COMPARATIVE STUDIES ON THE IMPLICATIONS OF CONDENSED TANNINS IN THE EVALUATION OF *HOLCUS LANATUS* AND *LOLIUM* SPP. SWARDS FOR SHEEP PERFORMANCE

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

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AUGUST, 1995

This thesis is dedicated to my darling wife Adriana who helped with it more than she will ever know.

It is great beauty of our science that advancement in it, whether in a degree great or small, instead of exhausting the subject of research, opens the doors of further and more abundant knowledge, overflowing with beauty and utility, Michael Faraday 1791 - 1867.

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ABSTRACT

Montossi, F.M. 1995. Comparative studies on the implications of Condensed Tannins in the evaluation of *Holcus lanatus* and *Lolium* spp. swards for sheep performance. PhD Thesis, Massey University, Palmerston North, New Zealand.

The series of experiments which form the basis of the present study concentrated on evaluations of: (i) diet selection, grazing behaviour, herbage intake, and sheep performance between *Holcus lanatus* (Yorkshire fog) and *Lolium* spp. (perennial or annual ryegrass) swards both associated with *Trifolium repens* (White clover), and in one study with the presence or absence of *Lotus comiculatus* (Birdsfoot trefoil), and (ii) the effects of condensed tannins (CT) on the behaviour and performance of sheep grazing those swards. The effects of CT on sheep production were assessed by twice daily oral administration of polyethylene glycol (PEG; Molecular weight 4,000) to half of the lambs on each sward combination.

Three grazing experiments are reported; the first two (Experiments 1 and 2) were carried out at Massey University (New Zealand) from 1992 to 1993, while the final trial was undertaken at INIA Tacuarembó Research Station (Uruguay) during 1994. In the first experiment (Chapter 3), relationships amongst sward, grazing behaviour, and animal performance variables were studied on perennial ryegrass/white clover and Yorkshire fog/white clover swards rotationally grazed by ewes at medium and high daily allowances (6% and 12% of liveweight as herbage dry matter respectively) during late autumn in 1992. The next experiment (Chapter 4) was designed to investigate the effects of low concentrations of condensed tannins (CT) on lambs grazing perennial ryegrass/white clover or Yorkshire fog/white clover swards at a constant height of approximately 6 cm from December 1992 to March 1993. The final experiment (Chapter 5) was carried out from August to early November 1994 to examine differences in behaviour and performance between annual ryegrass/white clover and Yorkshire fog/white clover swards, both with presence or absence of birdsfoot trefoil, rotationally grazed by lambs

Results from Experiments 1 and 2 showed that herbage intake achieved by sheep grazing perennial ryegrass swards was 15 - 27% higher than that achieved on *Holcus lanatus* swards. Bite weight was 13 - 38% greater for *Holcus lanatus* than for ryegrass, associated with the 15 - 25% greater sward bulk density. There was a consistent advantage (1 - 5%) in the organic matter digestibility of the herbage selected in favour of ryegrass swards. Sheep on both pasture types concentrated grass rather than clover in the diet. Sheep grazing on ryegrass swards had higher liveweight gains (8 - 51%), clean wool growth (6%), carcass weight (7%), GR values (22%), and carcass dressing out percentage (2%) than sheep grazing on Yorkshire fog swards. The stocking rate maintained on ryegrass plots was 25% greater than that on Yorkshire fog plots.

Similar low concentrations of CT were recorded in the diets of ryegrass and Yorkshire fog swards (≤ 0.2% on a DM basis). These results were confirmed by measurements of NH_3 concentration in the rumen fluid. The low levels of CT had no significant effects on diet selection, herbage intake, grazing behaviour patterns or lamb performance. However, the lambs grazing on Yorkshire fog swards showed small and non-persistent responses to CT in terms of faecal egg counts, wool growth and liveweight gain.

Experiment 3 indicated that the organic matter digestibility of the diet selected and the herbage intake of lambs grazing on Yorkshire fog swards were higher than those on annual ryegrass (5% and 24% respectively), reflecting the higher contents in the diet of grass green leaf and of legume and the lower content of dead material in favour of Yorkshire fog swards. Lambs grazing on both swards showed similar behaviour patterns. Those on Yorkshire fog swards had higher clean wool growth (15%), greater fibre diameter (48%), and longer fibre length (5%), greater liveweight gains (41%), final weight (11%), carcass weight (29%), carcass weight gains (29%), GR value (38%), and lower faecal egg count (FEC) values (20%).

Slightly higher CT dietary concentrations were recorded in Yorkshire fog swards than in annual ryegrass (0.420 vs 0.365 ± 0.02% on a DM basis). These low CT levels increased clean wool growth (11%), fibre diameter (4%), although differences in carcass measurements were relatively small, and tended to reduce FEC values (15%). The effects of CT on animal performance were greater in Yorkshire fog swards than in perennial ryegrass swards. CT had no significant effects on diet selection, herbage intake, or grazing behaviour patterns. The very small effects of lotus on sward composition, sward structure and on lamb performance were explained by its very low contribution to both swards.

The major conclusions of the first two experiments are as follows: (i) under high fertility conditions and intensive grazing management, perennial ryegrass/white clover swards appeared to have higher feeding value than Yorkshire fog/white clover swards for sheep production; (ii) the results of these experiments confirmed the presence of limited CT concentrations in *Holcus lanatus*, and provided further evidence that low CT concentrations also exist in perennial ryegrass; (iii) these low CT concentrations (≤ 0.2% on a DM basis) present in both swards did not influence sheep performance significantly. Finally, the conclusions of the last experiment were: (i) under low to moderate soil fertility conditions and lax rotational grazing management, Yorkshire fog swards had better composition and structure for lamb production than annual ryegrass, as a consequence of the early reproductive development in annual ryegrass; (ii) low CT concentrations (range 0.36 to 0.42% on a DM basis) consistently increased wool production and liveweight gains, particularly in Yorkshire fog swards.

The findings of these studies are discussed (Chapter 6) in the context of the role of *Holcus lanatus* for grazing systems and of the potential benefits of low dietary CT concentrations in *Holcus lanatus* and *Lolium* spp. for animal production.

Keywords: *Lolium perenne* (perennial ryegrass); *Lolium multiflorum* (annual ryegrass); *Holcus lanatus* (Yorkshire fog); *Trifolium repens* (White clover); *Lotus corniculatus* (Birdsfoot trefoil); Polyethylene glycol (PEG); Condensed tannins (CT); herbage intake; diet selection; grazing behaviour and lamb production.

ACKNOWLEDGEMENTS

I would like to express my deepest gratitude to my chief supervisor Professor J. Hodgson (Department of Plant Science, Massey University, New Zealand), who went far beyond the call of duty in providing warm guidance and close supervision throughout the course of this research project, for organizing and arranging a Ph.D programme for me to pursue, for the privilege of being one of his students; and to my co-supervisors, Dr. S.T. Morris (Department of Animal Science, Massey University, New Zealand) for his prompt and constructive editing of draft scripts and for his continuous enthusiastic encouragement and stimulation; and to Ing. Agr. D. Risso (National Institution of Agricultural Research, Uruguay) for his friendship, helpful comments, and unconditional support, and Ings. Agrs. G. Pigurina and J. Silva (INIA, Uruguay) for their support.

In addition to my supervisors, Drs. J.L. Corbett and M.G. Lambert (AgResearch, New Zealand Pastoral Agriculture Research Institute Ltd.) are gratefully acknowledged for their valuable and critical comments.

Thanks are due to my fellow researchers Y. Hu and F. Liu who co-laboured with me during the field and laboratory measurements of the experiments carried out in New Zealand and their generosity in sharing their information.

I gratefully acknowledge the continuous encouragement and generous financial support of the National Institution of Agricultural Research (INIA, Uruguay), and in particular the following members of the Institution: Mr J.P. Hounie (President), Mr. T. Pereira (INIA Board), Ing. Agr. C. Ceroni (INIA Board), Ing. Agr. M. Allegri (Human Resources Manager), Dr. E. Indarte (National Director), Dr. A. Rabuffeti (Former National Director), Ing. Agr. J. Grierson (National Deputy Director), and Dr. Gabriel Cerizola (Human Resources).

The New Zealand Ministry of Foreign Affairs and Trade is thanked for provision of a post-graduate stipend and financial assistance to cover the cost of this study, and the opportunity to spend time in this wonderful country and to know its friendly people.

My special sincere thanks to the former Director of INIA Tacuarembó Research Station, Ing. Agr. O. Pitalluga and all the staff of the Research Station for their valuable support during the execution of the project in Uruguay.

I am greatly indebted to the Manager of Glencoe Research Unit, Dr. E.J. Berreta for his camaraderie, provision of time, patience, wise and constructive help. I also wish to thank the staff of Glencoe, in particular to Tecs. Agrops. J. Levratto, M.A. Zarza, W. Zamit, and M. Guigou. My sincere thanks also to Tec. Agrop. J.P. Motta for his immeasurable assistance in the field and laboratory work during the last experiment of this study in Uruguay.

I wish to thank Professor T.N. Barry (Department of Animal Science, Massey University) for his advice on interpretation of information related to condensed tannins, Dr. I.L. Gordon (Department of Plant Science, Massey University) for invaluable criticism and advice on statistical analyses and data interpretation, Dr. S. Ganesh (Department of Statistics, Massey University) for providing advice on experimental design and in the use of the SAS package, Dr. C. Matthew (Department of Plant Science, Massey University) for providing generous and cordial answers to any doubt that I had at any time, Dr. B. Christie (Department of Plant Science, Massey University) for helping in the use of GLE graphics package, and finally, Mr P.N.P Matthews (Department of Plant Science), Mr P. Kemp (Department of Plant Science), Dr. I. Valentine (Department of Plant Science), and Dr. C.W. Holmes (Department of Animal Science) for their friendship and support.

Thanks are also due to Ms R. Hodgson who has been very kind with my wife, daughter, and relatives.

I am extremely grateful to H. Duran (National Co-ordinator of Animal Production Programmes, INIA) who gave me unconditional support, generous encouragement, inspiration, and excellent research instruction when I made my first steps into research.

Thanks are extended to the staff of the Departments of Plant Science and Animal Science of Massey University for their friendly and generous technical field and laboratory assistance. These helpers include: Mr D. Sollit, Mr T. Lynch, Mr M.A. Osborne, Mrs J. Cave, Ms C. McKenzie, Ms F. Brown, Mr G. Evans, Ms R.A. Watson, Mrs J. Harrigan, Mrs K. Hamilton, Mr D. Burnham, D. Cooper, and others.

Thanks are also due to many colleagues at INIA (Uruguay) who were generous in giving their time for discussion and data interpretation, in sharing information, or helped me in various ways: Ing. Agr. R. San Julián, Dra. A. Mederos, Ing. Agr. D. Cozzolino, Ing. Agr. A. Morón, and Ing. Agr. M. Bemhaja.

My grateful thanks to Dr. D. Castells (SUL, Uruguay) for operating and preparing the oesophageal fistulated sheep used in the Uruguayan experiment.

I really appreciate the unforgettable times that I shared with my fellow graduate students at Massey University, especially the friendships of my contemporaries: Dr. S.C. da Silva, Mr A. Garay-Hernandez, Mr M.U.H. Awan, Dr. H.M. Nodoushan, Dr. M.R. Ghannadha, Dr. H. Tavakoli, Mr G. DeNava, Mr D. Escallón, Mr J.V. Uribe, Mrs A. Del Pino, Mr W. Beskow, Mr D. Real, Mr C. Poli, Mr G. Bishop-Hurley, Mr C. Black, Mr B. Butler, Mrs G. Griffiths, Mr P. Sharp, Mrs S. Assuero, Mr Padilla, Mr G. Li, Mr X.R. Meng Fu, Mr C. Ammarante, Mr S. Oppong, Mr M. Hyslop, Mr Z. Nie, and others.

I am extremely grateful to my parents, uncle, aunt, and grandparents for their education, considerable encouragement, inspiration, and patience. My thanks are also due to my relatives, sister, brother, friends, and wife´s relatives for their encouragement.

Lastly, my immense unforgettable appreciation and recognition is to my devoted wife Adriana for her patience, dedication, physical and mental support during the "hard" days in the long time that we spent in New Zealand, especially in giving me a wonderful inspiration to complete the project, "our adorable daughter Maria Florentina".

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CHAPTER 1

INTRODUCTION AND OBJECTIVES

Traditionally, ruminant production systems in New Zealand are based almost entirely on pastoral farming, containing varying proportions of perennial ryegrass and white clover pastures being the predominant source of forage for grazing animals. Understanding the components of any system is essential before one can initiate large-scale studies of that system (Forbes, 1988a). In pastoral systems, grazing animals and grazed swards are highly interactive through: (i) the effect of defoliation by grazing animals on the utilization, composition, regrowth and persistence of the grazed sward and (ii) the effects of herbage characteristics and canopy structure on ingestive behaviour and herbage intake of grazing animals, and animal performance. The intake of pasture by grazing ruminants has a major influence in restricting animal performance (Hodgson, 1981).

In the scientific literature, general agreement has evolved about the fundamental importance of behavioural factors in controlling herbage intake under grazing conditions (Stobbs 1973a,b; Hodgson, 1977, 1981, 1985b, 1990; Burlinson, 1987; Poppi *et al.*, 1987). Commonly accepted theories of metabolic and physical control of appetite have been criticized by these authors because these theories do not take into account the potential influence of sward and animal characteristics on diet selection and herbage intake. This is a particularly important feature of the ecology of pastoral grazing systems which cannot easily be investigated in conventional nutrition studies (Hodgson *et al.*, 1994) and a multifactorial approach may be required to outline the interdependence of the many variables involved in the animal to pasture interface (Birrell, 1989).

Much of the research on foraging behaviour and diet selection of grazing ruminants has relied essentially upon a descriptive empirical approach (Hodgson, 1981; Gordon and Lascano, 1993) and most of the livestock forage research in the past has been concentrated on measuring output of a particular grazing system rather than the interaction between grazed sward and the grazing animal (Forbes, 1988a). An understanding of plant-animal interactions, in particular, knowledge of the components of sward structure and their influence on the mechanics of the grazing process (Hodgson, 1985b; Laca *et al.*, 1992; Gordon and Lascano, 1993) is limited by: (i) the numerous complex and strong interactions involved (Vallentine, 1990), (ii) the absence of information on the distribution of specific plant species or components within sward canopies (Hodgson *et al.*, 1994) and (iii) the practical difficulties of investigating multivariate problems under field conditions (Hodgson, 1985b). Research studies of the mechanisms involved in ingestive behaviour, diet selection, herbage intake, and their resulting interaction on animal performance are essential to improve understanding of the causative effects of particular sward attributes on animal productivity. However, the information available covering a range of different situations is limited (Hodgson, 1985b) and conflicting (Burlison, 1987).

The importance of secondary compounds in plant tissues on the diet selection and herbage intake of larger herbivores has been well documented (Provenza and Balph, 1987, 1988, 1990; Barry and Blaney, 1987; Provenza *et al.*, 1991). However, it is not easy to quantify their effects under grazing conditions, or relate them in any quantitative sense to the effects of sward structural characteristics (Hodgson *et al.*, 1994; Hodgson, 1993a). One of these secondary compounds is the tannin complex, which has potentially important effects on milk, meat and wool production by enhancing the efficiency of protein utilization (Waghorn *et al.*, 1990) and by reducing the effect of parasitism in grazing animals (Niezen *et al.*, 1993a). However, especially with temperate swards, information in relation to the influence of low concentrations of condensed tannins on diet selection, herbage intake and animal performance is scarce and more research is needed to generalize the available information.

The present research study was designed to explore some facets of the plant-animal interface and subsequent effects on animal production, with particular reference to the influence of condensed tannins on this interactive process. In the first instance, the study concentrated on the evaluation of grasses with low concentrations of condensed tannins, and then subsequently with combinations of grasses and legumes with and without tannins were studied. *Holcus lanatus* (Yorkshire fog) was chosen as the common gramineous species for these comparisons, because of its known low concentration of condensed tannins (Terrill *et al.*, 1992a,b) and interest in its potential as an alternative pasture species to perennial ryegrass (*Lolium perenne* L.) particularly in conditions of limited plant nutrient status (Watkin and Robinson, 1974; Haggar *et al.*, 1976; Harvey *et al.*, 1984; Morton *et al.*, 1992).

The objectives of the series of three experiments performed were:

(i) To investigate differences on herbage intake, diet selection, ingestive behaviour, and sheep performance between *Lolium* spp. (perennial or annual ryegrass) and *Holcus lanatus* (Yorkshire fog) swards both associated with *Trifolium repens* (White clover), and in one study with presence or absence of *Lotus corniculatus* (Birdsfoot trefoil).

(ii) To evaluate the effects of low concentrations of condensed tannins on the behaviour and performance of sheep grazing those swards.

CHAPTER 2

LITERATURE REVIEW

2.1 GENERAL INTRODUCTION

The following review of literature is divided into four main sections focused on:

(2.2) the importance of understanding behavioural constraints to herbage intake and ingestive behaviour.

(2.3) the significance of the influence of plant and animal factors in determining diet selection

(2.4) the evaluation of the effects of condensed tannins on diet selection and herbage intake.

(2.5) the significance of *Holcus lanatus* for animal production, with special attention to the potential value of its condensed tannins.

The purposes of section 2.2 are (i) to discuss the importance of behavioural limitations in the control of herbage intake under grazing conditions, and (ii) to review the relationships amongst ingestive behaviour components, the structural characteristics of the sward canopy and animal characteristics and their influence upon herbage intake. In this section, attention is mostly concentrated on the behavioural constraints of sward and animal origin given that they are of major importance in the present research study.

In section 2.3, a brief outline of all the theories involved in diet selection is given, but attention is concentrated on the influence of animal and plant factors on selective grazing and diet selection, and their consequences to herbage intake. The linked role of animal senses and the effects of previous experience on diet selection are reviewed briefly, based principally on the reviews of Arnold (1981), Arnold and Hill (1972), Vallentine (1990) and Provenza and Balph (1987, 1988, 1990) respectively.

Section 2.4 summarizes current knowledge of the effect of condensed tannins (CT) on diet selection and voluntary intake, particularly in tropical and semi-tropical regions, where plants containing CT are very important feed sources for ruminants. Attention is then given to the effect of CT on rumen metabolism and animal production in temperate regions. Features of the effect of CT on animal production in the two regions are discussed separately for ease of presentation and comprehension. Factors affecting the concentration of CT are also discussed and additionally some issues related to tannin analysis are mentioned.

Finally, in section 2.5 important agronomic and nutritional characteristics of *Holcus lanatus* are reviewed briefly, with particular reference to the connotations of the presence of CT in this grass for animal production.

2.2 HERBAGE INTAKE BY GRAZING ANIMALS

2.2.1 Introduction and overview

According to Ulyatt (1981) and Minson (1981), animal performance will be determined by three variables which define the feeding value of forage; (i) the quantity of food eaten; (ii) the proportion of each unit of food digested and (iii) the efficiency of utilization of the end products of digestion. The relative importance of each component in determining the feeding value cannot be assessed easily because they are correlated. However, the same authors stated that experimental results have shown that at least 50% of the differences in feeding value can be attributed to differences in voluntary intake. Additionally, the importance of level of herbage intake in determining productivity of grazing animals has been supported by several authors, who suggest that variation in intake of pasture by grazing ruminants has a major influence on animal performance (Stobbs, 1973a,b; Hodgson, 1977, 1981; Poppi *et al.,* 1987).

Considering the overall grazing system, the consumption of the herbage produced by grazing animals is one of the major factors which determines the efficiency of the grazing system (Hodgson, 1990). Therefore, a proper understanding of the interrelationships between grazing animals and grazed swards is a key factor for maximizing the output of grazing systems.

