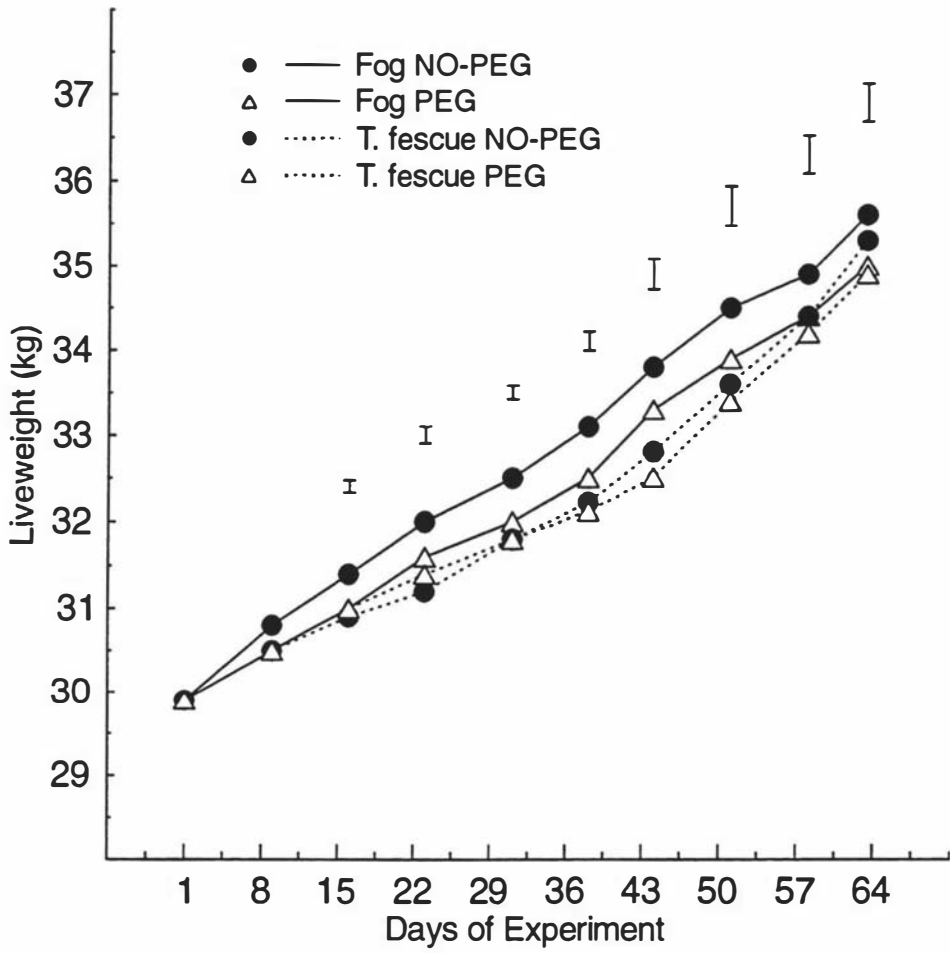


Figure 4.12 Liveweight (kg) of lambs grazing Yorkshire fog/ clover and tall fescue/clover pastures under rotational management in summer and early autumn, 1994.

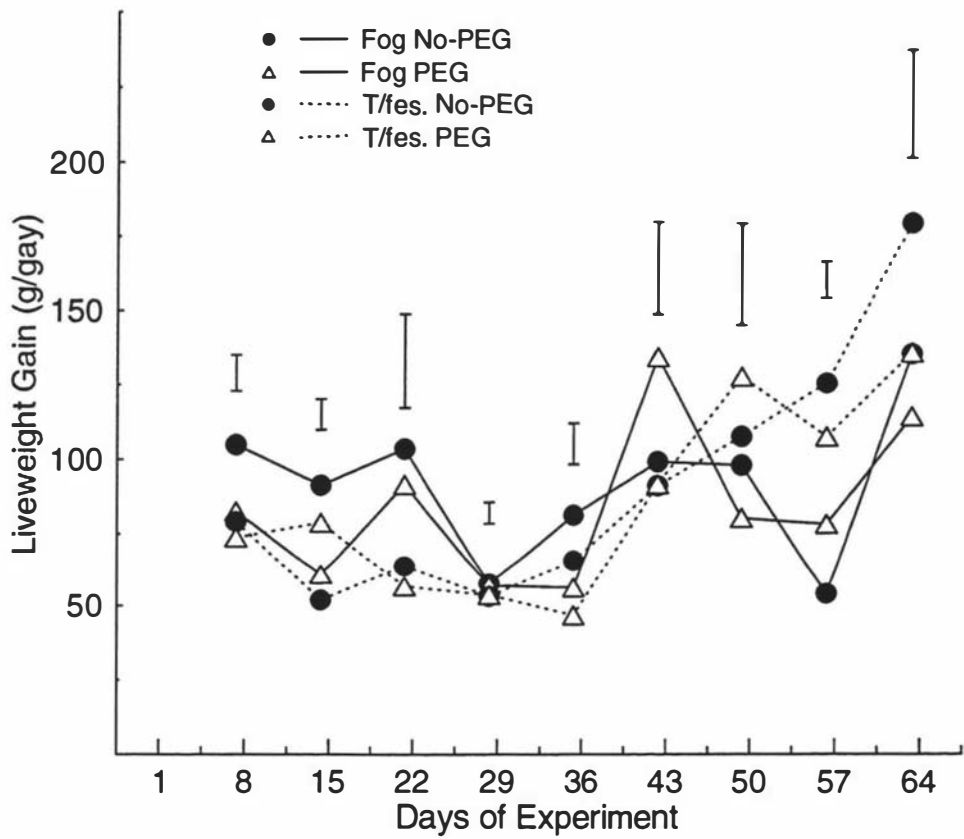


Figure 4.13 Liveweight gain (g/day) of lambs grazing Yorkshire fog/clover and tall fescue/clover pastures under rotational management in summer and early autumn, 1994

Table 4.14. Effects of previous pasture, current pasture, sex and condensed tannins (CT) on the liveweight gain, carcass weight, carcass weight gain and wool growth rate of lambs grazing Yorkshire fog/clover and tall fescue/clover pastures in summer and early autumn, 1994

n=16	Previous pasture				Current pasture				Sex				PEG			
	Ryegrass	Fog	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Male	Female	SEM	Sig.	Ctrl	PEG	SEM	Sig.
Liveweight gain (g/day)																
26/01/94 - 04/03/94	59	52	3.2	NS	57	54	2.9	NS	58	53	2.9	NS	58	53	3.3	NS
04/03/94 - 29/03/94	103	112	10.4	NS	104	111	9.4	NS	110	105	5.2	NS	104	111	6.5	NS
26/01/94 - 29/03/94	77	75	4.7	NS	77	76	4.4	NS	80	72	2.3	*	78	74	2.9	NS
Carcass weight (kg)																
	14.1	14.2	0.2	NS	14.2	14.1	0.2	NS	14.4	14.0	0.1	*	14.2	14.1	0.1	NS
Carcass weight gain (g/day)																
	30	31	3.0	NS	31	30	2.8	NS	33	27	1.7	*	31	29	2.0	NS
Dressing out %																
	44	44	0.4	NS	44	44	0.3	NS	44	43	0.3	NS	44	44	0.3	NS
GR (mm) Left																
	6	6	0.5	NS	6	6	0.6	NS	6	6	0.5	NS	7	6	0.5	NS
Right																
	6	6	0.9	NS	6	6	0.9	NS	7	6	0.6	NS	6	6	0.7	NS
Wool growth rate (mg/100cm² per day)																
26/01/94 - 04/03/94	91	106	4.5	+	100	98	4.4	NS	104	93	6.6	NS	103	94	6.2	NS
04/03/94 - 29/03/94	108	127	2.8	**	123	112	2.8	*	118	118	5.8	NS	123	1123	5.4	NS

liveweight gain in control lambs than in PEG drenched lambs in the initial period, although the difference was not significant.

4.5.2.2.7. The Rate of Wool Growth

There were significant effects of previous pasture and current pasture on the rate of wool growth in the second period of measurement (March). Lambs tended to have faster rate of wool growth on Yorkshire fog than on tall fescue in the second period ($P \leq 0.05$). There were no significant effects of sex and PEG administration on the rate of wool growth in the two periods of measurement.

4.6. DISCUSSION

4.6.1. Evaluation of Experimental Procedures

The proportions of grasses, clover and dead material differed between the two methods of hand separation and point quadrat analysis. There were higher proportions of live grasses and clover based on point quadrat data than based on hand separation samples, whereas dead material was a smaller proportion (Table 4.3 and Table 4.10). Hodgson (1981a) suggested that the inclined point quadrat underestimated the proportion of dead material in the canopy. This has been confirmed by Grant *et al.* (1985), who stated that the underestimation of the proportion of dead material by the inclined point quadrat was because the dead material was concentrated in the bottom strata which were too dense to record precisely.

The diets selected by experimental lambs were determined through analyses of oesophageal extrusa samples collected from OF sheep. Oesophageal extrusa samples were only recorded for three categories (grasses, legume and dead material) based on the visual observations. The proportions of grasses in the diets were significantly higher than those of swards offered to animals, while the

proportions of clover and dead material in the diets were consistently lower than those determined by hand separation for both swards. However, the proportions of grasses in the diets more closely reflected those measured based on point quadrat data than based on hand separation (Tables 4.3 and 4.10). In the upper strata above the post-grazing sward surface heights (>8 cm in December and >4 cm in February and March), the proportion of grasses was consistently greater than 90%, with the exception of 88% on tall fescue in March (Tables 4.3 and 4.10). The proportions of grasses in the diets selected by OF sheep from both the swards were similar (Table 4.2, 4.3, 4.9 and 4.10). This implied that point quadrat data should give the best comparison with extrusa composition from a gridded tray.

4.6.2. Sward Characteristics

The trials were not set up specifically to study sward performance, so evaluation is confined to differences in the characteristics between treatments.

Pre-grazing sward surface heights were consistently in the range of 10 - 23 cm throughout the two experiments, with little difference between Yorkshire fog and tall fescue treatments (Figures 4.1 and 4.7). Post-grazing sward surface heights declined from 6 - 10 cm in December to about 5 cm in February and March. The decline in post-grazing sward heights were mainly attributed to increased stocking rate owing to introduction of additional 6 RF wethers to the paddocks within each pasture to determine the ammonia concentration in February, the slow growth rate of sward in the dry season and increasing herbage intake in lambs.

Pre-grazing herbage masses were similar between Yorkshire fog and tall fescue swards over the two experiments (Tables 4.1 and 4.8), but Yorkshire fog had higher residual herbage mass than tall fescue in February and March (Table 4.8 and Appendix 4.6). This could be related to the fact that there was higher proportion of sown grass stem that was not prone to defoliation by animals

compared with grass leaf on Yorkshire fog than on tall fescue.

There was an increase in the proportion of dead material to a greater extent on post-grazing Yorkshire fog sward than on post-grazing tall fescue sward in February (Appendix 4.7). The higher proportion of dead material on Yorkshire fog swards is partially because of its slow rate of decomposition (Watt, 1978) which is associated with higher CT concentrations in Yorkshire fog, compared with tall fescue. The high accumulation of dead material was reported by Niezen *et al.* (1993a).

There was an invasion of other grasses to both Yorkshire fog and tall fescue swards (Tables 4.2 and 4.9). Invasion of other grasses to Yorkshire fog has been reported by other authors (Watkin and Robinson, 1974; Harvey *et al.*, 1984; Smith and Allcock, 1985; Watt, 1987; Morton *et al.*, 1992). Niezen (1993a) showed a smaller proportion of other species on Yorkshire fog than on ryegrass. The high proportions of other grasses in tall fescue sward is consistent with the results in several experiments (Butler, unpublished; Hodgson *et al.*, 1996). A consistently higher proportion of white clover found on tall fescue sward than on Yorkshire fog sward implied that clover grows in mixed sward more easily with tall fescue than with Yorkshire fog.

4.6.3. Herbage Consumption

Green grass was the main component of the diets selected, comprising more than 93% of the diets from both swards at all the periods of sampling (Tables 4.3 and 4.10). Although grass leaf and stem were not recorded separately in the extrusa samples, grass leaf made main contribution to the diets based on the visual observations. There was a lower proportion of dead material in the diets than in the swards. The lower proportion of dead material in the diets was probably related to the distribution of dead material in the bottom of sward which decreased opportunity for defoliation by the animals (Poppi *et al.*, 1987), and low

acceptability of dead material by animals (Clark *et al.*, 1982; Kenney and Black, 1984). These results suggested that the diets selected by lambs more closely reflect the botanical composition of the upper strata of swards. These findings have been supported by other authors (Hodgson, 1982, 1985b, 1990; Clark *et al.*, 1982; Milne *et al.*, 1982; Clark, 1993; L'Huillier *et al.*, 1984; Bootsma *et al.*, 1990; Barthram and Grant, 1984; Illius *et al.*, 1992). This indicates that the composition and distribution of the components in the upper strata is probably more important than selection by grazing animals in the determination of the botanical composition of the diets. The higher proportion of green material (or grass leaf) in the diet selected may also be related to little intake restriction for the sheep and the ease of prehension due to the low structural strength (Hodgson and Grant, 1982; Poppi *et al.*, 1987).

However, although there was a higher proportion of white clover in upper strata than in the sward as a whole, the proportion of clover in the diets did not reflect this, and the proportion of dead material was higher in the diets than in the upper strata of swards. Indeed, no dead material was found above the average post-grazing surface height of the swards (Tables 4.3 and 4.10 and Figures 4.3, 4.9a and 4.10a). This suggests that some lambs were grazing below measured post-grazing sward height.

The higher total N and OMD in the diets on Tall fescue than on Yorkshire fog in Period 1 of December (Table 4.4) were partially related to the fact that sown grass (leaf or seed head) contributed to all the upper strata of the sward canopy on tall fescue pasture, and partially to the lower proportion of sown grass stem on tall fescue than on Yorkshire fog in the period of sampling. The differences in total N and OMD in the diets between the two pastures were further confirmed by the results in Period 2 of February and in March (Table 4.11). However, the higher OMD in the diets from Yorkshire fog than from tall fescue in Period 1 of February (Table 4.11) was probably associated with the significantly higher proportion of green grass leaf and the lower proportion of dead material on

Yorkshire fog sward than on tall fescue sward offered to the animals.

The higher intake per bite of OF sheep grazing on Yorkshire fog than on tall fescue swards (Tables 4.5 and 4.12) was partially related to the higher proportion of sown grass leaf on Yorkshire fog than on tall fescue (Tables 4.2 and 4.9), and partially to greater bulk density on Yorkshire fog sward than that on tall fescue sward in December (Appendix 4.2) and in Experiment 3 (Table 4.8). However, the difference in intake per bite on both swards between different seasons, to greater extent on Yorkshire fog (Tables 4.5 and 4.12), may be explained by greater variations of leaf strength and cellulose content in Yorkshire fog (Evans, 1967). Evans (1967) emphasized the importance of leaf strength and cellulose content when Yorkshire fog was compared with ryegrass and *Poa trivialis* in leaf strength and cellulose content.

Lambs had faster rate of biting on Yorkshire fog than on tall fescue in Experiment 2 ($P \leq 0.05$) (Table 4.5), but had slower rate of biting on Yorkshire fog than on tall fescue in Experiment 3 ($P \leq 0.1$) (Table 4.12). The former was attributed to higher proportion of sown grass leaf on Yorkshire fog than on tall fescue (Table 4.2), the latter can be explained by greater bulk density on Yorkshire fog than on tall fescue after grazing (Table 4.8). A compensatory relationship between the rate of biting and the intake per bite was not found in the former period, but was very clearly found in the latter period.

The intakes calculated from the arithmetic product of grazing behaviour components were 128 and 109 g DOM/kg $W^{0.75}$ /day for Yorkshire fog and tall fescue respectively in Experiment 2 and 103 and 87 g DOM/kg $W^{0.75}$ /day for the same species in Experiment 3. These values are above the maximum likely intake (90 g DOM/kg $W^{0.75}$ /day) of lambs of this size suggested by other researchers (Weston, 1982; Weston and Davis, 1991; Dove, 1996; Weston, 1996). By contrast, the intakes estimated from faecal output and *in vitro* digestibility were 49 and 49 g DOM/kg $W^{0.75}$ /day for Yorkshire fog and tall fescue

respectively in Experiment 2 and 52 and 47 g DOM/kg $W^{0.75}$ /day for the same species in Experiment 3, well within the limits of likely intake in such animals. Hence, as in Experiment 1, the estimates of intake from the faecal output and *in vitro* digestibility are preferred.

There was not much difference in herbage OM intake in lambs between Yorkshire fog and tall fescue overall (Table 4.5 and 4.12), with the exception of late December, where there was a greater herbage OM intake on Yorkshire fog than on tall fescue (Appendix 4.5), and late February, where tall fescue had a greater herbage OM intake than Yorkshire fog (Appendix 4.11). The former may be related to the faster rate of biting on Yorkshire fog than on tall fescue (Table 4.5) and the latter was attributed to higher OMD on tall fescue than on Yorkshire fog in the period (Table 4.11). Male lambs had a greater herbage OM intake than females. PEG had a negative effect on herbage OM intake of lambs in Experiment 2, but no significant effect in Experiment 3.

There was a consistently higher total CT concentration in Yorkshire fog than in tall fescue at all periods of measurement. The low CT concentrations in Yorkshire fog have further confirmed the findings in Experiment 1 and are in accordance with the results of other researches (Terrill *et al.*, 1992a, 1992b; Douglas *et al.*, 1993; Montossi *et al.* 1994; Iason *et al.*, 1995). The CT values in the diets from Yorkshire fog differed at the different periods of measurements. This was related to the proportions of grass leaf and stem and their maturity. CT concentrations in green leaf are approximately twice those in green stem in Yorkshire fog (Douglas *et al.*, 1993; Iason *et al.*, 1995).

Rumen ammonia concentration was slightly increased by PEG supplementation in samples taken 4 hours after administration at 12:00 hour on Yorkshire fog in Experiment 3 (Figure 4.11). This suggests that small CT concentrations in Yorkshire fog would bind with proteins and therefore reduce protein degradation to ammonia by microorganisms. The evidence of effects of low CT level on

rumen ammonia concentration has been provided by Terrill *et al.* (1992b). Non-persistent effects of PEG on rumen ammonia concentration indicated that PEG administration twice daily could not completely eliminate binding of plant protein to CT in the rumen for a long time. There were no rumen ammonia concentration responses to PEG supplementation in tall fescue in Experiment 3. The absence of PEG effect on rumen ammonia concentration for tall fescue may suggest that the recorded low CT concentrations in tall fescue are an artifact of the current procedures of analysing CT contents. Estimates of rumen ammonia concentration were not made in Experiment 2.

Lambs were drenched prior to the experiment, at mid-point and before the end of each experiment. The drenching procedures were designed to control worm parasites rather than demonstrate differences. Faecal samples were taken two weeks after drenching, before the second drenching and at the end of each experiment to record egg counts. The procedures of sampling faeces could define the effectiveness of drenching. The comparison of the means of faecal egg counts before the second drenching and at the end of the experiment between treatments directly implied the effect of treatments on faecal egg counts. Therefore, some inferences of effects were drawn from the experiments.

Lambs had lower FECs on Yorkshire fog than on tall fescue, and female lambs had lower FECs than male lambs in Experiment 2. However, there was no significant effect of pastures and sexes on FECs in Experiment 3. The difference between the two experiments may be attributed to greater resistance for worm parasites in older lambs than young lambs.

The evidence of lower FECs on Yorkshire fog than on tall fescue has been provided by Niezen *et al.* (1993a). Niezen *et al.* (1995) suggested, based on the effect of CT on FEC in lambs grazing *Lotus* spp (Niezen *et al.*, 1993b) and sulla (Niezen *et al.*, 1994), that forages containing CT fed to animals might increase the post-ruminal availability of dietary protein and affect the establishment or

persistence of gastrointestinal nematodes, reducing the effect of parasitism. The results from Experiments 2 indicated that Yorkshire fog containing low CT concentrations could have a potential role in the control of worm parasites in lambs compared with tall fescue.

4.6.4. Animal Performance

There were no significant effects of previous grazing experience on liveweight gain. Lambs showed different responses of liveweight gain to the two pastures in the different periods. Lambs had faster liveweight gain on Yorkshire fog than on tall fescue in Experiment 2 ($P \leq 0.1$) (Table 4.7). The difference of liveweight gain in lambs was a consequence of different herbage OM intake, herbage OM intake being greater on Yorkshire fog than on tall fescue in Period 2 of December ($P \leq 0.05$) (Appendix 4.5). The higher herbage OM intake in lambs in March (Appendix 4.12) than in February (Appendix 4.11) resulted in double the liveweight gain on both swards in March to that in February. Carcass weight gain showed a similar pattern to liveweight gain, being higher for lambs grazing on Yorkshire fog than on tall fescue from late November to late January in Experiment 2 ($P \leq 0.05$), but no significant difference between pastures from February to March in Experiment 3.

Wool has a high sulphur content mainly as cystine (Hogan, 1975; Reis *et al.*, 1990) and wool growth rate has been increased by post ruminal supplementation with sulphur-containing amino acid (SAA) (Reis, 1979). CT can reduce SAA degradation in the rumen (McNabb *et al.*, 1993b; Wang *et al.*, 1994). Increased wool growth due to CT is also supported by reports of Terrill *et al.* (1992b) and Lee *et al.* (1992). The faster wool growth on Yorkshire fog than on tall fescue in January ($P \leq 0.1$) and in March ($P \leq 0.05$) may have been due to differences in the effects of low CT on absorption of essential amino acids and cystine availability for body synthetic reaction. However, effects of low CT concentrations in grasses on degradation and absorption of SAA were not measured in the current project.

Male lambs had faster liveweight gain than female lambs in the initial period when growth rates were high in Experiment 2, but the difference in liveweight gain became smaller as growth rates declined with time (Table 4.7). Therefore, carcass weight and carcass weight gain did not show big differences between sexes, although there was a faster liveweight gain in male lambs than in female lambs overall in Experiment 2 (Table 4.7). There were significantly faster liveweight gain, greater carcass weight and faster carcass weight gain in male lambs than in females in Experiment 3 (Table 4.14). These results are associated with the greater DOM intake in male lambs (Table 4.12).

PEG drenching reduced liveweight gain by 8.9% in Yorkshire fog in the first period of Experiment 2 ($P \leq 0.1$), but this effect did not persist to the end of the experiment. This is consistent with the results of Montossi (1995), but is not consistent with the finding by Terrill *et al.* (1992b), who showed that low CT in Yorkshire fog increased lamb liveweight gain in spring, where there was a higher CT concentrations in the diets compared with the current experiment (0.47% vs 0.2% on a DM basis). There were no significant effects of PEG on carcass weight and carcass weight gain in either experiment. These results indicated that small effects of low CT concentrations in the grasses in the initial period probably occurred in non-carcass components. There was no evidence of an effect of low CT in the grasses on the rate of wool growth in either experiment. However, the increasing interest in effects of low CT concentrations in the grasses on animal performance is reinforced by the increased rumen ammonia concentration in sheep grazing Yorkshire fog by PEG supplementation in Experiment 3 and the improved wool growth rate in lambs by the action of low CT in ryegrass in Experiment 1. Experiment 4 was therefore designed to evaluate the effects of low CT concentrations in Yorkshire fog on body growth and wool growth in lambs under limited selection opportunity.

4.7. CONCLUSIONS

Yorkshire fog had similar herbage mass to tall fescue in a dry summer. There were higher proportions of sown grass presented in Yorkshire fog than in tall fescue swards in spring and summer.

The diets selected by OF sheep contained more green material and less dead material than swards offered to the sheep. The composition of the diets was influenced to a greater extent by structure and distribution of the plant components in the upper layers of sward canopies than by the selection of grazing animals.

Grazing behaviour was not significantly affected by previous grazing experience, sex and PEG administration, but was influenced by current pasture. Nutritional factors such as OMD of the diets was more important in determining herbage OM intake than grazing behaviour. Animal production was largely influenced by current pasture and sex rather than previous pasture and PEG supplementation. Lambs grazing Yorkshire fog had slightly faster liveweight gain than those grazing tall fescue in late spring and early summer, but there was no difference between pastures in early autumn. Male lambs had faster gains than females.

Yorkshire fog had consistently higher CT concentrations than tall fescue, while 'CT' in tall fescue was an artifact. Low CT concentrations in the grasses did not have effects on grazing behaviour, diet election or herbage OM intake. The small CT concentrations in Yorkshire fog reduced rumen ammonia concentration, but were not enough to improve animal performance such as liveweight gain, carcass weight and wool growth. More research is needed to define the minimal effective CT concentration improving ruminant production in forages.

CHAPTER 5

EXPERIMENT 4: EFFECTS OF LEADER/FOLLOWER GRAZING REGIME AND CONDENSED TANNINS ON INGESTIVE BEHAVIOUR, HERBAGE INTAKE AND PERFORMANCE OF LAMBS GRAZING YORKSHIRE FOG PASTURE

ABSTRACT

A grazing experiment (Experiment 4) was conducted on Yorkshire fog (*Holcus lanatus* c.v. Massey Basyn)/white clover (*Trifolium repens* c.v. Grassland Tahora) pasture to assess the grazing behaviour, diet selection, herbage intake and performance of lambs as affected by low condensed tannin (CT) concentrations in the grass and grazing sequence under rotational grazing management in summer, 1994/1995.

Sixty castrated male lambs were used in the experiment. 12 lambs were slaughtered as the initial group at the start of experiment to measure the carcass weight of the lambs. Another 48 lambs were allocated to two groups in sets of twenty-four. A grazing rotation was set up on eight paddocks each of 0.1 ha, in which a Leader group of 24 lambs grazed each paddock for four days, followed by a similar Follower group of 24 lambs grazing for four days. Half of the lambs within each group were drenched with 10 g polyethylene glycol (PEG: MW 3350) twice daily at 0830 and 1630 hrs and the remaining lambs were drenched with water as a control.

Sward surface height decreased with grazing, and there were significant declines in herbage mass and increases in bulk density. There were higher proportions of grass leaf and white clover and lower proportions of grass stem and dead

material in the Leader sward than in the Follower sward. There were correspondingly higher proportions of green grass and white clover and a smaller proportion of dead material in the diets of Leader than of Follower lambs, and a higher proportion of green material and a lower proportion of dead material in the diets than in the swards offered to animals.