Over the past 25 years there have been many reviews on the control of voluntary intake in indoor conditions (Bell, 1970; Ellis, 1978; Forbes, 1986, 1988b) which explain the control of voluntary intake in terms of conventional theories of metabolic and physical control of appetite. However, several authors suggested that these theories do not take into account the potential influence of non-nutritional characteristics of vegetation (Poppi *et al.,* 1987) or behavioural constraints (Hodgson, 1990) on herbage intake under grazing conditions (McClymont, 1967; Stobbs, 1973a,b; Arnold, 1981, 1987; Hodgson, 1977, 1981, 1985a,b,c, 1990; Poppi *et al.,* 1987). Nutritional factors such as digestibility or crude protein content, the time feed stays in the rumen and concentrations of metabolic products appear to be important in controlling intake only if accessibility and availability of forage are unlimited. The factors determining herbage intake in the latter situation have been named by Poppi *et al.* (1987) as non-nutritional factors.

Characteristics of tropical and temperate swards, including herbage mass, canopy structure and sward species have been postulated as major factors limiting the ability of the grazing animal to meet its requirements through their influence on ingestive behaviour, herbage intake and diet selection. Animal attributes (mainly mouth size, mobility of the jaw, lips and tongue) are also related to the actual level of herbage intake (Arnold, 1981; Hodgson, 1990).

2.2.2 Regulation of herbage intake under grazing conditions

Many of the factors involved in the process of herbage intake control have been described in extensive reviews. These factors have been subdivided in several ways in order to explain and understand the mechanism of herbage control. Meijs (1981) suggested that they can be classified into those of animal origin, sward and management origin. Minson (1981) suggested that the quantity of herbage eaten by the grazing animals depends on three main factors: (i) the availability of suitable herbage; (ii) the physical and chemical composition of the herbage, and (iii) the nutrient requirements of the animal. Poppi *et al.* (1987) mentioned that the factors influencing pasture intake can be broadly classified as nutritional and non-nutritional factors, and showed that the relationship between pasture intake and sward characteristics (herbage mass, green herbage mass, sward height) is curvilinear, with two quite different sections on that curve. In the ascending part of the curve, the non-nutritional factors appear to be the most important in limiting pasture intake, principally via pasture structure and grazing behaviour of the animals. Components of grazing behaviour are grazing time, bite size, and rate of biting. In the second part of the curve (at the plateau), nutritional factors such as digestibility, the time feed stays in the rumen and concentration of metabolic products appear to be important in controlling intake. At a low herbage mass or sward height, the increased difficulty of harvesting herbage reduces intake, where factors like the digestibility of stem and dead material are of minor importance in determining the lower intake achieved. Though oversimplified, this classification of factors controlling herbage intake under grazing conditions given by Poppi *et al.* (1987) has been useful to understand the principles involved in the subject. However, there are still interesting questions about the relative importance of alternative effects.

Recently, Hodgson (1990) suggested that herbage intake is influenced by three main groups of factors: (i) those affecting herbage digestion, relating mainly to the maturity and nutrient concentration of the herbage eaten (*The sensation of physical satiety*); (ii) those affecting herbage ingestion, relating mainly to the physical structure of the sward canopy (*Behavioural constraints*) and (iii) those affecting the demand for nutrients and the digestive capacity and eating capability of the animal concerned, reflecting largely their maturity and productivity state (*Feeding drive*). The amount of herbage intake will be determined by the balance between these three different forces, where feeding drive is seen as a positive factor, and physical satiety and behavioural constraints as negative factors influencing herbage intake.

The drive to eat in ruminants represents the animal's present demand for nutrients, principally energy. However, other nutrients, mainly protein and minerals, are also important for high producing animals. Potential energy expenditure is a function of the size and stage of maturity of the animal, its productive stage and genetic capability for production (Hodgson, 1990).

The sensation of physical satiety is a function of the degree of distention of the alimentary tract, or of the abdomen, caused by the volume of digesta in the tract. The volume of the digesta is a function of the amount of food eaten recently, its digestibility, the rate of digestion and of passage of undigested residues (Hodgson, 1990). This factor is of dominant importance in controlling forage intake in housed animals (Freer, 1981; Minson, 1981) but, under grazing conditions, the ability of the ruminant to harvest forage may impose an additional limitation on intake.

Hodgson (1985a) mentioned that the inhibitory satiety stimulus and behavioural limitations may or may not reinforce one another, depending on sward conditions, and both appear to be sensitive to the magnitude of the nutrient deficit.

Behavioural constraints limit the potential rate of herbage consumption, and may relate to both sward and animal characteristics and their impact on intake per bite and rate of biting (Hodgson, 1990). Hodgson (1977, 1985a,b, 1990) suggested that behavioural inhibitions assume much greater importance under grazing conditions.

2.2.2.1 *Behavioural constraints to herbage intake and ingestive behaviour.*

Hodgson (1990) defined the amount of herbage eaten daily as the product of time spent grazing and the rate of herbage intake during grazing. Allden and Whittaker (1970) and Hodgson (1982) suggested the estimation of herbage intake through the following equation:

$$I = GT \times RB \times IB$$

where;

I = daily intake of herbage by a grazing animal (mg OM/kg LW).

RB = the rate of biting during grazing period (bites/minute).

IB = herbage intake per bite (mg OM/kg LW).

GT = the time spent grazing (min/day).

Animals attempt, by adjusting components of ingestive behaviour, to achieve an adequate level of intake in the face of constraints of sward structure and composition.

On temperate pastures, the three main components of grazing behaviour and their products are influenced mainly by sward height and herbage mass (Allden and Whittaker, 1970; Hodgson, 1985a,b,c, 1990; Poppi *et al.,* 1987), whereas with tropical pastures leaf/stem ratio and sward density become more relevant (Stobbs, 1973a,b, 1975; Chacon *et al.,* 1978).

2.2.2.1.1 Intake per bite

The importance of intake per bite has long been recognized, but attempts to quantify it in grazing situations have been made only relatively recently (Forbes, 1982). Several authors (Burlison *et al.*, 1992; Hodgson, 1985, 1990; Black, 1990; Illius *et al.*, 1992; Mitchell *et al.*, 1991) mentioned that the herbage intake of grazing ruminants tends to reflect closely the weight of material harvested per bite because a low bite weight cannot be adequately compensated for by increasing the number of bites and grazing time (Hodgson, 1982).

Intake per bite (IB) is the most sensitive animal response to variations in sward characteristics of the sward canopy. It has amply been documented with domesticated animals (mainly in sheep and cattle) grazing on temperate swards that IB increases linearly with increasing sward height (or tiller height) or herbage mass (or green herbage mass) (Allden and Whittaker, 1970; Hodgson and Milne, 1978; Hodgson and Jamieson, 1981; Forbes, 1982; Black and Kenny, 1984; Penning *et al.*, 1991; Burlison *et al.*, 1991; Laca *et al.*, 1992). On subtropical and tropical swards (Stobbs 1973a,b, 1975; Chacon and Stobbs, 1976), herbage bulk density, rather than sward height, has the dominant influence on IB. In addition, high density of leaf within the sward is considered another significant factor affecting IB. However, positive relationships between IB and sward height have also been established on tropical swards in the studies of Chacon *et al.* (1978).

Hodgson (1981) based on the results of Stobbs (1975) observed a decline in rate of herbage intake when the herbage bulk densities in the surface horizons of the sward were less than 25 kg DM ha^{-1} cm^{-1}. The low bulk density of the uppermost layers of the tropical swards is mainly related to low population density of leaves present in those horizons. As a consequence, it is difficult for animals to prehend large quantities of leaf in each bite. This is not the case for temperate swards.

Burlison *et al.* (1991) defined intake per bite (IB) as the product of bite volume (BV) and bulk density of the grazed horizon, and BV is a function of bite depth (BD) and bite area (BA). Since the pioneer experiment of Black and Kenny (1984) who measured bite dimensions in sheep with artificial swards, there have been several studies on the relationships amongst sward height, sward bulk density and IB, and in particular, the influence of sward characteristics on bite components. This provides a basis for understanding the effects of plant morphology and sward structure on IB in terms of variation in the physical dimensions of individual bites of herbage, and in the bulk density of herbage within the volume occupied at a bite (Hodgson, 1985b).

Sward height and bulk density have been negatively correlated both within and between swards (Burlison *et al.,* 1985; Hodgson, 1990; Laca *et al.,* 1992). Burlison *et al.* (1985) showed that in their experiment height had a far greater influence than bulk density or herbage mass on IB, BD and BV. In addition, Laca *et al.* (1992), working with *Paspalum dilatatum* and *Medicago sativa* swards grazed by steers at different combinations of heights and bulk densities showed that bite weight was more sensitive to variation in sward height than in bulk density, and the two components had independent effects on IB. In their experiment, sward height had positive effects on both bite area and depth, and was more indicative of instantaneous availability than mass per unit of area. Conclusively, the authors suggested that even in homogenous swards, IB cannot be described with a single value, it is necessary to know both height and density of the sward to predict bite dimensions.

Burlison *et al.* (1991) working with seventeen grass and oat swards grazed by sheep, showed that bite weight was positively related to surface height (range of 6 - 55 cm) which acted primarily upon bite depth and hence bite volume, and to the bulk density of the grazed stratum (range of 0.1 - 2.0 mg DM/cm^3) which influenced bite weight directly. The same authors reported that the effects of surface height and grazed stratum bulk density were independent and additive.

These findings are in agreement with those reported by Mitchell *et al.* (1991) on *Sorghum bicolor* swards grazed by deer and sheep. There was a positive effect of height on BD, on average 11 times as large as the negative effect of bulk density. On average, a 100% increase in height or bulk density resulted in a 64% vs 21% increase in IB respectively, reflecting the fact that BV increased in relation to height (39%) but decreased in relation to bulk density (18%). Finally, the authors concluded that sward height was the major determinant of BV and IB via its influence on BD.

Intake per bite might be expected to depend on the tensile strength of plant material. Thus size of a bite may be limited by the maximum force the animal is able to exert in prehending a bite. The choice by an animal of leaf or stem may be related to shearing strength and intake per bite would decrease as tensile strength of leaves increase (Poppi *et al.,* 1987). However, Inoue *et al.* (1993) working with two lines of perennial ryegrass selected for low or high leaf shear breaking load, found no significant differences between the lines in dry matter intakes, rumen retention times or liveweight gain in sheep.

Plant pseudostem has been found to act as a barrier to animal herbage intake on very short vegetative swards. Barthram and Grant (1984) explained that the pseudostem acts as a barrier to bite depth, and the reduction in bite depth is likely to limit IB and consequently also the daily herbage intake, because pseudostems are more difficult to gather than leaf (Hughes *et al.,* 1991). This may determine the height to which an animal prefers to graze. This limit appears to be reached for sheep in swards with a leaf horizon of less than 20 - 30 mm deep, but in swards with a deeper leaf horizon there is a slight proportional relation between sward surface height and bite depth (Hodgson, 1985b). Recently, Burlison *et al.* (1991) and Laca *et al.* (1992) found that bite depth did not appear to be constrained initially by the presence of pseudostems, even though the presence of dead leaf at the lower levels of the sward canopy might have had some influence. L´ Huillier *et al.* (1986) suggested that the distribution of green grass leaf determined which strata were grazed. Sheep grazed apparently indiscriminately at the surface of all swards with a high green leaf content in the upper strata, but defoliation was largely concentrated in the basal 3 cm of an 18 cm tall sward which had a very high content of dead flowering stem, with green herbage only in the basal stratum.

2.2.2.1.1.1 Sward attributes affecting bite components

On temperate sown swards, it has been precisely documented that a positive linear relationship exists between sward height and bite depth (Milne *et al.,* 1982; Burlison, 1987; Laca and Demment, 1990; Burlison *et al.,* 1991; Mitchell *et al.,* 1991; Laca *et al.,* 1992), with IB being the leading factor in determining daily herbage intake, and sward height being the best estimator of bite depth.

Bite area is far less sensitive to changing sward structure than bite depth (Burlison, 1987). In general, experimental evidence involving different temperate species sampled by sheep or cattle shows that bite area is affected positively by sward height (Burlison, 1987; Laca and Demment, 1990; Laca *et al.,* 1992) and negatively by sward bulk density (Laca and Demment, 1990; Mitchell *et al.,* 1991; Laca *et al.,* 1992). On very sparse swards the number of leaves and stems prehended at a bite is probably limited by a maximum bite area (Hodgson, 1985b), while on dense swards the number of plant units grazed at a bite may be limited by the effort required to sever the herbage (Hodgson, 1985b; Hughes *et al.,* 1991). As a result, on very dense swards, a deeper bite might result in a reduction in bite area (Hughes *et al.,* 1991). For bite volume, the general tendency is that this parameter of bite dimension increases as sward height increases (Burlison, 1987; Black and Kenny, 1984; Burlison *et al.,* 1991). Black and Kenny (1984) also observed a negative effect of sward bulk density on bite volume.

2.2.2.1.2 Rate of biting

Biting rates of 30 - 50 bites/minute appear to be common in both cattle and sheep (Vallentine, 1990), but a great variation exists between studies. In his review, Hodgson (1985b) reported for cattle a range of 21 - 66 bites/minute, and for sheep a range of 31 - 49 bites/minute. On tropical swards, Stobbs (1974) found that cattle bites ranged from 45 to 80 per minute and the number of grazing bites taken by cows during 24 hours period rarely exceeded 36,000 bites. This latter value may set an effective upper limit to the compensation for reduced intake per bite (Stobbs, 1973a,b, 1975).

A general negative relationship between rate of biting and sward height or rate of biting and herbage mass has been observed in both tropical and temperate swards grazed by sheep or by cattle (Chacon and Stobbs, 1976; Hodgson and Jamieson, 1981; Milne *et al.,* 1982; Phillips and Leaver, 1985; Burlison, 1987; Penning *et al.,* 1991; Mitchell *et al.,* 1993). An increase in biting rate, reflecting a decrease in sward height or herbage mass, has been found to be accompanied by a decrease in the ratio of manipulatory to harvesting bites in sheep (Penning, 1986; Penning *et al.,* 1991; Laca *et al.,* 1992). Penning *et al.* (1991) observed that as IB increased, a greater proportion of jaw movements were allocated to masticate and manipulate the herbage ingested and therefore biting rate fell but intake rate remained constant. These results indicate the need to record both head movements and jaw movements. Hodgson (1985b) stated that biting rate may be a direct response to sward conditions rather than a compensatory mechanism for a reduced bite weight.

2.2.2.1.3 Grazing time

Grazing animals exhibit a daily grazing cycle that is remarkably consistent and recurs each day with minimum change (Vallentine, 1990). Cattle and sheep normally divide their working day into alternating periods of grazing, rumination and rest. Major grazing periods begin near dawn and again in the late afternoon, ending near sunset, though short periods of night grazing are not uncommon (Arnold, 1981). There is usually a period of ruminating activity after each grazing period, but much of the rumination occurs at night (Hodgson, 1982, 1990). Freer (1981) commented that social factors and daylength may also contribute to reduction in grazing time. However, in tropical conditions, where the length of daylight varies little, some studies have shown that cattle graze predominately at night (Chacon *et al.,* 1978; Stobbs, 1975; Arnold, 1981). High producing cows can be identified by the extent of foraging during the night (Stobbs, 1975). Penning *et al.* (1991) suggested in their experiment that grazing and ruminating times were interchangeable; as grazing time increased there was a concomitant decrease in time spent ruminating, and time spent idling remained constant.

Grazing time rarely exceeds 12 - 13 hours/day, as beyond this time grazing would interfere with rumination and other behavioural requirements (Poppi *et al.,* 1987). Hodgson (1990) mentioned that a grazing time in excess of 8 - 9 hours/day is likely to be indicative of limiting sward conditions. On temperate sown swards, grazing time has been found to range from approximately 6.5 - 13.5 hours/day for sheep and 5.8 - 10.8 hours/day for cattle (Hodgson, 1990), depending on sward and animal conditions. However, Arnold (1981) mentioned extreme values of about 14 - 15 hours of grazing time in beef cattle.

Daily patterns of grazing activity, biting rate and grazing time are similar for cattle and sheep (Arnold, 1981). However, Hodgson (1990) suggested that sheep tend to have a lower biting rate than cattle and so spend more time grazing, though the differences are small and are not always consistent. These differences can be associated with the greater selectivity of grazing by sheep in most circumstances.

Variation in physiological state can have a marked impact on ingestive behaviour. Animals lactacting or pregnant, young animals (with high growth potential) and animals in poor condition, increase grazing time and rate of biting in order to compensate for higher food requirements (Hodgson, 1985a,b, 1990; Phillips and Leaver, 1985; Poppi *et al.,* 1987). However, Amold (1981) mentioned that the relative magnitude of these effects appears to differ in different circumstances.

Grazing time usually varies inversely with sward height and herbage mass (Allden and Whittaker, 1970; Phillips and Leaver, 1985; Burlison, 1987; Penning *et al.,* 1991). Animals may reduce their grazing time on very short swards (Chacon and Stobbs, 1976; Penning *et al.,* 1991). This mechanism is employed by animals to conserve energy (Stephens and Krebs, 1986; Penning *et al.,* 1991).

2.2.2.1.4 Compensatory relationships amongst ingestive behaviour components

The rate of biting and grazing time usually tend to increase with declining intake per bite, but the rate of increase in the rate of biting and the time spent in grazing, are seldom enough to prevent an associated decline in the short-term rate of herbage intake (IB x RB) (Allden and Whittaker, 1970; Hodgson, 1985a,b, 1977, 1990; Penning *et al.,* 1991).

Herbage mass influences the relative balance amongst components of grazing behaviour by altering pasture height and/or pasture density, both components of sward structure. In a review of 13 trials, Hodgson (1977) mentioned that the critical herbage mass below which herbage intake declined varied from 1100 - 4000 kg DM/ha for sheep grazing temperate swards. Intake per bite declines progressively with declining herbage mass; grazing time at first tends to increase but then declines with further reduction in herbage mass below about 1000 kg DM/ha (Allden and Whittaker, 1970; Morris *et al.,* 1993a).

On shorter swards any increases in biting rate or grazing time are inadequate to avoid the decline in intake per bite and rate of intake. In a series of experiments reviewed by Hodgson (1985a, 1990), the author found that for sward heights below 6 - 8 cm and 8 - 10 cm, the daily intake by sheep and cattle is restricted (mainly intake per bite) and the compensatory factors (GT and RB) have little impact in preventing the decline in daily herbage intake.

Increase in biting rate has been considered as a compensatory response by the grazing animal to prevent the decline of intake rate. But it appears to be due primarily to a reduction in the number of manipulative jaw movements and to an increase in prehending movements with declining sward height, consequently, total jaw movements per unit time remain constant (Penning *et al.*, 1991). The variation in biting rate should therefore be considered as a direct effect of variation in sward conditions (Hodgson, 1985b). The most readily apparent adaptative response to the decline of IB is the increase in grazing time which usually occurs when the rate of intake declines (Freer, 1981). But the decline in intake per bite cannot be fully compensated for, by increasing both grazing time and rate of biting (Hodgson, 1985b). As a corollary, Hodgson (1985b) concluded that variations in daily herbage intake reflected closely the observed variations in IB.

2.2.2.2 *The influence of sward characteristics on ingestive behaviour and herbage intake*

Animal intake and animal performance usually increase at a steadily decreasing rate towards a maximum value as herbage allowance (kg OM or DM/animal/day; kg OM/kg LW/day), herbage mass on offer, or sward height increase, reflecting the influence of herbage allowance, herbage mass on offer, and sward height on the amount of herbage consumed.

Herbage mass indicates the amount of herbage present above ground, usually per hectare (kg DM/ha), while herbage allowance only implies a managerial decision without clear indication of the amount of herbage and its distribution within the sward (Rodriguez Capriles, 1973). This latter term gives a better impression of the balance between herbage demand and supply (Hodgson, 1984), and acts effectively as a rationing process (Hodgson, 1990). Hodgson and Milne (1978) suggested that herbage weight per unit of area is more closely related to herbage intake than herbage weight per animal, but herbage weight per animal probably exerted an effect through its influence on the rate of change of herbage weight per unit area during a grazing period.