Leader lambs had greater intake per bite (79 vs 64 ± 3.9 mg OM/bite, $P \leq 0.001$) and consistently higher total N (2.67 vs 2.35 ± 0.065 % DM, $P \leq 0.01$) and OMD (78 vs 72 ± 0.7 %, $P \leq 0.001$) and spent more time in grazing (660 vs 620 ± 7 min, $P \leq 0.001$) than Followers, and herbage OM intakes were significantly greater (1025 vs 800 ± 16.0 g/day, $P \leq 0.001$). Leader lambs had lower faecal egg counts (71 vs 163 ± 23 eggs/g faeces, $P \leq 0.01$), faster liveweight gain (107 vs 37 ± 5.0 g/day, $P \leq 0.001$), carcass weight (15.0 vs 12.5 ± 0.2 kg, $P \leq 0.001$) and wool growth rate (109 vs 80 ± 2.9 mg/100cm² per day, $P \leq 0.001$) than Followers. There was no significant difference in CT concentrations between diets selected from the Leader and Follower swards. Consistent increase in rumen ammonia concentration by PEG administration indicated that the low CT concentrations in Yorkshire fog to some extent reduced the rate of protein degradation in the rumen. There were no significant effects of the low CT concentrations in the grass on herbage intake, body growth and wool growth rate of lambs.

From the experiment, it was concluded that: (i) The Leader/Follower grazing regime created the desired contrasts in the quality and quantity of herbage between Leader and Follower swards, while Leader lambs had the superiority of selection opportunity, diet quality and less possibilities of infection by worm parasites. Therefore, Leader lambs produced higher body growth and wool growth. (ii) Low CT concentrations in the Yorkshire fog had no effects on grazing behaviour, diet selection and herbage intake; (iii) Low CT concentrations consistently reduced rumen ammonia concentration in sheep, but were not enough to effectively increase animal production.

Keywords: Yorkshire fog (*Holcus lanatus*), condensed tannins, polyethylene glycol (PEG), grazing behaviour, diet selection, herbage intake, animal performance.

5.1. INTRODUCTION

Yorkshire fog has potential for pasture production in New Zealand, especially in low-fertility soils where ryegrass has limited production (Jacques, 1962; Dunbar, 1974; Vartha and Clifford, 1971; Watkin and Robinson, 1974; Clements and Easton, 1974). Condensed tannins (CT) as secondary compounds occur in the leaves and stem of species such as *Lotus* spp., sainfoin (*Onobrychis viciifolia*) and sulla (*Hedysarum coronarium*). Effects of CT in forages on the nutritional status of grazing animals largely depend upon CT concentration. Forages containing CT (20 - 40 g/kg DM) may have an advantage in reducing protein degradation in the rumen and increasing protein absorption from the small intestine (Barry, 1985; Waghorn *et al.*, 1987a; Barry, 1989; Waghorn *et al.*, 1990; Terrill *et al.*, 1992b; Wang *et al.* 1994). However, limited information is available on the effects of low CT concentrations (1 - 10 g/kg DM) in forages on animal performance.

The effects of low CT concentrations in Yorkshire fog on the nutritional status of growing lambs have been studied in different seasons in recent years (Terrill *et al.*, 1992a; Montossi *et al.*, 1994; Montossi, 1995; Experiments 1, 2 and 3), but all of the recent studies have been conducted at non-limiting levels of allowance. Herbage allowance is one of the important pasture factors affecting ingestive behaviour, herbage intake and performance of grazing animals. The purpose of the experiment reported in this chapter was to compare the grazing behaviour, diet selection, herbage intake and performance of growing lambs and to assess effects of low CT concentrations in Yorkshire fog on the performance of lambs offered herbage of contrasting quantity and nutritive value, and with differing

opportunity for selective grazing.

5.2. MATERIALS AND METHODS

5.2.1. Experimental Site and Duration

One grazing experiment (Experiment 4) was carried out at the Pasture and Crop Research Unit, Massey University from 1 December, 1994 to 30 January, 1995. The experimental site was located on a Tokomaru silt loam soil with Olsen P values in the range of 20-30 $\mu\text{g/g}$, classified as an Aeric Fragiaqualf (gleyed, yellow-grey earth). The monthly rainfall, mean soil temperature (10 cm depth) in late 1994 and early 1995 compared with 10-year average values in the site are presented in Appendix 5.1.

5.2.2. Swards

Yorkshire fog/white clover pasture, as described in Chapter 3 (Experiment 1), was used in the experiment. A grazing rotation was set up on eight paddocks each of 0.1 ha, in which a Leader group of lambs grazed for four days at a herbage allowance of 10% of liveweight, followed by a similar group of Follower lambs also grazing for four days. This created the desired contrasts in both the quantity and nutritive value of herbage available to the animals.

Daily herbage allowance was calculated as follows:

$$\text{Daily herbage allowance} = \frac{\text{Area of plot (ha)} \times \text{herbage mass (kg DM/ha)}}{\text{Total LW (kg)} \times \text{grazing days}}$$

(% of LW)

Two supplementary paddocks were used to keep sheep fistulated in the rumen

and in the oesophagus when necessary.

Broad-leaved weeds were removed by hoeing from all the pastures.

5.2.3. Animals and Treatments

Sixty male Suffolk X Romney lambs, with initial weight 27.9 ± 2.2 kg, were used. 12 lambs selected at random were slaughtered before the experiment to measure carcass weight and assess carcass gain over the study. 48 lambs were randomly allocated into two groups. The first group of 24 lambs as a Leader Group grazed one paddock for four days, and then the other group of 24 lambs as a Follower Group followed for four days. The two groups of lambs grazed rotationally eight paddocks of Yorkshire fog/white clover pasture to assess effects of contrasts in the amount and nutritive value of herbage available, and of CT in Yorkshire fog on grazing behaviour, herbage intake and animal performance. There were two complete grazing cycles between 30 November, 1994 and 30 January, 1995.

Half of the lambs in each group were drenched with 10 g polyethylene glycol (PEG; MW 3350) twice daily throughout the study to inhibit effects of CT on rumen fermentation. The remaining lambs were drenched with water as a control treatment.

All the lambs were drenched with Levamisol (Nilverm, Coopers-pitman-Moore, New Zealand Ltd.) to remove internal parasites prior to the experiment and in the middle of experiment.

5.3. MEASUREMENTS

The standard procedures in the present experiment refer to those used in Chapter 3 (Experiment 1). Only new procedures in the experiment are described here.

5.3.1. Sward Characteristics

Sward measurements were made before grazing (pre-grazing), at mid-grazing (when the Leader group of lambs was moved out and the Follower group of lambs was moved into a paddock) and after grazing each paddock.

Sward surface height was measured before, at mid-grazing and after grazing each paddock using a sward stick. Fifty measurements of the undisturbed foliage were made at random in each paddock.

Sward mass was estimated by cutting eight rectangular quadrats (0.1 m² area) to ground level in each paddock using an electric shearing head before, at mid grazing and after grazing. Five sward height measurements were made within each quadrat before the herbage was cut. *Bulk density* was calculated by dividing herbage mass (kg DM/ha) by sward surface height for each plot.

Botanical composition was determined with samples taken to ground level at the same time as sward mass was estimated. In the laboratory the samples were dissected into different species, and then into leaf, pseudostem and dead material within a species. The relative contribution of plant parts was calculated.

5.3.2. Ingestive Behaviour and Herbage Intake

All measurements of grazing behaviour were made in the two 4 - day periods respectively in both December and January.

Diet composition was determined by using two pairs of sheep fistulated in the oesophagus which were kept in adjoining paddocks for 4 - 5 days and then grazed in pairs with the two groups of experimental lambs. Estimates of diet composition were made in two 4-day periods in each month, the fistulates being switched between Leader and Follower groups between measurement periods.

Two samples were taken from each fistulate within each treatment during each period; thus 16 samples of extrusa were collected in each 4-day period.

Herbage OM intake was estimated as the procedures described in Chapter 3. The release rate of chromium was measured from CRCs collected from all lambs at slaughter, three weeks after a second capsule was administered.

5.3.3. Faecal Egg Counts (FECs)

The procedures of drenching lambs, sampling faeces and estimating faecal egg count were same as described in Chapter 4.

5.3.4. Rumen Ammonia Concentration

Ten wethers fistulated in the rumen were used to estimate rumen ammonia concentration in January, 1995. The sheep grazed an additional paddock of Yorkshire fog for two weeks. Five sheep were drenched with PEG at the same times and in the same quantity as the lambs. The remaining five sheep were drenched with water as a control group, to determine the effect of drenching PEG on rumen ammonia concentration (and hence on forage protein breakdown).

The rumen fluid was collected by syringe every four hours commencing at 0800 hours for a continuous 24 hours two weeks after PEG administration commenced. The animals were then switched between drenching treatments, and the same procedures repeated in a second period. The procedures were same as described in Chapter 4.

5.3.5. Animal Performance

Lamb liveweight and fasted weight were recorded as described in detail in Chapter 3. All the lambs were slaughtered when the experiment ended, hot

carcass weight was recorded and carcass GR was measured. Dressing out percentage was calculated based on fasted weight and hot carcass weight. Carcass weight gain was estimated using the initial predicted carcass weight and final carcass weight.

Wool samples were clipped at the beginning, mid-point and end of the experiment. Greasy wool samples were conditioned for 48 hours, weighed and scoured. The weight of clean wool was measured on each wool sample and subsequently the rate of wool growth per unit area was calculated. The procedures were described in Chapter 3.

5.4. STATISTICAL ANALYSIS

The experimental data were processed and analyzed using the SAS package (SAS Institute Inc., 1985 and 1990). The analysis procedures of sward measurement were same as described in Chapter 4. Analyses of covariance were used to assess the effects of grazing sequence and PEG supplementation and the interactions between them on animal performance such as liveweight gain, carcass weight, carcass weight gain, carcass dressing out %, carcass GR and wool growth based on a two-factor randomized design.

5.5. RESULTS

5.5.1. Sward Characteristics

5.5.1.1. Sward Surface Height

Surface heights significantly decreased with grazing and were maintained close to 15 cm pre-grazing, 9 cm mid-grazing and 5 cm post-grazing at the different dates of measurement over the experiment (Figure 5.1).

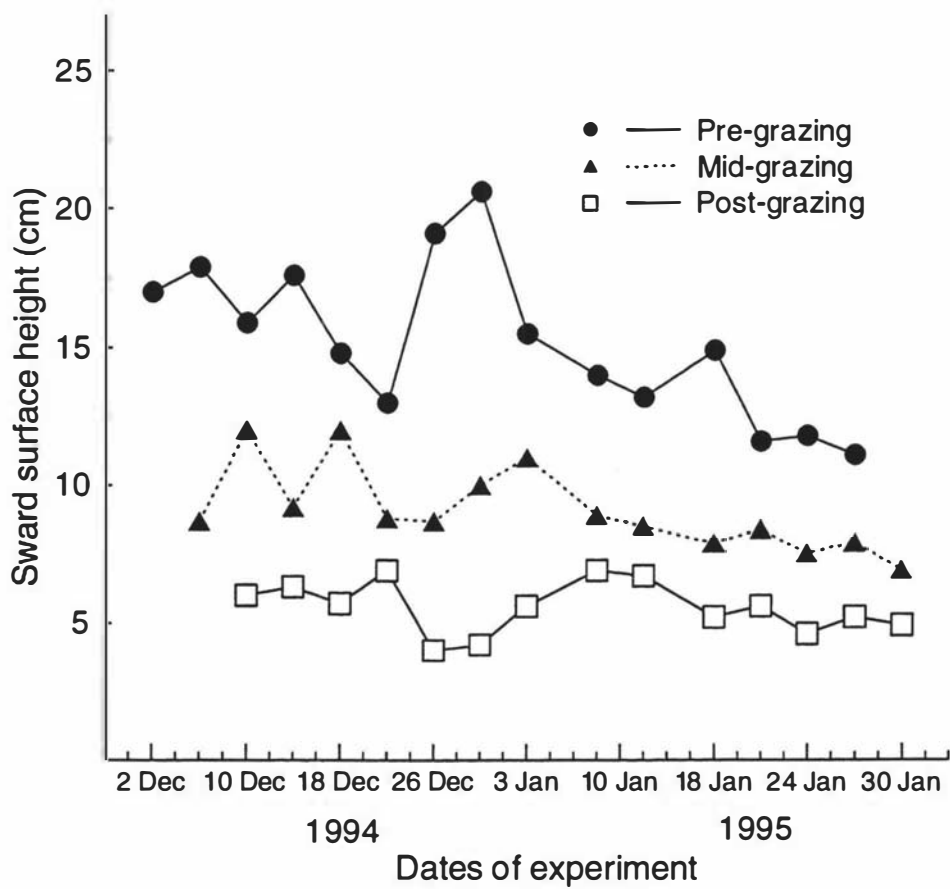


Figure 5.1. Sward surface height (cm) of "leader" and "follower" Yorkshire fog/clover pastures under rotational grazing management in summer, 1994/1995.

5.5.1.2. Herbage Mass and Bulk Density

Herbage masses and bulk densities of the swards are shown in Table 5.1. There were significant differences in herbage masses ($P \leq 0.001$) and bulk densities ($P \leq 0.001$) between pre-grazing, mid-grazing and post-grazing swards. Bulk density significantly increased with decreased sward surface height.

5.5.1.3. Botanical Composition of Swards

Botanical composition of swards by hand separation is shown in Figure 5.2 and Table 5.2. Yorkshire fog leaf and stem made major contributions to sward composition, although other grasses such as perennial ryegrass and *Poa* spp. were also present. The proportion of Yorkshire fog leaf decreased with grazing and was significantly different between the pre-grazing, mid-grazing and post-grazing swards ($P \leq 0.001$), but grass stem increased with grazing and the difference was significant ($P \leq 0.05$). There was a significant difference in the proportion of white clover between the swards ($P \leq 0.001$). Dead material consistently increased with grazing, and there was a higher proportion of dead material post-grazing than pre-grazing and mid-grazing.

5.5.2. Animal Measurements

5.5.2.1. Diet Composition - botanical and chemical

A comparison of composition of the samples selected by OF sheep and swards offered to sheep is shown at Table 5.3. The oesophageal extrusa samples were dissected into grass, legume and dead material, while weed was ignored because there was a very small proportion in the sward (Table 5.2). Grasses made main contributions to the diets selected by OF sheep in Leader and Follower groups, while white clover accounted for small proportions. There were higher proportions of green material ($P \leq 0.001$) and white clover ($P \leq 0.05$) and smaller proportions of

Table 5.1. Sward characteristics of Yorkshire fog/clover pasture under rotational grazing management in summer, 1994/1995

	Pre-grazing	Mid-grazing	Post-grazing	SEM	Sig.
Herbage mass (kg DM/ha)	4110	3090	2360	79	***
Bulk density (g/cm ³)	3.0	4.3	4.9	0.09	***

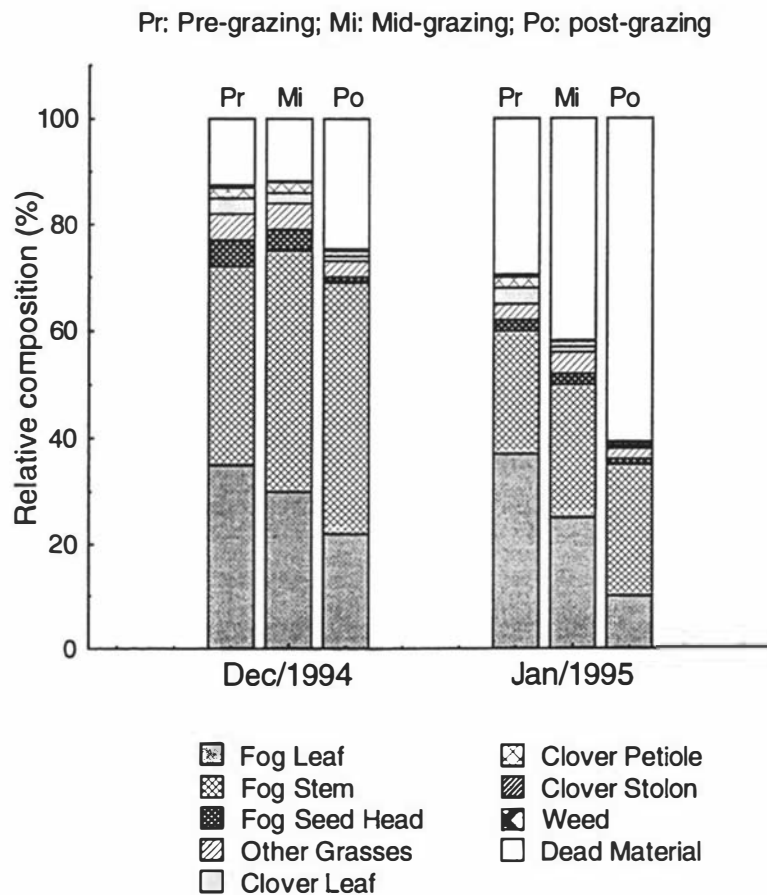


Figure 5.2. Botanical composition (%) of Yorkshire fog/white clover pasture under rotational grazing management in summer, 1994/95

Table 5.2. Relative contribution (%) of the components of Yorkshire fog pasture under rotational grazing management in summer, 1994/1995

	Pre-grazing	Mid-grazing	Post-grazing	SEM	Sig.
Fog leaf	36	27	15	1.3	***
Fog stem	29	33	34	1.6	*
Fog seed head	3	3	1	0.6	*
Total live fog	68	63	50	1.9	***
Other grasses	3	4	2	0.8	NS
Clover leaf	3	1	1	0.2	***
Clover petiole	2	1	1	0.2	***
Clover stolon	<1	<1	<1	0.1	NS
Total live clover	6	3	2	0.5	***
Weed	<1	0	0	0.1	NS
Dead Material	23	30	46	2.1	***

Table 5.3. Comparison of the botanical composition of the samples selected by OF sheep and the swards offered to the sheep

	Swards					Extrusa samples			
	Pre-grazing	Mid-grazing	Post-grazing	SEM	Sig.	"Leader" group	"Follower" group	SEM	Sig.
Grasses (%)	71	67	51	2.1	***	90	81	1.5	***
Clover (%)	6	3	2	0.5	***	2	1	0.3	*
Green material (%)	77	70	54	2.1	***	92	82	1.5	***
Dead material (%)	23	30	46	2.1	***	8	18	1.5	***

Table 5.4. Chemical composition of the samples selected by OF sheep in leader (L-G) and follower groups (F-G)

	L-G	F-G	SEM	Sig.
Total N (% DM)	2.67	2.35	0.65	**
OMD (%)	78	72	0.7	***
CT (g/kg DM)				
Extractable	0.91	0.86	0.045	NS
Protein-bound	1.23	1.06	0.101	NS
Fibre-bound	0.45	0.33	0.048	NS
Total	2.59	2.26	0.165	NS

dead material ($P \leq 0.001$) in the diets from Leader than from Follower sheep. There were higher proportion of grasses and lower proportions of white clover and dead material in the diets than in the swards.

The chemical composition of the samples selected is shown in Table 5.4. There were consistently higher total N ($P \leq 0.001$) and OMD ($P \leq 0.001$) in the diets from Leader sward than from Follower sward. There was no significant difference in CT concentrations in the diets between the swards.

5.5.2.2. Grazing Behaviour

Observations of grazing behaviour in lambs and intake per bite in OF sheep are summarized in Tables 5.5. Leader lambs had great intake per bite ($P \leq 0.001$), and spent more time in grazing ($P \leq 0.001$) and less time in ruminating ($P \leq 0.001$) than Followers. The rate of biting was slower in Leader lambs than in Followers ($P \leq 0.05$). However, there was no significant effects of PEG administration or the interaction of grazing sequence and PEG on the grazing activities of lambs.

5.5.2.3. Herbage Intake

Mean release rate of Cr_2O_3 was estimated from CRCs collected from experimental lambs at slaughter in January. There was no significant difference in release rate of CRCs from lambs amongst treatments. A common release rate of Cr_2O_3 (226.5 ± 3.64 mg/day) was used to determine the faecal output in lambs.

Leader lambs had significantly greater herbage OM intake than Follower lambs. There were no significant effects of PEG administration or the interaction of Leader/Follower groups and PEG on herbage OM intake.

Table 5.5. Grazing behaviour and herbage OM and DOM intakes of leader (L-G) and follower lambs (F-G) grazing Yorkshire fog/clover pasture in summer

	Main effects						Interaction of leader/follower (L/F) x PEG								
	Leader/Follower			PEG			L-G		F-G		SEM	F Value for			
	L-G	F-G	SEM	Ctrl	PEG	SEM	Ctrl	PEG	Ctrl	PEG		L/F	PEG	L/F x PEG	
Grazing time (min)	660	620	7	650	640	7	680	650	620	620	9	***	NS	+	
Ruminating (min)	310	350	5	320	320	5	290	320	350	340	7	***	NS	+	
Resting time (min)	410	410	6	410	420	6	410	410	420	420	9	NS	NS	NS	
Rate of biting (bites/min)	44	47	0.4	45	45	0.4	43	44	47	47	0.6	*	NS	NS	
Intake per bite (OM mg/bite)	79	64	3.9									***			
OM intake (g/day)	1025	800	16.0	913	912	16.0	1026	1023	800	801	22.8	***	NS	NS	
OM intake (g/kg W ^{0.75})	72	59	1.1	66	65	0.1	72	72	59	59	1.6	***	NS	NS	
DOM intake (g/day)	796	575	11.8	686	685	11.8	797	794	575	576	16.8	***	NS	NS	
DOM intake (g/kg W ^{0.75})	56	43	0.8	49	49	0.8	56	56	43	43	1.2	***	NS	NS	

5.5.2.4. Faecal Egg Counts (FECs)

There were lower faecal egg counts in Leader lambs than in Follower lambs ($P \leq 0.01$). There were no significant effects of PEG or the interaction between Leader/Follower groups and PEG on faecal egg counts over the experiment.

5.5.2.5. Rumen Ammonia Concentration

Rumen ammonia concentrations were consistently higher in rumen-fistulated wethers (RF) in the PEG-group than in the Control-group, especially in the time immediately after drenching in the morning ($P \leq 0.1$), but no significant difference was found at the other times of measurement (Figure 5.3).

5.5.2.6. Animal Performance

There was a tendency for both Leader and Follower lambs to have faster liveweight gain in the initial period and slower liveweight gain in the middle period and faster liveweight gain again in late period (Figures 5.4 and 5.5).

There were significantly faster liveweight gains ($P \leq 0.001$), greater carcass weights ($P \leq 0.001$), faster carcass weight gains ($P \leq 0.001$) and rates of wool growth in Leader lambs than in Followers (Table 5.7). Dressing out % was higher in Leader lambs than in Follower lambs. The Follower lambs had negative carcass weight gain because the lambs lost weight in the period of late December and early January. There was no effect of PEG or the interaction between Leader/Follower groups and PEG on liveweight gain, carcass weight and carcass weight gain and wool growth rate.

Table 5.6. Faecal egg counts (eggs/g faeces) of leader and follower lambs grazing Yorkshire fog/clover pasture in summer, 1994/1995.

	Main effects (n=24)						Interaction of Leader/follower (L/F) x PEG (n=12)					F value for		
	Leader/Follower			PEG			L-G		F-G		SEM			
	L-G	F-G	SEM	Ctrl	PEG	SEM	Ctrl	PEG	Ctrl	PEG		L/F	PEG	L/F x PEG
Faecal egg counts (eggs/g faeces)	71	163	23	138	96	23	71	71	204	121	32	**	NS	NS

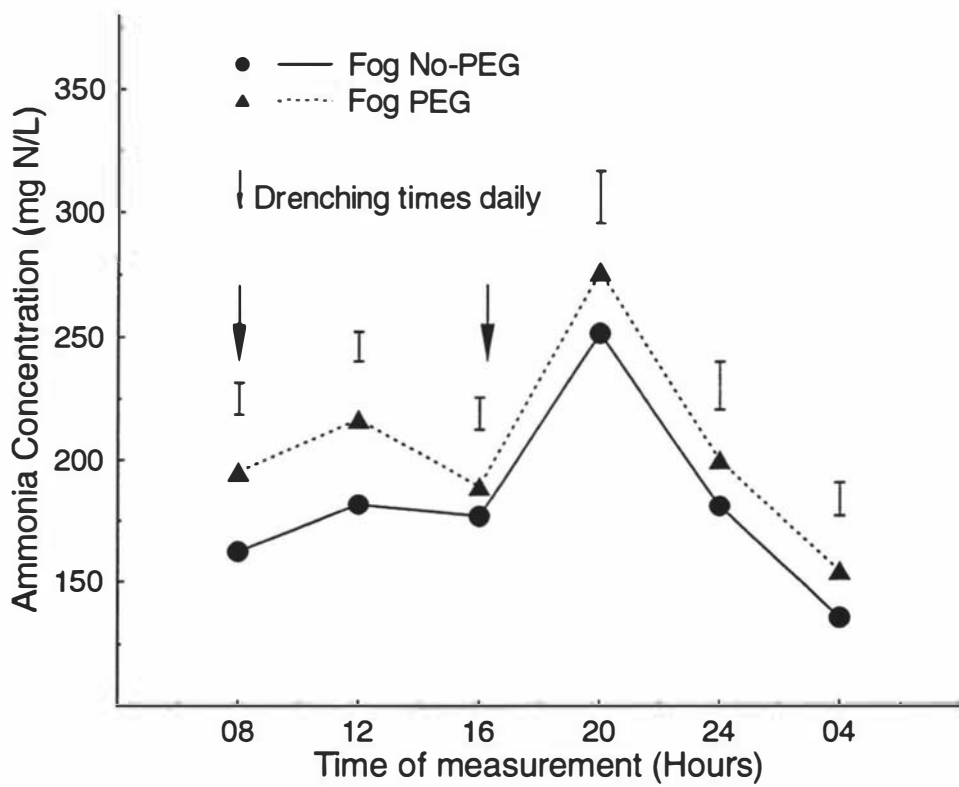


Figure 5.3. Ammonia concentration (mg N/L) of sheep fistulated in the rumen on Yorkshire fog/clover pastures in summer, 1995 (PEG drenching twice daily at 0800 and 1600 hrs).

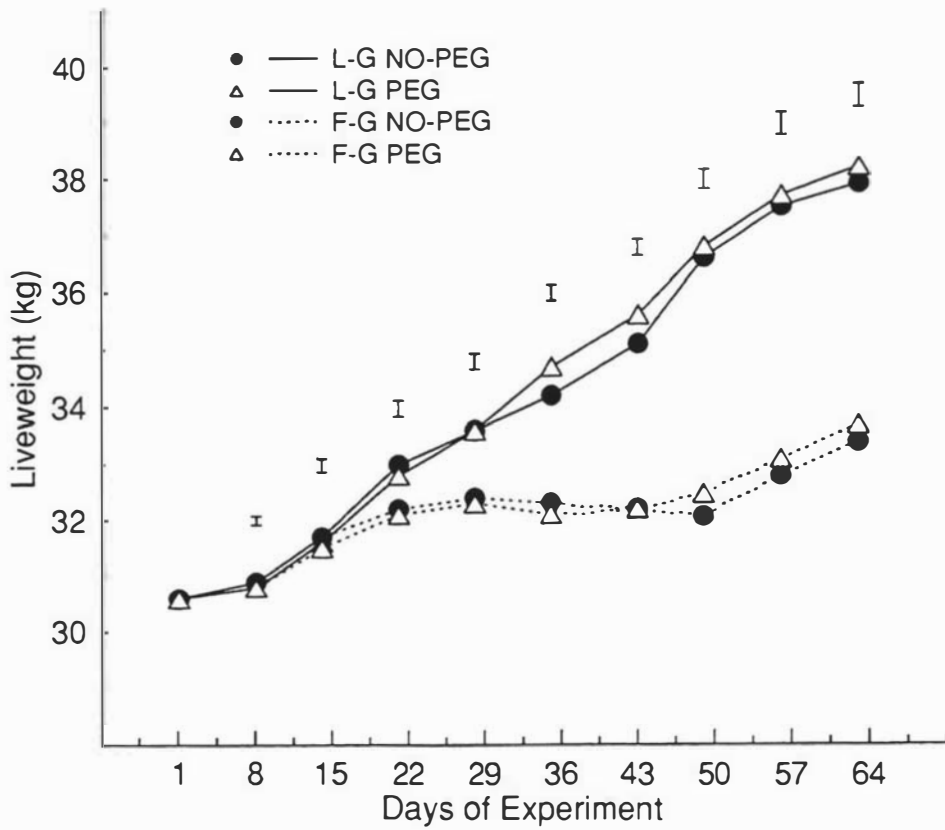


Figure 5.4. Liveweight (kg) of the "leader" (L-G) and "follower" (F-G) lambs grazing Yorkshire fog/clover pasture in summer, 1994/1995

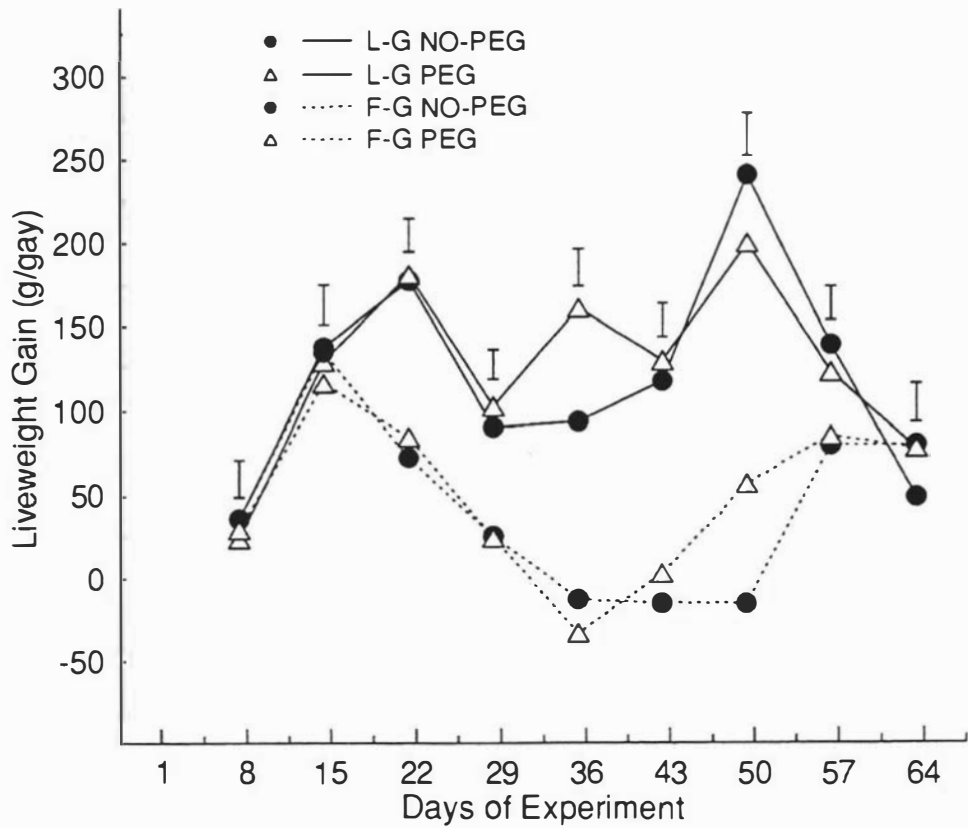


Figure 5.5. Liveweight gain (g/day) of the "leader" (L-G) and "follower" (F-G) lambs grazing Yorkshire fog/clover pasture in summer, 1994/1995

Table 5.7. Liveweight gain, carcass weight, carcass weight gain, dressing out % and wool growth rate of "leader" and "follower" lambs grazing Yorkshire fog in summer

	Main effects						Interaction of "Leader"/"Follower" (L/F) x PEG							
	Leader/Follower			PEG			Leader		Follower		SEM	F Value for		
	Leader	Follower	SEM	Ctrl	PEG	SEM	Ctrl	PEG	Ctrl	PEG		L/F	PEG	L/F x PEG
Liveweight gain (g/day)														
29/11/94 - 11/01/95	109	32	5.8	67	74	5.8	104	114	31	33	8.3	***	NS	NS
11/01/95 - 01/02/95	103	48	10.7	71	80	9.5	102	103	40	56	14.7	**	NS	NS
29/11/94 - 01/02/95	107	37	5.0	68	76	5.0	103	111	33	40	7.0	***	NS	NS
Carcass weight (kg)	15.0	12.5	0.2	13.6	13.9	0.2	14.7	15.3	12.4	12.5	0.3	***	NS	NS
Carcass weight gain (g/day)	40	-1	3.0	17	22	3.0	35	44	-1	<1	4.3	***	NS	NS
Dressing out %	43	41	0.4	42	43	0.4	43	44	42	41	0.5	***	NS	NS
Wool growth rate (mg/100cm ² per day)														
29/11/94 - 11/01/95	113	105	3.1	108	111	3.1	111	116	105	106	4.5	+	NS	NS
11/01/95 - 01/02/95	109	80	2.9	92	97	2.9	103	114	80	80	4.2	***	NS	NS

5.6. DISCUSSION

One of the aims of this experiment was to quantify the effect of low CT concentrations at a limiting level of sward allowance on animal production. This objective was achieved with grazing of a Leader group of lambs for four days, followed by a similar group of Follower lambs also grazing for four days. The Leader/Follower grazing regime, of course, created differences in the characteristics of the sward such as surface height, bulk density and botanical composition, and hence selection opportunity for lambs. Therefore, the desired contrast was conducted on the effects of the quality and quantity of forage on the grazing behaviour, herbage intake and performance of lambs on the Leader and Follower swards.

5.6.1. Sward Characteristics

Defoliation by Leader lambs resulted in significant differences in not only sward surface height, herbage mass and bulk density but also the proportion of the components between the Leader and Follower swards (Figure 5.1 and Table 5.1). Lower proportions of grass leaf and clover and higher proportions of grass stem and dead material in the Follower sward were attributed to defoliation by the Leader lambs (Table 5.2). This was also reflected in the composition of diets from the two swards.

5.6.2. Botanical and Chemical Composition of the Diet Selected

There was a considerable reduction in herbage mass and green leaf after defoliation by the Leader lambs, but green plant parts still made the main contributions to the Follower sward, so the diets selected by OF sheep comprised mainly green material (Table 5.3). Clover content in the swards decreased with grazing, but there were smaller proportions of clover in the diets than in the swards (Table 5.3). This may be partially attributed to a small proportion of clover

and its an irregular distribution in the swards, and partially to the ease of physical comminution of clover by chewing. Clover was disrupted and disintegrated into much smaller particles than Yorkshire fog in the mouth, as clover is more easily broken down by chewing than Yorkshire fog (Moseley, 1981; Wilman and Riley, 1993), resulting in underestimating of proportion of clover in the diets. Although there was an increased proportion of dead material in the sward with grazing, the diets contained more green grass and less white clover and dead material than swards offered to the animals (Table 5.3). This is consistent with the results in Chapters 3 and 4 (Tables 3.2, 4.3 and 4.10). However, the proportion of dead material was high in the diets in the current experiment, compared with that in the former experiments. The high proportion of dead material was a consequence of the considerable proportion of dead material in the swards, especially in the Follower sward.

The consistently higher total N and OMD in the diets from Leader sward than from Follower sward may be explained by the differences in proportions of grass leaf, stem and dead material between the two swards. The CT concentrations in Yorkshire fog were similar to the values in earlier experiments (Experiments 1, 2 and 3; Montossi *et al.*, 1994; Montossi, 1995). The difference in CT concentrations in the diets from the two swards in December (Appendix 5.2) may be associated with the relative contribution of Yorkshire fog leaf and stem to the composition of sward and with the maturity of the components (Figure 5.2). The temporal difference in CT concentrations between January (2.90 - 2.93 g/kg DM) and December (1.63 - 2.25 g/kg DM) (Appendices 5.2) can be explained by more dead material in the swards in January than in December (Figure 5.2), as CT concentrations are greater in dead leaf than in green leaf and stem in Yorkshire fog (Iason *et al.* 1995).

5.6.3. Grazing Behaviour and Herbage Intake

The slower rate of biting and greater intake per bite in Leader animals than in

Followers were attributed to greater surface height and herbage mass in Leader sward than in Follower sward (Table 5.5). There was a compensatory relationship between slower rate of biting and the greater intake per bite in the experiment. Consistently greater herbage OM intake in Leader lambs than in Followers was related to higher OMD of the diets and longer grazing time of lambs (Tables 5.5).

The intakes calculated from the arithmetic product of grazing behaviour components were 126 and 99 g DOM/kg $W^{0.75}$ /day for Leader and Follower lambs. These values are above the maximum likely intake (Weston, 1982; Weston and Davis, 1991; Dove, 1996; Weston, 1996). By contrast, the intakes estimated from faecal output and *in vitro* digestibility were 56 and 43 g DOM/kg $W^{0.75}$ /day for Leader and Follower lambs and were below the limit of likely intake in such animals. The estimates derived from faecal output and diet digestibility are therefore preferred, as for the previous three studies.

5.6.4. Internal Parasites

Lambs had higher faecal egg counts on Follower sward than on Leader sward. This may be related to lower herbage intake in Follower lambs and the faecal contamination of the sward by the Leader lambs when they grazed pasture, and to lower CT concentrations in Follower swards than in Leader swards in December, as forages containing condensed tannins appear to have an effect on the establishment or survival of nematodes in the alimentary tract of sheep (Niezen *et al.*, 1993b).

5.6.5. Rumen Ammonia Concentration

The higher rumen NH_3 concentrations of RF sheep with PEG than with water found immediately after administration indicated that PEG administration allowed increased protein breakdown in the rumen. This suggested that low CT concentrations in Yorkshire fog could reduce the rate of protein degradation in the

rumen of sheep. It would appear that there were consistently higher rumen NH_3 concentrations in PEG-group of sheep than in Control-group, but the differences were not significant at some times of measurements. The variation in rumen ammonia concentration in sampling periods indicated that PEG administration twice daily may not completely eliminate binding of plant protein to CT in the rumen for a full 24 hrs period. This is consistent with the results in earlier studies (Experiment 3; Montossi, 1995). Terrill *et al.* (1992b) also found an increased rumen ammonia concentration by PEG administration in the diets containing low CT concentration of 0.47 % on a DM basis.

5.6.6. Animal Performance

The animal performance in the experiment suggested that the Follower sward produced loss of liveweight of lambs during the middle of the experiment (Figures 5.4 and 5.5). The differences in liveweight gain, carcass weight and carcass weight gain reflected almost entirely the differences in the quality and quantity of forages (Tables 5.2 and 5.4) and the consequences of different herbage DOM intake between the Leader and Follower lambs (Table 5.5).

There was an effect of CT concentrations on rumen NH_3 concentration immediately after administration (Figure 5.3), but there were no significant differences in liveweight gain, carcass weight, carcass weight gain and wool growth rate between PEG-group and Control-group of lambs (Table 5.7). There were no effects of interaction between Leader/Follower swards and PEG administration on animal performance. These results indicated that low CT concentrations in Yorkshire fog were not enough to effectively increase the efficiency of nutrient utilization and hence promote increased animal production even at the restricted grazing, as the effects of CT should be expressed when protein supply is restricting animal production. This further confirmed the findings in the earlier experiments.

5.7. CONCLUSIONS

The Leader/Follower grazing regime created significant differences in herbage quantity and quality between the Leader and Follower swards, selection opportunity and diet quality for animals on the swards. There were higher proportions of green grass and clover and lower proportion of dead material in the Leader sward than in the Follower sward, while total N and OMD were significantly higher in the diets of Leader sheep than of Follower sheep. The greater herbage OM intake and less opportunity of infection by worm parasites resulted in faster liveweight gain, carcass weight gain and wool growth rate in Leader lambs than in Follower lambs.

The increased rumen ammonia concentration by PEG supplementation indicated that the low CT concentrations in Yorkshire fog to some extent reduced the rate of protein degradation in the rumen. However, the absence of effects of PEG administration and interaction between the Leader/Follower sward and PEG on liveweight gain, carcass weight gain and wool growth rate suggested that low CT concentrations were not enough to effectively increase animal production even at the restricted grazing. There were no significant effects of the low CT concentrations on grazing behaviour, diet selection, herbage intake, body growth and wool growth rate of lambs.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

6.1. INTRODUCTION

Most information on CT concentrations and their effects on digestion, metabolism and performance of ruminants is available for legumes or shrubby forages and relatively high CT concentrations (>20 g/kg DM). Accumulating evidence for the presence of low CT concentrations in grasses has been found in recent years (Terrill *et al.*, 1992a; Douglas *et al.*, 1993; Iason *et al.*, 1995; Montossi, 1995). The low CT present in ryegrass/clover pasture has been reported to decrease rumen ammonia concentration and increase wool growth rate (Terrill *et al.*, 1992b). This indicates that low CT concentrations in grasses have potentially important effects on protein digestion, metabolism and animal performance. The underlying aims in this thesis were to make comparative evaluations of Yorkshire fog with ryegrass and tall fescue with reference to grazing behaviour, herbage intake and performance of lambs, and to specifically assess effects of low CT concentrations of less than 1% on a DM basis in grasses on these parameters. The results of individual experiments have been discussed in detail in the preceding chapters. Following an evaluation of the experimental procedures used in the field studies, this chapter will focus general discussion on: 1) sward effects on selective grazing and herbage intake; 2) variation in CT concentrations in grasses and their effects on the performance of lambs; 3) brief evaluation of Yorkshire fog with ryegrass and tall fescue in terms of animal production;

6.2. EVALUATION OF THE EXPERIMENTAL PROCEDURES USED IN THE CURRENT RESEARCH PROGRAMME

One of the main objectives in this study was to do comparative studies of Yorkshire fog with ryegrass and tall fescue in terms of grazing behaviour,

herbage intake and animal performance. The non-nutritional factors such as sward surface height, sward structure, herbage mass and herbage allowance are most important in influencing these parameters. Sward surface height as an important indicator of sward characteristics was measured weekly in Experiment 1 and before and after grazing each paddock in Experiment 2, 3 and 4. Sward structure, herbage mass and botanical composition of swards were measured fortnightly in Experiment 1 and before and after grazing each paddock in other experiments. The results showed that similar sward surface height and herbage mass were maintained between experimental grass pastures in all experiments. This allowed direct comparisons of grazing behaviour, herbage intake and animal performance between swards with similar physical and morphological characteristics.

The botanical composition of the experimental swards was determined by hand separation of herbage samples and point quadrat set at 32.5° to the horizontal (Warren Wilson, 1963). The techniques demonstrated similar patterns of proportions of the components in each sward, though the proportions were estimated based on the weights of all plant parts by hand separation and based on the relative contacts of the parts using point quadrat. Point quadrat data resulted in an underestimation of the proportion of dead material in the sward, but the technique could still interpret the relative difference correctly (Hodgson, 1981a) and show the vertical distribution of plant parts within sward canopy.

The diet composition of the experimental lambs was determined by identifying oesophageal extrusa samples selected by mature OF sheep using a gridded tray technique (Clark and Hodgson, 1986) and calculating the proportions of grasses, legume and dead material on a relative area basis. Forbes and Beattie (1987) suggested that oesophageally-fistulated animals selected a diet similar in botanical composition and digestibility to that selected by non-fistulated animals of similar background and nutritional history, and that their ingestive behaviour in general was no different from non-fistulated animals. There is evidence that

mature oesophageally fistulated wethers can provide representative samples of the diets selected by lambs (Hughes *et al.*, 1984). Thus, the comparison of diet composition and point quadrat data should provide quantitative estimates of diet selection. Furthermore, the estimates of composition and structure in the upper strata of sward derived from the point quadrat were important in defining selective behaviour within these strata. Barthram and Grant (1984) observed that sheep selectively grazed the leaf horizon at the top of a vegetative ryegrass sward. However, there were lower proportions of clover in the diets than even in the upper strata of swards offered to sheep in Experiment 2 and 3. This may be related to the following factors: 1) the small contribution of clover to the experimental swards and its uneven distribution in the swards; 2) the ease of physical comminution for clover by chewing, resulting in much smaller particles and more difficult to distinguish compared with Yorkshire fog; and 3) possible differences between the oesophageal samples of OF sheep and the diets selected by the experimental lambs.

The relative proportions of CT fractions in the extrusa samples may change on chewing, compared with those from pasture samples, as a transfer of extractable CT to protein-bound CT might occur (Terrill *et al.*, 1992a). Also, CT concentrations may differ to some extent between diets and swards. Wang (1995) showed that there were higher CT concentrations in the diets than in the sward on offer when sheep grazed *Lotus corniculatus*. This has been confirmed by Terrill *et al.* (1992a). In the present project, the CT levels were estimated from oesophageal extrusa rather than from pasture components to assess the effects of CT concentrations in the diets on grazing behaviour, herbage intake and animal performance.

The levels of variability in the ingestive behaviour parameters were different, coefficients of variation (CVs) being small in total grazing time (8 - 13%) and the rate of biting (6 - 9%), but being moderate in intake per bite (20 - 36%) across treatments and experiments. The latter is in agreement with the coefficients of

variation of 16 to 32% for sheep reported by Hodgson (1982).

The values of herbage OM intake reported in this thesis were estimated from total faecal output and diet OM digestibility (Hodgson and Rodriguez, 1971). The total faecal output of the experimental lambs was estimated indirectly using intraruminal chromium controlled-release capsules (CRC) and the procedure described by Parker *et al.* (1989; 1990a; 1990b). Parker *et al.* (1991) reported that reliable estimates of group faecal output were obtained from the faecal concentration of Cr and the average digestibility of the feed. However, differences between capsules in marker release rate, and between-animal variations in the digestibility of the feed selected restrict the use of CRC for measuring individual animal intake (Parker *et al.*, 1990b). The digestibility was estimated based on herbage samples collected with oesophageally-fistulated animals. There were the following possible sources of error in estimating digestibility: 1) the difference in digestibility between the *in vitro* and *in vivo* estimates based on herbage samples collected with OF animals; 2) a single digestibility value is then applied to all the test lambs, regardless of any differences in the individual levels of intake; 3) the diet selected by individual test lambs may differ in digestibility from that selected by the OF animals. These errors can lead to errors in the estimate of herbage intake. The use of the alkane technique to measure herbage intake could have overcome the problems associated with the first two sources of error, and the estimate of herbage intake could be obtained in individual animals and with greater accuracy compared with the procedures of faecal output and *in vitro* digestibility (Dove and Mayes, 1991), the coefficients of variation being 13 - 24% in herbage intake in the current study.

The arithmetic product of grazing time (GT), rate of biting (RB) and intake per bite (IB) could be used to calculate herbage intake (Allden and Whittaker, 1970; Jamieson and Hodgson, 1979; Hodgson, 1982). The herbage OM intakes calculated in this way were 1.3 - 2.5, 2.2 - 2.6, 1.7 - 2.0 and 2.2 - 2.3 times greater than those estimated by faecal output and OMD respectively in

Experiments 1, 2, 3 and 4. Also, most of the values of herbage intake (digestible OM intake) calculated from the product of grazing behaviour data were above the maximum likely intake of lambs of this size suggested by some researchers (Weston, 1982; Weston and Davis, 1991; Dove, 1996; Weston, 1996). By contrast, the intakes estimated from faecal output and *in vitro* digestibility were well below the limit of likely intake in such animals. These comparisons were similar in all the experiments. The greater herbage DOM intakes calculated from the product of grazing behaviour data can be attributed to the following factors: (i) the rates of biting measured using the 20 consecutive bites during periods of peak grazing activity in the experiments would be faster than true average daily values (Hodgson, 1982); (ii) intake per bite estimated for mature OF sheep could be greater than that for the experimental lambs (Forbes, 1988a). Jamieson and Hodgson (1979) suggested that the lower value for intake per bite obtained from estimates of daily herbage intake and total daily bites resulted from overestimation both of rate of biting and of intake per bite derived from extrusa collection. In consideration with these reasons the herbage intake calculated by the arithmetic product of components of ingestive behaviour were not reported in this thesis. As Hodgson (1982) suggested, "it is probably prudent to think of measurements of ingestive behaviour as a means of explaining observed effects on herbage intake rather than as a means of estimating intake itself, and to measure intake independently".

The initial live weight, carcass weight and clean wool weight were used as covariates to analyze correspondingly liveweight gain, carcass weight gain and wool growth rate in the experiments. These procedures reduced variation in the statistical analyses. The coefficients of variations for liveweight gain, carcass weight gain and wool growth rate were respectively 10 - 19%, 18 - 22% and 11 - 22% in the first three experiments. The CVs for animal variables were larger in Experiment 4 because some follower lambs lost weight over the experiment.

6.3. EVALUATION OF HERBAGE AND ANIMAL PRODUCTION FOR THREE GRASS PASTURES

Comparisons of herbage production from ryegrass and Yorkshire fog pastures have shown a consistent superiority of Yorkshire fog under low fertilizer N and a general inferiority under high fertilizer N and cutting management (Haggar, 1976; Watt, 1987; Frame, 1992; Harvey *et al.*, 1984). The current experiments were not designed to investigate differences in herbage production, but ryegrass was superior to Yorkshire fog in improving liveweight gains of animals under continuous stocking management at similar herbage mass. The ryegrass had higher herbage OMD, which resulted in greater herbage OM and DOM intakes, and hence faster liveweight gain. The lower OMD of Yorkshire fog, compared with ryegrass, is consistent with the results of Morton *et al.* (1992) and Montossi (1995). The evidence of lower N content in ryegrass than in Yorkshire fog agrees with Montossi (1995), but is inconsistent with the finding by Wilman and Riley (1993).

A high invasion of other species in Experiments 2 and 3 indicated a considerable competitive disadvantage of tall fescue (Tables 4.2 and 4.9, Appendices 4.3 and 4.7). The factor responsible has been identified as slow root growth (Rhodes, 1968) and slow tillering (Tavakoli, 1993). Brock (1983) showed that severe moisture stress limited Roa tall fescue growth, but recovery with the occurrence of rain was rapid.

A superiority of tall fescue over ryegrass in terms of pasture production and similar liveweight gain and carcass weight between tall fescue and ryegrass have been reported in documented reviews (Watkin, 1975; Goold and van der Elst, 1979; Anderson, 1982; Brock, 1983; Wright *et al.*, 1985), but there are little comparative data for tall fescue and Yorkshire fog. Most values of total N and *in vitro* digestibility were in favour of tall fescue compared with Yorkshire fog in Experiments 2 and 3 (Tables 4.4 and 4.11), but tall fescue did not sustain higher

animal performance. The lower growth rate of lambs on tall fescue than on Yorkshire fog in Experiment 2 reflected the lower herbage intake in tall fescue (Appendix 4.5). During the particularly dry period of 1994, the advantage in liveweight gain between the lambs grazing Yorkshire fog over tall fescue pastures was 56% (Table 4.7). The superiority of Yorkshire fog over tall fescue in animal production is supported by other results (Niezen, 1993a). However, no differences in liveweight gain, carcass weight gain or wool production between Yorkshire fog and tall fescue were found in Experiment 3 in summer and early autumn.

Lower faecal egg counts on Yorkshire fog than on tall fescue in Experiment 2 demonstrated the beneficial effect of Yorkshire fog in limiting worm parasite infestation (Table 4.6). This evidence is supported by Niezen *et al.* (1993a) and Hodgson *et al.* (1996). There was no significant difference in faecal egg count between pastures in Experiment 3 (Table 4.13). However, the drenching programme used in these studies would be expected to limit the advantage of Yorkshire fog over tall fescue in control of worm parasites.

The Leader/Follower grazing regime in Experiment 4 created the desired contrasts in both the quantity and quality of herbage available to the animals. One of the main interests was to investigate the effects of restricted grazing on CT concentrations in the diet and effects of PEG administration on the performance of lambs grazing Yorkshire fog. The regime forced the lambs on the Follower sward to graze lower digestibility herbage, while minimizing selective grazing and limiting herbage OM intake. The effect of Leader/Follower grazing on animal performance was predictable considering the differences in the quantity and quality of herbage. These results further defined the importance of herbage quantity and quality in determining herbage OM intake, and hence animal body growth and wool growth. The higher dietary CT concentrations in Leader diets than in Follower diets in December (Table 6.1, Experiment 4) were attributed to more opportunity for selecting green leaf for the Leader sheep at this grazing regime. There were no effects of PEG or interaction between PEG and grazing

sequence on grazing behaviour, diet selection, herbage intake and animal performance. These results further indicate that CT concentrations in Yorkshire fog were not high enough to improve animal production.

6.4.SWARD EFFECTS ON SELECTION AND HERBAGE INTAKE OF ANIMALS

The low proportions of sown grasses present in both pastures in Experiments 2 and 3, especially in tall fescue, were of some concern. These proportions were 42 - 43 % and 32 - 38 % for Yorkshire fog and tall fescue in Experiment 2 (Table 4.2 and Appendix 4.3) and 63 - 66 % and 36 - 65 % for Yorkshire fog and tall fescue in Experiment 3 (Table 4.9 and Appendix 4.7) before grazing, compared with 72 - 77 % and 69 - 72 % for ryegrass and Yorkshire fog in Experiment 1 (Figure 3.2 and Appendix 3.2). The high invasion of other grasses to tall fescue pasture has been reported in several studies (Butler, unpublished; Hodgson *et al.*, 1996). The small proportions of sown grasses in the current experiments could have limited the magnitude of treatment effects, but should not mislead the interpretation of results.

There was generally more green material and less dead material in the diets than in the swards offered to animals (Tables 3.3, 4.3, 4.10 and 5.3). The diets selected mainly comprised grass leaf at most dates of sampling based on visual observations, with the exception of the diets selected by animals on Follower sward in Experiment 4, although leaf and pseudostem were not separated in extrusa samples. Strong preference for green leaf has been shown in several studies (Hodgson, 1982; 1986; 1990; Clark *et al.*, 1982; L'Huillier *et al.*, 1984). Clark *et al.* (1982) found that sheep had a strong preference for green grass and strong dislike for dead material, but neither preference nor rejection of legume material. This has been confirmed by the results in the current experiments (Tables 4.3, 4.10 and 5.3). Animals ate dead material on the Follower sward in Experiment 4 as the proportion of dead material increased and the availability of green material and the possibility of selecting for it by animals became less, but

the diets still contained less dead material than the swards offered to the animals (Table 5.3).