Estimates of herbage intake as a function of variations of herbage allowance have been extensively studied for the more important domesticated animal species, this relationship being documented for sheep (Rattray *et al.,* 1987; Gibb and Teacher (1976), cited by Meijs, 1981); beef cattle (Nicol and Nicoll, 1987; Hull *et al.,* (1961), Marsh and Murdoch (1974), Jamieson and Lambert, 1987, cited by Meijs (1981); dairy cattle (Holmes, 1987; Holmes *et al.,* 1992; Hoogendoom *et al.,* 1992; Holmes and Wilson, 1987; Meijs, 1981); goats (Collins and Nicoll, 1986, cited by McCall and Lambert, 1987), and deer (Fennessy and Milligan, 1987).

Dairy cow intakes normally approach a maximum at allowances 3 - 4 times greater than the amount eaten, but only start to decline markedly when the allowance is less than twice intake (Le Du *et al.,* 1979; Hodgson 1975, 1984), and declines rapidly when the allowance falls below 40 g OM/kg LW/day (Hodgson, 1975). This is also supported by recent information published by Dougherty *et al.* (1992) studying allowance-intake relationships of beef cattle grazing on tall fescue. This relationship is affected by the level of milk production. The herbage intake of high-yielding cows is more sensitive to restrictions in herbage allowance than that of low-yielding cows (Combellas *et al.,* 1979). Leaver (1985) mentioned that animals of higher production potential have greater voluntary intakes, amounting to 0.2 - 0.4 kg DM increase in intake/kg milk. Reduced herbage intakes at low allowances are related to the increasing difficulty of prehending and ingesting herbage as swards are grazed down by grazing animals (Poppi *et al.,* 1987). This effect can be seen mainly in reductions of intake per bite (Stobbs, 1973a,b; Jamieson and Hodgson, 1979) and in extreme conditions, grazing time and rate of biting are also reduced. At high pasture allowance, nutritional factors such a digestibility, the time feed stays in the rumen and concentration of metabolic products appear to be important in controlling intake (Poppi *et al.,* 1987).

Laca and Demment (1990) argued that herbage mass in itself does not affect intake rate of cattle, but some of its components, namely sward height and sward bulk density.

Research on allowance-animal response relationships with sheep in New Zealand has historically related to ewe liveweight changes, wool growth and ovulation rate rather than to herbage allowance-intake relationships, because of the difficulty in obtaining reliable estimates of herbage intake in grazing sheep (Rattray *et al.,* 1987). The use of the herbage allowance method is a very useful tool for grazing systems involving short grazing periods of 1 - 3 days, where concurrent pasture growth can be largely ignored (Hodgson, 1977, 1984). Hodgson (1977, 1984) criticized the management rules based on herbage allowance or residual DM, because they are affected by sward conditions. In this sense, several researchers (Le Du *et al.,* 1979; Hodgson 1984; Baker, 1985; Geenty and Rattray, 1987; Morris *et al.,* 1992) suggested that residual herbage mass or stubble height mass may be more useful than herbage allowance as general predictors of herbage intake and animal performance.

It has been suggested by several studies, mainly by Hodgson (1981, 1984, 1985b, 1990), Parker and McCutcheon (1992) and Morris *et al.,* (1994), that height of the undisturbed sward appears to be the most useful indicator for predicting both animal and sward responses, particularly under continuous stocking management. The point at which intake approaches the maximum can be regarded as the critical height. There is little point in providing swards above this critical threshold, because further increases in sward height will not improve intake and will result in a reduction in digestibility, ultimately counterbalancing some of the potential advantages of the increased height (Hodgson, 1990).

Under continuous stocking, critical stubble heights have been recommended for sheep by several authors on ryegrass dominant swards: (i) from 4 - 7 cm for spring-lambing ewes (Hodgson, 1990; Orr *et al.,* 1990; Penning *et al.,* [illegible]1; Chestnutt, 1992; Parker and McCutcheon, 1992; Morris *et al.,* 1994), but a greater height (9 cm) has been suggested for early lactation (Orr *et al.,* 1990; Chestnutt, 1992), (ii) 4 cm for winter-lambing ewes and for late winter-pregnancy (Morris *et al.,* 1993a), (iii) 4 cm for ewes prior to and after mating in autumn (Burnham *et al.,* 1994).

Swards of 12 - 15 cm height and 8 - 10 cm height are required to achieve maximum steer and bull performance in autumn and spring pastures respectively (Morris *et al.,* 1993b). Hodgson (1990) recommended sward heights from 9 - 10 cm for beef cows and weaned calves to maintain levels of herbage intake and animal performance close to maximum. In addition, Baker (1985) and Hodgson (1990) under set-stocking situations suggested critical values of sward height at which intake and performance of dairy cows can be affected, suggesting that intake and milk production are restricted when sward heights are smaller than 7 - 9 cm. With rotational grazing conditions, the critical post-grazing stubble height is approximately 8 - 10 cm.

On temperate sown swards, intake per bite and rate of herbage intake have been found to be positively and linearly/asymptotically (Allden and Whittaker, 1970; Forbes, 1982; Penning, 1986) or quadratically (Penning *et al.*, 1991) related to sward height for various classes of stock.

2.2.3 Conclusions

Animal performance will be determined by three main variables: (i) the quantity of food eaten; (ii) the proportion of each unit of feed digested and (iii) the efficiency of utilization of the products of digestion. In this sense, the relative importance of both voluntary intake (i) and nutritive value (ii and iii) in determining feeding value cannot be assessed easily because the two components are correlated. However, it is estimated that intake accounts for at least 50 % of the total variation observed in feeding value.

Herbage intake is influenced by many unrelated and related factors, therefore, intake cannot be predicted accurately from a simple factor. The level of herbage intake achieved will be determined by the balance between positive factors (feeding drive; demand for nutrient) and negative factors (such as physical satiety and behavioural constraints). According to Hodgson (1990), this concept implies that it is risky to link herbage intake with any single variable. In other words, an improvement on herbage digestibility will result in an increase of herbage intake only if it is not accompanied by adverse changes in sward height or herbage density (Hodgson, 1990).

Daily herbage intake appears to be closely correlated with bite weight because when this component of grazing behaviour is reduced, it cannot be adequately compensated for, by increasing the number of bites or by increasing the grazing time. Bite weight also, is the most important behavioural variable for grazing animals responding to changing sward conditions.

Bite weight increases with both the height and density of the pasture. On temperate sown swards at a vegetative stage of growth, sward height is the principal determinant of bite weight. On the other hand, in swards at a reproductive stage of growth the relative proportions of leaves and stems also become important in determining bite weight because of the effect of selective grazing. On tropical swards, bulk density and leaf/stem ratio of the pasture are of prime importance on bite weight.

Of the components of bite dimension, bite depth appears to be positively related to sward surface height and makes a far greater contribution to bite volume (hence bite weight), than does bite area.

Sward height appears to be the most useful field indicator in order to predict herbage intake and hence animal performance under set stocking conditions. However, pasture allowance is the most used pasture management tool to estimate the DM intake of rotationally grazed dairy cows.

Herbage intake of grazing cows is depressed once the cows are forced to consume more than 50% of herbage on offer, or to graze the sward down to a mean height of less than 8 - 9 cm (rotational grazing) or 9 - 10 cm (set-stocking). Under set stocking management, herbage intake may be expected to start to decline when surface height of the sward falls below 6 - 7 cm for grazing sheep and 9 - 10 cm for cattle.

2.3 DIET SELECTION

2.3.1 Introduction and overview

Food selection has been interpreted by Robbins *et al.* (1987b) as " a dynamic, multifactorial process integrating animal requirements and metabolic capabilities with a vast array of plant and community chemistries and spatial configurations that create absolute and relative values for all food items".

Over the last two decades much effort has been made by diet selection theorists to find conceptual models that could explain the complexity of diet selection. Their purpose has been to develop appropriate models to describe diet selection, rather than to attempt to seek a generalized foraging theory (Milne, 1991). These models may be useful tools for understanding the complexities of plant-animal relationships (Gordon and Lascano, 1993; Taylor, 1993).

Despite a huge amount of literature available in ruminant diet selection, it is not possible to extrapolate specific principles to general situations. This fact relates to the diversity of the population of plants and animals involved in diet selection, and the complexity of their interactions. Several researchers (Black and Kenny, 1984; Hodgson, 1985a; Malechek and Balph, 1987; Provenza and Balph, 1990; Milne, 1991; Taylor, 1993; Hodgson *et al.,* 1994) have highlighted the necessity for greater emphasis on diet selection research to understand the complexity of this phenomen.

2.3.2 Theories of diet selection

Provenza and Balph (1990) have analyzed and summarized the five conceptual models of diet selection in grazing ruminants. The models, which are not mutually exclusive, include: (i) *Nutritional wisdom or euphagia*; (ii) *Hedyphagia*; (iii) *Morphophysiology and size*; (iv) *Optimal foraging*, and (v) *Learning by consequences.*

Provenza and Balph (1990) criticize euphagia and hedyphagia theories because these do not take into account the post-ingestive consequences to animals of selecting a specific diet. They argue that, with the exception of sodium, the experimental evidence has failed to demonstrate that animals can directly sense mineral nutrients from the foods that they eat. Marten and Andersen (1975) and Vallentine (1990) stated that the existence of generalized nutritional wisdom of grazing animals about the forage they consume is now widely rejected. On the contrary, evidence exists to demonstrate that plant species with high digestibility or high crude protein content may be less palatable to animals (Vallentine, 1990). Moreover, the outcome of foraging choices may not become clear until after consumption and digestion, therefore the significance of individual foraging choices for a specific nutrient is likely to be lost (Illius and Gordon, 1990).

Optimal foraging theory (Crawley and Krebs, 1992) states that as a result of evolutionary selection pressures, animals will tend to hunt or graze (eg ruminants) for their food efficiently. There are a number of grounds for questioning this assumption, including the individual variation in diet selection which is partially genetic and partially experimental (Provenza and Balph , 1990). Additionally, Illius *et al.* (1992) argued that herbivores may not show intake maximizing behaviour because they may face an inherently difficult task in discriminating between the profitability of alternative foods. Furthermore, it has been claimed (Westoby, 1974, 1978) that for hervibores, maximizing the rate of energy consumed may be less important than obtaining a balanced diet and avoiding toxins or other anti-nutritional plant compounds. This suggestion has been refuted by Stephens and Krebs (1986) who claimed that the evidence that herbivores select nutrients to balance their diets is weak, and that particular dietary or anti-nutritional factors can be incorporated into rate-maximizing models by specific constraints. The complexity of vegetation structure and composition and the necessity for consumption of a mixed diet to balance intake, play an important and fundamental role in limiting nutrient intake rate (Illius and Gordon, 1993). Optimal foraging theory was postulated to explain food selection by predators where the quality of prey tissue is of little importance, relative to the rate at which prey can be obtained. In comparison, plants differ markedly in their nutritive value (Malechek and Balph, 1987). Additionally, Provenza and Cincotta (1993) remarked that economic models do not consider the dynamic nature of the adaptative processes and cannot explain why animals within a species express different dietary habits.

Foraging theorists have generally ignored the influence of digestion and nutrient absorption on foraging decisions, assuming that digestive efficiency is high and constant for an ample range of food items as well as across individuals (Illius and Gordon, 1990, 1993). The morphophysiology and size of species theory has received the same criticisms as the optimal foraging theory because it ignores the potential individual variation within a species resulting from both genetic factors and experience through learning (Provenza and Balph, 1990).

Finally, learning by consequences (Provenza and Balph, 1987, 1988, 1990; Provenza and Cincotta, 1993) is based on positive and negative pre and post-ingestional consequences and experiences which may be either social or individual trial and error experiences. This is essentially a conceptual model and is still in its early stages (Provenza and Cincotta, 1993). In some aspects, learning by consequences concerns all the five challenges that ruminants face during grazing (Provenza and Balph, 1990), which were properly defined by those authors as: (i) the foraging environment is highly variable in the quantity of energy, protein and minerals offered in different dietary items; (ii) ruminants have to cope with plant chemical defences, which reduce or interfere with metabolic processes and may cause death; (iii) ruminants have to cope with plant morphological defences, such as the cases of standing dead material in some grasses, thorns in forbs and woody plants, differences in sward canopy shape and architecture, etc; (iv) the spatial and temporal variation in the opportunity to obtain food efficiently, and (v) the presence of unfamiliar foraging environments, where ruminants have to move and feed due to abiotic or catastrophic events, such as fire, rain, etc, which rapidly and significantly alter the vegetation available.

These five theories are not mutually exclusive. They have different origins in diverse fields including animal science, behavioral ecology, and psychology (Provenza and Balph, 1990), and they are complementary in several aspects. Lynch *et al.* (1992) evaluated the five theories and he concluded that learning by consequences appears to be the broadest, though some of the other theories may be involved in explaining ruminant diet selection. Hodgson *et al.* (1994) stated that simpler explanations for animal choices can be applied to explain diet selection, relating to the ease of harvesting and the accessibility of plant components within a sward.

Recently, Bazely (1989, 1990), Laca *et al.* (1993) and Demment *et al.* (1993) developed a patch model based on the marginal value theorem (Charnov, 1976; Krebs and McCleery, 1984, cited by Bazely, 1990). The model of Laca *et al.* (1993) predicts patch or site selection and utilization, arguing that prediction of intake rate on the basis of sward measurements necessitates theoretical developments to predict site selection by grazers. Their model is based principally on the optimal foraging model and partially on the morphophysiology and size of species model, and does not take into account the retrospective effects of post-ingestion factors. The model estimates the instantaneous intake rate (IIR) as a function of distances between patches and difference between patch heights. There was a close agreement between the variables observed and predicted, but IIR was consistently over-estimated by the model.

According to Taylor (1993) all the models currently used to interpret diet selection have low predictive value, specially in relation to spatial and temporal heterogeneity.

2.3.3 Factors affecting selection between alternative forage sources

2.3.3.1 *The linked role of animal senses*

All the senses of grazing animals (sight, touch in the lips and mouth, taste, smell and hearing) appear to be involved in diet selection (Arnold and Hill, 1972; Arnold 1981; Vallentine, 1990). However, their interactions are complex, and no sense seems to predominate in every situation (Arnold, 1966b; Vallentine, 1990). The investigation of the role of animal senses in the selection of their diets has often been avoided by researchers because of the confounded experimental results associated with the interactive relationships between senses, animal prior experience and memory, and the rapid adaptation of animals to loss of a sense (Arnold, 1966b; Lynch *et al.,* 1992). Additionally, it has been suggested that blindfolded sheep do not behave normally (Arnold, 1966a, 1981; Arnold and Dudzinski, 1978; Bazely, 1990).

The role of hearing and olfaction in diet selection have been shown to be of limited importance (Arnold, 1966b, 1981; Vallentine, 1990; Lynch *et al.,* 1992). Tactile and taste cues used in diet selection operate while the sheep is biting, whereas both olfactory and visual cues may operate over distance (Bazely, 1990). Marten (1978) and Vallentine (1990) argued that the sense of sight is of importance to sheep for mainly orientating themselves in space, but not for selecting species within a grazing site.

The sense of touch is important in that grazing animals generally select against rough, harsh, or spiny material (Vallentine, 1990). There is evidence to show that the sense of touch may be involved in animal preferences (Garner, 1963; Marten, 1978). Ivins, (1952, 1955) and Garner (1963) suggested that hairiness in Yorkshire fog affects its palatability. Taste seems to be implicated in the motivation of food acceptance (Goatcher and Church, 1970a,b; Vallentine, 1990), although Provenza and Balph (1988) argued that the effect of this sense on diet selection can be shaped by the foraging environment.

In a renowned experiment, Arnold (1966b) found similar liveweight gains between sheep with intact senses of smell and taste and those with impaired senses. The author concluded that animal senses are not always critically involved in total intake of nutrients.

Arnold and Hill (1972) and Arnold (1981) reviewed the information related to the plant chemical factors influencing taste and smell preferences. In both reviews, the authors arrived at the same conclusions: (i) animals cannot recognize and respond to molecular concentrations in the form in which they occur in plants, with some exceptions such as sodium or potassium salts and sugars; (ii) animal preferences are questionably linked with plant nutrient components; (iii) any positive or negative association between animal preferences and a particular plant compound cannot establish causal or consequential relationships because of the multi-dimensional nature of the process of selection.

Simons and Marten (1971), Arnold and Hill (1972), Marten and Jordan, (1974), and Marten (1978) working with several plant species (*Phalaris arundinacea*, *Dactylis glomerata*, etc) found that certain alkaloids and tannins were disliked by sheep. Recently, investigation on features of the biochemistry of dietary preferences has been very active (Crawley, 1983), particularly focused on the role of the secondary plant compounds (eg condensed tannins) upon selection strategies (Barry and Blaney, 1987; Malechek and Balph, 1987; Provenza and Balph, 1987, 1988, 1990).

2.3.3.2 *The effect of previous experience of animals on diet selection*

Previous experience by animals early in life and the presence of the mother have been mentioned as important factors affecting the development of dietary preferences in browsing and grazing ruminants (Hodgson, 1971; Provenza and Balph, 1987, 1988, 1990; Nolte *et al.,* 1990; Provenza and Burrit, 1991; Burrit and Provenza, 1991; Lascano *et al.,* 1985; Ramos and Tennessen, 1992; Lynch *et al.,* 1992). Experimental evidence of learning through consequences is the principal source of the learning diet selection theory postulated by Provenza and Balph (1987, 1988, 1990).

Burrit and Provenza (1990) suggested that ruminants can acquire aversions to food that contains toxins by associating the flavour (taste and odour) of the food with aversive post-ingestive feedback, which is apparently caused by stimulation of the emetic system. Food aversions can start as soon as the drug has been released in the rumen. This suggestion could be applied, for instance when goats are feeding on plants containing high CT levels (Provenza *et al.*, 1993).

Young ruminants can learn which foods to eat or avoid through interactions with their mothers (Squibb *et al.,* 1990; Thorhallsdottir *et al.,* 1990a,b; Mirza and Provenza, 1990, 1992; Nolte *et al.,* 1990; Ramos and Tennessen, 1992) and other conspecifics (Thorhallsdottir *et al.,* 1990c) and through post-ingestive feedback from nutrient and toxins (Provenza *et al.,* 1990; Burrit and Provenza, 1989, 1991; Provenza and Burrit, 1991). After weaning, lambs become independent of their mothers, and it is probable that learning about food preferences through trial and error becomes important (Burrit and Provenza, 1991). Provenza and Balph (1987, 1988) and Burrit and Provenza (1989) discussed the practical application of this knowledge, suggesting that animal production can be increased by training young animals early in life to avoid harmful plant species or to reduce intake of toxic plants.

Comparing sheep with previous experience, in several contrasting nutritional environments, Arnold and Maller (1977) found that only small differences in experience in early life, resulted later in marked differences in grazing preferences, herbage intake and liveweight gain, but small differences in wool production. In lambs and goats, the positive effects of previous experience can persist for several months (Lynch and Bell, 1987; Nolte *et al.,* 1990; Squibb *et al.,* 1990; Distel and Provenza, 1991) or for years (Arnold and Maller, 1977). Food preferences in lambs nurtured by their mothers are more persistent than in lambs reared alone (Nolte *et al.,* 1990; Thorhallsdottir *et al*, 1989), probably because presence of the mother increases a lamb´s attention to the forage.

2.3.3.3 *Animal factors influencing diet selection*

Experimental studies explicitly demonstrate that ruminant diet selection can be influenced by body size and related variables (Van Dyne *et al.,* 1980; Arnold, 1981; Demment and Van Soest, 1985; Hodgson, 1985b, 1990, 1994; Illius and Gordon, 1987, 1990, 1993; Demment and Greenwood, 1988; Gordon and Illius, 1988; Black, 1990; Milne, 1991; Gordon and Lascano, 1993). Demment and Van Soest (1985) suggested that small animals have higher metabolic costs per unit volume of rumen than do larger animals. As a consequence, small ruminants have to select forages with quicker fermentation rates, rapid energy yields and faster rates of passage than larger ruminants. Larger animals can utilize poorer quality foods better than small animals, because they can eat and retain plant cell walls for longer permitting a better digestion.