No evidence of selection for white clover in preference to grass has been provided in these trials. The results suggested that diet composition was mainly dependent on the botanical composition and structure of the swards offered to grazing animals rather than on deliberate selection. There was no evidence that low CT concentrations affected diet selection. Animals selected the components which would be expected to have higher CT levels (Iason *et al.*, 1995), but the low CT levels in Yorkshire fog were unlikely to have a selectively advantageous defensive role against herbivores. This has been confirmed in studies with *Lotus pedunculatus* (Waghorn *et al.*, 1990), Yorkshire fog (Douglas *et al.*, 1993) and *Lotus comiculatus* (Wang *et al.*, 1994).

Herbage intake is usually related to diet digestibility. From the concept of 'forage consumption constraint' (FCC), the constraints of intake (or the difference between actual intake and maximum theoretical intake) increase markedly as digestibility decreases (Weston, 1996). In the current experiments, the intakes actually achieved ranged from 46 to 70 g DOM/kg^{0.75} day⁻¹ and were within the maximum theoretical intake (90 g DOM/kg^{0.75} day⁻¹) for 30 kg weaners recommended by Weston and Davis (1991). Freer and Jones (1984) in a study of the digestibility and voluntary feed consumption of two grasses and two legumes, found that the intake from legumes was 100-200 g OM day⁻¹ more than from grasses, while the intake of both classes of plant increased by 16-19 g OM day⁻¹ for each unit increase in digestibility. In the current study, intake increased by 62 g OM day⁻¹ for each unit increase in digestibility when Yorkshire fog and ryegrass was compared in Experiment 1, declined by 23 g OM day⁻¹ for Yorkshire fog and tall fescue in Experiment 2, increased by 59 g OM day⁻¹ for Yorkshire fog and tall fescue in Experiment 3 and 38 g OM day⁻¹ for the Leader and Follower swards in Experiment 4. These effects may be explained in part by treatment differences in the digestibility of diets, but it seems clear that variations in sward

structural characteristics affecting grazing behaviour and selection of animals also had an important role in determining herbage intake (see also Poppi *et al.*, 1987).

6.5. VARIATION OF CT CONCENTRATIONS IN GRASSES AND THEIR EFFECT ON RUMEN AMMONIA CONCENTRATION

6.5.1. Variation of CT Concentrations in Grasses

It has generally been considered that grasses from temperate and cool temperate climate contain no CT (Bernays *et al.*, 1989; Iason *et al.*, 1995). Perennial ryegrass pasture was originally thought to be a non CT-containing forage and was used as a control to compare with CT-containing forages by Terrill *et al.* (1992b), who suggested that the CT content in ryegrass pasture in their studies might be attributed to Yorkshire fog mixed in the sward. Actually, ryegrass diets contained slightly higher CT level (Table 3.4) than Yorkshire fog diets in Experiment 1. This has been confirmed by the results of Montossi (1995). Low CT concentrations have been found in the diets of sheep grazing several grasses in this series of studies (Table 6.1). In the oesophageal extrusa, a low proportion of total CT was extractable and most CT was protein-bound (Tables 4.4, 4.13 and 5.4), except for Experiment 1 in winter (Table 3.4). The higher protein-bound and total CT concentrations in the diets from Leader swards than from Follower swards in December in Experiment 4 (Table 5.4) can be explained by the relative contributions of live leaf and stem to the swards (Table 5.2), as Yorkshire fog leaf contains much higher CT concentration than stem (Iason *et al.*, 1995). The differences in CT concentrations between the different periods of sampling in Experiment 4 (Appendix 5.2) were due to more dead material in the swards in January than in December. This has been confirmed by Iason *et al.* (1995) who also reported that dead leaf contained higher CT than live leaf, stem and flowers in a Yorkshire fog sward.

Table 6.1. CT concentrations in plant material and in the diets selected by sheep grazing grass pastures.

Pasture/species	CT level (g/kg DM)	Sampling duration	References
Perennial ryegrass/clover:			
ryegrass/fog/clover			
1.	2.9	Aut., 1989	Terrill <i>et al.</i> , 1992b
2.	4.7	Spr., 1989	Terrill <i>et al.</i> , 1992b
ryegrass/clover			
1.	2.0†	1990/1991	Douglas <i>et al.</i> , 1993
2.	1.3†	1990/1991	Douglas <i>et al.</i> , 1993
3.	2.1	May, 1992	Montossi <i>et al.</i> , 1994
4.	2.1	June., 1993	Exp. 1
Yorkshire fog/clover:			
1.	2.5	May, 1992	Montossi <i>et al.</i> , 1994
2.	1.9	Dec., 1992	Montossi, 1995
3.	1.7	Jan., 1993	Montossi, 1995
4.	1.8	June, 1993	Exp. 1
5.	4.2	Sept., 1993	Montossi, 1995
6.	1.8	Dec., 1993	Exp. 2
7.	2.1	Feb., 1994	Exp. 3
8.	1.7	March, 1994	Exp. 3
9.	2.3 (1.6)‡	Dec., 1994	Exp. 4
10.	2.3 (1.7)	Dec., 1994	Exp. 4
11.	3.2 (3.2)	Jan., 1995	Exp. 4
12.	2.7 (2.7)	Jan., 1995	Exp. 4
Tall fescue/clover:			
1.	1.3	Dec., 1994	Exp. 2
2.	1.1	Dec., 1994	Exp. 2
3.	1.2	Jan., 1995	Exp. 3
4.	1.3	Jan., 1995	Exp. 3
Annual ryegrass/clover:			
1.	3.7	Sept., 1994	Montossi, 1995
2.	4.0	Oct., 1994	Montossi, 1995 (in Uruguay)

†: Data refer to swards offered; other results refer to extrusa samples;

‡: The data within the bracket show values for follower group.

6.5.2. Evaluation of the Effect of CT Content on Rumen Ammonia Concentration

Polyethylene glycol (PEG) can specifically bind with CT or displace CT from a pre-formed CT:protein complex, then form much stronger chemical bonds with CT than do plant proteins, hence preventing CT from reacting with protein or releasing protein from the CT-protein complex in the rumen. PEG has been assumed to specifically bind and inactivate CT without influencing the digestion of other nutrients (Jones and Mangan, 1977; Barry and Manley, 1986; Barry, 1989; Wang *et al.* 1994; Wang *et al.*, 1995b), and to completely bind available CT and release protein from CT-protein complex in the ratio of 1.8:1 for PEG and CT (Barry, 1989). Much research has been done by spraying forages (Barry and Duncan, 1984; Barry 1985) or orally drenching animals with PEG (Waghorn *et al.*, 1987a; 1994a; 1994b; Terrill *et al.*, 1992b; Wang *et al.*, 1994; 1996; Montossi, 1995) to study the effects of CT in forages on digestion, metabolism and production of ruminants.

The effects of CT on rumen ammonia concentrations are assessed using administration of PEG to the animals to bind and inactivate CT and a comparison of rumen ammonia concentration between control and PEG drenched animals. Rumen ammonia concentration has been reduced by high CT concentrations (>50 g/kg DM) in *Lotus pedunculatus* (Barry *et al.*, 1986; McNabb *et al.*, 1993a; Waghorn *et al.*, 1994a) and by moderate CT (20 - 40 g/kg DM) in *Lotus corniculatus* (Waghorn *et al.*, 1987; Wang *et al.*, 1994; 1996). PEG was administered to the wethers fistulated in the rumen in Experiments 3 and 4 to assess the effect of low CT concentrations in grasses on rumen ammonia concentration. PEG supplementation increased rumen ammonia concentration immediately after drenching in sheep grazing Yorkshire fog in Experiment 3 (Figure 4.11) and at most sampling times in Experiment 4 (Figure 5.5). This finding is consistent with the results in Yorkshire fog/clover reported by Montossi (1995) and in ryegrass/Yorkshire fog/clover pasture reported by Terrill *et al.*

(1992b). The evidence suggests that low CT levels in the grasses to some extent reduce protein degradation in the rumen, and that the effective range of CT concentration in reducing the rate of protein degradation in the rumen is very wide. The reduced protein degradation in the rumen by CT can be explained by the fact that CT-protein complex, formed during chewing, is not dissociated at rumen pH, hence preventing or reducing the rate of protein degradation by rumen microorganisms. The variations in the response of rumen ammonia concentration to PEG over the sampling periods indicated that PEG supplementation twice daily did not completely eliminate binding of plant proteins to CT in the rumen for a full 24 hr period. This is in agreement with the results reported by Terrill *et al.* (1992b) and Montossi (1995). The absence of responses in rumen ammonia concentration to PEG drenching in tall fescue indicates that the components estimated as CT may have been an artifact of the method of analysing CT.

6.6. EFFECTS OF CT IN GRASSES ON PERFORMANCE OF RUMINANTS

The effects of low CT concentrations in grasses on nutrient digestion and metabolism were not examined in the current studies. Much research on the effects of CT concentrations of more than 20 g/kg DM on digestion, metabolism and performance of ruminants has been done in recent years. Effects of low CT concentrations (< 10 g/kg DM) in forages on animal performance are less understood, compared to the effects of moderate to high CT level (>20 g/kg DM). Wang (1995) suggested that an extractable CT level of more than 9 g/kg DM could increase the abomasal non-ammonia nitrogen (NAN) flux in lambs and hence improve nutrient utilization in the small intestine. Barry (1989) suggested that the range of CT concentration 20 - 40 g/kg DM could improve the nutritive value of forages, reducing the rate of protein degradation in the rumen and increasing the quantity of nutrient digestion in the small intestines, and hence improve animal performance. This has been supported by other researchers (Waghorn *et al.*, 1990; McNabb *et al.*, 1993a; Wang *et al.*, 1994; Douglas *et al.*, 1995). The low CT concentrations of less than 10 g/kg DM present in grasses

Table 6.2. Effects of CT concentrations in the grass-based pastures on liveweight gain, carcass weight, carcass weight gain and wool growth rate.

Pasture/species	CT level (g/kg DM)	Liveweight gain (g/d)				Carcass weight (g/d)				Carcass weight gain (g/d)				Wool growth (mg/100 cm ² per day)			
		Ctrl	PEG	Dif. %	Sig.	Ctrl	PEG	Dif. %	Sig.	Ctrl	PEG	Dif. %	Sig.	Ctrl	PEG	Dif. %	Sig.
Yorkshire fog/ clover																	
1.	1.8	144.9	142.3	-1.8	NS	16.3	16.2	-0.6	NS	71.2	69.1	-2.9	NS	86.8	74.3	-14.4	NS
2.	1.8	103.1	95.0	-7.8	NS	15.0	14.5	-3.3	NS	36.1	28.5	-21.1	NS	116.1	119.3	+2.8	NS
3.	2.1	80.0	73.4	-8.1	NS	14.4	14.1	-2.1	NS	33.6	28.7	-14.6	NS	113.6	110.6	-2.6	NS
4.	2.6	68.3	75.5	+10.5	NS	13.6	13.9	+2.2	NS	16.9	22.3	+32.0	NS	101.8	105.6	+3.7	NS
5.	1.8	129	113	-10.1	NS	16.2	16.4	+1.2	NS	-	-	-	-	109	109	0.0	NS
6.	4.2	174	135	-29	**	19.3	18.7	-3	NS	-	-	-	-	154	140	-10	*
Ryegrass/clover																	
7.	2.1	173.3	173.8	+0.3	NS	17.0	17.1	+0.6	NS	87.1	90.0	+3.3	NS	77.6	90.6	+16.8	*
8.	1.9	130	131	+0.8	NS	17.3	17.6	+1.7	NS	-	-	-	-	108	121	+12.0	*
9.	4.7	175	136	-22.3	*	19.2	18.3	-4.7	NS	-	-	-	-	115	97	-15.7	*
Tall fescue/ clover																	
10.	1.2	77.0	75.0	-2.6	NS	14.0	13.9	-0.7	NS	20.6	18.8	-8.7	NS	112.5	110.0	-2.2	NS
11.	1.3	76.9	74.7	-2.9	NS	14.1	14.1	0.0	NS	29.2	29.8	+2.1	NS	111.1	98.2	-11.6	NS
Annual ryegrass/ clover 12	3.7	111	105	-5.4	NS	17.1	17.0	-0.6	NS	-	-	-	-	134	122	-9.0	*

Ctrl: control group (CT acting); PEG: PEG supplementation group (CT inactivated);

Dif. (%) = (PEG - Ctrl)/Ctrl x 100;

References for the data: 1 & 7 (Exp. 1); 2 & 10 (Exp. 2); 3 & 11 (Exp. 3); 4 (Exp. 4); 5, 6, 8 & 12 (Montossi, 1995); 9 (Terrill *et al.* 1992b).

have demonstrated potential effects on ruminant digestion and performance (Terrill *et al.*, 1992b; Montossi, 1995). However, a minimal level of CT concentration in forages to effectively improve animal production has not been clearly defined. The effects of low CT concentrations in grasses on animal performance have been assessed using comparative studies of control (CT acting) and PEG administration (CT inactivated) treatments in recent years. The general comments which follow are drawn from the results of a series of studies on the effects of low CT concentrations in grass-based pastures on animal performance (Table 6.2).

1) Low dietary CT concentrations of 4 - 20 g/kg DM in grasses could to some extent enhance animal performance, but concentrations of < 3 g CT/kg DM in grasses were not high enough to effectively improve animal performance (Table 6.2). Terrill *et al.* (1992b) showed that a CT level of 4.7 g/kg DM resulted in a significant improvement in wool growth rate and liveweight gain on ryegrass/Yorkshire fog/clover pasture in spring. Beneficial effects of similar low CT concentrations (4.2 g/kg DM) on liveweight gain and wool growth rate were observed in Yorkshire fog/clover/*Lotus* pasture in Uruguay by Montossi (1995). Lower CT concentrations (2 - 3 g/kg DM) had small effects on liveweight gain in the initial period in the current studies, but did not persist until the end of each experiment. The results of Experiment 4 indicated that CT concentrations in Yorkshire fog were not high enough to effectively enhance animal production even at the restricted grazing. These results indicate that minimal effective CT concentrations of close to 4 g/kg DM in diets are required to significantly improve animal performance. Research is needed in the range of 4 - 20 g CT/kg DM basis to define the minimal effective range of CT in plants on grazing ruminants.

Similar small and non-persistent effects of CT on animal responses were observed by Montossi (1995). Treatments of "previous experience", in which lambs grazed pastures of ryegrass or Yorkshire fog for four weeks before they were used for further field experiments, were designed in Experiments 2 and 3

to quantify this apparent transient response of lambs to PEG administration. There were no effects of previous experience or interaction between previous experience and current pasture on liveweight gain in these experiments. These results indicate that the low CT concentrations in Yorkshire fog could have a small effect on lamb performance in the initial period. The explanation for such limited influence on animal performance was probably that grazing animals showed partial adaptation to the dietary CT. The partial adaptation of ruminants to high dietary CT concentrations has been reported by Barry (1985) and Lowther and Barry (1985). Robbins *et al.* (1987b) confirmed some buffering effects of sheep's saliva against high dietary CT concentrations.

There was a tendency for higher responses in liveweight gain to PEG administration on Yorkshire fog swards than on perennial ryegrass swards, despite the fact that there were similar CT concentrations in the extrusa samples between ryegrass and Yorkshire fog pastures. This is consistent with the results observed by Montossi (1995). The difference in responses of liveweight gain between Yorkshire fog and ryegrass might be attributed to different molecular weights of CT between the two species affecting the capacity for precipitating plant proteins. Barry (1989) reported differences in the capacity to precipitate protein in legumes which had different molecular weights of CT.

2) There were no significant effects of low CT concentrations on carcass weight or carcass weight gain. The small increases in liveweight gain in the initial period to low CT concentrations in the grasses were not reflected in carcass weight differences in the current studies. This is in agreement with the results of Montossi (1995). These results indicated that the small increase in liveweight gain probably occurred in non-carcass components (Terrill *et al.*, 1992b). Lower responses in carcass fatness to CT concentrations were observed by some authors (Purchas and Keogh, 1984; Terrill *et al.*, 1992b), presumably due to increasing protein deposition and reducing fat as a proportion of the carcass, but this has not been supported by the results of the current experiments.

3) An unexpected increase in wool growth associated with PEG administration was observed in ryegrass pasture in Experiment 1, and significant improvements in liveweight gain following the use of PEG in ryegrass pasture have been reported by other researchers (Terrill *et al.*, 1992b; Niezen *et al.*, 1993a; Montossi, 1995). These increases in wool growth rate and liveweight gain by use of PEG in ryegrass are difficult to explain. It has been suggested that the effects may reflect the influence of PEG on fungal toxins with a multi-ring structure similar to CT (Barry and Blaney, 1987; Reid and Lauren, 1989; Terrill *et al.*, 1992b), but further evidence is required. Whatever the explanation, it is clear that perennial ryegrass is not strictly appropriate as a control to assess the effects of CT concentrations on animal performance.

6.7. CONCLUSIONS

The following general conclusions can be drawn from this series of experiments:

- 1) Diet composition was determined largely by the structure and distribution of sward components rather than by the diet selection of animals. Herbage OM intake was influenced to a greater extent by nutritional factors than by behavioral limitations.
- 2) Perennial ryegrass/white clover pasture produced higher animal production than Yorkshire fog/white clover pasture under continuous grazing management in winter. Yorkshire fog pasture produced higher animal production than tall fescue under rotational grazing management in late spring and early summer, but both pastures had similar animal production in summer and early autumn. Of greater significance was the higher quality of the green herbage in tall fescue than Yorkshire fog. Tall fescue should have a potential role in New Zealand agricultural systems if herbage quality and acceptability to stock are controlled through grazing management.

- 3) In a final study, a leader/follower grazing regime created desired contrasts in herbage quantity and quality. The difference in sward allowance, selection opportunity, diet quality and less possibility of larval infection resulted in the superior performance of the leader lambs over follower lambs in animal production.
- 4) Low CT concentrations (1.8 - 3.2 g/kg DM) were present in perennial ryegrass and Yorkshire fog, but estimates of comparable CT contents in tall fescue may have been artifacts. The low CT concentrations in the grasses had no effect on grazing behaviour, diet selection or herbage intake.
- 5) The low CT concentrations in Yorkshire fog to some extent reduced rumen ammonia concentration and had small effects on liveweight gain in the first weeks after exposure, but were not enough to effectively improve animal production overall. Lower faecal egg counts found in lambs on Yorkshire fog swards compared with tall fescue swards under rotational grazing management indicated the potential of Yorkshire fog in the control of internal worm parasites. This may be related to low CT concentrations in the Yorkshire fog. More research is needed to define the potential benefits of low CT concentration in Yorkshire fog for parasite control.

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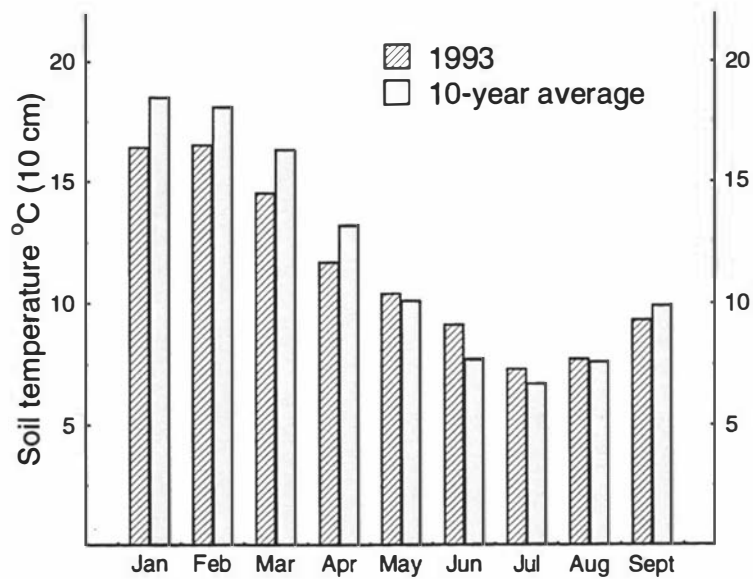
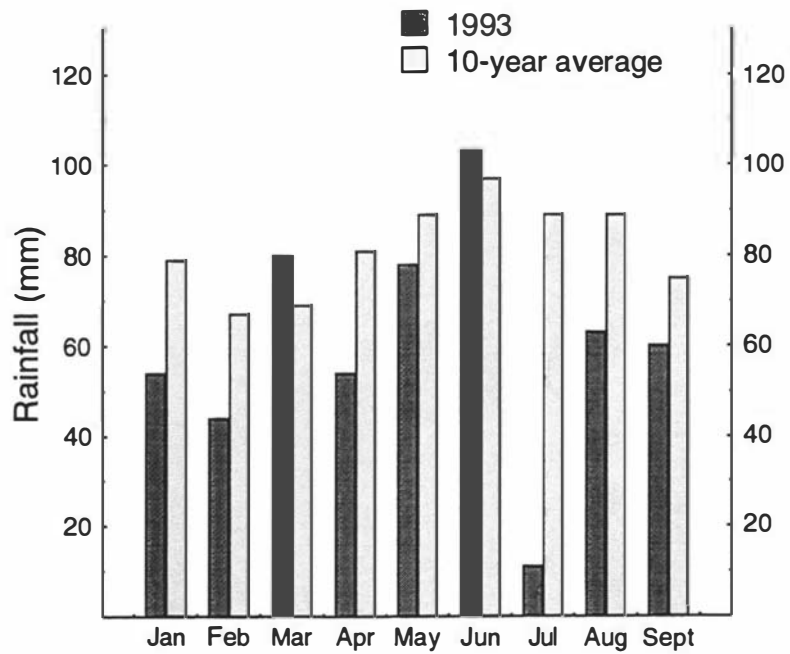
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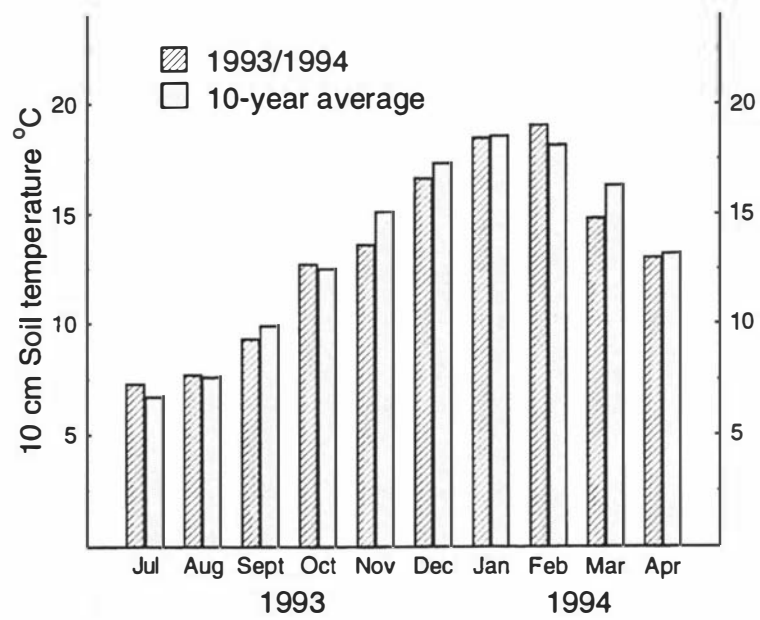
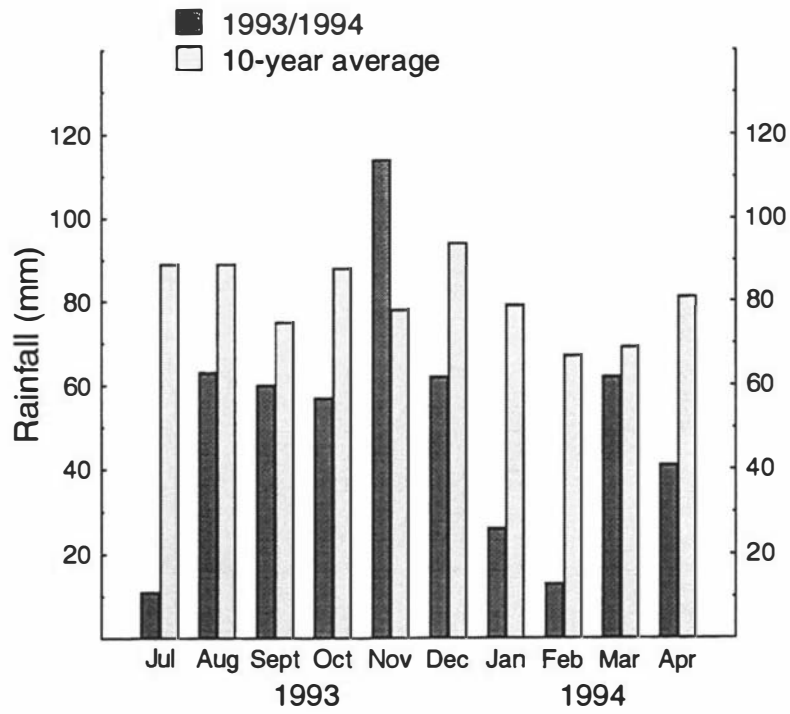
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Appendix 3.1 Rainfall (mm) and mean 10 cm soil temperature(°C) in 1993 compared with 10-year average values from the same site.



Appendix 4.1 Rainfall (mm) and mean 10 cm soil temperature(°C) in 1993/94 compared with 10-year average values from the same site.

Appendix 4.2. Sward characteristics of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in late spring and early summer, 1993/1994.

		Herbage mass (DM kg/ha)								Bulk density (DM mg/cm ³)							
		Pre-grazing				Post-grazing				Pre-grazing				Post-grazing			
		Fog	Tall fescue	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Fog	Tall fescue	SEM	Sig.	Fog	Tall fescue	SEM	Sig.
Dec/1993	Per 1	4050	3650	166	NS	2820	2480	139	NS	2.2	2.0	0.11	NS	4.1	4.0	0.34	NS
	Per 2	4240	3930	180	NS	3230	3040	187	NS	2.1	2.0	0.10	NS	3.3	3.0	0.13	+
Jan/1994	Per 3	3710	3880	264	NS	2750	2540	170	NS	2.4	2.6	0.22	NS	3.8	4.5	0.34	NS
	Per 4	3390	3550	200	NS	2480	2520	146	NS	2.6	2.4	0.13	NS	4.5	5.6	0.52	NS

Appendix 4.3. The proportion of components of Yorkshire fog/clover and tall fescue/clover swards before and after grazing under rotational grazing management in late spring and early summer, 1993/1994.