Both rumen and body size vary between species, resulting in dissimilar digestive ability for degrading fibrous grasses, trees and shrubs (Demment and Van Soest, 1985). However, there are exceptions to this causal relationship, given by the differential ability between ruminants to consume plants containing high CT concentrations. Deer reduce the effect of condensed tannins through their ability to produce proline-rich salivary proteins (Robbins *et al.,* 1987b). Goats cope by different mechanisms explained by Kumar and Vaithiyanathan (1990) and by Distel and Provenza (1991).

The dental morphology of grazing animals (broad and flattened incisor arcade) interferes with the efficiency of selecting individual plant parts, while the presence of narrower and more pointed incisor arcades in browsing animals allows better selectivity (Gordon and Illius, 1988). The incisor arcade breadth dimension has been used to explain why cattle are less able to discriminate between forage components than sheep (Gordon and Illius, 1988; Black, 1990; Milne, 1991).

Researchers (Dudzinski and Arnold, 1973; Langlands and Sanson, 1976; Jamieson and Hodgson, 1981; Hughes *et al.,* 1984; Grant *et al.,* 1985, 1987; Hodgson, 1990) showed that sheep select diets containing more live components than cattle, resulting in diets of better nutritive value. Because of the larger jaw and the use of the tongue in cattle, this species is less accurate in selecting plant parts from a sward, in comparison with sheep, particularly when green and dead material are well mixed. Sheep have a greater ability to select from fine-scale mixtures (Grant *et al.,* 1985; Grant *et al.,* 1987). However, the stronger jaws and the jerking action of the head of cattle gives an advantage to this species in dealing with more fibrous components of pastures.

Some evidence suggests that sheep can graze deeper within the sward canopy than do cattle (Grant *et al.,* 1985; Hodgson, 1993a, 1990). However, Hodgson (1985b) summarized several experimental works and suggested that there is little evidence to demonstrate major differences in diet selection between species across a range of conditions in temperate swards.

The influence of metabolic state of the animal on diet selection has not been studied in detail (Milne, 1991). Arnold (1981) reported no differences in diet selection amongst pregnant, lactating or dry cattle and sheep grazing sown pastures. Variations in diet selection associated with age have been very small (Arnold, 1981; Hodgson, 1982; Hughes *et al.,* 1984), probably reflecting the more unstable patterns of diet selection of young animals (Hodgson, 1990). Also, very similar diets have been documented with adult and juvenile goats feeding on brush (Provenza and Malechek, 1986). However, young goats lost more weight than adults, probably reflecting more energy expended on foraging due to lack of foraging skills and faster rates of passage.

It has been well documented that there are marked differences between individual members of the same animal species in their preferences for plant species (Marten, 1978; Walton, 1983; Grant *et al.,* 1985; Grant *et al.,* 1987). Diet selection may vary substantially between individuals in the same day as well as for the same individual on different days (Vallentine, 1990).

2.3.3.4 *Sward characteristics affecting diet selection*

Diet selection influences the digestibility of the diet eaten by animals compared with the pasture on offer and affects intake by influencing bite size (Poppi *et al.,* 1987). Sheep reduce intake when they penetrate the surface canopy to obtain green grass leaf in summer ryegrass pastures (L´Huillier *et al.,* 1984). Animals selecting between alternative bites in a sward, probably take smaller bites than animals which are not discriminating, indicating that selective grazing behaviour "should not necessarily be seen as an advantage to the animal in nutritional terms" (Hodgson, 1985b) because the lower rate of herbage consumption may not be compensated for by the better quality of the bites taken.

In defining selection mechanisms several authors have utilized the concept of a two-phase process, including "site selection or grazing station" and "bite selection" (Hodgson, 1982; Milne, 1991; Gordon and Lascano, 1993). However, there are contradictory definitions of these terms between authors: site selection being used to define grazing selectivity at grazing patch level (Milne, 1991; Gordon and Lascano, 1993) or at plant community level (Hodgson and Grant, 1982). In this review, site selection refers principally to selection in a horizontal plane on a large scale whereas bite selection reflects selection of individual bites of herbage from the vegetation at a chosen site involving both the horizontal and vertical planes in small scale areas (eg, grazing patch) (Hodgson and Grant, 1982). On relatively short temperate swards, selective grazing is likely to be related to vegetation patch rather than to individual plants or plant components (Hodgson *et al.,* 1994). Relevant aspects of bite selection will be discussed here. Those related to site selection are not of particular interest in the present study.

Bite selection is influenced by preference for specific plant components and their relative abundance and accessibility (Hodgson and Grant, 1982). The description and discussion of bite selection within a sward will be divided into the following sections: (2.2.3.4.1) selection of plant parts in a pasture and (2.2.3.4.2) selection of plant species in a pasture, the latter with special reference to selection of white clover from perennial ryegrass in temperate swards.

2.3.3.4.1 Selection of plant parts in a pasture

It has been clearly documented that the diet eaten by grazing animals usually contains higher proportions of leaf and live plant tissue, and lower proportions of stem and dead tissue, than are found in the sward on offer (Chacon and Stobbs, 1976; Van Dyne, 1980; Arnold, 1981; Clark *et al.,* 1982; Hodgson, 1982, 1985b, 1990; L'Huillier *et al.,* 1984; Vallentine, 1990). Dead material may be rejected because of low preference or its inaccessibility in the base of the pasture (Poppi *et al.,* 1987; Vallentine, 1990). In addition, a high proportion of green leaf in the diet selected may be due to its ease of prehension, as leaf has lower structural strength and shear force than stem (Hodgson and Grant, 1982; Poppi *et al.,* 1987) rather than to any immediate discemment by the animal of nutritional advantages of eating leaves (Hodgson *et al.,* 1994). When pastures contain more than 70% of dead material, the difficulty of harvesting preferred pasture components is one of the major factors influencing the lower intake achieved (Poppi *et al.,* 1987).

Detailed experimental evidence (Kenny and Black, 1984; Black and Kenny, 1984; Arnold, 1987; Bazely, 1990; Black, 1990; Illius and Gordon, 1990; Laca and Demment, 1991; Illius *et al.,* 1992, Demment *et al.,* 1993; Laca *et al.,* 1993) suggests that sheep and cattle prefer forage that could be eaten at a faster rate, in spite of the fact that this might result in a diet of lower digestibility (Gordon and Lascano, 1993; Clark, 1993). The choice between altemative forage sources is strongly influenced by potential intake rate, which is principally controlled by the height and bulk density of sward canopies, by the vertical or horizontal distribution of the sward components and plant components (Allden and Whittaker, 1970; Stobbs, 1973a, 1973b, 1975; Hodgson, 1985b, 1990; Burlison *et al.,* 1991; Mitchell *et al.,* 1991; Laca and Demment, 1991; Laca *et al.,* 1992; Clark, 1993), by the animal´s immediate experience (Newman *et al.,* 1992) and long term experience (Flores *et al.,* 1989a,b), and ultimately by the degree of hunger of the animal (Newman *et al.,* 1994).

Clark *et al.* (unpublished results cited by Gordon and Illius (1988) and Gordon and Lascano (1993)) working with sheep, cattle and goats as well as Black and Kenny (1984) with sheep, showed that animals prefer tall and sparse swards rather than short and dense ones. Additionally, in Clark´s experiment sheep were less sensitive than goats to height differences, taking shallower bites from the sward surface. These findings are also supported by Gong *et al.* (1993).

2.3.3.4.2 Selection of plant species in a pasture: with special reference to selection of white clover from perennial temperate swards

Hodgson (1981) mentioned that selection will depend upon the preference contrasts between alternative components of the sward as well as their distribution within the canopy. On temperate swards, there is some experimental evidence suggesting that the diets of oesophageally fistulated animals clearly reflect the composition of the top horizons of the sward, showing a substantially unselective grazing (Milne *et al.,* 1982; Barthram and Grant, 1984; Illius *et al.,* 1992; Clark, 1993). However, some examples in the literature show deliberate selection by animals for white clover (Hodgson and Grant, 1980; Briseño *et al.,* 1981; Bootsma *et al.,* 1990; Amstrong *et al.,* 1993) or for leaf components at the base of the sward (L´ Huillier and Poppi, 1984; Grant *et al.,* 1985). Poppi *et al.* (1987) suggested that sheep appear to select white clover preferentially, but this appears to be the case when clover is present in a high proportion in the grazed horizon. The differences between clover content of the sward and of the diet may disappear when the comparison is based on the clover content of the surface horizons of the sward (Milne *et al.,* 1982; Clark and Harris, 1985; Bootsma *et al.,* 1990; Milne, 1991). These findings demonstrate the complexity of interpreting diet selection without information on sward structure (Hodgson, 1981; Milne *et al.,* 1982; Bootsma *et al.,* 1990; and Hodgson *et al.,* 1994).

Hodgson *et al.* (1989) showed that white clover selection was determined principally by the size and weight of the leaves and their vertical distribution within the sward canopy, while cyanogenic levels and leaf mark had little effect. Leaf mark has been suggested as an important factor determining visual selection of morphs of white clover by sheep (Cahn and Harper, 1976), but in this study there was no evaluation of possible relationships between leaf mark and canopy distribution of alternative morphs (Hodgson, 1989; Hodgson *et al.,* 1994).

Nicol and Collins (1990) working with different combinations of sheep, cattle and goats showed that many of the differences in diet composition could be explained principally by choice of grazing horizons, and the discrimination within horizons was of less importance in influencing diet composition. However, cattle showed, on average, less discrimination between components than sheep or goats. These findings in goats are in accord with the results of Clark *et al.* (1982) and Nicol *et al.* (1987). The available evidence suggests that sheep appear to be less selective for white clover than deer (Bootsma *et al.,* 1990).

Illius *et al.* (1992), studying discrimination and patch choice by sheep grazing clover swards, mentioned that patch selection was influenced by sward height and by clover content, and their effects were additive. Tall patches with intermediate contents of white clover (40 to 50%) were preferred, and patches with low or high levels of white clover were avoided. Anti-preference factors such as secondary compounds may be involved at the highest levels of clover (Hodgson *et al.,* 1994). Preferential avoidance of high white clover levels in swards have also been found in other studies (Milne *et al.,* 1982; Clark and

Harris, 1985). In the experiment of Illius *et al.* (1992), during frequent switching between patches, components of the functional response such as bite depth, bite weight and intake rate were modified by patch composition and also by the composition of the alternate patch. Sheep did not take the opportunity of exploring heterogeneity in surface clover content moving to a new grazing patch only after bouts of 20 - 30 bites, probably indicating that the individual bite does not provide sufficient information to influence selection (Illius and Gordon, 1990). Milne (1991) supported the conclusion of the latter authors, saying that since a grazing animal takes between 10,000 and 40,000 bites in a day, the ability to gain information on bites taken is complex and difficult. Finally, Illius *et al.* (1992) argued that sheep make restricted use of previous consumption experience and rely more on the information gained during short periods of grazing, evidence on the role of the animal´s memory in selective grazing being circumstantial (Illius and Gordon, 1990). This is probably the basis for patch sampling and selective constraints in highly heterogeneous swards.

Newman *et al.* (1992), comparing sheep preferences between white clover and ryegrass, found that sheep preferred the opposite species to the one that they had been previously grazing. The explanations given by the authors for this foraging behaviour are: (i) animals try to obtain a balanced diet, (ii) animals should behave to maximize their intake rates and (iii) a physiological response to a novel diet. This experiment emphasizes the significance of previous dietary experiences in grazing selectivity.

Armstrong *et al.* (1993) found no differences in clover selection in relation to variations in patch size and in the distance between patches. However, Laca *et al.* (1993) showed that instantaneous intake rates in ryegrass were directly and inversely correlated with patch heights and patch distances respectively, thus sheep were looking for instantaneous intake rate maximization. This pattern was also observed by Demment *et al.* (1993), where steers appeared to select patches more on the basis of height than of density, concentrating their grazing on patches offering greater intake rate potential.

Differences in canopy heights between legumes and grasses appear to be more important than the relative stage of herbage maturity in determining sheep and goat preferences (Illius *et al.*, 1992; Gong *et al.*, 1993; Hodgson *et al.*, 1994).

2.3.3.5 *Hunger and diet selection*

Several authors have suggested that hungry animals normally accept less pleasant foods (Newman *et al.*, 1994) and increase rate of intake (Chacon and Stobbs, 1976; Dougherty *et al.*, 1989; Newman *et al.*, 1994) compared with fully-fed animals. However, others have found no effects of fasting on the quality of the diet selected by grazing animals (Langlands, 1967; Hodgson, 1981; Jung and Koong, 1985; Greenwood and Demment, 1988). Several effects of increasing length of fasting have been mentioned, such as: (i) reduction in mastication time (Greenwood and Demment, 1988) and (ii) longer retention times of plant material in the reticulo-rumen (Dougherty *et al.*, 1989), and hence passage rate might be slower (Newman *et al.*, 1994).

Newman *et al.* (1994) studying the effect of fasting on sheep preference for white clover and grasses, concluded that fasting not only increased the drive to eat, but also interfered with foraging behaviour, affecting diet composition. Fasted sheep spent a significantly lower proportion of their grazing time on white clover than unfasted ones (82% vs 95%).

The disagreement between authors can be related to the length of the fasting period used in each experiment (eg 24 hours for Newman´s experiment). In terms of the implications of fasting in diet selection research, oesophageal-fistulated animals (OF) are rarely kept in pens more than 4 hours before sampling. Therefore, proper management of OFs should make this factor irrelevant in diet selection studies.

2.3.4 Conclusions

When Provenza and Balph (1990) reviewed the five prevailing conceptual models of diet selection, they concluded " it is likely that most of the researchers responsible for the development of a particular explanation were unfamiliar with details of the other". This concept explicitly shows the necessity of major collaborative effort between researchers with diverse background origins, as in the case of behavioural ecologists and nutritionists. Hodgson *et al.* (1994) addressed the importance in the next 25 years for collaborative work between ecologists and nutritionists to develop research programs to "investigate one of the most interesting interface areas in animal science today". Rogers and Blandel (1991) argued about the benefits of viewing the problem of diet selection from an ecological perspective, saying that "nutritional requirements have to be satisfied within the context of fluctuations in the availability of foods, and competition with other biologically essential activities".

The comments expressed by Provenza and Balph (1990), Rogers and Blandel (1991), and Hodgson *et al.* (1994) show clearly the great potential for the development of diet selection as an interdisciplinary subject. The ultimate dietary choice of a ruminant will be pre-conditioned by the complex world of pre-ingestive (food gathering associated with animal and plant characteristics) and post-ingestive factors affecting the products of rumen digestion as well as learning the consequences of selective grazing.

The literature explicitly demonstrates that the animal senses *per se*, are not always critically and exclusively involved in diet selection, and therefore in animal intake and animal production. However, despite the earlier works of Arnold, this is a research field where the literature is scarce, and general conclusions could be hazardous.

In the last two decades, the learning by consequences theory has made great contributions in our understanding of ruminant diet selection processes by including important factors such as individual positive and negative ingestional consequences of foraging and social learning to explain diet selection.

It has been suggested that the size of a ruminant´s mouth plays a very important role in diet selection, resulting in differential discrimination abilities amongst animal species to select amongst forage components. The literature is not conclusive on this aspect, but effects of previous experience of grazing conditions could be involved in some of the experiments, resulting in confounding effects. Additional experimental evidence with sheep and cattle suggests that age, breed, productive status, and sex differences within species do not seem to be important factors affecting diet selection. However, more research is needed in this area.

Grazing animals have been shown to harvest green leaf in preference to green stem and dead material, so green material is an important factor in determining the grazed horizon. This is related to the fact that the green component of the sward is largely selected by its accessibility and by its ease of prehension by grazing animals and hence it can be eaten at a faster rate.

The choice between alternative forage sources is strongly influenced by potential intake rate, which is principally controlled by the height and bulk density of sward canopies, by the vertical or horizontal distribution of the sward components and by previous dietary experiences.

Recent evidence shows that when white clover and grass leaf are distributed together in the upper horizons of the sward canopy, they are selected in proportion to their distribution. Therefore, pastures must not only contain a high proportion of white clover in order to increase animal production but it must be accessible to the grazing animal.

Several research studies suggest that sheep appear to select white clover preferentially, however this appears to be the case when clover is present in a high proportion in the grazed horizon, but these differences disappear when the comparison is based on the clover content of the surface horizons of the sward. This highlights the significance of including information on sward structure in diet selection research.

High concentrations of white clover (> 50%) in the pasture on offer are rejected by grazing animals, probably reflecting the presence of secondary compounds.

Gordon and Lascano (1993) inferred that conclusions drawn from temperate regions on diet selection, where the digestibility of white clover and perennial ryegrass are little different, cannot be generally applied to other regions of the world because of the greater heterogeneity and complexity of the factors involved in diet selection in such circumstances.

Depending on the severity of the fasting period, diet composition may also be affected by the degree of animal hunger.

2.4 CONDENSED TANNINS AND ANIMAL PRODUCTION

2.4.1 Condensed tannins: definition, classification and ecological role

Tannins are classified as secondary compounds, which seem to have no direct essential function for the basic biochemical reactions required to sustain the growth and development of plants (Vickery and Vickery, 1981). Tannins are defined as polymeric phenolic compounds with strong binding properties. In particular, CT are considered an important quantitative defence of plants against herbivory (Freedland and Janzen, 1974; Roades and Cates, 1976; Swain, 1979; Zucker, 1983; Robbins *et al.*, 1987a,b). Zucker (1983), summarizing research on tannins, proposed that they play a significant ecological mixed function: (i) a defence mechanism against living-plant enemies (fungus, bacteria, insects and hervibores) and (ii) a delay mechanism in plant decomposition, when plant tissue becomes litter.

During disintegration of plant material by animal chewing, CT react with plant protein by hydrogen bonding to form a complex (Barry and Blaney, 1987). Tannins also combine with cellulose, hemicellulose and pectin to form stable complexes (Zucker, 1983; Mangan, 1988). However, Barry (1989) mentioned that tannins have a greater affinity for protein than for cellulose, which has been attributed to the strong hydrogen bond affinity of the carbonyl oxygen of the peptide group. Although tannins are chemically not well defined, (Jansman, 1993), they were classified by Swain (1979) into two groups based on chemical structure, molecular weight, water solubility and action: the hydrolyzable tannins and the condensed tannins. Condensed tannins are by far the most widely distributed in higher plants (McLeod, 1974; Swain, 1979); hydrolyzable tannins are restricted to the Angiosperms (Swain, 1979).

2.4.2 Factors affecting the concentration of condensed tannins in forages

Tannins occur commonly in both woody (about 80%) and herbaceous (about 15%) dicotyledonous plant species (Provenza *et al.,* 1990).

The concentration of CT in plants varies with: (i) plant species (Lowther *et al.,* 1987; Telek, 1989; Terrill *et al.,* 1992a,b; Jansman, 1993; Douglas *et al.,* 1993); (ii) plant cultivars (John and Lancashire, 1981; Lowther *et al.,* 1987; Wang and Ueberschar, 1990); (iii) plant components (Jones *et al.,* 1973; Provenza and Malechek, 1984; Barry, 1989; Terrill *et al.,* 1992a,b; Jansam, 1993; Douglas *et al.,* 1993); and (iv) the soil fertility and temperature conditions where plants are growing (Barry and Forss, 1984; Lowther *et al.,* 1987; Douglas *et al.,* 1993).

Condensed tannins are present in leaves and stems of several important agronomic temperate legumes ((*Lotus* spp. (birsfoot trefoil), *Hedysarum coronarium* (sulla), and *Onobrychis vicifolia* (sainfoin)) (Barry, 1989) and in *Holcus lanatus* (Terrill *et al.*, 1992b; Douglas *et al.*, 1993). They also appear to exist in the flower petals only of white and red clovers (Barry, 1989). However, Horigome and Uchida (1981) found CT traces in leaves of red clover and of Italian ryegrass. Jones *et al.* (1973) also found CT trace amounts in the stems and extremities of the petioles and medium amounts in petals of white clover and red clover plants, but CT were not present in the leaves of these species. In sulla, the stems, leaves and flowers contain 1.3, 3.6, 6.9% (on a DM basis) of CT respectively (Terrill *et al.*, 1992b). The same authors did not find CT in perennial ryegrass but found medium levels (CT = 2.44%) in *Chichorium intybus*. Of 11 species evaluated in terms of the CT distribution within plants, 10 had a leaf lamina-stem ratio of CT concentration superior to 1, the highest ratio being for *Lotus comiculatus* (5.13) and the lowest (0.96) for *Lotus tenuis* (Douglas *et al.*, 1993). Plants with CT concentrations greater than 2%, often had CT levels in their lamina, 2 - 5 times higher than that in their stems.