	Before grazing								After grazing							
	December, 1993				January, 1994				December, 1993				January, 1994			
	Fog fescue	Tall	SEM	Sig.	Fog fescue	Tall	SEM	Sig.	Fog fescue	Tall	SEM	Sig.	Fog fescue	Tall	SEM	Sig.
Sown grass leaf	24	18	1.9	NS	28	25	2.9	NS	15	10	0.3	**	14	16	0.2	*
Sown grass stem	17	12	1.5	NS	14	12	1.4	NS	27	19	1.4	+	18	11	2.1	NS
Sown grass seed head	1	2	1.1	NS	1	1	0.7	NS	3	1	0.3	*	0	<1	0.3	NS
Total sown grass	42	32	3	+	43	38	4.6	NS	45	30	1.7	*	32	27	2.0	NS
Other grass leaf	16	25	1.1	*	10	16	0.7	*	12	18	0.7	*	8	10	0.5	NS
Other grass stem	12	15	0.1	**	6	10	1.0	NS	17	23	1.1	+	11	19	0.7	*
Other grass seed head	8	8	1.1	NS	1	3	0.3	*	3	3	0.5	NS	<1	1	0.4	NS
Total other grasses	36	48	2.2	+	17	29	1.0	*	32	44	0.3	**	19	30	1.3	*
Clover leaf	2	3	0.6	NS	4	6	0.7	NS	2	2	0.1	NS	1	2	0.4	NS
Clover petiole	1	2	0.3	NS	3	5	0.5	NS	2	1	0.4	NS	1	2	0.2	+
Total clover	3	5	0.9	NS	7	11	0.2	**	4	3	0.5	NS	2	4	0.7	NS
Weed	<1	0	0.2	NS	0.0	<1	0.1	NS	0	0	0.0	NS	0	0	0.0	NS
Dead Material	19	15	2.6	NS	33	22	4.1	NS	19	23	1.8	NS	47	39	2.1	NS

Appendix 4.4. Grazing behaviour of lambs grazing Yorkshire fog/clover and tall fescue/clover in late spring and early summer, 1993/1994.

Period 1 Main effects (n=16)	Previous pasture			Current pasture			Sex			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Grazing time (min)	550	570	10	580	540	10	560	560	13	560	560	13
Ruminating time (min)	280	270	6	290	260	6	280	280	10	280	270	10
Resting time (Min)	520	510	11	480	550	11	520	510	12	510	520	12
Rate of biting (bites/min)	42	44	0.2	43	43	0.2	43	43	0.5	44	42	0.5
Intake per bite (mg OM/bite)				83.0	68.9	5.1 +						
Interaction of previous pasture x current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x SPP		
Grazing time (min)	560	540	590	540	15	NS	+	NS	NS	NS		
Ruminating time (min)	310	250	280	270	9	NS	*	NS	NS	+		
Resting time (min)	480	560	480	540	16	NS	**	NS	NS	NS		
Rate of biting (bites/min)	43	44	43	42	0.3	**	NS	NS	+	*		
Period 2												
Main effects (n=16)	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Grazing time (min)	560	560	15	560	560	15	570	560	12	550	570	12
Ruminating time (min)	310	290	10	300	300	10	320	280	11	300	300	11
Resting time (Min)	480	500	13	490	490	13	470	510	19	500	480	19
Rate of biting (bites/min)	42	41	0.3	42	41	0.3	42	41	0.5	41	42	0.5
Intake per bite (mg OM/bite)				87.1	80.1	4.7 NS						
Interaction of previous pasture x current pasture (n = 8)												
Previous species	Ryegrass		Fog		SEM	F value for						
Grazing species	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x SPP		
Grazing time (min)	570	560	560	560	21	NS	NS	NS	NS	NS		
Ruminating time (min)	290	320	300	280	13	NS	NS	+	NS	NS		
Resting time (min)	490	470	490	520	18	NS	NS	NS	NS	NS		
Rate of biting (bites/min)	43	41	42	41	0.4	NS	*	NS	NS	NS		

Appendix 4.5. Herbage OM intake of lambs grazing Yorkshire fog/clover and tall fescue/clover in late spring and early summer, 1993/1994.

Period 1	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
OMI (g/day)	708	830	31.6	757	781	31.6	810	728	42.7	817	722	42.7
OMI (g/kg W ^{0.75})	55	67	3.1	60	62	3.1	64	59	3.7	65	58	3.7
Interaction of previous pasture x current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x Spp		
OMI (g/day)	710	706	805	856	44.7	+	NS	NS	NS	NS		
OMI (g/kg W ^{0.75})	55	56	65	69	4.4	+	NS	NS	NS	NS		
Period 2	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
OMI (g/day)	828	772	15.8	835	765	15.8	846	752	24.4	830	770	24.4
OMI (g/kg W ^{0.75})	63	61	0.9	64	59	0.9	64	59	1.8	65	59	1.8
Interaction of previous pasture x current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x Spp		
OMI (g/day)	869	787	802	742	22.3	*	*	*	NS	NS		
OMI (g/kg W ^{0.75})	66	60	63	59	1.3	NS	*	+	+	+		

Appendix 4.6. Sward characteristics of Yorkshire fog/clover and tall fescue/clover pastures under rotational grazing management in summer and early autumn, 1994.

		Herbage mass (DM kg/ha)								Bulk density (DM mg/cm ³)							
		Pre-grazing				Post-grazing				Pre-grazing				Post-grazing			
		Fog	Tall	SEM	Sig.	Fog	Tall	SEM	Sig.	Fog	Tall	SEM	Sig.	Fog	Tall	SEM	Sig.
		fescue				fescue				fescue				fescue			
Feb./1994	Per 1	3370	3380	160	NS	2190	1820	93	*	2.3	2.7	0.10	**	4.9	4.1	0.24	*
	Per 2	3040	3130	196	NS	2140	1970	177	NS	2.9	2.8	0.11	NS	4.1	4.0	0.11	NS
March/1994	Per 3	2570	2420	187	NS	1650	1480	61	+	2.8	2.6	0.13	NS	3.3	3.4	0.15	NS
	Per 4	2470	2580	75	NS	1750	1610	50	+	2.8	2.7	0.18	NS	3.5	3.4	0.10	NS

Appendix 4.7. The proportion of components of Yorkshire fog/clover and tall fescue/clover swards before and after grazing under rotational grazing management in summer and early autumn, 1994.

	Before grazing								After grazing							
	February, 1994				March, 1994				February, 1994				March, 1994			
	Fog fescue	Tall	SEM	Sig.	Fog fescue	Tall	SEM	Sig.	Fog fescue	Tall	SEM	Sig.	Fog fescue	Tall	SEM	Sig.
Sown grass leaf	45	28	2.7	*	43	48	2.9	NS	10	16	0.4	***	27	36	1.7	*
Sown grass stem	21	8	1.6	**	20	17	1.8	NS	23	11	0.7	***	25	16	1.4	**
Sown grass seed head	<1	0	0.3	NS	0	0	0.0	NS	0	0	0.0	NS	0	0	0.0	NS
Total sown grass	66	36	2.6	**	63	65	4.6	NS	33	27	1.0	*	52	52	3.1	NS
Other grass leaf	4	9	1.5	+	5	6	1.4	NS	2	5	0.2	**	3	3	0.5	NS
Other grass stem	2	12	1.0	**	3	3	0.7	NS	4	12	0.4	***	8	7	0.7	*
Other grass seed head	0	2	0.5	+	0	0	0.0	NS	0	0	0.0	NS	0	0	0.0	NS
Total other grasses	6	23	2.2	**	8	9	2.0	NS	6	17	0.5	***	11	10	1.1	NS
Clover leaf	3	4	0.6	NS	3	5	0.6	*	<1	1	0.2	NS	1	4	0.4	**
Clover petiole	1	4	1.2	NS	1	3	0.4	*	<1	<1	0.1	NS	<1	3	0.4	*
Total clover	4	8	1.7	NS	4	8	1.0	*	1	1	0.3	NS	1	7	0.8	*
Weed	<1	0	0.1	NS	0	0	0.0	NS	0	0	0.0	NS	0	0	0.0	NS
Dead Material	23	33	1.0	**	25	18	5.3	NS	60	55	1.2	*	35	31	4.2	NS

Appendix 4.8. The proportion of components in the diets selected by OF sheep grazing fog/clover and tall fescue/clover in summer and early autumn, 1994.

	Yorkshire fog				Tall fescue				Diets from			
	Sward samples ¹		Sward canopy ²		Sward ¹		Sward canopy ²		Fog	Tall fescue	SEM	Sig.
	Pre-grazing	Post-grazing	Overall	>4cm	Pre-grazing	Post-grazing	Overall	>4cm				
February												
Grasses (%)	72	39	82	90	60	44	82	92	94	94	0.9	NS
Clover (%)	4	1	10	10	9	1	12	8	1	4	0.4	NS
Weed (%)	<1	0	0	0	0	0	0	0	0	0	0.0	NS
Dead material (%)	23	60	8	0	31	55	6	0	5	5	0.8	NS
March												
Grass (%)	72	64	88	96	73	62	88	88	95	96	0.8	NS
Clover (%)	4	1	11	4	8	6	12	12	2	2	0.5	NS
Weed (%)	0	0	0	0	0	0	0	0	0	0	0	NS
Dead material (%)	24	35	1	0	19	32	<1	0	3	2	0.6	NS

¹: Herbage samples by hand separation;

²: Point quadrat data.

Appendix 4.9. Grazing behaviour of lambs grazing Yorkshire fog/clover and tall fescue/clover in summer (February, 1994)

Period 1	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
Grazing time (min)	560	550	10	560	550	10	570	540	17	560	550	17
Ruminating time (min)	320	300	14	300	320	14	300	320	14	310	310	14
Resting time (Min)	520	540	21	530	530	21	530	530	16	520	530	16
Rate of biting (bites/min)	44	45	0.8	45	44	0.8	45	44	1.0	45	44	1.0
Intake per bite (mg OM/bite)				72.7	69.6	4.4 NS						
Interaction of previous pasture x current pasture (n = 8)						F value for						
Previous pasture	Ryegrass		Fog		SEM							
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x SPP		
Grazing time (min)	580	540	550	550	15	NS	NS	NS	NS	NS		
Ruminating time (min)	320	320	290	320	21	NS	NS	NS	NS	NS		
Resting time (min)	500	530	560	520	31	NS	NS	NS	NS	NS		
Rate of biting (bites/min)	44	44	45	45	1.2	NS	NS	NS	NS	NS		
Period 2	Previous pasture			Current pasture			SEX			PEG		
Main effects (n=16)	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Grazing time (min)	640	640	13	610	670	13	630	650	11	670	610	11
Ruminating time (min)	300	270	11	290	280	10	280	290	17	290	280	18
Resting time (Min)	450	490	20	490	450	19	480	460	19	440	500	19
Rate of biting (bites/min)	46	45	0.6	44	48	0.6	47	45	1.1	47	45	1.2
Intake per bite (mg OM/bite)				71.4	52.1	3.7 **						
Interaction of previous pasture x current pasture (n = 8)						F value for						
Previous pasture	Ryegrass		Fog		SEM							
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x SPP		
Grazing time (min)	620	670	610	670	20	NS	*	NS	*	NS		
Ruminating time (min)	300	300	280	250	17	*	+	NS	NS	NS		
Resting time (min)	480	430	500	470	31	NS	NS	NS	+	NS		
Rate of biting (bites/min)	44	49	44	47	0.9	NS	**	NS	NS	NS		

Appendix 4.10. Grazing behaviour of lambs grazing Yorkshire fog/clover and tall fescue/clover in early autumn (March, 1994)

Period 1 Main effects (n=16)	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Grazing time (min)	620	630	14	610	640	13	610	640	17	630	620	17
Ruminating time (min)	260	280	16	260	270	18	290	250	27	270	270	27
Resting time (Min)	510	490	19	530	480	19	500	500	30	490	510	30
The rate of biting (bites/min)	51	51	0.6	51	51	0.6	51	51	1.5	52	50	1.5
Interaction of previous pasture x current pasture (n = 8)							F value for					
Previous pasture	Ryegrass		Fog		SEM							
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x SPP		
Grazing time (min)	590	660	630	620	22	NS	*	NS	NS	+		
Ruminating time (min)	280	240	250	310	28	NS	NS	NS	NS	NS		
Resting time (min)	530	490	520	470	30	NS	+	NS	NS	NS		
The rate of biting (bites/min)	52	51	50	51	1.0	NS	NS	NS	NS	NS		
Period 2 Main effects (n=16)	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Grazing time (min)	610	590	13	600	600	13	580	620	24	590	600	22
Ruminating time (min)	260	250	13	260	250	13	250	260	9	260	260	9
Resting time (Min)	530	560	10	540	540	10	570	520	25	550	540	3
The rate of biting (bites/min)	51	52	1.1	51	52	1.1	51	52	1.1	52	51	1.2
Intake per bite (mg OM/bite)				60.0	57.5	6.3 NS						
Interaction of previous pasture x current pasture (n = 8)							F value for					
Previous pasture	Ryegrass		Fog		SEM							
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x Spp		
Grazing time (min)	589	628	601	570	19.4	NS	NS	NS	NS	NS		
Ruminating time (min)	278	237	241	266	19.4	NS	NS	NS	NS	+		
Resting time (min)	529	530	553	559	15.4	NS	NS	NS	NS	NS		
The rate of biting (bites/min)	51	52	51	52	1.8	NS	NS	NS	NS	NS		

Appendix 4.11. Herbage OM intake of lambs grazing Yorkshire fog/clover and tall fescue/clover in summer (February, 1994)

Period 1	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
OMI (g/day)	800	670	64.5	725	745	64.5	827	643	70.3	825	644	70.3
OMI (g/kg W ^{0.75})	60	51	5.1	55	56	5.1	62	49	5.3	59	54	6.5
Interaction of previous pasture x current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x Spp		
OMI (g/day)	767	834	683	656	91.2	NS	NS	+	NS	+		
OMI (g/kg W ^{0.75})	58	62	52	51	7.2	NS	NS	NS	NS	NS		
Period 2	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
OMI (g/day)	737	772	58.9	639	870	62.1	835	674	36.3	805	703	39.8
OMI (g/kg W ^{0.75})	55	59	4.6	47	66	4.9	62	51	2.8	60	53	2.8
Interaction of previous pasture x current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp x Spp		
OMI (g/day)	660	814	617	927	96.2	NS	*	**	NS	NS		
OMI (g/kg W ^{0.75})	49	60	46	71	7.5	NS	*	*	NS	NS		

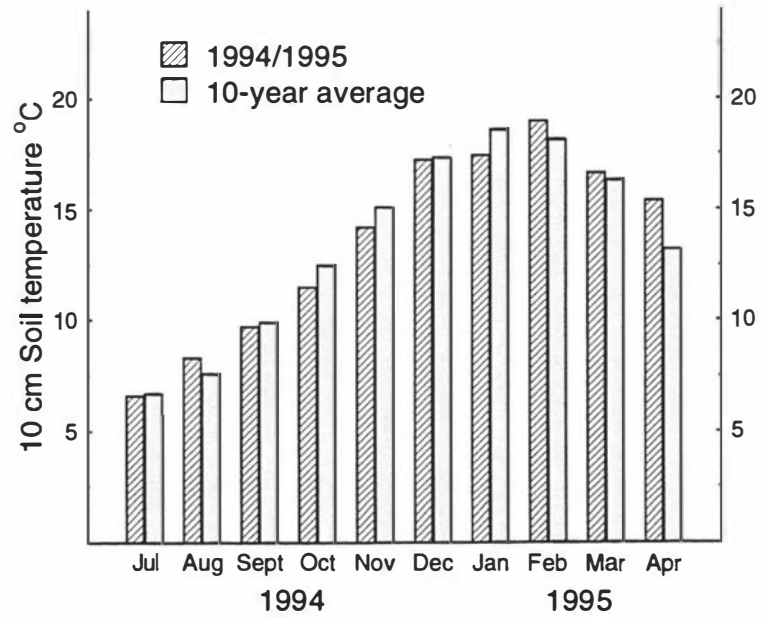
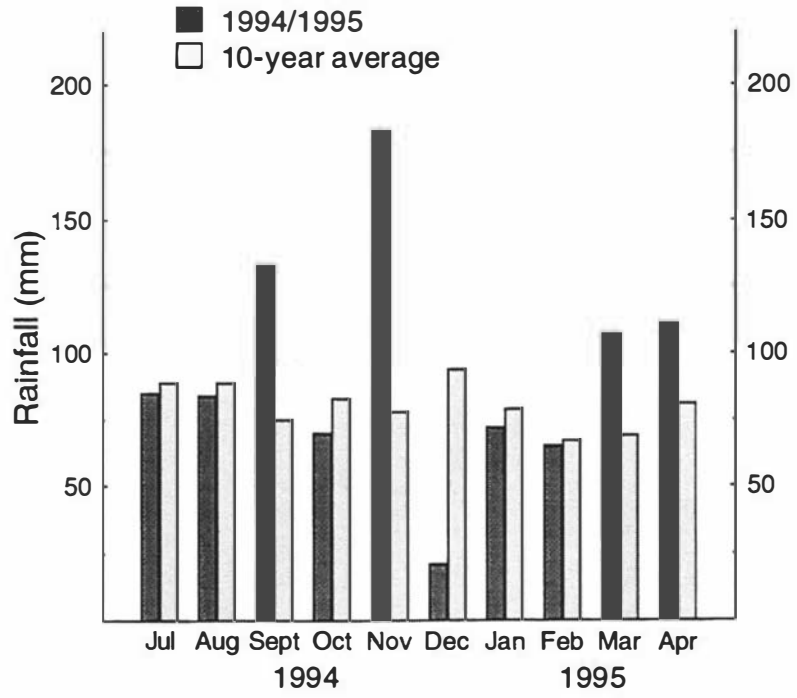
Appendix 4.12. Herbage OM intake of lambs grazing Yorkshire fog/clover and tall fescue/clover in early autumn (March, 1994)

Period 1	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
OMI (g/day)	1153	1097	101.0	1167	1084	110.0	1196	1054	115.5	1232	1018	116.9
OMI (g/kg W ^{0.75})	80	77	7.3	82	76	7.3	84	81	6.6	85	72	8.5
Interaction of previous pasture × current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp × Spp		
OMI (g/day)	1251	1055	1083	1113	156.4	NS	NS	NS	NS	NS		
OMI (g/kg W ^{0.75})	87	73	76	79	11.4	NS	NS	NS	NS	NS		
Period 2	Previous pasture			Current pasture			SEX			PEG		
	Ryegrass	Fog	SEM	Fog	Tall fescue	SEM	Male	Female	SEM	Ctrl	PEG	SEM
Main effects (n=16)												
OMI (g/day)	1151	1093	83.2	1071	1170	85.6	1236	1008	88.9	1197	1048	95.2
OMI (g/kg W ^{0.75})	79	76	5.6	74	81	5.8	84	71	6.0	81	74	6.4
Interaction of previous pasture × current pasture (n = 8)												
Previous pasture	Ryegrass		Fog		SEM	F value for						
Current pasture	Fog	Tall fescue	Fog	Tall fescue		Prvsp	Spp	Sex	PEG	Prvsp × Spp		
OMI (g/day)	1031	1274	1118	1069	121.0	NS	NS	+	NS	NS		
OMI (g/kg W ^{0.75})	71	88	78	74	8.7	NS	NS	NS	NS	NS		

Appendix 4.13. Effects of current pasture species and CT on rumen ammonia concentration of sheep grazing Yorkshire fog/clover and tall fescue/clover pastures in summer and early autumn, 1994.

Time	Main effects						Interaction of species * PEG					F value for		
	Effect of species			Effect of PEG			Fog		Tall fescue		SEM	F value for		
	Fog	Tall fescue	SEM	Ctrl	PEG	SEM	Ctrl	PEG	Ctrl	PEG		Spp	PEG	Spp x PEG
8:00	263	343	19.2	309	298	18.5	270	257	347	340	30.1	*	NS	NS
12:00	405	448	76.7	362	492	73.7	268	542	456	440	120.0	NS	NS	NS
16:00	254	360	23.5	316	298	22.6	257	251	375	345	36.9	**	NS	NS
20:00	386	481	40.4	426	441	38.9	364	407	487	474	63.5	+	NS	NS
24:00	316	377	35.0	342	351	33.6	298	333	386	368	54.9	NS	NS	NS
4:00	251	302	23.3	280	273	22.4	249	253	311	292	36.5	+	NS	NS

PEG drenching twice daily at 0830 and 1630 hrs.



Appendix 5.1 Rainfall (mm) and mean 10 cm soil temperature(°C) in 1994/95 compared with 10-year average values from the same site.

Appendix 5.2. Chemical composition of the diets selected by OF sheep in leader (L-G) and follower groups (F-G) on Yorkshire fog pasture in summer, 1994/1995.

	December		January		SEM	F values for		
	L-G	F-G	L-G	F-G		Month	L/F	L/F x Month
Total N (% DM)	2.97	2.52	2.38	2.18	0.131	***	**	NS
OMD (%)	81	74	74	70	1.1	**	*	NS
CT (g/kg DM)								
Extractable	0.80	0.78	1.03	0.95	0.055	**	NS	NS
Protein-bound	1.08	0.65	1.38	1.48	0.156	**	NS	NS
Fibre-bound	0.38	0.20	0.53	0.45	0.059	**	+	NS
Total	2.25	1.63	2.93	2.90	0.220	***	NS	NS

APPENDIX DATA

Appendix Data 3.1. Grazing behaviour in winter, 1993*

Lamb No.	SPP	PEG	Period 1				Period 2			
			GT	RUT	RST	BTRT	GT	RUT	RST	BTRT
02	1	1	585	370	440	54	480	390	525	63
05	1	2	585	395	415	52	585	360	450	70
11	1	2	555	345	495	53	600	360	435	65
14	1	2	570	410	415	58	530	330	535	63
35	1	1	570	365	460	57	615	360	420	69
38	1	1	615	390	390	56	645	345	405	72
08	2	1	585	310	500	53	570	330	495	57
18	2	2	525	395	475	60	585	390	420	59
23	2	1	600	385	410	56	585	360	450	60
45	2	2	585	385	425	53	585	360	450	56
40	2	2	540	340	515	53	630	345	420	57
50	2	1	540	385	470	60	645	375	375	63

*:Two observations were made in early June (Period 1) and late June (Period 2); Total time of observation used was 1395 minutes, and 55 minutes were used for drenching each period;

Spp: 1 = ryegrass; 2 = Yorkshire fog; PEG: 1 = NO PEG; 2 = PEG;

GT: Grazing time (min); RUT: Ruminating time (min); RST: Resting time (min); BTRT: The rate of biting (bites/min).

Appendix Data 3.2. Intake per bite (mg OM/bite), the botanical composition (%) and OMD of the diets selected By sheep in winter, 1993

Sheep	No.	Spp	Plot	IB	Botanical composition				OMD
					Grass	Clover	GRNM	DDM	
Period 1									
29	1	1	1	30.8	95.1	3.3	98.4	1.6	80.47
27	1	1	1	50.8	92.8	5.4	98.2	1.8	80.00
04	1	2	2	60.9	93.2	3.0	96.2	3.8	80.52
63	1	2	2	53.8	91.2	4.4	95.6	4.4	79.62
29	1	3	3	55.3	100.0	0.0	100.0	0.0	81.07
27	1	3	3	34.9	96.8	0.0	96.8	3.2	79.80
04	2	1	1	59.3	91.2	1.9	93.1	6.9	78.34
63	2	1	1	27.5	93.9	2.0	95.9	4.1	78.51
27	2	2	2	56.3	98.3	0.0	98.3	1.6	76.82
29	2	2	2	37.7	97.5	0.0	97.5	2.3	77.12
04	2	3	3	95.1	96.0	2.0	98.0	2.0	76.90
63	2	3	3	37.4	95.7	2.6	98.3	1.7	76.45
Period 2									
04	1	1	1	50.0	95.2	0.0	95.2	4.8	79.65
63	1	1	1	48.5	96.7	0.0	96.7	3.4	77.43
27	1	2	2	50.0	89.4	2.7	92.1	7.9	77.76
29	1	2	2	33.7	90.8	0.0	90.8	9.2	77.92
04	1	3	3	84.1	92.0	0.0	92.0	8.0	80.55
63	1	3	3	34.3	89.2	3.0	92.2	7.8	79.06
27	2	1	1	55.9	97.0	0.0	97.0	3.0	77.03
29	2	1	1	47.3	95.4	1.6	97.0	3.0	76.28
04	2	2	2	91.1	90.6	7.2	97.8	2.2	76.59
63	2	2	2	80.5	96.5	0.0	96.5	3.5	75.79
27	2	3	3	81.5	87.9	0.0	87.9	12.1	78.01
29	2	3	3	53.1	93.4	1.2	94.6	5.4	76.50

IB: Intake per bite; GRNM: Green material; DDM: Dead material.

Appendix Data 3.3. Condensed tannin concentration (CT: g/kg DM) in the diets from ryegrass/clover and Yorkshire fog/clover pastures in winter, 1993.

Pasture	Extractable	Protein-bound	Fibre-bound	Total CT
<u>Period 1</u>				
Yorkshire fog				
1	1.01	0.52	0.14	1.67
2	1.09	0.45	0.21	1.75
3	1.15	0.49	0.17	1.81
Ryegrass				
1	1.18	0.62	0.28	2.08
2	1.19	0.30	0.27	1.76
3	1.16	0.24	0.11	1.51
<u>Period 2</u>				
Yorkshire fog				
1	1.14	0.61	0.48	2.23
2	1.14	0.75	0.31	2.20
3	1.21	0.65	0.16	2.02
Ryegrass				
1	1.32	0.66	0.08	2.06
2	1.14	0.49	0.20	1.83
3	0.59	1.40	0.20	2.19

Appendix Data 3.4. Herbage intake (g OM/day) in lambs in winter, 1993

Lamb No.	SPP	PLOT	PEG	Period 1		Period 2	
				INTK1	MTTK1	INTK2	MTTK2
02	1	1	1	1324.5	99.0	1044.4	73.4
05	1	1	2	1110.4	78.4	1177.7	79.3
11	1	1	2	1044.8	75.9	1167.5	79.9
14	1	1	2	1017.7	76.1	846.3	59.5
35	1	1	1	1684.1	129.8	1308.0	93.9
38	1	1	1	1339.6	98.4	999.4	67.7
03	1	2	1	1260.8	89.5	818.5	54.8
25	1	2	1	1058.8	83.1	1002.4	76.3
27	1	2	2	1269.8	89.7	1470.8	96.1
32	1	2	1	989.2	74.4	996.5	70.0
33	1	2	2	1420.3	106.8	999.4	71.4
42	1	2	2	1026.6	83.8	1117.1	83.5
07	1	3	2	1243.1	91.9	845.2	58.7
12	1	3	1	955.8	69.8	825.5	58.3
17	1	3	2	1217.4	86.5	1034.8	70.0
36	1	3	1	959.7	73.0	1263.8	89.8
46	1	3	1	1381.5	100.9	1278.2	83.5
48	1	3	2	962.3	77.5	755.2	56.1
08	2	1	1	733.1	51.8	950.6	65.0
18	2	1	2	1222.8	89.3	1040.7	71.9
23	2	1	1	715.2	55.1	905.8	64.0
40	2	1	2	741.9	53.9	946.2	65.4
45	2	1	2	1009.9	78.8	967.1	69.5
50	2	1	1	672.9	56.0	897.9	68.3
04	2	2	1	1232.6	89.5	984.1	67.7
13	2	2	2	721.9	62.2	785.5	62.5
24	2	2	1	1030.2	81.4	800.8	58.2
30	2	2	2	1049.6	77.6	869.9	62.1
37	2	2	2	1292.1	104.1	1289.4	94.2
49	2	2	1	623.2	51.9	741.0	56.4
06	2	3	1	1088.6	79.1	1182.8	80.5
15	2	3	2	684.1	54.4	817.9	61.5
22	2	3	2	980.9	70.1	1208.3	81.0
26	2	3	2	789.5	60.8	971.6	70.2
28	2	3	1	745.5	56.4	956.5	67.2
47	2	3	1	1180.5	96.3	662.8	50.8

INTK: Herbage intake (g OM/day);

MTTK: Herbage intake (g OM/kg $W^{0.75}$ /day).

Appendix Data 3.5. Liveweight (kg), fasted weight (kg) and carcass weight (kg) of lambs at slaughter in winter, 1993

Lamb No	SPP	PLT	PEG	Liveweight							Fasted weight		Carcass weight		
				W1	W2	W3	W4	W5	W6	W7	FSW1	FSW2	CCS	LGR	RGR
02	1	1	1	29.0	32.0	34.5	34.5	35.0	35.5	36.0	27.5	33.5	16.5	16	16
05	1	1	2	32.0	34.5	36.0	37.0	38.5	39.5	40.5	30.0	37.5	18.5	18	17
11	1	1	2	30.5	33.5	35.5	36.0	38.0	39.0	39.5	28.5	36.5	18.5	8	8
14	1	1	2	29.0	32.5	34.0	35.0	37.5	38.5	39.5	27.0	36.5	17.5	7	7
35	1	1	1	28.0	31.0	33.0	33.5	35.5	36.5	37.0	25.5	34.5	16.5	10	10
38	1	1	1	30.0	33.5	36.0	36.5	37.5	38.5	39.0	28.5	36.0	17.5	5	5
03	1	2	1	31.5	34.5	36.0	37.5	39.0	40.5	41.0	29.5	37.0	18.5	13	12
25	1	2	1	26.5	29.0	30.5	31.5	32.5	33.5	34.5	25.0	31.5	15.0	6	8
27	1	2	2	31.5	35.0	37.5	38.5	40.0	40.5	41.5	29.5	38.0	19.0	7	10
32	1	2	1	29.5	32.5	34.5	34.5	35.5	36.5	37.0	27.5	34.0	16.5	9	9
33	1	2	2	29.0	32.0	33.5	34.0	35.0	36.0	36.5	27.5	34.0	17.0	10	10
42	1	2	2	25.5	29.0	31.5	32.0	33.0	33.0	33.5	23.0	30.5	14.0	9	10
07	1	3	2	31.5	33.5	34.5	35.5	36.0	38.0	39.0	29.5	35.5	17.0	5	5
12	1	3	1	31.5	33.0	34.0	34.5	35.5	36.5	37.5	29.5	35.0	17.0	8	8
17	1	3	2	31.0	34.5	36.0	36.5	38.0	39.0	40.0	29.5	37.0	18.5	8	9
36	1	3	1	29.0	32.0	33.5	34.0	36.0	36.5	38.0	27.0	35.0	17.5	7	9
46	1	3	1	30.5	34.5	37.5	38.5	39.5	41.0	42.0	28.5	39.0	18.5	10	10
48	1	3	2	27.0	29.5	31.5	32.5	33.0	34.0	34.5	25.5	31.5	15.5	9	9
08	2	1	1	33.0	34.5	35.5	36.0	36.5	38.0	38.5	31.0	35.0	17.5	10	13
18	2	1	2	31.0	33.0	35.0	35.5	36.5	37.5	37.5	29.5	34.5	17.0	12	10
23	2	1	1	29.0	31.5	33.5	35.0	36.5	37.0	37.5	27.5	33.0	16.5	9	10
40	2	1	2	31.5	33.5	35.0	35.5	36.0	37.5	38.5	30.0	35.5	18.0	7	10
45	2	1	2	28.5	31.5	33.0	34.0	35.0	36.0	36.0	27.0	33.0	16.0	6	6
50	2	1	1	25.5	28.5	30.5	31.5	32.5	32.5	33.0	24.0	30.5	14.5	8	8
04	2	2	1	31.5	33.5	35.0	36.0	37.0	38.5	39.0	29.5	36.0	18.0	11	15
13	2	2	2	25.0	26.5	29.0	29.5	30.5	31.5	32.0	24.0	29.5	14.0	5	5
24	2	2	1	27.0	30.0	32.5	33.5	34.5	35.5	36.0	26.0	33.0	15.0	5	6
30	2	2	2	31.5	33.0	33.5	34.0	35.0	36.5	37.0	29.5	34.0	16.5	4	5
37	2	2	2	26.0	29.5	32.5	33.0	34.0	35.5	36.0	24.0	33.0	15.0	9	10
49	2	2	1	26.0	28.5	30.5	31.5	32.5	34.0	34.5	24.5	31.5	15.0	8	8
06	2	3	1	31.5	33.5	35.5	36.5	38.0	39.5	40.5	29.5	37.0	18.0	17	17
15	2	3	2	28.0	29.5	31.5	31.5	32.5	34.0	34.5	26.5	32.5	15.0	8	7
22	2	3	2	32.5	34.0	36.5	37.0	38.5	39.5	40.5	30.5	37.5	19.5	16	15
26	2	3	2	30.5	31.5	33.0	33.5	34.5	35.5	37.0	27.5	34.0	15.5	10	9
28	2	3	1	29.0	32.0	34.5	34.5	35.5	36.5	37.0	27.5	34.5	16.0	10	9
47	2	3	1	26.0	29.0	30.5	31.0	32.0	33.0	33.5	25.0	30.5	14.5	8	8

W1..W7: Liveweight recorded weekly; FSW1 & FSW2: Initial and final fasted weight;
CCS: Carcass weight at slaughter; LGR & RGR: GR on the left and right sides.

Appendix Data 3.6. Wool weight (g/100cm²) and wool growth rate (mg/100cm²) in winter, 1993.

Lamb No.	SPP	PLT	PEG	CWL1	CWL2	WLGTH
02	1	1	1	10.78	2.94	70.00
05	1	1	2	7.13	2.55	60.71
11	1	1	2	13.11	3.94	93.81
14	1	1	2	12.20	4.26	101.43
35	1	1	1	13.64	3.58	85.24
38	1	1	1	12.84	3.54	84.29
03	1	2	1	12.16	3.73	88.81
25	1	2	1	9.49	2.40	57.14
27	1	2	2	13.33	4.44	105.71
32	1	2	1	10.19	2.91	69.29
33	1	2	2	14.07	4.96	118.10
42	1	2	2	11.43	3.45	82.14
07	1	3	2	10.63	4.05	96.43
12	1	3	1	8.46	3.66	87.14
17	1	3	2	10.59	3.46	82.38
36	1	3	1	13.48	4.32	102.86
46	1	3	1	12.08	3.28	78.10
48	1	3	2	10.39	4.11	97.86
08	2	1	1	8.70	2.92	69.52
18	2	1	2	7.68	2.14	50.95
23	2	1	1	10.40	3.54	84.29
40	2	1	2	10.80	3.21	76.43
45	2	1	2	9.47	2.73	65.00
50	2	1	1	8.92	2.92	69.52
04	2	2	1	9.84	2.41	57.38
13	2	2	2	13.94	2.78	66.19
24	2	2	1	11.99	4.44	105.71
30	2	2	2	9.16	3.03	72.14
37	2	2	2	10.19	4.62	110.00
49	2	2	1	9.35	3.82	90.95
06	2	3	1	9.25	4.38	104.29
15	2	3	2	9.85	2.71	64.52
22	2	3	2	11.09	3.43	81.67
26	2	3	2	12.28	2.95	70.24
28	2	3	1	8.94	3.38	80.48
47	2	3	1	11.39	3.50	83.33

CWL1 & CWL2: initial and final wool weights;
WLGTH: Wool growth rate.

Appendix Data 4.1. The rate of biting in spring and early summer, 1993/1994.

Lamb No.	PRVSP	SPP	SEX	PEG	BTRT1	BTRT2
03	1	1	1	1	46	41
04	1	1	2	2	43	44
05	1	1	2	1	43	43
12	1	1	1	2	40	43
14	1	1	2	1	43	44
15	1	1	2	2	43	40
22	1	1	1	1	41	43
26	1	1	1	2	41	44
33	2	1	1	1	41	44
35	2	1	2	1	44	38
39	2	1	2	1	44	38
46	2	1	1	2	41	44
47	2	1	1	2	43	41
53	2	1	1	1	43	40
54	2	1	2	2	44	43
56	2	1	2	2	43	46
02	1	2	1	1	43	41
09	1	2	2	1	43	41
10	1	2	2	2	40	40
19	1	2	1	2	40	43
20	1	2	1	2	41	40
25	1	2	2	2	43	41
27	1	2	1	1	44	43
30	1	2	2	1	40	38
34	2	2	1	1	46	41
37	2	2	1	2	44	40
41	2	2	1	1	43	38
42	2	2	1	2	44	43
55	2	2	2	2	43	40
58	2	2	2	2	43	40
59	2	2	2	1	48	41
60	2	2	2	1	43	40

Prvsp (previous pasture): 1 = ryegrass; 2 = fog; Spp (current pasture): 1 = fog; 2 = Tall fescue; Sex: 1 = Male; 2 = Female; PEG: 1 = NO PEG; 2 = PEG;

Appendix Data 4.2. Grazing behaviour in spring and early summer, 1993/1994

Sheep No.	PRVSP	SPP	SEX	PEG	Period 1			Period 2		
					GT	RUT	RST	GT	RUT	RST
03	1	1	1	1	585	300	465	495	360	495
04	1	1	2	2	570	300	480	570	285	495
05	1	1	2	1	525	315	510	540	285	525
12	1	1	1	2	645	255	450	555	300	495
14	1	1	2	1	555	285	510	660	330	360
15	1	1	2	2	615	300	435	570	255	525
22	1	1	1	1	510	300	540	555	270	525
26	1	1	1	2	510	405	435	615	270	465
33	2	1	1	1	630	315	405	570	330	450
35	2	1	2	1	540	285	525	600	225	525
39	2	1	2	1	555	270	525	450	225	675
46	2	1	1	2	600	255	495	555	375	420
47	2	1	1	2	540	270	540	600	285	465
53	2	1	1	1	615	255	480	615	315	420
54	2	1	2	2	645	270	435	540	315	495
56	2	1	2	2	615	315	420	540	345	465
02	1	2	1	1	450	240	660	510	375	465
09	1	2	2	1	585	285	480	570	390	390
10	1	2	2	2	555	195	600	585	330	435
19	1	2	1	2	510	270	570	570	285	495
20	1	2	1	2	600	225	525	615	360	375
25	1	2	2	2	525	255	570	510	270	570
27	1	2	1	1	540	285	525	570	315	465
30	1	2	2	1	540	255	555	510	270	570
34	2	2	1	1	585	225	540	570	285	495
37	2	2	1	2	555	240	555	645	300	405
41	2	2	1	1	495	270	585	480	315	555
42	2	2	1	2	525	285	540	525	300	525
55	2	2	2	2	510	255	585	570	255	525
58	2	2	2	2	450	270	630	555	255	540
59	2	2	2	1	540	270	540	540	210	600
60	2	2	2	1	645	330	375	585	285	480

GT: grazing time; RUT: Ruminating time; RST: Resting time.

Appendix Data 4.3. Intake per bite (mg OM/bite), the botanical composition (%) and OMD (%) of the diets in spring and early summer, 1993/1994.

Sheep No	Spp	Day [#]	IB	Botanical composition %				OMD
				Grass	Clover	GRNM	DDM	
Period 1								
04	1	1	75.7	97.4	2.6	98.7	1.3	82.08
27	1	1	83.5	97.7	2.3	98.9	1.1	80.90
29	1	2	97.0	98.8	1.3	97.6	2.4	77.62
63	1	2	55.9	97.7	2.3	98.9	1.1	79.43
04	1	3	86.3	98.8	1.3	97.6	2.4	77.01
27	1	3	96.9	99.0	1.0	96.0	4.0	77.07
29	1	4	97.8	97.3	2.8	96.1	3.9	75.83
63	1	4	63.7	100.0	0.0	97.4	2.6	78.81
04	1	5	89.8	98.8	1.3	96.4	3.6	74.96
27	1	5	83.3	100.0	0.0	96.6	3.3	80.15
63	2	1	62.2	97.5	2.5	100.0	0.0	85.04
29	2	1	106.1	95.4	4.6	98.5	1.5	84.05
04	2	2	68.0	97.4	2.6	97.4	2.6	79.46
27	2	2	70.7	98.5	1.5	98.5	1.5	84.41
29	2	3	62.8	97.7	2.3	96.6	3.4	81.58
63	2	3	64.3	96.8	1.6	98.4	1.6	80.71
04	2	4	74.7	98.6	1.4	100.0	0.0	77.01
27	2	4	65.5	100.0	0.0	99.0	1.0	79.15
63	2	5	52.2	100.0	0.0	97.8	2.2	80.77
29	2	5	63.1	98.8	1.3	96.4	3.6	81.55
Period 2								
04	1	1	87.7	97.9	2.1	97.9	2.1	80.23
27	1	1	97.9	98.8	1.2	98.9	1.1	81.45
63	1	2	75.3	100.0	0.0	90.7	9.3	80.81
29	1	2	114.6	98.8	1.2	96.4	3.6	80.50
27	1	3	107.8	98.4	1.6	95.5	4.5	79.43
04	1	3	74.6	98.8	1.2	95.4	4.6	78.08
63	1	4	68.5	100.0	0.0	96.3	3.8	77.74
29	1	4	74.7	97.7	2.3	95.6	4.4	78.49
27	1	5	84.7	98.6	1.4	95.8	4.2	80.27
04	1	5	85.3	98.7	1.3	96.3	3.7	79.61
63	2	1	96.5	96.5	3.5	100.0	0.0	81.43
29	2	1	81.7	96.8	3.2	100.0	0.0	71.86
27	2	2	75.3	98.6	1.4	97.3	2.7	81.58
04	2	2	95.9	100.0	0.0	98.6	1.4	80.56
63	2	3	83.3	98.4	1.6	98.4	1.6	81.52
29	2	3	55.0	98.6	1.4	98.6	1.4	81.59
27	2	4	73.8	98.2	1.8	96.5	3.5	81.46
04	2	4	78.2	98.6	1.4	98.6	1.4	72.15
29	2	5	86.9	97.0	3.0	100.0	0.0	76.85
63	2	5	74.6	97.6	2.4	98.8	1.2	76.86

*: A continuous five day sampling was made in each pasture.

Appendix Data 4.4. Condensed tannin concentration (CT: g/kg DM) and N (% DM) in the diets from Yorkshire fog/clover and tall fescue/clover pastures in late spring (Dec., 1993).

Pasture	CT			Total CT	N
	Extractable	Protein-bound	Fibre-bound		
Period 1					
Yorkshire fog					
1	0.14	1.31	0.44	1.89	3.403
2	0.15	1.31	0.42	1.88	3.454
Tall fescue					
1	0.08	0.76	0.36	1.20	3.157
2	0.21	0.83	0.39	1.43	2.896
Period 2					
Yorkshire fog					
1	0.20	1.59	0.33	2.12	3.558
2	0.15	1.31	0.42	1.88	3.566
Tall fescue					
1	0.22	0.63	0.24	1.09	2.835
2	0.17	0.66	0.33	1.16	3.097

Appendix Data 4.5. Herbage intake (g OM/day) in spring and early summer, 1993/1994

Lamb No.	PRVSP	SPP	SEX	PEG	Period 1		Period 2	
					INTK1	MTTK1	INTK2	MTTK2
03	1	1	1	1	825.6	66.1	951.0	73.3
04	1	1	2	2	384.3	31.6	681.7	54.6
05	1	1	2	1	878.8	73.2	879.5	71.3
12	1	1	1	2	824.0	62.7	876.7	65.2
14	1	1	2	1	717.8	54.6	985.9	73.3
15	1	1	2	2	566.9	44.2	750.1	57.8
22	1	1	1	1	896.1	67.4	920.8	67.6
26	1	1	1	2	728.0	54.1	905.1	65.0
33	2	1	1	1	742.8	60.2	849.6	66.3
35	2	1	2	1	721.6	61.8	751.9	61.8
39	2	1	2	1	921.5	74.7	738.9	59.2
46	2	1	1	2	828.9	67.0	739.3	60.7
47	2	1	1	2	636.0	47.8	895.4	65.0
53	2	1	1	1	647.0	50.5	854.6	64.3
54	2	1	2	2	1089.2	90.7	748.1	59.9
56	2	1	2	2	850.6	66.4	836.5	62.9
02	1	2	1	1	1039.2	81.1	860.4	64.7
09	1	2	2	1	675.1	57.0	747.3	61.4
10	1	2	2	2	518.0	40.4	626.5	47.7
19	1	2	1	2	810.1	63.2	1007.8	76.7
20	1	2	1	2	467.2	36.9	721.1	55.6
25	1	2	2	2	854.7	66.7	774.5	57.6
27	1	2	1	1	878.9	67.7	806.9	60.7
30	1	2	2	1	405.1	31.2	753.1	56.6
34	2	2	1	1	856.1	65.2	814.5	61.3
37	2	2	1	2	739.4	59.9	720.1	56.9
41	2	2	1	1	1166.3	99.9	883.6	72.6
42	2	2	1	2	877.4	66.8	742.9	55.2
55	2	2	2	2	866.5	71.2	757.3	62.2
58	2	2	2	2	645.2	53.7	532.3	43.7
59	2	2	2	1	740.8	60.9	633.8	51.4
60	2	2	2	1	955.3	77.4	849.7	67.1

INTK: Herbage intake; MTTK: Intake in terms of metabolic weight (kg W^{0.75})

Appendix Data 4.6. Liveweight (kg) of lambs measured weekly in spring and early summer, 1993/1994.

Lamb No.	SPP	PRVSP	SEX	PEG	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
03	1	1	1	1	28.5	29.0	30.5	31.5	32.5	33.0	33.5	34.5	36.5	37.0
04	1	1	2	2	27.5	28.0	29.0	29.5	30.0	30.5	30.5	31.0	32.0	32.5
05	1	1	2	1	27.0	27.5	28.5	29.5	30.0	30.5	31.5	32.5	33.0	33.5
12	1	1	1	2	30.5	31.0	32.0	32.5	33.0	33.5	34.0	34.5	35.0	36.0
14	1	1	2	1	30.5	31.0	32.0	33.5	34.0	35.0	36.0	36.5	37.5	38.0
15	1	1	2	2	29.5	30.0	30.5	31.5	32.5	33.0	34.0	34.5	35.5	36.5
22	1	1	1	1	30.5	31.5	32.5	33.5	35.0	36.0	36.5	38.0	39.5	41.0
26	1	1	1	2	31.0	32.0	33.5	34.5	36.0	36.5	37.0	38.5	39.5	40.5
33	1	2	1	1	28.0	28.5	30.0	31.0	32.0	33.0	33.5	34.0	35.5	35.5
35	1	2	2	1	26.0	26.5	28.0	29.0	29.5	30.0	31.0	32.0	32.5	34.0
39	1	2	2	1	28.0	28.5	29.0	29.5	30.0	30.5	31.0	32.0	33.0	34.0
46	1	2	1	2	26.5	27.0	28.0	28.5	30.0	30.5	31.0	32.0	32.5	33.5
47	1	2	1	2	31.0	31.5	33.0	33.5	34.5	35.5	36.0	37.0	38.0	38.5
53	1	2	1	1	29.5	30.0	31.5	32.5	33.5	34.0	34.5	36.0	37.0	37.5
54	1	2	2	2	27.5	27.5	29.0	29.5	30.0	30.5	31.0	32.5	33.5	34.0
56	1	2	2	2	29.0	30.0	31.5	32.5	33.0	34.0	35.0	36.0	37.5	38.5
02	2	1	1	1	29.5	30.0	31.5	32.5	33.0	33.5	33.5	34.0	34.5	35.0
09	2	1	2	1	26.5	27.0	28.0	29.0	29.5	30.0	30.5	31.0	32.5	33.0
10	2	1	2	2	29.5	30.0	31.0	32.0	32.5	33.0	33.5	33.5	34.5	35.5
19	2	1	1	2	29.5	30.0	31.0	31.5	32.5	33.5	34.0	34.5	35.0	36.0
20	2	1	1	2	29.0	29.5	30.5	31.5	32.0	32.5	33.0	34.5	35.5	35.5
25	2	1	2	2	29.5	30.0	32.0	33.0	33.5	34.0	34.5	35.0	35.5	35.5
27	2	1	1	1	29.5	30.5	31.5	33.0	34.0	35.0	35.5	36.0	37.0	37.5
30	2	1	2	1	30.0	30.5	31.5	32.5	33.5	34.5	35.0	35.5	36.5	36.5
34	2	2	1	1	30.5	31.0	31.5	32.5	33.0	33.5	34.0	35.0	35.5	35.5
37	2	2	1	2	28.0	28.5	29.5	30.0	30.5	30.5	31.0	31.5	32.5	32.5
41	2	2	1	1	26.0	26.5	28.0	28.5	29.0	29.5	30.0	30.5	31.5	32.5
42	2	2	1	2	30.0	31.0	32.0	33.0	34.0	34.5	34.5	35.0	35.5	36.0
55	2	2	2	2	27.5	28.0	28.0	28.5	29.5	30.0	30.5	31.5	32.5	32.5
58	2	2	2	2	27.0	27.5	28.0	29.0	30.0	30.5	31.0	32.0	32.5	33.0
59	2	2	2	1	27.5	28.0	28.5	29.5	30.0	30.0	30.5	31.0	31.0	31.5
60	2	2	2	1	27.5	28.5	29.5	30.5	31.0	31.5	32.0	33.0	33.5	34.0

W1..W10: Liveweight of lambs recorded weekly.

Appendix Data 4.7. Fasted weight (kg) and carcass weight (kg) in lambs in spring and early summer, 1993/1994.

Lamb No.	PRVSP	SPP	SEX	PEG	FSW1	FSW2	FSW3	CCSW	LGR	RGR
3	1	1	1	1	26.5	30.0	34.0	-	-	-
4	1	1	2	2	26.0	28.0	30.0	13.5	4.0	4.0
5	1	1	2	1	25.5	28.0	31.0	14.5	4.0	4.5
12	1	1	1	2	28.0	30.0	33.0	14.5	7.0	5.0
14	1	1	2	1	28.5	32.5	34.5	15.0	4.0	5.0
15	1	1	2	2	27.0	30.0	33.5	15.5	4.0	5.0
22	1	1	1	1	28.0	32.5	37.0	16.5	6.0	6.0
26	1	1	1	2	29.0	33.0	36.5	-	-	-
33	2	1	1	1	26.0	29.0	32.5	-	-	-
35	2	1	2	1	24.5	27.0	31.0	14.0	8.0	9.0
39	2	1	2	1	25.5	28.0	31.5	-	-	-
46	2	1	1	2	25.0	28.0	30.5	-	-	-
47	2	1	1	2	28.5	31.5	35.5	16.0	8.0	9.0
53	2	1	1	1	27.5	31.0	34.5	15.0	5.0	5.0
54	2	1	2	2	25.0	27.0	30.0	13.5	3.0	3.5
56	2	1	2	2	27.0	30.5	35.0	-	-	-
2	1	2	1	1	27.5	30.5	32.0	13.5	3.0	3.0
9	1	2	2	1	24.5	27.5	30.0	-	-	-
10	1	2	2	2	28.0	30.5	33.5	15.0	5.0	4.0
19	1	2	1	2	27.0	29.5	32.5	14.0	4.0	5.0
20	1	2	1	2	27.0	29.5	32.5	13.5	4.0	3.0
25	1	2	2	2	27.5	31.0	32.5	-	-	-
27	1	2	1	1	27.5	31.5	34.0	15.0	5.5	4.5
30	1	2	2	1	28.0	31.5	33.0	-	-	-
34	2	2	1	1	28.0	30.0	32.5	14.5	5.0	6.0
37	2	2	1	2	26.5	28.5	30.0	13.5	3.0	3.0
41	2	2	1	1	24.0	27.0	30.0	13.0	2.0	3.0
42	2	2	1	2	28.5	31.5	32.5	14.5	6.0	8.0
55	2	2	2	2	25.0	27.0	29.0	13.0	5.0	5.0
58	2	2	2	2	25.0	28.0	30.5	13.5	4.0	4.0
59	2	2	2	1	25.5	27.5	29.0	13.0	6.0	8.0
60	2	2	2	1	25.5	28.5	31.0	14.0	3.0	3.0

FSW: Fasted weight. CCS: Carcass weight; -: Missing data.

Appendix Data 4.8. Wool weight (g/100cm²) and wool growth rate (mg/100cm² per day) in spring and early summer, 1993/1994.

Lamb No.	PRVSP	SPP	SEX	PEG	CWL1	CWL2	CWL3	WLGTH1	WLGTH2
03	1	1	1	1	10.90	3.45	4.46	127.66	127.32
04	1	1	2	2	14.64	2.89	4.51	107.13	128.97
05	1	1	2	1	13.26	3.35	4.60	124.07	131.35
12	1	1	1	2	14.46	3.79	3.82	140.38	109.24
14	1	1	2	1	11.74	2.61	3.47	96.72	99.01
15	1	1	2	2	12.33	3.40	4.08	125.75	116.50
22	1	1	1	1	7.94	2.23	3.05	82.55	87.14
26	1	1	1	2	9.61	3.42	3.76	126.80	107.42
33	2	1	1	1	11.59	2.82	4.06	104.35	116.02
35	2	1	2	1	15.35	3.79	5.12	140.34	146.15
39	2	1	2	1	9.74	3.39	3.19	125.71	91.17
46	2	1	1	2	11.28	3.26	3.79	120.57	108.29
47	2	1	1	2	12.59	2.80	3.75	103.82	107.04
53	2	1	1	1	10.73	2.95	4.13	109.33	117.95
54	2	1	2	2	11.06	3.92	3.68	145.07	105.01
56	2	1	2	2	15.18	3.22	5.73	119.15	163.62
02	1	2	1	1	8.93	2.96	3.03	109.78	86.52
09	1	2	2	1	11.87	3.22	3.72	119.26	106.17
10	1	2	2	2	11.91	3.29	3.12	122.03	89.21
19	1	2	1	2	11.99	3.36	3.11	124.26	88.80
20	1	2	1	2	11.12	3.21	3.99	119.04	114.14
25	1	2	2	2	12.46	3.04	3.77	112.46	107.82
27	1	2	1	1	9.68	2.79	3.53	103.28	100.96
30	1	2	2	1	10.97	2.99	3.77	110.90	107.72
34	2	2	1	1	13.71	3.55	3.26	131.43	93.10
37	2	2	1	2	11.53	3.51	3.42	130.04	97.70
41	2	2	1	1	10.79	3.18	3.80	117.72	108.54
42	2	2	1	2	11.28	2.72	3.37	100.64	96.43
55	2	2	2	2	15.58	3.96	3.84	146.70	109.80
58	2	2	2	2	15.35	3.37	3.57	124.92	102.12
59	2	2	2	1	15.23	4.11	3.62	152.35	103.40
60	2	2	2	1	11.70	3.51	3.44	130.11	98.40

CWL: Wool weight. WLGTH: Wool growth rate.