Condensed tannins in *Lotus pedunculatus* ranged from 2% to 8% (on a DM) when this species grew in low fertility, acid soils under cold conditions compared with high fertility soils under warm conditions (Barry and Forss, 1984). Douglas *et al.* (1993) comparing CT levels of 11 herbaceous species growing at two sites, found that CT concentrations at the moist-cool site were higher than at the drier-warm site (7.1 vs 5.8% on a DM basis). In all the experiments mentioned above, no explanations were offered for the variation of CT associated with both soil fertility and temperature.

Lowther *et al.* (1987) established that CT concentrations for *Lotus comiculatus* cultivars ranged from 0.13 to 3.9% (on a DM basis) and for *Lotus pedunculatus* cultivars from 5.8 to 9.76%. Within *Lotus comiculatus*, semi-erect cultivars had lower concentration (0.13 - 0.84%) than erect types (1.16 - 3.9%).

John and Lancashire (1981) also found that *Lotus comiculatus* (cv. Empire) growing in the same conditions had a lower concentration of CT (0.25%) than *Lotus comiculatus* (cv. Maitland) (1.45%). Cultivars of *Lotus comiculatus* contain lower concentrations of CT than does *Lotus pedunculatus* (Barry and Forss, 1984). These results were confirmed by Douglas *et al.* (1993). Seasonal variation of CT has also been documented in *Serica lespedeza*, where CT increased with advancing season and plant maturity (Cope *et al.,* 1971).

2.4.3 The effects of condensed tannins on diet selection and herbage intake

Diet selection and herbage intake in ruminants are associated negatively with the concentration of CT in plants (Cope and Bums, 1971; Barry and Manley, 1984, 1986; Provenza and Malechek, 1984; Barry and Duncan, 1984; Barry *et al.,* 1984; Barry, 1989; Terrill *et al.,* 1989; Provenza *et al.,* 1990, Provenza and Balph, 1990; Kumar and Vaithiyanathan, 1990; Distel and Provenza, 1991; Nuñez-Hemadez *et al.,* 1991; Pritchard *et al.,* 1992). Most of the experimental evidence mentioned above has been focused on evaluation with animals browsing brush plants or with temperate pasture species grazed by sheep under low fertility conditions, where the CT levels in the plant are normally medium to high. However, there is a lack of information on the effect of CT on diet selection when the levels are low. Nevertheless, the information generated with browsers fed on high CT plants will give a good framework to discuss this issue under the circumstances of the present study.

Recently, the importance of secondary compounds in plant tissues on the diet selection of large herbivores has been well documented (Freedland and Janzen, 1974; Barry and Blaney, 1987; Provenza and Balph, 1987, 1988, 1990; Provenza *et al.,* 1991). However, it is difficult to incorporate the effects of these compounds in diet selection models due to the associative effects of physical characteristics of plants (Hodgson, 1993a). Some authors (Feeny, 1969, 1976, Roades and Cates, 1976, Swain, 1979, cited by Clausen *et al.,* 1990) and

(Zucker, 1983; Barry *et al.,* 1984; Barry and Manley, 1986) suggest that CT reduce plant preferences by inhibiting principally protein digestion and secondly carbohydrate digestion. However, the adverse effects of CT on dry matter digestion have been questioned by Robbins *et al.* (1987a,b, 1990), who argued that the common *in vitro* techniques may maximize digestive reduction associated with the effect of CT and that these effects must be studied *in vivo* or with more sophisticated *in vitro* systems than those commonly used.

Kumar and Vaithiyanathan (1990) suggested that tannins might reduce intake in the following ways: (i) diminishing the permeability of the gut wall, giving false signals of ruminal distension; (ii) influencing the production of cholecystokinin and bombesin hormones, which have been observed to reduce intake in animals; (iii) affecting palatability because of the astringent taste in the mouth of animals when salivary proteins precipitate tannins; and (iv) reducing rumen digestion by causing bacteriostatic and bactericidal effects on rumen microbes.

There is no conclusive evidence that CT affects mineral utilization and more research is needed in this area (Kumar and Vaithiyanathan, 1990). However, studies reviewed by Jansman (1993) reveal that tannins affect vitamin and mineral metabolism, reducing vitamin A and vitamin B_{12} absorption. They also decrease iron availability and absorption in rats. Waghorn *et al.* (1987b) working with *Lotus* spp. suggested that CT reduced the apparent absorption of sulphur, potassium and magnesium in sheep.

Other researchers (Freedland and Janzen, 1974; Robbins *et al.,* 1987a,b; Provenza *et al.,* 1990; Provenza and Balph, 1990; Provenza *et al.,* 1990; Clausen *et al.,* 1990) claim that in ruminants CT reduce plant intake by their toxicity effects rather than by reducing digestibility of cell walls or protein availability. Freedland and Janzen (1974) suggest that animals attempt to avoid toxic effects of forages containing secondary compounds by eating plants or plant parts that do not contain them, or where they are present in lower concentrations. Animals should learn to avoid secondary compounds, or eat non-toxic quantities to minimize post-ingestive effects by memory, associating flavours and tastes with plant species and plant parts. Provenza *et al.* (1990) verified this hypothesis with goats, which recognize and avoid consumption of plants containing CT by associating the flavour with adverse post-ingestive consequences. The toxicity of tannins is related to gastritis, irritation and oedema of the intestine (Provenza *et al.,* 1990; Jansman, 1993). Despite the information mentioned above, little is known about the toxic effects of CT in animal production (see review by Jansman, 1993). It is normally accepted that CT are relatively resistant to hydrolysis in the gut and are too large to pass the intestinal membranes.

Natural selection can increase the efficiency of degradation of secondary compounds and can force animals to have mixed diets. It is generally accepted that browsing ruminants have developed mechanisms of CT detoxification and elimination through extensive selection for adaptation in dealing with tannins (Robbins *et al.,* 1987a,b; Kumar and Vaithiyanathan, 1990; Provenza and Balph, 1990; Provenza *et al.,* 1990).

The strategies developed to avoid the adverse effects of secondary compounds were summarized by Freedland and Janzen (1974) as: (i) detoxification by microsomal enzymes; within a range these enzymes degrade secondary compounds, but there is a great variability in their efficiency amongst species and individuals and also their efficiency relies on the animal´s size, age, sex, sexual state, and previous experience; (ii) detoxification in the gut, but this depends on the microflora developed in the gut; (iii) subsidiary mechanisms, like synthesizing particular chemicals that inhibit secondary compounds; formation of non-toxic complexes in the gut (eg interactions between alkaloids and tannins). Microsomal enzymes and gut floras are not able to manage large quantities of secondary compounds.

Few attempts have been made to demonstrate and understand these defence mechanisms in domestic deer, sheep, cattle or goats. Robbins *et al.* (1987b) described an adaptative procedure in deer to cope with diets containing high CT levels by producing salivary proteins that bind tannins in a highly specific manner, forming protein-tannin complexes, where dietary tannins would not affect cell wall digestion. The occurrence of such proline-rich salivary proteins in deer produced by the parotid gland can be related to its feeding habits. In this experiment, deer saliva had higher levels of proline richness and a greater tannin-binding capacity than either sheep or cattle saliva. However, these authors found some buffering effects of sheep´s saliva against CT, and suggested that domestic sheep are not true grazers but are grass-preferring intermediate feeders. Furthermore, sheep may adapt to diets high in CT (Barry, 1985; Lowther and Barry, 1985), but according to the latter researchers the reasons for this adaptation are unknown. Provenza and Malechek (1984) suggested that salivary or plant proteins consumed by domestic goats might bind with as much as 50% of dietary tannins during ingestion. This defensive strategy developed in goats, as in deer can also be connected with the significant amounts of tanniferous forages consumed by those animal species, particularly in goats. Additionally, an active tannase enzyme has been documented in goats by Kumar and Vaithiyanathan (1990).

Recent evidence (Distel and Provenza, 1991) shows that goats consuming plants containing CT early in life, ingested more tanniferous forages later in life than inexperienced goats. Despite the significant and persistent effects of previous experience on CT consumption in goats, the results of this experiment also suggest: (i) experienced goats were better capable of detoxifying tannins; (ii) neither experienced nor inexperienced goats showed evidence of producing proline-rich proteins in saliva; (iii) the capacity of the reticulo-rumen was increased in experienced goats but this effect was not permanent; (iv) there was some evidence that inexperienced goats ingest tannins in amounts that they can detoxify. In these experiments, plants were chopped to avoid the possible selective effects of plant forms and foraging skills.

Additional evidence (Clausen *et al.,* 1990; Jansman, 1993) suggests that differences in tannin structure can have profound effects on the rate of detoxification and on the final products of detoxification. These factors affect herbivore preferences, but the authors proposed that more investigation is necessary in this area.

Hagerman *et al.* (1992), comparing the different abilities of hydrolyzable and condensed tannins to precipitate proteins and the metabolic fate of these compounds, found that in both sheep and deer hydrolyzable tannins were hydrolysed soon after ingestion and totally excreted in the urine. CT were excreted 100% and 60% in deer and sheep respectively. This result in sheep suggests that some CT may be absorbed in the digestive tract (Mehansho *et al.,* 1987). Murdiati *et al.* (1992), studying in sheep: the toxic effects of gallic acid, tannic acid and hydrolyzable tannins with *Terminalia oblongata*, explained that rumen metabolism appeared to prevent toxicity from gallic and tannic acids at a dose rate of < 0.4 g/kg liveweight/day. *Terminalia oblongata* toxicity probably occurs under circumstances when animals ingest leaf containing high levels of hydrolyzable tannins without prior conditioning.

In vivo information on the capacity of intestinal or ruminal microflora to degrade CT is not available (Jansman, 1993). The observed deleterious effects of CT in sheep, deer, rats and mice during prolonged consumption of tannin-rich tree leaves suggest that proline-rich salivary proteins are the first line of animal defence, but this is an inadequate procedure in the long term for dealing with high CT diets (Kumar and Vaithiyanathan, 1990). Differences between species have lead some researchers (quoted by Kumar and Vaithiyanathan, 1990) to postulate threshold levels of toxicity for tannins of 3 - 5% for cattle and of 8 - 10% for goats on a DM basis. In addition, important individual differences in toleration of CT adverse effects are cited in the literature (Arnold and Hill, 1972; Kumar and

Vaithiyanathan, 1990; Distel and Provenza, 1991; Jansman, 1993).

2.4.4 The particular effect of condensed tannins on wool growth, liveweight gain, carcass composition, parasite infestation and bloating under temperate conditions

Traditionally, ruminant animal production in New Zealand pastoral agricultural systems is based on pasture, containing varying proportions of perennial ryegrass and white clover. Over the last two decades, numerous research studies, summarized by Waghorn and Barry (1987), Barry (1989), and Waghom *et al.* (1990) showed that nitrogen digestion is inefficient on these pastures due to the excessive degradation of soluble protein exceeding the capacity of rumen micro-organisms to synthesize protein from ammonia. Waghom and Barry (1987) stated that with fresh forages containing high quantities of crude protein, about 70% is degraded in the rumen and only 30% escapes to the small intestine for absorption. This excessive degradation has been mentioned as the cause of (i) the high incidence of frothy bloat in dairy cattle (Jones *et al.,* 1973) and (ii) amino acid deficiencies in lactating sheep (Penning *et al.,* 1988), in dairy cows (Rogers *et al.,* 1979) and also in growing sheep (Barry, 1981; Poppi *et al.,* 1988).

Furthermore, increases in liveweight gain or nitrogen retention have been observed in response to increasing post-ruminal protein or amino acid supply of animals consuming fresh pasture (Barry, 1981; Poppi *et al.,* 1988). This suggests that ruminants offered fresh, high quality pastures, may be absorbing insufficient protein, so that there are specific amino acid limits (Fraser *et al.,* 1990). Experimental evidence has highlighted the importance of condensed tannins (CT) as an effective route to avoid this significant constraint to animal production under intensive grazing systems (Jones *et al.,* 1976; Barry, 1985, 1989; Waghom 1987a,b; Waghom and Jones, 1989; Waghom *et al.,* 1990; Terrill *et al.,* 1992b; Wang *et al.,* 1994).

The strength and degree of interaction between CT and protein is determined by the nature of both the CT and proteins (Jansman, 1993) being affected by temperature, pH, ionic strength, incubation time and molecular weight of proteins and tannins. High concentration of CT (6 - 10% on a DM basis) and low molecular weight (7,000) in *Lotus* spp. depress voluntary intake and carbohydrate digestion but are highly efficient at reducing plant protein degradation and increasing amino acid supply to animals (Barry and Reid, 1984).

Condensed tannins bind to proteins forming a stable and insoluble complex in the pH range of 3.5 - 7.0; this becomes unstable and releases protein at pH below 3.5 and above 8.0 (Jones and Mangan, 1977). Therefore, proteins in legume and grasses containing tannins should be protected from microbial degradation in the rumen, and in theory be released in the abomasum for absorption in the small intestine (Waghom, 1985).

Additionally, Waghom and Barry (1987), Waghom *et al.* (1987a,b), and Waghom *et al.* (1990) suggested that CT provide a selective protection of essential amino acids during the process of digestion. As a consequence, tannin-containing plants have higher ratios of essential amino acids to non essential amino acids, increasing body nitrogen retention in sheep. It is generally accepted that CT can increase the availability and absorption of essential amino acids by 60%, compared with equivalent CT-free forages (Waghorn *et al.,* 1990). The effect of CT on the digestion and metabolism of methionine and cysteine has been documented by McNabb *et al.* (1993a,b) showing that CT increased the absorption of these sulphur essential amino acids at the small intestine level. These findings are in agreement with the results of Wang *et* al. (1994) for cysteine, but not for methionine. The inappropriate dietary supply of sulphur amino acids in sheep limits wool production (Reis, 1979; Reis *et al.,* 1990).

The effect of CT on animal production is generally tested by including polyethylene glycol (PEG) in their diets, which binds CT and forms a stable complex. PEG can be used to either prevent protein reacting with CT or to displace protein from pre-formed CT:protein complexes (Barry, 1989).

Condensed tannins in *Lotus comiculatus* (CT = 3.4% on a DM basis) increased the amount of cysteine available for wool growth and liveweight gain, producing increments of 11% and 8% in wool growth and liveweight gain rates respectively (Wang *et al.,* 1994). These results are in agreement with those of Lee *et al.* (1992), who reported that high CT in *Lotus pedunculatus* significantly improved cysteine supply and utilization at the whole body level, resulting in increments of 29% in wool growth and of 8% in liveweight gain in comparison with a control treatment. Dry matter intake was markedly depressed with *Lotus pedunculatus*, confounding the results of this experiment. The authors did not provide information related to the concentration of CT for each species, so it is difficu lt to generalize conclusions from this experiment. Conversely, the rates of liveweight gain and wool growth of lambs fed on high CT, *Lotus pedunculatus* (CT = 7.6 - 9% on a DM basis) were reduced by 61% and by 22% respectively (Barry, 1985). *Lotus pedunculatus* (CT = 4 - 10%) (Barry and Manley, 1984; Barry and Duncan, 1984; Barry *et al.,* 1986) and *Lotus comiculatus* (CT = 3.5 - 4.9%) (Chiquette *et al.,* 1988; Wang *et al.,* 1994) showed depressive effects of CT on readily fermentable carbohydrates, pectins and hemicellulose, but not cellulose.

Under high soil fertility conditions, lambs performed better on swards of *Lotus pedunculatus* (CT = 2%, 153 - 315 g/day) and *Onobrychis vicciifolia* (CT = 6%, 182 - 230) than on *Medicago sativa* (123 - 267 g/day), *Trifolium pratense* (127 - 234 g/day) or *Lolium perenne* (88 - 198 g/day) swards, but a *Trifolium repens* sward had the highest feeding value (190 - 354 g/day) (John and Lancashire, 1981). Conversely, under low fertility conditions where the level of CT is normally increased, lambs fed on *Lotus pedunculatus* (CT = 7.6 - 8.9% on a

DM basis, 27 - 125 g/day) drenched with water (CT effective) performed worse than lambs fed on the same sward but drenched with PEG (CT not effective) (Barry and Reid, 1984). These results clearly show the beneficial and harmful effects of CT according to their concentration in plant tissue.

Purchas and Keogh (1984) and Terrill *et al.* (1992a) found that the carcass fat content of lambs grazing CT-containing plants (*Lotus pedunculatus* and *Hedysarum coronarium*) to be lower than that of lambs grazing white clover/ryegrass pastures, presumably due to increasing protein deposition and reducing fat as a proportion of the carcass. However, low CT levels of *Plantago lanceolata* (CT = 0.955% on a DM basis) and of *Cichorium intybus* (CT = 0.136% on a DM basis) did not produce leaner lambs than white clover or ryegrass swards (Dearker *et al.,* 1994).

Free tannin negatively affects voluntary intake and animal performance, forming complexes with protein which react and precipitate microbial and digestive enzymes (McLeod, 1974; Barry and Duncan, 1984; Barry and Manley, 1984, 1986). In *Lotus* spp., free tannins increased linearly with increments in total CT in a range of 0 to 9% (Barry and Manley, 1986). Bound and free tannins seem to be the respective indices of the nutritionally beneficial and detrimental effects of CT in fresh forage diets consumed by ruminant animals: with bound tannins increasing amino acid supply and free tannins probably being responsible for depressions in rumen carbohydrate digestion and voluntary intake (Barry and Manley, 1986). Hydrolyzable tannins have never been detected in fresh forages grown under New Zealand conditions (Jones unpublished, cited by Barry and Manley, 1986; Barry and Blaney, 1987).

Animal adaptation to the consumption of birdfoot trefoil forage with high CT concentration has been recorded by Barry (1985), who found that the liveweight gain of lambs with previous experience (5 weeks) of consuming high CT levels were greater than that of unconditioned lambs. The author proposed that sheep adapt to the high CT concentration to some degree.

Despite the considerable research effort in Australia and New Zealand, studying the effect of condensed tannins in ruminant nutrition and animal production, few attempts have been made to evaluate diet selection in these circumstances. Waghorn *et al.* (1990) suggested that palatability is unlikely to mediate the effect of CT on intake. In experiments with sheep fed on *Lotus pedunculatus*, the stem fraction (containing 2.2% CT) was rejected, but leaflets containing high levels (CT = 8.8%) were preferred and eaten. Furthermore, Jones and Mangan (1977) showed that CT from sainfoin was unable to form insoluble complexes with submaxillary mucoprotein, so that the lubricating properties of the salivary mucoprotein, and palatability, were unaffected. Dairy cows preferred dock leaves with higher CT concentrations (2 - 3 times) than dock stems (Waghorn and Jones, 1989).

It has been suggested (Niezen *et al.*, 1993a) that feeding plants containing CT might reduce the effect of parasitism by increasing the post-ruminal availability of dietary protein and, as a result, affect the establishment or persistence of gastrointestinal nematodes. In a series of experiments evaluating the effect of CT on liveweight gain and faecal egg counts (FEC), Niezen *et al.* (1993a) and Niezen *et al.* (1994) showed that lambs fed on CT-containing plants (*Lotus pedunculatus, Lotus corniculatus,* and *Hedysarium coronarium*) had lower FEC and higher liveweight gains than those grazing conventional ryegrass or non-CT-containing pastures. In some cases the effects of CT on FEC persisted for a short period (21 - 42 days). The effects of CT on liveweight and on FEC levels were not consistent across comparisons. From the observations on FEC, the reduction in worm burdens was modest.

Niezen *et al.* (1993b) comparing the effect of four grass species on lamb parasitism and growth, using suppression drenching (each 15 days) and trigger-drenching (threshold of 1500 epg) schemes, found that suppressively and trigger-drenched lambs on ryegrass swards were heavier than those on the other grasses, but trigger-drenched lambs grazing on *Holcus lanatus* were heavier than lambs grazing on tall fescue or browntop. In general, the sequence in the level of FEC was Browntop > Tall fescue > Yorkshire fog > or = Ryegrass. The liveweight gains of suppressively drenched lambs were always higher than those of the trigger-drenched lambs, but this difference was much smaller for lambs grazing the *Holcus* sward, suggesting a possible effect of CT on body growth and on parasite control.

A good example of the importance of sward structure on larvae population was given by Moss and Vlassoff (1993), who found that chicory swards offer good opportunity to reduce larval intake in grazing animals in comparison with perennial ryegrass, prairie grass and luceme swards, because this herb had the lowest larval populations per unit of herbage mass.

The results of the series of trials performed by Niezen and collaborators are not conclusive. More experimental work has to be done in order to isolate nutritional and non-nutritional effects (eg sward attributes) which may be confounded, and to evaluate the effect of CT on lamb parasitism. FEC may not be a good indicator of this effect.

Leathwick and Atkinson (1995) further argued that plants containing CT, such as *Lotus* spp., could have considerable potential for a future role in the integrated management of flystrike and dags.

Beneficial effects of dietary tannins also appear to be important in reducing the risk of bloat by binding proteins which are responsible for ruminal foam formation and decreasing the activity of gas-producing microflora in the rumen (Jones and Littleton, 1971; Reid *et al.,* 1974; Mangan, 1988; Waghorn *et al.,* 1990). However, with the "cell rupture" theory of legume pasture bloat (Howarth *et al.,* 1978), the role of CT seems to be secondary, and the assumption that CT interferes with digesting enzymes *in vivo* is doubtful. This theory is supported by the results of Lees *et al.* (1981) where bloat-safe legumes (*Lotus comiculatus, Onobrychis vicicifolia* and *Astragal cicer* L.) had strong to moderate cell walls and higher degrees of tissue strength than the bloat causing legumes (*Medicago sativa, Trifolium repens*, and *Trifolium pratense*).

In New Zealand, a series of research studies (Terrill *et al.,* 1992a) in *Lotus* spp has shown that for ruminant nutrition the optimal concentration of CT in forage diets is approximately 2.2% on a DM basis. Values exceeding 5% are recognized as being detrimental in ruminant diets, affecting fibre digestion and voluntary intake (Barry, 1989; Waghorn *et al.,* 1990). However, as yet the minimal effective concentration has not been defined (Terrill *et al.,* 1992a). Evidence published by Waghorn and Jones (1989) showed that when the diet of dairy cattle contained only 0.17% of CT on DM basis, bloat was absent.

Recently Terrill *et al.* (1992a), comparing animal production during different seasons between *Lolium perenne/Holcus lanatus/Trifolium repens* (CT = 0.2 - 0.6%) and sulla (*Hedysarium coronarium*) (CT = 4 - 6%), found that the rates of body and wool growth (derived from lambs drenched or undrenched with PEG) were higher for lambs grazing on sulla than those grazing on pasture, and on average CT increased wool growth and liveweight gain, the increases being (4 - 11%; 1.7 - 19.3%) for sulla and (4 - 18.5%; 24 - 29%) for pasture respectively. The CT responses were always higher in both swards in spring rather than in autumn or winter. The authors suggested that animal responses to CT could be associated with the presence of CT in *Holcus lanatus* (CT = 0.2%). Additionally, they argued that low CT concentrations probably have some nutritional function in reducing rumen protein degradation, resulting in increments in protein supply which can contribute towards body and wool growth.

Waghom *et al.* (1990), reviewing the nutritional value of plants containing CT for animal production in temperate conditions, concluded that ruminant production of milk, meat and wool could be increased by 10 - 15% if grazed pasture contained 2 - 3% of CT on a DM basis, suggesting that these levels would be achieved if white clover (*Trifolium repens*) could be engineered to contain 7 - 8% of CT in its foliage. Australian and New Zealand laboratories are transferring genes coded for leaf production of CT from sainfoin and birdfoot trefoil into legumes that have greater agronomic potential, such as luceme and white clover (Barry and Blaney, 1987).

2.4.5 Analytical methods available for the measurement of tannins in plants

Comprehensive reviews of tannin analyses have been recently published by Deshpande *et al.* (1986), Makkar, (1989), Okuda *et al.* (1989), cited by Jansman, (1993).

Methods of tannin analysis can be classified into three main groups: colorimetric methods, protein binding methods, and other methods, but none of these methods provide completely satisfactory results because of the chemical complexity of tannins (Jansman, 1993). The colorimetric methods are widely employed for quantitative determinations of CT in fruits, grains, forage legumes and grasses. Protein binding methods are based on the ability of tannins to precipitate proteins, which might provide useful information about the nutritive value of foods and feeds which contain them (Hagerman and Butler, 1978). Other methods include evaluation of CT in plants by near infrared reflectance spectroscopy (Windham *et al.,* 1988) and others.

The colorimetric methods include the following assays: Vanillin assay, Folin Denis assay, Prussian blue assay and Acid butanol assay. In New Zealand (Barry and Blaney, 1978), CT in legumes and grasses are determined by the vanillin-HCl procedure, or ultimately by the modified butanol-HCL procedure, which includes a sub-routine for extraction of free CT (Terrill *et al.,* 1992b). The modified butanol-HCl procedure gives total CT in the forages into extractable, protein-bound, fibre-bound fractions, but it has some limitations in detecting low CT concentrations (< 1% on a DM basis), while the vanillin-HCl procedure is very sensitive (Terrill *et al.,* 1992b). However, the latter method can give false interpretations due to the confounding effect of the presence of anthocyanin in plant materials (Sarkar and Howarth, 1976). Broadhurst and Jones (1978) mentioned that the Vanillin assay suffers from reported lack of reproducibility between samples, days and laboratories.

Ahn *et al.* (1989) mentioned that there is considerable variation in CT content between browse species, depending on the analysis used and on the method of drying. Drying the browse at 60ºC in a forced-draught oven resulted in variable losses of CT in all species. However, this system of drying resulted in highly significant increases in nitrogen digestibility. These results are supported by Swain (1979) using temperatures of 50ºC. Grinding of forage samples in preparation for analysis has also been shown to affect CT extractability (Terrill *et al.,* 1990).

2.4.6 Conclusions

The presence of secondary compounds, and in particular of tannins in plants, must be considered as a defensive, anti-herbivore strategy and the complexity of diet selection in these circumstances must be assessed with this in mind.

In general, many researchers have directly or indirectly attributed the low browser preferences and low intake for several tropical plants to the relatively high CT in their tissues. Additionally, as plants contain high CT levels in tropical regions, ruminants living in these environments have developed defensive mechanisms through natural selection against the deleterious effects of CT.

Recently, additional evidence suggests that herbivores instinctively recognize and avoid tannin-containing plant parts in response to post-ingestive adverse effects, and that the exposure of animals early in life to plants containing CT may give an advantage to animals later in life to deal with this secondary compound (Provenza and Balph, 1990).

In the literature, the term "tannins" has been used in a general context without using precise definitions of their structure and classification. Hydrolyzable and condensed tannins are of most agricultural significance. The distinction is important, particularly when they differ in their nutritional significance and toxic effects (Murdiati *et al.,* 1992). Hydrolyzable tannins are degraded in the rumen by microorganisms and absorbed through ruminal walls producing toxic effects, while condensed tannins are not in fact degraded in the gut.

The information available related to the influence of CT on diet selection for domesticated ruminants is very scarce, especially when they are feeding on temperate pastures containing low CT levels. More research is needed to generalize the available information.

Robbins *et al.* (1987a) stated that "the interpretation of plant-animal interaction as affected by tannins is far more complex and important than most ruminant ecologists have realized" and the understanding of these interactions is an excellent ground for testing theories of plant and ruminant coevolution. The level and type of tannins, the length of the test period, as well as differences among animal species and their differences in age and in production level, may explain the contrasting results in the literature with respect to the effect of tannins on feed intake, diet selection and hence on animal production. Moreover, tannic acid has been frequently used to study the responses of animals to the effect of secondary compounds. However, some researchers argue that isolated tannins from feedstuffs or standards of commercial tannins (eg tannic acid) cannot be representative of tannins in a number of feedstuffs (Hagerman *et al*, 1992;

Jansman, 1993). This hypothesis has been proved by Hagerman *et al.* (1992) comparing tannic acid (a hydrolyzable tannin) versus quebracho tannin (a CT) in terms of their capacity to precipitate protein. Jansman (1993) suggested that the large number of variables that tend to modify the harmful effects of tannins limits the usefulness of direct comparison between the different studies. Hagerman *et al.* (1992) suggested that generalizations about the effects and functions of tannins should not be based on studies with tannins from a single source.

Several studies conducted principally in New Zealand clearly indicate that an optimal CT concentration in forage diets (2 - 3% on a DM basis) could increase ruminant production of milk, wool and meat by 10 to 15%, whilst depression of rumen digestion occurs at 4%, and animal intake and animal productivity are severely affected with CT levels in the range of 6 - 10%. So far, the minimal effective CT concentration has not been defined (Terrill *et al.*, 1992b). However, some evidence indicates that low CT levels (0.2%) are useful in preventing bloat in cattle (Waghorn and Jones, 1989). There is no information for meat and wool production in those circumstances.

New information is becoming available which shows additional benefits of CT plants in animal production, such as: (i) a way to reduce carcass fatness (Purchas and Keogh, 1984; Terrill *et al.*, 1992a) (ii) a control of internal parasites in sheep (Niezen *et al.*, 1993a,b; Niezen *et al.*, 1994), and (iii) a supplementary tool to be incorporated into integrated management control of flystrike and dags in sheep (Leathwick and Atkinson, 1995). More research is needed in this area before attempting to draw any general conclusion.

Condensed tannin concentrations in forages vary significantly according to: plant species, plant cultivars, plant components, soil fertility and temperature. Increased concentrations of CT have been found in CT-containing plants under environmental stress, but reason(s) for this plant behaviour have not been given in the literature.

None of the colorimetric assays for tannin determination are very specific, however most of them are appropriate for screening purposes, with the Vanillin and Acid Butanol assays being the most broadly used (Jansman, 1993). The perfection of the current analytical techniques used to measure tannins in plants, or the development of new economical and less laborious methods, are required in order to improve the volume and quality of our information.

2.5 THE POTENTIAL OF *HOLCUS LANATUS* (YORKSHIRE FOG) FOR ANIMAL PRODUCTION

In New Zealand over the last decade much effort has been made by plant breeding scientists to find viable alternatives to perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*) in seasons or environments where the production of the traditional New Zealand pasture is limited. There is interest in the potential value of Yorkshire fog as an alternative species for low to moderate soil fertility conditions and poor drainage conditions (Watkin and Robinson, 1974; Jacques, 1974; Haggar, 1976; Harvey *et al.*, 1984; Morton *et al.*, 1992), as well as due to its probable nutritional benefits in enhancing the efficiency of dietary protein utilization associated with its CT content (Terrill *et al.*, 1992a; Douglas *et al.*, 1993) or its potential effect on lamb parasitism (Niezen *et al.*, 1993b).

Holcus lanatus has been the subject of several reviews and investigations in the past (Cameron, 1979; Muangthong, 1989). These reviews have been concentrated on agronomic aspects of *Holcus*, dealing with genotype variability (Muangthong, 1989) and with sward characteristics affecting acceptability to sheep (Cameron, 1979).

Cameron (1979) reported that 11 *Holcus lanatus* characters (leaf tensile strength, leaf width, clump height and diameter, clump erectness, leaf flavour level, soluble sugar concentration, rust infestation, dead leaf, sheath material, proportion of inflorescences) only explained 20 - 25% of the variation in sheep preference, and he concluded that the unexplained variation may be related to high variance amongst sheep preferences and with unassessed plant characteristics.

Low CT levels have been reported in *Holcus lanatus* (CT = 0.16 - 0.18%, Terrill *et al.,* 1992a,b) and (CT = 0.13 - 0.20%, Douglas *et al.,* 1993). The low concentrations of CT observed in *Holcus lanatus* could be associated with positive effects on animal production (Waghom and Jones, 1989; Terrill *et al.,* 1992a,b).

Studies of herbage intake and sheep performance on Yorkshire fog swards appear to be limited to the earlier experiments of Watkin and Robinson (1974) and to the recent trials published by Morton *et al.* (1992) and Niezen *et al.* (1993b), which show the potential of *Holcus* for animal production. However, there is no information evaluating *Holcus* swards in terms of sward structure, diet selection and ingestive behaviour. In addition, there is no information on the effect of the CT content of Yorkshire fog upon liveweight gain, wool growth and rumen metabolism.

CHAPTER 3

EXPERIMENT 1: A COMPARATIVE STUDY OF HERBAGE INTAKE, INGESTIVE BEHAVIOUR AND DIET SELECTION IN SHEEP GRAZING *HOLCUS LANATUS* AND *LOLIUM PERENNE* SWARDS IN LATE AUTUMN

3.1 ABSTRACT

Relationships amongst sward characteristics, grazing behaviour, diet selection, and herbage intake of ewes in mid-pregnancy were studied on *Lolium perenne* (perennial ryegrass)/*Trifolium repens* (White clover) and *Holcus lanatus* (Yorkshire fog)/*Trifolium repens* (White clover) swards rotationally grazed at medium and high daily allowances (6% and 12% of liveweight as herbage dry matter respectively) during late autumn.

Estimates of herbage mass and sward surface height for the ryegrass and *Holcus lanatus* swards respectively were 2250 vs 2880 ± 169 kg DM ha^{-1} and 13 vs 13.9 ± 0.8 cm.

Herbage intake achieved by sheep grazing ryegrass swards was 35% higher than that achieved on *Holcus lanatus* swards (1410 vs 1100 ± 29 g DM ewe^{-1} day^{-1}) and the difference between grazing allowances was 25% in favour of high allowance (1370 vs 1150 ± 50 g DM ewe^{-1} day^{-1}). Bite weight was 38% greater for *Holcus lanatus* than for ryegrass (139 vs 86 ± 7 g OM bite^{-1}) and 30% greater for high allowance than for medium allowance (130 vs 90 ± 7 g OM bite^{1}). The higher intake per bite of *Holcus lanatus* swards was associated with the greater sward bulk density recorded (210 vs 168 ± 20 kg DM ha^{-1} cm^{-1}). Grazing time increased for ryegrass swards and for medium allowances to compensate

for limitations in intake per bite (610 vs 500 ± 34 mins and 620 vs 495 ± 27 mins), whereas the changes in rate of biting were small.

There was a small, but consistent advantage in the organic matter digestibility of the herbage selected in favour of ryegrass swards (85.7 vs 82.2 ± 0.3 %), while no differences were found between herbage allowances. Animals on both pasture types concentrated on grass rather than clover in the diet, and extrusa samples from both showed evidence of limited concentrations of condensed tannins. The low contribution of white clover in the diet of both swards (1.5%) was explained by the limited contribution of this species in the total herbage mass during late autumn and by its distribution at the base of sward canopy.

It is concluded that herbage intake was influenced more by nutritional than behavioural constraints, but that these effects need to be investigated in animals of higher productive potential and nutrient demand.

Keywords: *Holcus lanatus*; *Lolium perenne*; white clover; grazing allowance; sheep; ingestive behaviour; diet selection and herbage intake.

3.2 INTRODUCTION

Traditionally New Zealand livestock systems rely on pasture, perennial ryegrass and white clover being the most important forage species. However, there is interest in alternative species in seasons and environments where ryegrass production is limited. Yorkshire fog (*Holcus lanatus* L.) is an alternative species to perennial ryegrass (*Lolium perenne* L.) for low to moderate soil fertility conditions (Watkin and Robinson, 1974; Haggar, 1976; Harvey *et al.*, 1984, and Morton *et al.*, 1992) and for the potential value of its condensed tannins in enhancing the efficiency of dietary protein utilisation (Terrill *et al.*, 1992b). However, there is a lack of information on herbage intake, diet selection, ingestive behaviour and animal performance of sheep grazing Yorkshire fog. The aim of the present study was to investigate differences in these variables between Yorkshire fog and perennial ryegrass.

A preliminary report of this experiment was published in the Proceedings of the New Zealand Society of Animal Production 1994, Volume 54 (see Appendix 3.1).

3.3 MATERIALS AND METHODS

3.3.1 Site preparation and management

The experiment was carried out at Massey University (41° 10′ S), Palmerston North, New Zealand from May to June 1992. The experimental site, on a Tokomaru silt loam soil , classified as an Aeric Fragiaqualf (gleyed, yellow-grey earth) was sown in March 1988 with perennial ryegrass (*Lolium perenne* L. cv. 'Grasslands Nui') or Yorkshire fog (*Holcus lanatus* L. cv. 'Massey Basyn') both with white clover (*Trifolium repens* L. cv. 'Grasslands Tahora') in plots of 0.2 ha. The sowing rates were 18, 3, and 2 kg ha^{-1} for perennial ryegrass, Yorkshire fog and white clover respectively. A soil fertility test performed on June 1991 showed that the average level (from four paddocks of each species) of pH, Olsen-P (µg/ml), exchangeable K (meq/100 g of soil), and SO_4-S (µg/g of soil) were similar for both swards, being 5.7, 27.5, 0.61, and 5.2 *vs* 5.7, 24.5, 0.65, and 4.25 for *Holcus* and ryegrass swards respectively. Experimental swards were managed under continuous stocking with sheep for two years. Nitrogen and phosphate fertilisers (50 Kg of Urea and 300 Kg of superphosphate ha^{-1} respectively) were applied to the experimental area in April 1992, and plots were grazed and then left to accumulate herbage.

Long-run temperatures on the experimental site range from 7 ºC (July) to 18 ºC (January) and the average annual precipitation is 1000 mm. The monthly rainfall for the months May-June 1992 was 30 mm and 75 mm respectively, compared with respective averages of 90 mm and 95 mm. Temperatures for May and June 1992 were similar to long-run averages (9 and 7.2 ºC vs 10 and 7.5 ºC respectively).

3.3.2 Experimental design

The trial was conducted on four 0.2 ha paddocks for each sward species, and each paddock was divided into two by electric fences in the ratio 2:1 to give two daily herbage allowances representing 6% (medium) and 12% (high) of the liveweight of the experimental animals respectively on a dry matter basis. During the experimental period, the four replicate paddocks of each species were grazed for periods of 7 days in sequence. The average instantaneous stocking rates were 90 and 45 ewes ha^{-1} for medium and high allowances respectively.

A total of 48 adult Romney ewes in mid-pregnancy (mean weight 64 ± 7.2 SE Kg) were used in the present study. The first group of 24 ewes grazed the experimental plots during weeks 1 and 2 and the remaining group (n = 24) grazed new plots during weeks 3 and 4. Six ewes grazed in each plot. The ewes were randomized amongst treatments according to fasted liveweight, and grazed adjacent plots for one week before measurements commenced.

3.3.3 Sward measurements

Herbage mass was estimated by cutting six 0.1 m^2 quadrats to ground level with an electric shearing handpiece in each plot before and after grazing. The samples were washed and then dried in a forced-draught oven for 72 hours at a temperature of 70 - 80º C. Sub-samples were clipped adjacent to each quadrat, bulked within each replicate and subsequently dissected into categories for morphology (leaves, stems, live and dead tissue) and species, then dried and weighed as above.

Sward surface height (SSH) was measured before and after grazing using a sward stick (Bircham, 1981; Barthram, 1986). Five readings were made inside each quadrat when herbage mass samples were collected, giving 30 readings for each plot. Within each plot 40 extra readings were then taken randomly.

Sward bulk density (SBD) was calculated by dividing the herbage mass estimated for each quadrat cut, by the corresponding SSH average (mean of 5 readings).

The vertical distribution of plant tissue within the sward canopy was measured using an inclined point quadrat (Warren Wilson, 1963) set at 32.5º to the horizontal; 100 contacts were recorded in each plot before and after grazing. Contacts were recorded for species, morphology (leaf, stem, petiole), and state (live and dead).