Appendix Data 4.9. The rate of biting in summer and early autumn, 1994

Lamb No.	SPP	PRVSP	SEX	PEG	Feb.		March	
					BTRT1	BTRT2	BTRT3	BTRT4
101	1	2	2	2	35	40	46	48
102	1	2	2	2	46	48	57	57
106	1	2	2	1	43	43	55	50
113	1	2	1	1	46	46	55	52
114	1	2	2	1	48	41	55	55
116	1	2	1	2	52	43	-	-
118	1	2	1	2	44	44	46	50
119	1	2	1	1	43	43	44	52
131	1	1	2	2	43	41	48	52
135	1	1	1	2	46	46	52	52
136	1	1	1	1	48	48	50	50
137	1	1	2	1	40	43	50	44
142	1	1	1	2	46	44	55	52
143	1	1	2	1	46	43	55	57
144	1	1	2	2	-	-	-	-
151	1	1	1	1	43	43	52	48
103	2	2	2	2	46	50	52	55
104	2	2	1	1	44	46	-	-
109	2	2	2	1	48	48	52	52
111	2	2	2	1	43	50	50	55
112	2	2	2	2	39	39	52	52
115	2	2	1	2	48	46	50	50
120	2	2	1	2	44	-	-	-
124	2	2	1	1	44	55	52	52
132	2	1	1	1	48	46	50	50
138	2	1	2	2	43	43	-	-
139	2	1	1	2	43	50	52	52
140	2	1	1	2	41	52	52	55
145	2	1	1	1	44	50	55	48
147	2	1	2	1	43	52	57	57
148	2	1	2	1	44	48	50	57
149	2	1	2	2	46	50	46	50

-: Missing data; BTRT: The rate of biting;

PRVSP: 1=ryegrass; 2=Fog; SPP: 1= Fog; 2= Tall fescue.

Appendix Data 4.10a. Grazing behaviour in summer (Feb., 1994).

Lamb No.	SPP	PRVSP	SEX	PEG	Period 1			Period 2		
					GT	RUT	RST	GT	RUT	RST
101	2	1	2	2	525	285	585	585	390	420
102	2	1	2	2	600	300	495	630	240	525
106	2	1	2	1	525	255	615	585	315	495
113	2	1	1	1	630	285	480	675	255	465
114	2	1	2	1	495	375	525	645	390	360
116	2	1	1	2	480	225	690	525	225	645
118	2	1	1	2	480	225	690	600	195	600
119	2	1	1	1	630	330	435	615	255	525
131	1	1	2	2	555	405	435	570	330	495
135	1	1	1	2	630	285	480	555	375	465
136	1	1	1	1	615	330	450	675	270	450
137	1	1	2	1	555	270	570	660	210	525
142	1	1	1	2	615	315	465	585	375	435
143	1	1	2	1	525	315	555	570	345	480
151	1	1	1	1	585	240	570	630	285	480
103	2	2	2	2	645	300	450	690	225	480
104	2	2	1	1	480	405	510	690	375	330
109	2	2	2	1	525	315	555	690	255	450
111	2	2	2	1	525	300	570	750	225	420
112	2	2	2	2	480	285	630	645	225	525
115	2	2	1	2	540	345	510	570	255	570
120	2	2	1	2	570	390	435	-	-	-
124	2	2	1	1	660	225	510	735	210	450
132	1	2	1	1	450	330	615	675	315	405
138	1	2	2	2	510	270	615	690	330	375
139	1	2	1	2	540	240	615	615	210	570
140	1	2	1	2	600	285	510	660	255	480
145	1	2	1	1	600	315	480	720	255	420
147	1	2	2	1	585	360	450	600	240	555
148	1	2	2	1	540	360	495	660	375	360
149	1	2	2	2	525	390	480	720	285	390

GT: Grazing time (min); RUT: Ruminating time (min); RST: Resting time (min).

Appendix Data 4.10b. Grazing behaviour in early autumn (March, 1994) (Cont.).

Lamb No.	PRVSP	SPP	SEX	PEG	Period 3			Period 4		
					GT	RUT	RST	GT	RUT	RST
101	2	1	2	2	600	285	510	570	270	555
102	2	1	2	2	615	195	585	690	270	435
106	2	1	2	1	600	315	480	645	255	495
113	2	1	1	1	615	240	540	615	240	540
114	2	1	2	1	630	270	495	600	240	555
118	2	1	1	2	630	210	555	570	225	600
119	2	1	1	1	690	285	420	555	180	660
131	1	1	2	2	585	240	570	585	285	525
135	1	1	1	2	615	240	540	600	315	480
136	1	1	1	1	570	360	465	600	150	645
137	1	1	2	1	600	195	600	600	315	480
142	1	1	1	2	615	345	435	525	330	540
143	1	1	2	1	585	315	495	660	240	495
151	1	1	1	1	540	240	615	540	270	585
103	2	2	2	2	690	225	480	600	240	555
109	2	2	2	1	735	240	420	555	255	585
111	2	2	2	1	570	255	570	675	255	465
112	2	2	2	2	735	315	345	540	285	570
115	2	2	1	2	555	405	435	585	225	585
124	2	2	1	1	615	270	510	540	345	510
132	1	2	1	1	675	375	345	630	225	540
139	1	2	1	2	570	315	510	570	240	585
140	1	2	1	2	585	210	600	570	225	600
145	1	2	1	1	690	180	525	675	240	480
147	1	2	2	1	765	180	450	690	210	495
148	1	2	2	1	645	285	465	570	225	600
149	1	2	2	2	705	210	480	645	270	480

Appendix data 4.11. Intake per bite (mg OM/bite), the botanical composition (%) and OMD (%) of the diets in summer and early autumn, 1994.

Sheep No	SPP	PER	DAY	IB	Botanical composition %				OMD
					Grass	Clover	GRNM	DDM	
27	1	1	1	78.0	98.8	1.2	100.0	0.0	77.45
63	1	1	1	90.3	95.4	1.4	96.8	3.2	72.85
27	1	1	2	71.4	92.4	1.0	93.4	6.6	72.80
63	1	1	2	47.7	93.1	1.2	93.3	6.7	73.13
04	1	1	3	99.5	95.5	1.3	96.8	3.2	75.76
29	1	1	3	63.5	90.9	2.3	93.2	6.8	74.80
04	1	1	4	72.4	89.2	1.0	90.2	9.8	69.08
29	1	1	4	58.8	94.4	1.2	95.6	4.4	72.02
04	1	2	1	104.0	95.6	1.2	96.8	3.2	75.78
29	1	2	1	83.6	94.6	0.0	94.6	5.4	67.02
27	1	2	2	69.6	93.5	3.3	96.8	3.2	69.72
63	1	2	2	63.5	91.7	3.0	94.7	5.3	69.77
04	1	2	3	65.0	95.6	1.2	96.8	3.2	67.04
29	1	2	3	56.6	96.6	0.6	97.2	2.3	70.09
27	1	2	4	73.8	90.0	0.0	90.0	10.0	59.41
63	1	2	4	54.6	94.0	1.1	95.1	4.9	62.63
04	1	3	1	106.3	80.2	15.1	95.3	4.7	79.36
63	1	3	1	51.9	97.7	2.3	100.0	0.0	79.31
27	1	3	2	66.8	95.1	1.9	97.0	3.0	76.47
29	1	3	2	50.5	96.3	2.5	98.8	1.2	78.18
04	1	3	3	84.6	96.7	1.3	98.0	2.0	76.62
63	1	3	3	45.8	96.1	1.1	97.2	2.8	74.39
27	1	3	4	48.1	91.1	3.3	94.4	5.6	75.70
29	1	3	4	49.9	94.4	2.1	96.5	3.5	74.79
04	1	3	5	60.1	96.7	0.0	96.7	3.3	75.99
63	1	3	5	36.0	90.5	4.5	95.0	5.0	78.08
04	2	1	1	92.1	94.5	4.5	99.0	1.0	71.24
29	2	1	1	78.1	97.6	0.0	97.6	2.4	76.66
04	2	1	2	57.3	84.9	2.9	87.8	12.2	68.55
29	2	1	2	65.5	96.8	0.0	96.8	3.2	70.62
27	2	1	3	56.6	92.7	3.7	96.3	3.7	70.97
63	2	1	3	51.6	91.0	1.2	92.2	7.8	73.39
27	2	1	4	76.5	89.3	0.0	89.3	10.7	68.71
63	2	1	4	79.6	93.5	0.0	93.5	6.5	69.57
27	2	2	1	57.0	97.2	0.0	97.2	2.8	68.71
63	2	2	1	51.7	93.3	1.5	94.8	5.2	71.13
04	2	2	2	57.1	97.5	0.0	97.5	2.5	77.08
29	2	2	2	50.4	96.0	0.0	96.0	4.0	75.20
27	2	2	3	65.0	93.3	4.0	97.3	2.7	74.74
63	2	2	3	49.3	97.6	0.0	97.6	2.4	68.68
04	2	2	4	43.3	98.6	0.0	98.6	1.4	71.27
29	2	2	4	55.5	94.0	2.2	96.2	3.8	69.00
27	2	3	1	73.3	96.7	2.2	98.9	1.1	80.66
29	2	3	1	64.5	94.0	2.2	96.0	4.0	78.07
04	2	3	2	95.7	97.6	0.0	97.6	2.4	81.85
63	2	3	2	51.2	94.6	1.4	96.0	4.0	82.02
27	2	3	3	69.7	94.8	4.1	98.9	1.1	77.68
29	2	3	3	56.0	97.7	1.8	99.5	0.5	72.76
04	2	3	4	50.6	93.4	2.0	95.4	4.6	77.32
63	2	3	4	36.9	94.9	3.3	98.2	1.8	77.43
27	2	3	5	44.3	94.2	2.1	96.3	3.7	78.72
29	2	3	5	32.6	97.8	0.8	98.6	1.4	80.06

Appendix Data 4.12. Condensed tannin concentration (CT: g/kg DM) and N (% DM) in the diets from Yorkshire fog/clover and tall fescue/clover pastures in summer and early autumn, 1994.

Pasture	CT				N
	Extractable	Protein-bound	Fibre-bound	Total	
Period 1					
Yorkshire fog					
1	0.24	1.28	0.49	2.01	3.179
2	0.47	1.24	0.54	2.25	3.084
Tall fescue					
1	0.04	0.95	0.39	1.38	3.006
2	0.05	0.84	0.40	1.29	3.011
Period 2					
Yorkshire fog					
1	0.41	1.12	0.51	2.04	2.892
2	0.44	1.22	0.51	2.17	2.928
Tall fescue					
1	0.00	0.72	0.36	1.08	3.242
2	0.00	0.85	0.38	1.23	3.227
Period 4*					
Yorkshire fog					
1	0.51	0.79	0.35	1.65	3.851
2	0.52	0.85	0.39	1.76	3.876
Tall fescue					
1	0.00	0.82	0.30	1.12	3.847
2	0.00	0.83	0.40	1.23	3.871

*: Extrusa samples were collected in late March, not in early March (Period 3).

Appendix Data 4.13a. Herbage intake (g OM/day) in lambs in summer (Feb., 1994).

Lamb No.	SPP	PRVSP	SEX	PEG	Period 1		Period 2	
					INTK1	MTTK1	INTK2	MTTK2
101	2	1	2	2	288.0	23.0	224.1	17.7
102	2	1	2	2	730.8	56.3	687.1	51.7
106	2	1	2	1	838.4	60.9	729.4	52.4
113	2	1	1	1	713.7	51.8	596.8	43.3
114	2	1	2	1	833.0	63.4	655.5	48.7
116	2	1	1	2	400.7	32.1	382.4	30.2
118	2	1	1	2	918.7	72.6	823.8	64.3
119	2	1	1	1	743.4	55.3	838.3	60.9
131	1	1	2	2	1119.1	85.2	463.3	34.8
135	1	1	1	2	649.3	48.3	735.7	54.0
136	1	1	1	1	852.2	62.6	848.3	60.9
137	1	1	2	1	577.0	46.2	649.7	50.5
142	1	1	1	2	901.1	69.4	763.3	56.7
143	1	1	2	1	631.1	46.9	635.0	46.6
144	1	1	2	2	318.3	23.7	-	-
151	1	1	1	1	1086.2	78.9	755.2	53.1
103	2	2	2	2	829.4	64.7	978.6	76.3
104	2	2	1	1	716.4	55.9	994.4	76.7
109	2	2	2	1	483.9	38.7	857.6	67.7
111	2	2	2	1	694.6	55.6	688.4	54.4
112	2	2	2	2	191.3	15.7	-	-
115	2	2	1	2	783.2	61.1	996.4	76.8
120	2	2	1	2	352.4	25.3	-	-
124	2	2	1	1	1199.4	87.1	1042.9	74.9
132	1	2	1	1	1034.6	79.6	828.7	63.8
138	1	2	2	2	290.7	22.4	-	-
139	1	2	1	2	819.5	60.9	984.5	71.5
140	1	2	1	2	1018.2	76.6	961.4	72.3
145	1	2	1	1	1047.2	76.9	874.4	62.8
147	1	2	2	1	703.8	50.5	969.4	69.6
148	1	2	2	1	1054.1	75.7	930.5	66.1
149	1	2	2	2	703.8	56.3	477.9	38.2

INTK: Herbage OM intake;

MTTK: Intake based on metabolic weight ($\text{kg } W^{0.75}$).

Appendix Data 4.13b. Herbage intake (g OM/day) in lambs in summer (March, 1994) (Cont.).

Lamb No.	PRVSP	SPP	SEX	PEG	Period 3		Period 4	
					INTK3	MTTK3	INTK4	MTTK4
101	2	1	2	2	924.7	69.5	1216.1	90.4
102	2	1	2	2	1164.3	81.8	1131.1	78.6
106	2	1	2	1	1190.9	79.4	1041.3	68.0
113	2	1	1	1	1028.7	70.0	829.8	55.9
114	2	1	2	1	987.8	69.4	947.1	65.8
118	2	1	1	2	1014.2	73.7	1269.4	91.2
119	2	1	1	1	1506.7	104.7	1349.9	92.8
131	1	1	2	2	1141.1	81.0	914.5	64.2
135	1	1	1	2	1199.3	82.5	988.5	66.6
136	1	1	1	1	862.2	56.9	1065.4	69.6
137	1	1	2	1	1982.2	147.3	994.4	72.2
142	1	1	1	2	1566.2	108.8	1153.9	79.3
143	1	1	2	1	1349.9	92.8	1034.1	70.4
151	1	1	1	1	854.8	57.0	1346.8	88.0
103	2	2	2	2	1548.4	113.8	1403.9	100.8
109	2	2	2	1	1278.8	93.9	819.1	59.5
111	2	2	2	1	1147.3	84.3	676.9	49.2
112	2	2	2	2	524.1	40.9	542.4	41.8
115	2	2	1	2	1076.2	75.6	1014.1	70.5
124	2	2	1	1	1702.8	113.5	1540.6	100.7
132	1	2	1	1	1394.5	99.0	1467.3	102.0
139	1	2	1	2	1507.8	101.5	1285.8	84.8
140	1	2	1	2	1703.5	122.3	1221.3	85.8
145	1	2	1	1	1261.3	84.9	1597.7	105.4
147	1	2	2	1	1394.5	92.0	1646.5	106.5
148	1	2	2	1	625.2	41.7	875.6	57.2
149	1	2	2	2	287.2	20.9	1069.9	79.5

Appendix Data 4.14. Liveweight (kg) of lambs in summer and early autumn, 1994.

Lamb No.	PRVSP	SPP	SEX	PEG	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
101	2	1	2	2	28.0	28.5	29.0	29.5	30.0	30.0	30.5	31.0	31.5	32.0
102	2	1	2	2	29.5	30.0	30.5	31.5	32.0	32.5	33.5	34.0	34.5	35.0
106	2	1	2	1	31.0	32.0	33.0	33.5	34.0	34.5	35.5	36.5	37.0	38.0
113	2	1	1	1	31.5	32.5	33.0	33.0	33.5	34.0	34.5	35.5	36.0	36.5
114	2	1	2	1	29.5	30.0	31.0	32.0	32.5	33.0	33.5	34.0	34.5	35.0
116	2	1	1	2	28.0	28.5	29.0	29.5	29.5			
118	2	1	1	2	28.5	29.0	29.5	30.0	30.5	31.0	32.0	32.5	33.0	33.5
119	2	1	1	1	30.5	31.5	32.0	33.0	33.5	34.0	34.5	35.0	35.0	35.5
131	1	1	2	2	30.5	31.0	31.0	31.5	32.0	32.5	33.0	33.5	34.0	34.5
135	1	1	1	2	30.5	31.5	32.0	32.5	33.0	33.5	34.5	35.0	35.5	36.5
136	1	1	1	1	31.0	32.0	32.5	33.5	34.0	35.0	36.0	37.0	37.5	38.0
137	1	1	2	1	28.5	29.0	29.0	29.5	30.0	30.5	31.0	31.5	32.0	33.0
142	1	1	1	2	29.5	30.0	30.5	32.0	32.5	33.0	34.0	34.5	35.0	35.5
143	1	1	2	1	30.5	31.5	32.0	32.5	33.0	33.5	34.0	35.0	35.5	36.0
144	1	1	2	2	30.0	31.0	31.5	31.5	32.0			
151	1	1	1	1	31.0	32.0	33.0	34.5	35.0	35.5	36.0	36.5	37.0	38.0
103	2	2	2	2	29.0	29.5	30.0	30.0	30.5	30.5	31.0	31.5	32.5	33.5
104	2	2	1	1	29.0	29.5	30.0	30.5	30.5	31.0	...			
109	2	2	2	1	28.5	29.0	29.0	29.5	30.0	30.5	31.0	31.5	32.5	33.0
111	2	2	2	1	28.0	28.5	29.0	29.5	30.0	30.5	31.0	32.0	32.5	33.0
112	2	2	2	2	27.0	27.5	28.0	28.0	28.5	29.0	29.5	29.5	30.0	30.5
115	2	2	1	2	29.0	29.5	30.0	30.5	30.5	31.0	31.5	33.5	34.5	35.0
120	2	2	1	2	32.0	33.0	33.5					
124	2	2	1	1	31.5	32.5	33.0	33.5	34.0	34.5	35.0	36.0	37.0	38.0
132	1	1	1	1	29.0	30.0	30.5	30.5	31.0	31.5	32.5	33.5	34.0	35.0
138	1	1	2	2	29.5	30.0	30.5	31.5	32.0	32.0		
139	1	1	1	2	30.5	31.0	32.0	33.0	33.5	34.0	34.5	35.5	36.5	37.5
140	1	1	1	2	30.5	31.0	31.5	31.5	32.0	32.0	32.5	33.0	33.5	34.5
145	1	1	1	1	32.0	32.5	32.5	33.5	34.0	34.5	35.0	35.5	36.5	37.5
147	1	1	2	1	32.0	33.0	33.5	33.5	34.0	34.5	35.0	36.5	37.5	38.5
148	1	1	2	1	32.5	33.0	33.5	34.0	34.5	35.0	35.5	36.0	37.0	38.0
149	1	1	2	2	28.0	28.5	29.0	29.0	29.5	30.0	30.5	31.0	31.5	32.0

W1..W10: Liveweight recorded weekly.

Appendix Data 4.15. Fasted weight (kg), carcass weight (kg) and GR (mm) in lambs in summer and early autumn, 1994.

Lamb No.	SPP	PRVSP	SEX	PEG	FST1	FST2	FST3	CCS	LGR	RGR
101	2	1	2	2	26.0	27.5	29.0	12.0	4	3
102	2	1	2	2	27.5	29.0	32.0	14.0	8	9
106	2	1	2	1	29.0	31.5	35.0	16.0	9	1
113	2	1	1	1	29.5	31.0	33.5	15.0	5	6
114	2	1	2	1	27.0	29.5	32.0	14.0	8	8
118	2	1	1	2	27.0	28.5	31.0	13.5	6	6
119	2	1	1	1	28.0	30.0	32.5	14.0	4	4
131	1	1	2	2	28.0	30.0	32.0	14.0	5	5
135	1	1	1	2	28.5	31.0	34.5	15.5	7	7
136	1	1	1	1	28.0	31.0	34.5	16.0	5	5
137	1	1	2	1	26.0	27.5	30.0	13.0	3	3
142	1	1	1	2	27.5	30.0	33.0	14.5	9	9
143	1	1	2	1	28.5	30.5	33.0	14.5	7	7
151	1	1	1	1	28.5	32.0	35.0	15.0	6	7
103	2	2	2	2	26.5	28.0	30.5	13.0	5	6
104	2	2	1	1	26.5	28.5	-	-	-	-
109	2	2	2	1	26.5	28.5	30.5	13.0	6	5
111	2	2	2	1	26.5	28.0	30.5	13.0	5	5
112	2	2	2	2	25.0	26.5	28.0	11.5	3	3
115	2	2	1	2	27.0	29.0	31.5	14.0	7	8
124	2	2	1	1	29.0	31.5	35.0	15.5	7	7
132	1	2	1	1	26.5	28.5	31.5	13.5	5	6
138	1	2	2	2	26.5	29.0	-	-	-	-
139	1	2	1	2	28.5	31.0	34.5	15.0	5	5
140	1	2	1	2	28.0	29.5	31.5	14.0	5	4
145	1	2	1	1	29.5	31.5	34.5	15.5	9	9
147	1	2	2	1	30.0	32.0	35.5	16.0	8	8
148	1	2	2	1	30.0	32.5	35.0	15.5	8	8
149	1	2	2	2	26.5	28.0	30.0	12.5	5	5

FST: fasted weight; CCS: Carcass weight.

Appendix Data 4.16. Wool weight (g/100cm²) and wool growth rate (mg/100cm² per day) in summer and early autumn, 1994.

Lamb No.	PRVSP	SPP	SEX	PEG	CWL1	CWL2	CWL3	WLGTH1	WLGTH2
101	2	1	2	2	23.06	4.07	3.12	110.09	124.77
102	2	1	2	2	21.65	3.29	3.82	88.97	152.99
106	2	1	2	1	15.48	3.53	3.51	95.45	140.29
113	2	1	1	1	12.79	4.34	3.75	117.34	150.18
114	2	1	2	1	15.62	4.38	3.17	118.40	126.96
118	2	1	1	2	11.66	4.09	3.07	110.47	122.96
119	2	1	1	1	18.61	3.87	3.29	104.54	131.63
131	1	1	2	2	16.92	3.76	2.62	101.60	104.66
135	1	1	1	2	13.93	3.55	3.14	95.86	125.72
136	1	1	1	1	10.99	2.97	2.88	80.16	115.18
137	1	1	2	1	16.01	3.70	3.23	100.00	129.03
142	1	1	1	1	10.12	3.23	2.58	87.41	103.19
143	1	1	2	1	14.71	2.95	2.99	79.61	119.53
151	1	1	1	1	14.36	3.32	2.70	89.67	107.96
103	2	2	2	2	13.08	3.81	2.99	103.11	119.41
109	2	2	2	1	11.22	3.93	3.28	106.21	131.27
111	2	2	2	1	18.20	4.56	3.38	123.16	135.21
112	2	2	2	2	16.22	3.65	2.64	98.65	105.50
115	2	2	1	2	13.11	3.39	2.60	91.67	104.06
124	2	2	1	1	17.83	4.61	3.34	124.53	133.83
132	1	2	1	1	13.13	2.54	2.13	68.66	85.13
139	1	2	1	2	16.12	2.62	2.43	70.84	97.06
140	1	2	1	2	17.43	4.24	2.69	114.48	107.72
145	1	2	1	1	13.53	4.15	2.86	112.18	114.54
147	1	2	2	1	16.45	3.71	2.93	100.23	117.06
148	1	2	2	1	12.74	2.55	2.24	68.99	89.60
149	1	2	2	2	16.11	3.40	2.76	91.84	110.26

CWL: Wool weight;
WLGTH: Wool growth rate.

Appendix Data 5.1. The rate of biting (bites/min) in leader and follower (L/F) lambs in summer, 1994/1995*.

Lamb No.	L/F	PEG	BTRT1	BTRT2	BTRT3	BTRT4
02	1	2	43	44	46	41
04	1	2	48	40	39	44
09	1	1	46	33	44	39
15	1	1	40	38	44	41
20	1	2	40	44	48	44
22	1	2	39	40	48	40
25	1	1	41	46	46	41
26	1	2	46	43	44	41
27	1	1	44	46	46	40
28	1	2	44	50	41	43
29	1	2	43	48	46	44
32	1	2	38	39	50	39
33	1	1	46	48	48	34
34	1	2	48	46	50	41
35	1	1	46	41	46	44
37	1	1	41	44	44	43
39	1	2	39	44	48	48
44	1	2	44	39	46	40
45	1	1	46	40	52	41
50	1	2	43	43	48	40
52	1	1	40	40	43	48
57	1	1	40	48	50	36
58	1	1	48	41	43	44
62	1	1	48	44	48	38
01	2	2	43	46	48	43
03	2	1	57	55	44	46
07	2	1	55	60	52	48
08	2	1	39	44	40	48
11	2	2	41	46	44	48
14	2	1	43	52	44	44
17	2	2	50	46	57	52
18	2	2	34	52	46	50
19	2	1	41	48	44	41
24	2	2	44	44	48	48
30	2	2	46	50	52	46
31	2	1	55	48	44	39
38	2	2	41	46	46	46
40	2	1	44	44	46	55
41	2	2	41	48	44	44
43	2	1	39	50	48	41
47	2	1	39	46	44	48
48	2	1	48	44	44	55
49	2	1	48	46	46	48
54	2	1	52	36	48	46
55	2	2	50	48	50	46
56	2	2	50	46	50	44
59	2	2	50	43	46	43
61	2	2	44	50	40	55

*: Four periods of observation were made in Dec., 1994 and Jan., 1995; BTRT1..BTRT4: The rate of biting was measured in the four periods.

Appendix Data 5.2a. Grazing behaviour in leader and follower lambs in summer (Dec., 1995).