Tiller population was estimated from 20 tiller cores (diameter = 53 mm) collected from each plot before grazing. The core samples were hand separated into species (ryegrass, Yorkshire fog, white clover, other grasses, and weeds), and the number of units (tillers or nodes) of each was calculated. Ten tillers and 10 nodes were sub-sampled from the 6 quadrats taken in each plot, and hand separated into pseudostem, grass leaf, petiole and clover leaf. The materials of each category were measured for length, weight and area and then oven dried for 48 hours and weighed. Leaf area was estimated for clover leaf using the method of Williams *et al.* (1964).

3.3.4 Animal measurements

Ewe liveweights were recorded at the beginning and at the end of the trial. Two pairs of castrated male sheep fistulated at the oesophagus, were rotated between treatment replicates on a daily basis and one extrusa sample was collected from each animal from each plot. The extrusa samples taken in the field were sealed in polythene bags, immediately frozen under crushed ice, and subsequently stored at -20º C. The frozen extrusa samples were divided into two portions. On one portion, the proportions of grasses and white clover in the total diet were assessed by suspending a sample of herbage in water in a gridded tray and identifying plant material at grid intersections (Clark and Hodgson, 1986). The proportion of each sward component was subsequently expressed as a percentage of the total contacts with herbage particles. The other portion was freeze-dried and ground (1 mm diameter sieve) and then subjected to laboratory analyses for *in vitro* digestibility (Roughan and Holland, 1977), total nitrogen determined by the Kjeldahl method, carbohydrates and lignin (Bailey, 1967), and condensed tannins (CT) by the Butanol/HCl procedure (Terrill *et al.*, 1992b).

Faecal output of the grazing animals was estimated using intraruminal controlled release capsules (CRC; Captec (NZ) Ltd., Auckland), according to procedures described by Parker *et al.* (1989). Individual faecal samples were taken daily at 0830 to 0930 hours from the rectum of each ewe. Seven days after CRC dosing, there were two consecutive periods of 5-days faecal sampling. Faecal samples were oven dried at 80º C to constant weight and then bulked within 5-day periods for each ewe. The concentration of chromium (Cr) in faeces was assessed by atomic absorption spectrophotometry (Parker *et al.*, 1989). The chromic oxide release rates were determined from capsules recovered from 12 ewes (3 per treatment) slaughtered at the end of the trial.

Herbage organic matter intake (**HOMI**) was estimated from equation (**1**) (Parker *et al.*, 1992), using *in vitro* organic matter digestibility (**OMD**) values obtained from the extrusa samples collected from oesophageal fistulated sheep.

$$HOMI\ (g\ OM\ day\text{-}1) = (RR / FC) / (1 - OMD) \qquad (1)$$

Where RR = Rate of marker release (g Cr day^{-1})

FC = Concentration of Cr in the faeces (g Cr/g OM)

Two 24 hour grazing behaviour studies were carried out during each faecal collection period. Time spent in grazing, ruminating and resting was manually recorded for each ewe at intervals of 15 minutes. Night time observations were recorded using an infra-red nightscope (Varo Noctron V.). Rate of biting (bites/minute) was obtained for each animal using a 20-bites technique (Jamieson and Hodgson, 1979) recorded by stop-watch during grazing periods at dawn, mid-morning, early afternoon and dusk. This measure provides an indication of the maximal biting rate for the sward in question. The weight of herbage taken in individual bites was determined using the oesophageal fistulated wethers. The procedure used involved counting the number of bites taken during the collection of extrusa samples (Stobbs, 1973a,b). The weight per bite was calculated by dividing the weight of the sample by the number of bites taken (Forbes, 1982). Estimates of herbage recovery rates were obtained by offering 4 samples of fresh forage (200g) to each fistulate and by weighing the forage recovered in the collecting bags.

3.3.5 Statistical analysis

The pasture and animal data were analyzed using the statistical package SAS (SAS, 1985), based on a Split-Plot Design using 4 blocks, with species (Yorkshire fog or perennial ryegrass) as the main plot and grazing allowances (medium or high) as the split-plot factor. Pasture measurements before and after grazing were separately analyzed, based on plot means. A point quadrat package (Butler, 1991) was used in the analysis of inclined point quadrat data. The variances of means were calculated using Students t test (Steel and Torrie, 1981). Liveweight gain results were adjusted by co-variance for initial weight.

3.4. RESULTS

Interactions between species and grazing allowances were not significant for any sward or animal variable, so results are presented as main effects only.

3.4.1 Sward measurements

3.4.1.1 *Herbage mass, surface sward height and sward bulk density*

The results of estimates of herbage mass, surface sward height and sward bulk density are given in Table 3.1.

Before grazing, there were no significant differences in herbage mass between species or grazing allowances, but Yorkshire fog swards had a significantly higher post-grazing herbage mass than ryegrass swards. This resulted in a higher proportion of herbage removed in ryegrass swards than in Yorkshire fog swards (40% vs 27% respectively). After grazing, high allowance treatments had higher post-grazing herbage mass than medium allowance treatments. On average, 45% and 23% of the pre-grazing herbage mass were removed at medium and high allowances respectively.

SSH for Yorkshire fog and ryegrass swards were similar before and after grazing. High allowance plots had a significantly greater sward height than medium allowance after grazing, but this difference was not significant before grazing. There were no significant differences in SBD between grazing allowances before or after grazing, though the SBD of Yorkshire fog was 30 % higher ($P < 0.06$) than ryegrass swards before grazing and 29% higher after grazing.

3.4.1.2 *Sward composition*

The botanical composition of each sward before and after grazing is shown in Table 3.2. Sown grasses formed the major components of both Yorkshire fog and ryegrass swards before and after grazing. The proportion of white clover in the swards was identical (5%) before grazing, but it was slightly, though not significantly, higher in ryegrass swards than in Yorkshire fog swards after grazing.

Table 3.1. The effect of species and allowance on herbage mass (kg DM ha^{-1}), sward height (cm) and sward bulk density (kg DM ha^{-1} cm^{-1}) before and after grazing.

Before and after grazing	SPECIES				ALLOWANCES			
	Ryegrass	Yorkshire fog	SEM[‡]	Sign.[§]	Medium	High	SEM	Sign.
Herbage Mass (Before)	2246	2884	169	NS	2443	2686	170	NS
Herbage Mass (After)	1361	2099	58	**	1379	2082	152	**
% Mass defoliated	40	27	–	–	45	23	–	--
Sward height (Before)	13	14.9	0.78	NS	13.3	13.6	0.56	NS
Sward height (After)	7.2	8.3	0.35	NS	6	9.6	0.37	**
Sward bulk density (Before)	161	230	17	NS	197	194	6.2	NS
Sward bulk density (After)	204	286	15	NS	221	269	19.6	NS

SEM[‡] = Standard error of the mean
Sign.[§] = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

Table 3.2. The proportions of components of ryegrass and Yorkshire fog swards estimated from hand separation (DM basis).

Before Grazing	SPECIES				GRAZING ALLOWANCES			
	Ryegrass	Fog	SEM‡	Sign.§	Medium	High	SEM	Sign.
Ryegrass	60	18	6.2	*	44	34	3.1	NS
Yorkshire fog	0	45	2.2	**	21	24	4.3	NS
White clover	5	5	1.0	NS	6	5	0.7	NS
Other grasses	25	14	3.1	NS	18	20	1.8	NS
Weeds	1	4	2.4	NS	1	4	2.0	NS
Dead Material	9	14	2.0	NS	10	13	1.1	NS
After Grazing	**SPECIES**				**GRAZING ALLOWANCES**			
	Ryegrass	Fog	SEM	Sign.	Medium	High	SEM	Sign.
Ryegrass	54	12	3.6	**	31	34	2.4	NS
Yorkshire fog	0	54	2.5	**	28	27	4.3	NS
White clover	8	5	1.3	NS	5	7	0.6	*
Other grasses	24	10	3.7	NS	19	16	1.6	NS
Weeds	1	0	0.1	**	1	1	0.6	NS
Dead Material	13	19	1.0	*	16	15	2.2	NS

SEM‡ = Standard error of the mean. Sign.§ = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

The contents of other grasses did not differ significantly between swards, and weeds were a minor component. There was a tendency for a higher proportion of dead material in Yorkshire fog swards than in ryegrass swards, which was significant in the comparison after grazing. The proportion of dead material increased in both pastures during grazing.

Comparing grazing allowances, the white clover component was significantly higher at high allowances than at medium allowances after grazing, while there was no significant difference before grazing. There were no significant differences for other sward components between grazing allowances before or after grazing.

3.4.1.3 *Tiller and node populations*

Tiller and node populations are given in Table 3.3. Tiller density of Yorkshire fog in Yorkshire fog swards was substantially higher than that of ryegrass in ryegrass swards. White clover nodes had a very similar population density in both sown swards. The tiller density of other grasses was considerable in both swards, but the value was significantly higher in ryegrass swards than in Yorkshire fog swards. The population of weeds was insignificant and similar in both swards. Total tiller and node population was similar for Yorkshire fog and ryegrass swards.

3.4.1.4 *Tiller and node dissection*

Table 3.4 shows that the mean pseudostem length per tiller before grazing was substantially greater in Yorkshire fog than in ryegrass both before and after grazing. There was no significant difference in stem weight and leaf number per tiller, length or weight per leaf between species or grazing allowances, though ryegrass leaves tended to be longer and heavier than Yorkshire fog leaves. During grazing, a similar proportion of leaf length was removed from ryegrass and

Table 3.3. Tiller and node population density in ryegrass and Yorkshire fog swards (Tillers or nodes/m^2, data based on tiller and node separation).

Sward components	Ryegrass sward	Yorkshire fog sward	SEM‡	Sign.§
Sown grass tillers	6505	10355	918.7	**
White clover nodes	2365	2680	439.7	NS
Other grass tillers	8545	5088	373.3	**
Weeds	232	164	48.7	NS
Total	17647	18287	—	—

SEM‡ = Standard error of the mean
Sign.§ = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

Table 3.4. Tiller dissection results of ryegrass and Yorkshire fog tillers in the corresponding swards.

Before Grazing	SPECIES				GRAZING ALLOWANCES			
Mean value (per stem/node)	Ryegrass	Fog	SEM[‡]	Sign.[§]	Medium	High	SEM	Sign.
Stem length/per tiller (mm)	35.0	62.3	2.8	**	48.8	48.4	3.4	NS
Stem weight/per tiller (mg)	11.0	12.0	1.0	NS	11.0	12.0	0.7	NS
Leaf number/per tiller	3.0	2.9	0.1	NS	2.9	3.0	0.1	NS
Leaf length/per leaf (mm)	96.2	79.6	5.1	NS	89.5	86.3	6.2	NS
Leaf weight/per leaf (mg)	9.0	7.0	0.4	NS	8.0	8.0	3.0	NS
After Grazing	**SPECIES**				**GRAGING ALLOWANCES**			
Mean value (per stem/node)	Ryegrass	Fog	SEM	Sign.	Medium	High	SEM	Sign.
Stem length/per tiller (mm)	37.0	51.9	2.6	*	41.8	47.1	3.2	NS
Stem weight/per tiller (mg)	13.0	12.0	2.0	NS	12.0	13.0	0.8	NS
Leaf number/per tiller	2.6	2.7	0.1	NS	2.4	2.9	0.1	*
Leaf length/per leaf (mm)	49.9	42.4	4.2	NS	40.4	51.8	6.4	NS
Leaf weight/per leaf (mg)	6.0	5.0	0.6	NS	4.0	6.0	0.6	NS

SEM[‡] = Standard error of the mean
Sign.[§] = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

Yorkshire fog tillers (51% vs 53% respectively), but the proportion was much greater at medium allowances than at high allowances (60% vs 45% respectively). Leaf number per tiller was significantly lower after grazing ($P < 0.05$) at medium than at high allowances.

Before grazing, white clover nodes (Table 3.5) were similar in leaf number, leaf area, and leaf weight amongst swards and grazing allowances, but petiole length and petiole weight tended to be higher in Yorkshire fog than in ryegrass swards. After grazing, leaf area and weight, and petiole length and weight, were similar between white clover plants in the two swards and the two grazing allowances, but the leaf number per node was higher in ryegrass swards than in Yorkshire fog swards. The proportion of white clover lost during grazing on Yorkshire fog swards was higher than on ryegrass swards (18% vs 6.5% respectively). The reductions in white clover leaf area and leaf weight, were more severe on Yorkshire fog swards and at medium grazing allowances than on ryegrass swards and at high grazing allowances respectively, but these differences were not significant.

3.4.1.5 *Canopy structure*

Before grazing the proportions of live sown grasses, white clover and other grasses estimated from point quadrat contacts were all higher in ryegrass than in Yorkshire fog swards (Table 3.6a,b) but, in contrast, the proportion of dead material was higher in Yorkshire fog swards. With the exception of white clover, these differences increased after grazing. In ryegrass swards, the proportions of live and dead material were similar before and after grazing. In contrast, in Yorkshire fog swards the proportion of dead material increased significantly during grazing. Less Yorkshire fog was recorded by point quadrat in ryegrass swards than ryegrass in Yorkshire fog swards, though no Yorkshire fog plants appeared in ryegrass swards recorded by hand separation. Other grasses and weeds were recorded in small proportions in both sown swards, but the

Table 3.5. Node dissection results of white clover in ryegrass and Yorkshire fog swards.

Before Grazing	SPECIES				GRAZING ALLOWANCES			
Mean value (per leaf/node)	Ryegrass	Fog	SEM[‡]	Sign.[§]	Medium	High	SEM	Sign.
Petiole length (mm)	32.6	37.4	3.3	NS	34.4	35.6	3.3	NS
Petiole weight (mg)	1.4	1.7	0.2	NS	2.0	2.0	0.2	NS
Leaf number/per node	3.1	2.8	0.1	NS	2.9	3.0	0.1	NS
Leaf area (cm^2)	0.9	0.9	0.1	NS	0.9	0.9	0.1	NS
Leaf weight (mg)	2.6	2.0	0.3	NS	3.0	2.0	0.2	NS
After Grazing	SPECIES				GRAZING ALLOWANCES			
Mean value (per leaf/petiole)	Ryegrass	Fog	SEM	Sign.	Medium	High	SEM	Sign.
Petiole length (mm)	30.6	35.1	0.8	NS	32.2	33.5	3.0	NS
Petiole weight (mg)	1.5	1.7	0.2	NS	1.4	1.8	0.2	NS
Leaf number/per node	2.9	2.3	0.1	*	2.6	2.6	0.1	NS
Leaf area (cm^2)	0.8	0.7	0.1	NS	0.7	0.8	0.1	NS
Leaf weight (mg)	1.9	1.6	0.2	NS	1.4	2.1	0.2	NS

SEM[‡] = Standard error of the mean
Sign.[§] = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

Table 3.6. Botanical composition of ryegrass and Yorkshire fog swards determined from inclined point quadrat contacts (proportion of total hits).

(a) Overall proportion of sward components							
Treatments	Ryegrass	Clover	Fog	Other Grasses	Weeds	Total live (%)	Dd.M.[3] (%)
Ryegrass BG[1]	81.1	13.7	2.5	2.4	0.3	91.2	8.8
Ryegrass AG[2]	88.4	8.0	—	3.7	—	86.4	13.7
SEM[‡]	3.5	2.5	—	0.9	—	1.9	1.8
Sign.[§]	NS	NS	—	NS	—	NS	NS
Yorkshire BG	11.5	11.5	76.7	0.9	0.3	87.9	12.4
Yorkshire fog AG	8.9	6.9	80.4	3.8	—	76.0	24.0
SEM	0.9	1.4	2.2	1.2	—	1.1	1.1
Sign.	NS	NS	NS	NS	—	**	**

(b) Leaf proportions of main species (compared with stem/petiole)				
Grazing	Ryegrass	Clover in ryegrass	Fog	Clover in Fog
Before Grazing	84.3	56.5	80.3	93.4
After Grazing	72.7	68.9	77.5	85.4
SEM	4.4	12.5	1.8	1.8
Sign.	NS	NS	NS	NS

[1]BG = Before grazing, [2]AG = After grazing, [3]Dd. M. = Dead Material, SEM calculated from Student t test
SEM[‡] = Standard error of the mean   Sign.[§] = * P < 0.05 ** P < 0.01 NS = Not Significantly different

proportion of other grasses was higher in ryegrass swards than in Yorkshire fog swards.

There was a tendency for leaf proportions to decrease and stem proportions to increase during grazing (Table 3.6b), the leaf decline being 68% greater in ryegrass swards than in Yorkshire fog swards. The proportion of clover leaf relative to petiole in ryegrass swards increased 22% after grazing, while it decreased by 9% in Yorkshire fog swards. However, none of these differences were significant.

3.4.1.6 *Defoliation height*

Table 3.7 indicates the mean values of the highest point quadrat contacts for grasses and white clover in the plots before and after grazing. Measured grazed height fell by 41% (NS) and by 48% ($P < 0.05$) for ryegrass and for Yorkshire fog swards during grazing and by 50% ($P < 0.05$) and by 45% (NS) for white clover in the corresponding swards. The surface height of the grazed stratum was lower for white clover than the corresponding sown grasses. The heights of defoliation for white clover were 3 cm at both medium and high allowances in ryegrass swards and 5 cm for Yorkshire fog swards. These values were taken as the basal grazed stratum heights for clover in ryegrass and Yorkshire fog swards respectively.

Before grazing only 5.6% of the total contacts above 3 cm from ground level were recorded as white clover in ryegrass swards, while 8.5% of the total contacts were recorded as white clover above 5 cm in Yorkshire fog swards (Table 3.8a). The corresponding values for ryegrass and Yorkshire fog were 91.8% and 80.5%. Proportions of white clover and other grasses above grazed height in Yorkshire fog swards were higher than those in ryegrass swards. There was a tendency for higher proportions of sown grasses and other grasses and lower proportions for white clover in the grazed strata than in the whole canopy

Table 3.7. Comparison of maximum values of sward heights (cm) for grass and clover components before and after grazing (measured by point quadrat).

Grazing	Ryegrass	Clover in ryegrass	Fog	Clover in Fog
Before	17	6	23	9
After	10	3	12	5
SEM‡	3.3	0.5	2.8	3.5
Sign.§	NS	*	*	NS

SEM‡ = Standard error of the mean   Sign.§ = * P < 0.05 ** P < 0.01 NS = Not Significantly different

Table 3.8. Comparison of proportions (%) of botanical components above grazing height before and after grazing (measured by point quadrat).

(a) The proportion of live material in grazed stratum before and after grazing (hits proportion of point quadrat)

Grazing	Above 3 cm from ground level			Above 5 cm from ground level		
	Ryegrass	Clover in ryegrass	Other grasses in ryegrass	Yorkshire fog	Clover in fog	Other grasses in fog
Before	91.8	5.6	2.6	80.5	8.5	11.0
After	98.5	0.0	1.5	81.5	0.0	18.5

Grazing	(b) The maximum height of contact (cm) with dead material in both sward canopies			
	Ryegrass Medium allowance	Ryegrass High allowance	Yorkshire fog Medium allowance	Yorkshire fog High allowance
Before	3	15	14	12
After	5	11	6	10

(Table 3.7 and Table 3.8a).

The maximum height of dead material (Table 3.8b) in ryegrass swards was lower than that in Yorkshire fog swards before grazing. With the exception of ryegrass medium allowance, those heights decreased in the rest of the treatment combinations after grazing.

3.4.2 Animal measurements

3.4.2.1 *Chemical composition of the diet selected*

Chemical analyses of oesophageal boluses for total nitrogen, cellulose, hemicellulose, lignin, total fibre, ash and condensed tannins contents are given in Table 3.9.

Yorkshire fog extrusa samples contained a significantly higher proportion of total nitrogen and hemicellulose than ryegrass extrusa samples, but a significantly lower content of cellulose. There were no differences in lignin, total fibre, or ash content, between extrusa samples from the two swards.