Lamb No.	L/F	PEG	Period 1			Period 2		
			GT	RUT	RST	GT	RUT	RST
02	1	2	570	330	480	585	300	495
04	1	2	705	270	405	750	210	420
09	1	1	750	360	270	690	270	420
15	1	1	645	255	480	750	315	315
20	1	2	615	390	375	525	330	525
22	1	2	705	330	345	600	300	480
25	1	1	720	240	420	675	285	420
26	1	2	615	375	390	645	225	510
27	1	1	720	225	435	765	270	345
28	1	2	645	345	390	540	285	555
29	1	2	570	285	525	570	300	510
32	1	2	675	240	465	645	300	435
33	1	1	690	210	480	735	195	450
34	1	2	630	345	405	585	255	540
35	1	1	660	360	360	690	315	375
37	1	1	690	240	450	495	330	555
39	1	2	465	360	555	480	315	585
44	1	2	660	300	420	645	270	465
45	1	1	735	255	390	705	225	450
50	1	2	765	225	390	690	210	480
52	1	1	615	345	420	615	240	525
57	1	1	660	300	420	570	255	555
58	1	1	630	240	510	690	255	435
62	1	1	690	195	495	615	300	465
01	2	2	555	390	435	555	330	495
03	2	1	645	270	465	585	345	450
07	2	1	630	270	480	675	240	465
08	2	1	540	285	555	570	390	420
11	2	2	675	225	480	615	300	465
14	2	1	675	360	345	540	405	435
17	2	2	615	315	450	570	270	540
18	2	2	675	315	390	645	360	375
19	2	1	525	435	420	555	330	495
24	2	2	585	375	420	480	420	480
30	2	2	645	315	420	615	300	465
31	2	1	630	435	315	645	315	420
38	2	2	600	360	420	615	285	480
40	2	1	645	375	360	540	330	510
41	2	2	615	315	450	525	360	495
43	2	1	570	270	540	480	360	540
47	2	1	600	345	435	645	270	465
48	2	1	735	270	375	615	210	555
49	2	1	690	330	360	735	195	450
54	2	1	600	345	435	555	345	480
55	2	2	705	240	435	645	300	435
56	2	2	690	330	360	645	285	450
59	2	2	555	330	495	600	270	510
61	2	2	570	360	450	585	330	465

GT: Grazing time (min); RUT: Ruminating time (min); RST: Resting time (min).

Appendix Data 5.2b. Grazing behaviour in leader and follower lambs in summer (Jan., 1995).

Lamb No.	L/F	PEG	Period 3			Period 4		
			GT	RUT	RST	GT	RUT	RST
02	1	2	735	300	345	735	270	375
04	1	2	675	330	375	630	375	375
09	1	1	795	330	255	765	285	330
15	1	1	720	315	345	660	360	360
20	1	2	750	345	285	675	375	330
22	1	2	615	330	435	705	240	435
25	1	1	645	375	360	720	240	420
26	1	2	555	345	480	585	390	405
27	1	1	750	300	330	690	345	345
28	1	2	690	315	375	600	360	420
29	1	2	735	270	375	735	330	315
32	1	2	675	375	330	750	285	345
33	1	1	705	315	360	600	345	435
34	1	2	645	375	360	750	330	300
35	1	1	720	285	375	765	285	330
37	1	1	720	315	345	615	330	435
39	1	2	570	315	495	720	375	285
44	1	2	645	315	420	705	345	330
45	1	1	645	345	390	585	435	360
50	1	2	645	390	345	735	420	225
52	1	1	645	345	390	660	240	480
57	1	1	690	345	345	660	300	420
58	1	1	645	360	375	735	255	390
62	1	1	615	315	450	735	255	390
01	2	2	525	375	480	585	405	390
03	2	1	645	345	390	645	390	345
07	2	1	720	255	405	705	315	360
08	2	1	540	300	540	690	405	285
11	2	2	555	375	450	630	405	345
14	2	1	645	330	405	645	360	375
17	2	2	675	300	405	630	435	315
18	2	2	735	375	270	735	330	315
19	2	1	540	390	450	675	360	345
24	2	2	555	285	540	735	240	405
30	2	2	600	405	375	570	405	405
31	2	1	615	345	420	600	435	345
38	2	2	630	375	375	690	375	315
40	2	1	630	375	375	525	450	405
41	2	2	630	360	390	570	390	420
43	2	1	630	420	330	570	450	360
47	2	1	570	405	405	645	330	405
48	2	1	645	360	375	405	435	540
49	2	1	720	405	255	750	285	345
54	2	1	660	375	345	585	450	345
55	2	2	705	375	300	765	285	330
56	2	2	615	465	300	660	330	390
59	2	2	660	375	345	690	345	345
61	2	2	570	420	390	555	345	480

Appendix Data 5.3. Intake per bite (mg OM/bite) and the botanical composition of the diet selected by sheep in "leader" and "follower" swards.

Sheep No	Period	L/F	Day	IB	Botanical composition %				OMD
					Grass	Clover	GRNM	DDM	
4	1	1	1	130.4	97.1	0.0	97.1	2.9	82.30
27	1	1	1	86.9	93.2	4.1	97.3	2.7	83.37
63	1	1	1	37.1	94.6	3.6	98.2	1.8	81.19
4	1	1	2	76.6	93.8	2.5	96.3	3.7	80.79
27	1	1	2	106.5	94.3	0.0	94.3	5.7	80.30
63	1	1	2	41.2	100.0	0.0	100.0	0.0	80.34
4	1	2	1	90.2	97.4	0.0	97.4	2.6	81.15
27	1	2	1	74.3	96.6	1.7	98.3	1.7	83.31
63	1	2	1	37.8	94.4	0.0	94.4	5.6	82.84
4	1	2	2	79.4	91.8	0.0	91.8	8.2	80.50
27	1	2	2	81.6	95.2	0.0	95.2	4.8	78.95
63	1	2	2	39.7	85.5	1.3	86.8	13.2	76.04
4	2	1	1	92.1	100.0	0.0	100.0	0.0	76.76
27	2	1	1	74.6	98.2	1.8	100.0	0.0	78.69
63	2	1	1	56.7	95.0	5.0	100.0	0.0	81.44
4	2	1	2	89.0	100.0	0.0	100.0	0.0	74.60
27	2	1	2	73.5	95.2	1.6	96.8	3.2	72.83
63	2	1	2	65.8	98.4	1.6	100.0	0.0	77.50
4	2	2	1	76.9	100.0	0.0	100.0	0.0	73.63
27	2	2	1	63.9	92.7	0.0	92.7	7.3	70.01
63	2	2	1	52.1	91.8	0.0	91.8	8.2	74.95
4	2	2	2	83.0	94.3	1.4	95.7	4.3	69.10
27	2	2	2	88.0	77.8	0.0	77.8	22.2	72.29
63	2	2	2	53.7	93.9	2.0	95.9	4.1	66.08
4	3	1	1	103.3	91.5	1.7	93.2	6.8	77.20
27	3	1	1	78.3	87.1	6.9	94.1	5.9	68.66
63	3	1	2	58.6	87.1	3.5	90.6	9.4	73.69
303	3	1	2	47.7	86.8	4.4	91.2	8.8	76.60
4	3	1	3	88.7	83.8	0.0	83.8	16.2	69.45
27	3	1	3	77.7	73.0	0.0	73.0	27.0	78.71
63	3	1	4	80.9	83.0	0.0	83.0	17.0	77.21
303	3	1	4	60.7	82.5	5.0	87.5	12.5	80.01
63	3	2	1	61.4	76.7	4.7	81.4	18.6	73.89
303	3	2	1	61.9	68.9	0.0	68.9	31.1	74.00
4	3	2	2	85.0	74.3	1.4	75.7	24.3	71.16
27	3	2	2	54.1	86.4	0.0	86.4	13.6	66.35
63	3	2	3	60.9	50.8	0.0	50.8	49.2	73.66
303	3	2	3	33.3	51.4	1.4	52.9	47.1	78.92
4	3	2	4	72.3	71.6	0.0	71.6	28.4	76.34
27	3	2	4	51.6	64.3	0.0	64.3	35.7	74.18
4	4	1	1	100.9	94.2	0.0	94.2	5.8	71.33
27	4	1	1	60.9	90.3	0.0	90.3	9.7	74.15
4	4	1	2	122.1	79.2	0.0	79.2	20.8	70.86
27	4	1	2	80.5	82.7	3.8	86.5	13.5	71.11
63	4	1	3	65.3	78.9	2.6	81.6	18.4	68.08
303	4	1	3	57.5	75.8	0.0	75.8	24.2	74.59
4	4	1	4	102.7	83.1	1.3	84.4	15.6	67.30
27	4	1	4	90.9	86.4	0.0	86.4	13.6	62.95
63	4	2	1	60.7	85.2	0.0	85.2	14.8	72.31
303	4	2	1	61.0	77.4	0.0	77.4	22.6	70.86
63	4	2	2	74.5	78.8	0.0	78.8	21.2	65.82
303	4	2	2	50.9	86.8	0.0	86.8	13.2	75.42
4	4	2	3	67.3	60.0	2.0	62.0	38.0	69.34
27	4	2	3	58.5	53.4	0.0	53.4	46.6	68.48
63	4	2	4	59.2	3.6	0.0	63.6	36.4	62.56
303	4	2	4	31.5	66.7	0.0	66.7	33.3	73.64

Appendix Data 5.4. Condensed tannin concentration (CT: % DM) and N (% DM) in the diets from "leader" and "follower" swards in summer, 1994/1995.

Pasture	CT			Total	N
	Extractable	Protein-bound	Fibre-bound		
<u>Period 1</u>					
Leader sward					
1	0.08	0.10	0.03	0.21	2.79
2	0.08	0.12	0.04	0.24	2.49
Follower sward					
1	0.08	0.06	0.01	0.15	2.36
2	0.08	0.06	0.02	0.16	2.53
<u>Period 2</u>					
Leader sward					
1	0.08	0.11	0.05	0.24	3.40
2	0.08	0.10	0.03	0.21	3.19
Follower sward					
1	0.08	0.07	0.03	0.18	2.39
2	0.07	0.07	0.02	0.16	2.78
<u>Period 3</u>					
Leader sward					
1	0.10	0.15	0.04	0.29	2.51
2	0.10	0.18	0.07	0.35	2.46
Follower sward					
1	0.08	0.12	0.03	0.23	2.27
2	0.12	0.22	0.06	0.40	2.31
<u>Period 4</u>					
Leader sward					
1	0.09	0.13	0.04	0.26	2.36
2	0.12	0.09	0.06	0.27	2.17
Follower sward					
1	0.09	0.12	0.05	0.26	2.29
2	0.09	0.13	0.04	0.27	1.85

Appendix Data 5.5. Herbage intake (g OM/day) in leader and follower lambs in summer, 1994/1995.

Lamb No.	L/F	PEG	Period 1		Period 2		Period 3		Period 4	
			INTK1	MTTK1	INTK2	MTTK2	INTK3	MTTK3	INTK4	MTTK4
02	1	2	985.9	72.4	924.4	67.1	1116.0	74.1	906.8	59.2
04	1	2	990.8	80.3	1251.8	97.7	1072.1	75.3	1167.7	81.2
09	1	1	1051.9	80.7	1081.6	81.0	1024.6	68.7	1048.3	69.2
15	1	1	1087.7	83.8	1191.2	87.5	947.0	63.8	1023.6	68.2
20	1	2	1049.2	81.8	1118.0	84.7	1040.6	70.5	1064.2	69.5
22	1	2	953.0	72.2	950.9	69.9	992.4	69.0	769.5	53.5
25	1	1	1140.4	87.9	982.7	73.9	1148.0	78.1	1177.5	78.5
26	1	2	1032.9	80.6	914.5	69.3	997.3	70.1	924.6	64.3
27	1	1	705.3	55.0	1239.6	95.5	979.4	70.3	949.5	67.4
28	1	2	1086.2	79.4	1069.4	76.8	1014.2	67.6	877.2	57.9
29	1	2	872.0	60.6	875.7	60.2	1161.3	71.4	975.8	60.0
32	1	2	969.2	78.2	980.2	75.2	1334.2	91.7	1084.6	73.0
33	1	1	996.9	67.6	1440.7	74.1	1093.6	67.3	1162.9	70.5
34	1	2	751.0	57.2	991.7	73.7	1060.8	72.9	903.9	60.2
35	1	1	965.7	69.3	1148.2	78.6	1355.0	85.2	1090.9	67.3
37	1	1	790.3	58.1	1038.9	73.5	1150.2	77.9	1068.2	69.5
39	1	2	886.5	69.2	1008.7	75.9	979.4	68.1	984.3	66.3
44	1	2	823.6	57.9	1007.4	68.3	938.1	59.0	1261.8	77.9
45	1	1	927.6	66.6	918.9	66.0	1010.8	66.4	1005.4	64.4
50	1	2	1266.7	85.8	1138.0	74.1	1261.3	77.1	1362.3	81.1
52	1	1	1202.0	92.6	1011.4	74.8	1064.5	74.0	952.7	64.8
57	1	1	938.5	78.1	949.7	78.0	860.2	66.8	770.5	58.6
58	1	1	806.2	63.7	895.2	68.1	1000.7	70.3	867.7	59.0
62	1	1	1070.2	73.6	1122.9	75.6	1007.4	62.2	795.5	48.5
01	2	2	714.6	54.8	730.4	55.6	838.4	62.3	959.2	70.5
03	2	1	716.9	55.9	670.3	51.6	801.9	60.3	847.2	63.0
07	2	1	706.0	55.8	874.7	68.2	922.2	69.4	1018.7	74.8
08	2	1	457.2	33.6	566.1	41.1	657.0	48.0	774.0	56.2
11	2	2	850.7	64.0	770.9	57.3	883.0	68.0	786.4	60.6
14	2	1	736.5	48.1	720.1	46.6	823.1	55.4	866.5	57.8
17	2	2	895.4	62.0	808.6	55.6	848.4	56.9	1010.3	67.1
18	2	2	765.2	57.3	787.5	58.5	725.9	53.1	764.4	55.5
19	2	1	806.2	57.3	779.1	54.1	945.0	65.0	786.4	53.5
24	2	2	891.7	66.3	848.7	62.8	712.4	52.3	1020.8	74.1
30	2	2	822.6	65.0	732.4	56.4	895.7	68.2	819.0	61.3
31	2	1	793.4	57.6	684.6	49.2	2174.6	157.2	698.4	49.9
38	2	2	739.9	53.1	785.1	55.2	939.6	66.0	801.7	55.1
40	2	1	579.6	44.7	578.9	44.4	774.5	58.2	751.6	55.2
41	2	2	880.8	61.2	826.8	56.8	704.4	48.7	808.3	55.3
43	2	1	760.7	59.3	825.5	64.1	883.0	67.2	1029.3	76.5
47	2	1	735.7	59.6	678.3	55.0	762.6	61.5	933.8	76.7
48	2	1	896.7	69.6	704.3	54.3	779.3	60.0	-	-
49	2	1	804.2	55.3	740.9	50.2	881.4	61.9	953.7	66.0
54	2	1	687.2	54.3	671.2	51.5	545.4	43.1	781.4	61.0
55	2	2	773.5	61.1	726.2	56.7	849.8	65.5	712.5	54.2
56	2	2	682.9	51.4	752.9	55.3	752.3	54.0	964.9	67.8
59	2	2	764.3	60.1	724.2	56.2	835.6	64.4	839.9	63.9
61	2	2	561.5	48.1	592.2	49.3	722.8	58.3	803.0	63.4

INTK: Herbage OM intake; MTTK: Intake based on a metabolic weight (kg W^{0.75}).

Appendix Data 5.6. Liveweight (kg) of leader and follower lambs in summer, 1994/1995.

Lamb No.	L/F	PEG	W1	W2	W3	W4	W5	W6	W7	W8	W9	W10
02	1	2	31.0	31.0	32.5	33.0	33.5	35.2	35.7	37.2	38.0	39.0
04	1	2	29.5	29.0	28.5	30.0	32.0	32.5	33.5	34.5	35.0	36.0
09	1	1	30.0	30.0	30.7	31.7	32.7	33.5	34.2	36.7	37.5	37.5
15	1	1	29.5	30.5	30.5	32.5	33.2	33.5	35.0	36.5	37.0	37.7
20	1	2	29.5	29.0	30.0	31.2	31.5	32.7	33.5	36.2	38.0	38.0
22	1	2	30.0	30.5	31.2	32.5	32.7	34.0	34.0	35.0	35.0	36.5
25	1	1	30.0	30.0	30.5	31.5	32.0	34.2	34.5	36.0	37.0	37.7
26	1	2	27.5	29.0	30.0	31.2	31.5	32.7	33.5	34.5	35.0	34.5
27	1	1	29.0	29.0	30.0	30.5	31.0	32.0	32.5	33.5	34.0	34.7
28	1	2	32.5	32.0	32.7	33.5	34.5	34.7	36.5	37.0	37.5	38.0
29	1	2	33.5	34.0	35.0	35.5	36.7	38.5	40.0	41.2	41.2	41.5
32	1	2	28.5	28.5	28.7	30.7	31.7	33.5	34.2	35.5	36.5	37.2
33	1	1	35.0	35.0	36.2	38.0	39.2	40.5	39.5	41.2	42.0	42.5
34	1	2	30.0	30.5	31.0	32.0	32.5	34.0	35.0	35.5	37.0	37.7
35	1	1	32.0	32.5	33.5	35.7	35.7	36.5	38.5	40.0	41.0	41.0
37	1	1	30.5	31.5	32.5	34.2	34.5	34.7	35.7	36.2	38.2	39.2
39	1	2	28.5	29.0	30.0	31.5	32.2	32.2	33.7	35.0	36.5	36.5
44	1	2	33.0	33.0	34.5	36.2	36.5	37.7	38.5	40.0	41.0	41.0
45	1	1	32.5	32.5	33.5	33.5	34.5	34.5	36.0	37.7	39.0	39.5
50	1	2	35.5	35.5	36.2	38.2	38.7	39.7	40.5	41.5	43.0	44.0
52	1	1	28.0	29.0	30.5	32.2	32.5	33.0	33.5	35.0	36.0	35.7
57	1	1	27.0	26.5	27.5	28.0	28.5	28.5	29.5	30.2	31.0	31.5
58	1	1	29.0	29.0	29.5	31.0	31.5	31.7	33.2	34.5	36.0	36.2
62	1	1	35.0	35.0	35.5	36.5	37.5	38.0	39.0	41.0	41.7	41.0
01	2	2	29.5	30.0	30.7	31.0	31.2	31.2	31.5	32.0	32.5	33.2
03	2	1	28.5	28.5	30.0	30.5	30.7	31.2	31.0	31.5	32.0	32.2
07	2	1	29.0	29.0	29.5	30.0	30.5	30.5	31.0	31.5	32.5	32.5
08	2	1	32.0	32.0	32.5	33.0	33.0	33.0	32.7	32.7	33.0	33.5
11	2	2	30.0	30.5	31.5	32.0	31.7	31.5	31.0	30.5	30.5	30.5
14	2	1	36.5	37.0	38.0	38.5	38.0	37.5	36.7	36.5	37.0	38.0
17	2	2	34.0	34.5	35.2	35.5	36.0	36.0	36.5	36.7	37.2	37.7
18	2	2	31.0	31.5	31.7	32.0	32.5	32.0	32.2	32.7	33.0	33.2
19	2	1	32.0	32.5	34.0	35.0	35.0	35.0	35.2	35.5	36.0	37.5
24	2	2	32.0	32.0	32.0	32.2	32.5	32.2	32.2	32.5	33.0	33.5
30	2	2	29.5	29.0	29.5	30.5	30.5	31.2	30.5	31.0	31.7	32.2
31	2	1	30.0	31.5	33.0	33.5	34.7	34.0	33.5	33.2	33.7	34.2
38	2	2	33.0	33.0	33.5	34.5	34.5	34.2	34.0	34.5	35.5	36.2
40	2	1	29.5	30.0	30.5	30.7	30.7	31.0	31.2	31.5	32.5	32.7
41	2	2	34.0	34.5	35.0	35.5	35.0	35.2	35.7	35.2	35.7	36.5
43	2	1	28.0	29.0	30.0	30.2	30.7	30.5	31.0	31.0	32.0	33.2
47	2	1	29.5	29.0	28.5	28.5	28.5	28.7	29.5	28.7	28.0	28.5
48	2	1	30.5	29.5	30.2	30.5	30.5	31.2	31.0	30.5	-	-
49	2	1	34.0	34.5	35.5	36.2	36.5	35.7	35.0	34.5	35.2	35.5
54	2	1	29.0	29.0	29.5	30.7	30.7	30.2	30.0	29.5	30.0	30.5
55	2	2	28.0	28.5	29.5	30.0	30.5	29.7	30.0	30.5	31.0	32.2
56	2	2	30.0	30.0	31.5	32.5	33.0	32.5	32.7	33.5	34.5	34.5
59	2	2	28.5	28.5	29.7	30.2	30.2	29.7	29.5	30.5	31.0	32.0
61	2	2	26.0	26.0	26.5	27.5	28.0	27.5	28.5	28.7	29.5	30.2

W1.. W10: Liveweight of lambs recorded weekly.

Appendix Data 5.7. Fasted weight (kg), carcass weight (kg) and GR (mm) in leader and follower lambs in summer, 1994/1995.

Lamb No.	L/F	PEG	FST1	FST2	FST3	CCS	LGR	RGR
02	1	2	29.0	32.5	35.5	15.65	4	5
04	1	2	27.5	30.5	32.5	13.65	2	2
09	1	1	27.0	31.2	34.0	14.35	4	3
15	1	1	27.0	33.5	34.0	14.30	5	6
20	1	2	27.5	30.7	34.0	14.60	2	2
22	1	2	27.5	31.5	32.7	14.70	7	6
25	1	1	28.0	31.5	34.0	14.40	2	2
26	1	2	25.0	31.0	31.2	13.85	3	3
27	1	1	27.0	29.5	31.5	13.20	3	3
28	1	2	29.0	34.2	35.5	14.75	3	4
29	1	2	31.0	37.0	39.5	17.90	5	5
32	1	2	25.0	31.0	33.7	15.35	7	6
33	1	1	31.0	34.0	37.5	16.05	3	3
34	1	2	27.5	32.0	34.0	15.95	8	8
35	1	1	28.5	34.7	37.0	16.60	7	7
37	1	1	28.0	33.5	35.7	16.00	8	8
39	1	2	26.5	31.2	33.0	13.60	1	1
44	1	2	29.5	35.7	37.5	17.45	7	8
45	1	1	29.0	34.0	35.5	14.60	3	2
50	1	2	32.5	37.5	40.7	17.25	5	5
52	1	1	26.0	30.7	32.5	13.90	5	5
57	1	1	25.0	27.0	28.7	11.65	3	3
58	1	1	26.0	30.2	33.0	14.00	4	4
62	1	1	31.5	36.5	37.5	17.05	6	6
01	2	2	26.5	27.5	29.5	11.20	1	1
03	2	1	26.0	28.0	29.0	12.40	1	1
07	2	1	27.0	28.0	29.0	12.55	1	1
08	2	1	30.0	30.5	31.0	12.85	3	3
11	2	2	28.0	28.5	27.5	11.85	2	2
14	2	1	33.5	33.5	34.5	14.05	3	3
17	2	2	31.0	33.7	34.5	14.75	4	3
18	2	2	28.5	29.0	30.0	12.50	1	1
19	2	1	28.5	32.5	34.0	14.60	1	1
24	2	2	29.0	29.0	29.7	12.65	2	3
30	2	2	26.5	27.5	28.7	11.25	3	4
31	2	1	28.0	29.5	31.0	12.50	2	3
38	2	2	29.5	31.0	32.5	13.60	2	3
40	2	1	27.0	28.5	29.5	11.25	2	3
41	2	2	31.5	33.2	33.5	13.95	3	2
43	2	1	25.0	27.5	30.0	12.05	5	5
47	2	1	27.0	26.5	25.7	10.35	1	1
48	2	1	26.5	28.2	26.7	10.85	2	2
49	2	1	30.5	30.7	32.2	13.75	2	2
54	2	1	26.0	27.0	27.2	12.25	4	4
55	2	2	24.5	27.2	28.5	11.20	2	2
56	2	2	27.0	29.7	31.5	13.65	3	2
59	2	2	25.0	26.5	28.5	11.50	2	3
61	2	2	24.5	25.5	27.2	10.80	2	1

FST 1..FST3: Fasted weight (kg); CCS: Carcass weight (kg);
LGR and RGR: GR on left and right side of carcass.

Appendix Data 5.8. Wool weight (g/100cm²) and wool growth rate (mg/100cm² per day) in leader and follower lambs in summer, 1994/1995.

Lamb No.	L/F	PEG	CWL1	CWL2	CWL3	WLGTH1	WLGTH2
02	1	2	15.44	4.15	2.71	118.61	123.09
04	1	2	17.87	4.69	2.94	134.05	133.65
09	1	1	11.32	3.79	2.58	108.17	117.13
15	1	1	15.43	4.52	3.26	129.22	148.21
20	1	2	13.40	3.67	2.48	104.73	112.77
22	1	2	12.70	3.63	2.34	103.84	106.32
25	1	1	11.62	4.03	2.73	115.26	124.20
26	1	2	12.23	3.71	2.53	105.92	115.09
27	1	1	16.28	5.02	2.00	143.54	90.76
28	1	2	11.02	3.96	2.24	113.18	101.88
29	1	2	13.13	4.01	2.47	114.54	112.07
32	1	2	12.18	4.65	3.10	132.80	140.89
33	1	1	13.68	4.16	1.82	118.84	82.73
34	1	2	16.93	3.81	2.38	108.77	108.10
35	1	1	12.06	3.30	2.35	94.30	106.69
37	1	1	12.88	3.53	2.01	100.79	91.40
39	1	2	13.95	3.96	2.37	113.28	107.56
44	1	2	13.49	5.48	2.62	156.67	119.22
45	1	1	12.40	3.52	2.05	100.49	93.37
50	1	2	15.94	4.08	2.13	116.59	96.87
52	1	1	9.71	3.78	2.17	108.03	98.53
57	1	1	12.83	3.06	1.83	87.32	82.99
58	1	1	11.88	3.90	2.02	111.49	91.82
62	1	1	12.33	3.73	2.44	106.62	111.12
01	2	2	11.88	4.26	1.75	121.57	79.77
03	2	1	11.26	4.02	1.94	114.91	88.26
07	2	1	10.23	2.73	1.72	78.10	78.07
08	2	1	18.19	3.45	1.35	98.70	61.27
11	2	2	11.80	3.38	1.74	96.45	78.90
14	2	1	10.54	3.80	1.64	108.70	74.76
17	2	2	14.45	3.89	1.65	111.21	75.19
18	2	2	14.10	3.63	2.07	103.65	94.14
19	2	1	12.21	3.38	1.76	96.45	79.91
24	2	2	11.57	3.57	1.80	101.89	82.00
30	2	2	16.19	4.68	2.00	133.82	90.80
31	2	1	10.40	3.86	1.65	110.34	75.07
38	2	2	12.22	4.07	1.90	116.20	86.35
40	2	1	15.99	4.08	2.01	116.58	91.16
41	2	2	11.95	3.51	1.49	100.36	67.57
43	2	1	11.56	4.21	2.35	120.42	106.98
47	2	1	13.69	2.79	1.75	79.80	79.58
48	2	1	11.95	3.57	1.74	102.13	79.06
49	2	1	13.89	4.78	1.94	136.58	88.06
54	2	1	13.51	3.38	1.36	96.50	61.75
55	2	2	10.10	3.24	1.43	92.62	65.01
56	2	2	8.48	3.39	1.74	96.92	78.95
59	2	2	10.28	3.44	1.66	98.19	75.33
61	2	2	12.68	2.53	1.85	72.31	84.13

CWL1..CWL3: Wool weight (g/100cm²);
 WLGTH 1 & 2: Wool growth rate (mg/100cm² per day).