The total condensed tannins (CT) in the diet selected from ryegrass and Yorkshire fog swards did not differ significantly. Protein-bound CT was consistently higher for Yorkshire fog sward, whereas the differences in fibre-bound CT and free CT between swards were not significant. All the concentrations were relatively low, and close to the lower limits of estimation (Terrill *et al.*, 1992b)

3.4.2.2 *Diet selection, diet digestibility, herbage intake and animal performance*

Data for the botanical components of the diet, diet digestibility, herbage intake and animal performance are presented in Table 3.10.

Table 3.9. Chemical composition of the diet selected (g/kg DM).

Components	Ryegrass extrusa	Yorkshire fog extrusa	SEM‡	Sign.§
Total Nitrogen	382	410	2.3	**
Cellulose	184	170	1.6	**
Hemicellulose	186	191	0.5	**
Lignin	118	125	2.8	NS
Total fibre [1]	488	486	25	NS
Ash	156	153	3.4	NS
Free CT[2]	0.684	0.721	0.059	NS
Protein-bound CT	1.352	1.475	0.026	*
Fibre-bound CT	0.039	0.283	0.105	NS
Total CT	2.075	2.480	1.749	NS

Note: [1] = Cellulose + Hemicellulose + Lignin
[2]CT = Condensed Tannins
Means of pooled samples within plots and within extrusa samples.

SEM‡ = Standard error of the mean
Sign.§ = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

Table 3.10. Results from diet selection, diet digestibility, herbage intake and animal performance.

	SPECIES				GRAZING ALLOWANCES			
	Ryegrass	Fog	SEM[‡]	Sign.[§]	Medium	High	SEM	Sign.
Diet selection[1]								
Grasses (%)	98.7	98.3	0.32	NS	98.7	98.2	0.30	NS
White clover (%)	1.3	1.7	0.33	NS	1.3	1.8	0.33	NS
Organic Matter Digestibility (%)	85.7	82.2	0.3	*	83.6	84.3	0.10	NS
Organic Matter Intake (g OM/ewe)	1412	1104	29.4	**	1149	1368	50.1	*
Liveweight[2] gain (g/ewe/day)	169	111	19.00	NS	121	159	19.85	NS

[1] = Proportion of white clover and grasses in the total diet.
[2] = Values adjusted by covariance (initial weight).

SEM[‡] = Standard error of the mean
Sign.[§] = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

Grasses were the main constituents of the diet selected on all treatment combinations. There were no significant differences in the relative proportions of grasses to white clover selected between swards and allowances, but there was a tendency for a higher proportion of white clover in Yorkshire fog swards than in ryegrass swards. This tendency is in agreement with point quadrat results and tiller/node dissection results. The proportion of white clover also tended to be higher at high allowance than at medium allowance. Proportions of dead tissue in the extrusa samples were negligible.

Organic matter digestibility (OMD) of the diet selected by oesophageal fistulated sheep was 3.5% units higher for ryegrass swards than for Yorkshire fog swards, but there was no significant difference between grazing allowances.

There was no significant difference in the release rate of chromic oxide (Cr_2O_3) amongst treatments, therefore a common release rate of 185.5 mg Cr_2O_3 day^{-1} was used for all the treatments. OM intakes were 22% greater for ryegrass swards than for Yorkshire fog swards and 16% greater for high allowance than for medium allowance.

Liveweight gain was 34% ($P < 0.06$) greater on ryegrass swards than on Yorkshire fog swards. Liveweight gain was similar in both grazing allowances.

3.4.2.3 *Ingestive behaviour*

The results of two 24-hour grazing behaviour studies are shown in Table 3.11. The mean bite size on Yorkshire fog swards was significantly higher than on the ryegrass swards. On average, the recovery rate of oesophageal samples taken in both swards was 89%. Bite size values from both swards were corrected for this rate. Rates of biting did not differ between swards. Grazing time and ruminating time tended to be higher on ryegrass swards than on Yorkshire fog swards, but the differences were not significant. Most of the grazing activity on

Table 3.11. The effect of species and grazing allowances on bite size, rate of biting, grazing time, ruminating time and resting time.

Behavioural Components		SPECIES				GRAZING ALLOWANCES			
		Ryegrass	Fog	SEM‡	Sign.§	Medium	High	SEM	Sign.
Mean Bite Size (mg OM/bite)		86	139	7.0	*	90	130	7.0	*
Rate of biting (bites/min^{-1})		52.7	47.5	2.2	NS	51.9	48.3	2.5	NS
Grazing time (min)	Daylight[1]	402	245	24	NS	359	285	19	NS
	Night[2]	210	256	55	NS	253	211	4	*
	24 hr[3]	612	501	34	NS	612	496	27	NS
Ruminating time (min)	Daylight	145	183	10	NS	158	170	6	NS
	Night	240	188	7	NS	212	216	3	NS
	24 hr	385	371	4	NS	370	386	22	NS
Resting time (min)	Daylight	134	232	35	NS	143	204	23	NS
	Night	308	339	62	NS	313	353	28	NS
	24 hr	442	571	26	NS	456	557	28	NS

[1]Daylight = Between 0730 - 1830 hours, [2]Night = Between 1830 - 0730 hours, [3]24 hr = Daylight + Night

SEM‡ = Standard error of the mean
Sign.§ = * $P < 0.05$ ** $P < 0.01$ NS = Not Significantly different

ryegrass swards (70%) occurred during daylight (from 0730 to 1830 hours), but on Yorkshire fog swards, 50% of the total grazing time occurred from 1830 to 0730 hours. Much of the ruminating activity (62%) occurred at night in ryegrass swards, but the period of rumination was equally distributed between night and day in Yorkshire fog swards. Resting time was mainly concentrated in the night period for both swards (74% for ryegrass and 59% for Yorkshire fog).

Reduction in herbage allowance from 12% to 6% depressed mean bite size by 31%. No effect of grazing allowance on the rates of biting was evident. Grazing time tended to be higher at medium than at high grazing allowance, though only the night-time contrast was significant. Resting time and ruminating time were higher (12% and 19%) at high grazing allowance than at medium grazing allowance, but these differences were not significant.

3.5 DISCUSSION

Comparative studies of sheep performance and herbage intake between perennial ryegrass and Yorkshire fog swards appear to be limited to the earlier experiments of Watkin *et al.* (1974) and to the recent trial published by Morton *et al.* (1992). There is no comparative information on sward structure, diet selection, and ingestive behaviour.

No significant interactions between species and allowances were observed in sward and animal data and therefore the main sources of variation are discussed separately.

3.5.1 Herbage mass, sward height and sward composition

The comparison between herbage mass and sward height data (Table 3.1) before and after grazing, indicate that ryegrass swards were defoliated more severely than Yorkshire fog swards at equivalent herbage allowance, and is in agreement with the results of Morton *et al.* (1992). The higher proportion of dead material may have contributed to the higher post-grazing residuals on Yorkshire fog swards than on ryegrass swards (Table 3.2). The proportion of herbage mass defoliated and post-grazing sward heights were higher and lower on medium grazing allowance than high grazing allowance, reflecting the higher grazing pressure of medium allowance treatments.

The higher proportion of other grasses on the ryegrass plots than on Yorkshire fog plots was not consistent with the results of other autumn observations (Harvey *et al.*, 1986; Morton *et al.*, 1992). Watkin *et al.* (1974) suggested than the aggressive nature of Yorkshire fog was the main factor associated with the low content of other grasses in comparison with ryegrass swards. The discrepancies between these reports are partially explained by the differences in frequency or severity of cutting or grazing applied in each experiment. Watt and Haggar (1980) showed that close and frequent defoliation reduced the DM yield and the proportion of *Holcus lanatus* to a much greater extent than that of *Lolium perenne*, whether the species were grown in monoculture or mixture.

Previous studies have indicated differences in the white clover content of Yorkshire fog and ryegrass swards, though differences have not been consistent (Watkin *et al*, 1974; Smith and Allcock, 1985; Morton *et al.*, 1992). The low white clover concentration of both swards (Table 3.2) reflected the low content normally found in winter (Korte *et al.*, 1987), and the similar clover content in both swards is mainly explained by the previous continuous stocking management (Watkin *et al.*, 1974).

3.5.2 Sward bulk density, tiller-node dissection and tiller density

The higher bulk density of Yorkshire fog swards than that of ryegrass swards was closely related to the longer and heavier pseudostems of Yorkshire fog tillers (Tables 3.3 and 3.4) as well as its higher distribution in the sward canopy (Hu, 1993). After grazing, the difference in sward bulk density between the swards was increased by 65%. This increase may be explained by the same factors mentioned above, plus the extra effect of the higher concentration of dead material of Yorkshire fog swards below the grazed stratum (Tables 3.2 and 3.6a,b). Hodgson (1993b) showed that, under continuous sheep stocking situations, the high degree of adaptability of Yorkshire fog and ryegrass swards to different grazing heights through the compensating effects between tiller population and tiller weight. In all the comparisons, the tiller population of Yorkshire fog swards was at least double that of ryegrass swards.

The higher population of Yorkshire fog tillers might have provided more shade to lower canopy layers and this could have increased the proportion of dead material in Yorkshire fog swards. The same argument can be used to explain the longer white clover petiole length found in Yorkshire fog swards in comparison with ryegrass swards (Tables 3.5, 3.6a,b) and thus the higher vertical distribution of white clover in Yorkshire fog swards.

The tillers of other grasses were much smaller and distributed in lower layers of the sward canopy, principally on Yorkshire fog swards. This probably contributed to increase the differences in sward bulk density in the grazed stratum between swards in favour of Yorkshire fog (Hu, 1993) (Table 3.7). *Poa annua* tillers formed the major component of other grasses. Bircham and Hodgson (1983) reported that the laminae of *Poa annua* tillers occupied an inferior position in the canopy of mixed-species swards of *Lolium perenne*, suggesting that *Poa annua* and *Trifolium repens* are less accessible to the grazing animals than *Lolium perenne*.

Leaf length results provide more evidence for the difference in defoliation rate between grass species. Longer and slightly heavier leaves in ryegrass formed the major components in the grazed strata and therefore were grazed more severely than was Yorkshire fog leaf (Table 3.4). There was also a higher proportion of leaves removed on ryegrass than on Yorkshire fog tillers. The mean leaf number per tiller in Yorkshire fog swards was still maintained at a higher value than ryegrass (Table 3.4).

3.5.3 Diet selection and sward structure

The vertical distribution of the sward components in the ryegrass canopy was similar to the results reported by L'Huillier *et al.* (1986) and Bootsma *et al.* (1990) in autumn swards, where the greater grazing intensity was confined to the surface horizons mainly consisting of green leaf. Selection of a high green leaf component in the diet has been documented by several authors (Arnold, 1981; Barthram and Grant, 1984; L'Huillier *et al.*, 1986). Leaf and pseudostem components could not be distinguished in extrusa samples, but visual appraisal suggested that green leaf was the main component of the diet selected. However, for Yorkshire fog swards, it was also presumed that pseudostems were incorporated in the diet, an assumption supported by point quadrat data (Tables 3.6a,b). The proportion of grass leaves in the swards decreased after grazing, to a greater extent in ryegrass swards.

The grazed heights for defoliated white clover were used to define the penetration by the animals within the swards (Table 3.7). This is an estimate of extreme height rather than of mean height, and implications of this assumption have to be considered, but the extreme height gave the best available estimate of vertical discrimination of defoliation. Bootsma *et al.* (1990) indicated that clover was subjected to a severity of defoliation which was at least equal to that of grasses, despite the fact that clover foliage was positioned lower and well protected by grasses in the sward canopy. This result is in accord with the present experiment. White clover was harvested by oesophageal fistulated sheep in a lower proportion than its presence in the total sward or in the grazed stratum (Table 3.8a). The vertical distribution of grass leaf was higher than that of white clover in both sward canopies, limiting the accessibility of the clover. These findings agree with the results reported by L'Huillier *et al.* (1986) and by Bootsma *et al.* (1990), where they explained that in autumn swards, the lower vertical distribution of white clover relative to green leaf, may negatively influence the consumption of white clover.

The higher vertical distribution of white clover in the Yorkshire fog sward canopy than in ryegrass, providing greater accessibility for the grazing sheep, may explain the higher proportion of clover in Yorkshire fog extrusa samples.

The concentration of white clover in the diet selected was only marginally higher at high allowances than at medium allowances (1.8% vs 1.3%), despite the greater opportunity for selection at high allowance.

Some dead material was dispersed in the grazed strata in both swards, and the proportion was much higher in Yorkshire fog swards than in ryegrass swards (Table 3.8b), but dead material was not detected in the extrusa samples. This may be related to its low acceptability (Kenny and Black, 1984) or its reduction in the grazed stratum due to trampling by the animal during grazing.

3.5.4 Chemical composition of the diet selected

In vitro digestibility of the diet was not affected by grazing allowance and only to a limited extent by sward species. The significantly lower OMD of extrusa samples taken from Yorkshire fog swards compared to ryegrass swards is in accord with the results of Morton *et al.* (1992). However, this result is in contrast to other published evidence (Harvey *et al.*, 1984; Watt, 1987) for differences in OMD between *Holcus lanatus* L. cv. 'Massey Basyn' and perennial ryegrass.

However in the latter experiments, pasture samples were taken by sward cutting techniques. The fistulated animals concentrated their grazing activity in the surface horizons where the green leaf was mainly distributed. The moderate, absolute difference in OMD between ryegrass and Yorkshire fog was predictable considering that some pseudostems were distributed in the grazed stratum of the Yorkshire fog swards. The relative contribution of white clover in the diet was not large enough to influence diet digestibility.

The low values for total fibre and lignin in the diet for both sward species substantiate the high OMD values. These results are in agreement with the findings of Morton *et al.* (1992) who reported no significant differences in total fibre content of herbage on offer between *Holcus lanatus* L. cv. 'Massey Basyn' and perennial ryegrass. However the fibre content of the diet selected in the latter experiment was higher than the values found in this experiment, probably reflecting the higher grazing pressure and the method of sampling used by Morton *et al.* (1992).

Terrill *et al.* (1992a,b) found that Yorkshire fog and perennial ryegrass contain trace amounts of CT, these values being slightly higher for Yorkshire fog, especially for the CT fraction bound to protein. The results of this experiment confirm these findings. However, it is unlikely that CT had any influence on animal performance in the conditions of the present experiment because of: (i) the low CT concentration in the diet (0.2% and 0.25% on a DM basis for ryegrass and Yorkshire fog respectively), (ii) the high grazing allowance utilized, (iii) the higher N content of the diet selected and (iv) the low bypass-protein requirements of the experimental ewes, which were in mid-gestation. There was no indication that the small differences in tannin content influenced discrimination between the grass and legume components of the two swards.

3.5.5 Herbage intake, liveweight gain, and grazing behaviour

The average herbage consumed (g OM ewe^{-1} day^{-1}) and the liveweight gain (g ewe^{-1} day^{-1}) achieved, were similar to those suggested by Geenty and Rattray (1987) for grazing ewes in mid-pregnancy, under New Zealand pasture conditions. Despite the high herbage allowances, herbage intakes were moderate compared with the potential achievable, probably reflecting the lower feeding drive of the mature ewes.

The higher intake per bite found in Yorkshire fog swards in comparison with ryegrass swards can be explained, at least partially, by the higher sward bulk density of the Yorkshire fog sward canopy (Table 3.3), and taken with the information on diet composition, indicates no particular behavioural constraints on intake of *Holcus*. In contrast, daily herbage intake was greater from ryegrass swards than from *Holcus* swards (Table 3.10). There are no previous reports in the literature of an inverse relationship between the two variables. Evidence from the behavioural studies clearly indicate that the advantage to *Holcus* in terms of bite weight was offset by lower bite rate and grazing time. These factors do not explain the inverse relationship between bite weight and daily intake in strict quantitative terms, so there is clearly a need for more detailed work on the components of ingestive behaviour. However, the above contrasts are supported by evidence from later trials in the present research project and by further evidence of Liu *et al.* (unpublished data). Liveweight gains tended to be higher on ryegrass than on Yorkshire fog swards, probably reflecting the effects of the higher OMD values and intakes achieved by the ewes grazing on ryegrass swards compared to those of the ewes grazing on Yorkshire fog swards.

Reducing the daily herbage allowance from 12 to 6% of LW depressed daily herbage intake by 16%. This decline appears to be related principally to reductions in intake per bite, (90 vs 130 mg OM bite^{-1} for medium and high allowances respectively). OMD values were similar for both allowances. Grazing time increased and idling time decreased with declining herbage allowance, but these effects were not completely compensatory, while rate of biting was similar in both allowances. Similar relationships amongst grazing behaviour components and declining herbage mass, sward height and herbage allowance have been reported (Allden and Whittaker, 1970; Jamieson and Hodgson, 1979; Hodgson, 1981, 1985a,b; Penning *et al.*, 1991; Morris *et al.*, 1992). Liveweight gain was 25% higher at high allowance, probably reflecting the influence of allowance on the amount of herbage consumed (Hodgson, 1981). However, levels of variation were high, relative to the low weight increments of the ewes.

3.6 CONCLUSIONS

Evidence from this trial confirms the limited concentration of condensed tannins in *Holcus lanatus*, and provides further evidence that a low concentration exists in perennial ryegrass. There was no evidence of differences in the degree of selectivity between the grass and legume components in the two swards.

Levels of herbage intake per sheep were substantially lower for *Holcus lanatus* swards than for perennial ryegrass swards. Though not conclusive, the evidence suggests that the most important limits were nutritional rather than behavioural in origin, and reflected differences in diet digestibility rather than in bite weight. This evidence requires substantiation for animals with higher growth potential and nutrient demand, and over an expan ded range of growing seasons.

CHAPTER 4

EXPERIMENT 2: A COMPARATIVE STUDY OF HERBAGE INTAKE, INGESTIVE BEHAVIOUR AND DIET SELECTION, AND EFFECTS OF CONDENSED TANNINS UPON BODY AND WOOL GROWTH IN LAMBS GRAZING *HOLCUS LANATUS* AND *LOLIUM PERENNE* SWARDS IN SUMMER

4.1 ABSTRACT

A comparative study was undertaken to investigate the effects of low concentration of condensed tannins (CT) on diet selection, herbage intake and animal performance in lambs grazing on four 0.2 ha paddocks each of *Lolium perenne* (perennial ryegrass)/*Trifolium repens* (White clover) or *Holcus lanatus* (Yorkshire fog)/*Trifolium repens* (White clover) swards, continuously grazed at a constant height of approximately 6 cm from December 1992 to March 1993. The effects of CT on rumen metabolism and animal production were assessed by twice daily oral administration of polyethylene glycol (PEG; Molecular weight 4,000) to half of the lambs on each sward.

The organic matter digestibility (OMD) of the herbage selected was higher in ryegrass swards in December (81 vs. 78 ± 0.04 %, $P < 0.01$), but not in January (80 vs. 79 ± 0.05 %). The herbage intake achieved by lambs grazing ryegrass swards was 23% higher than that achieved on Yorkshire fog swards in December (990 vs. 800 ± 36 g OM lamb^{-1} day^{-1}, $P < 0.05$), whereas, in January, herbage intakes did not differ significantly (1370 vs. 1190 ± 57 g OM lamb^{-1} day^{-1}, $P < 0.11$). Conversely, bite weight was greater for Yorkshire fog swards than for ryegrass swards during January (111 vs. 85 ± 5 mg OM bite^{-1}, $P < 0.01$), but not in December (90 vs. 80 ± 5 mg OM bite^{-1}). The higher bite weight of Yorkshire

fog swards apparently reflected the greater sward bulk density recorded on these swards (669 vs. 581 ± 31 kg DM ha^{-1} cm^{-1}, $P < 0.10$). In both December and January, grazing, ruminating, and idling times were similar between swards, while in January, the rate of biting in ryegrass swards was much higher than in Yorkshire fog swards (64 vs. 61 ± 1 bites min^{-1}, $P < 0.05$).

Lambs grazing on ryegrass swards had higher clean wool growth (1147 vs. 1085 ± 15 μg cm^{-2} day^{-1}, $P < 0.10$), carcass weight (17.5 vs. 16.3 ± 0.22 kg, $P < 0.05$), GR values (6.7 vs. 5.5 ± 0.59, $P < 0.10$) and carcass dressing out percentage (46 vs. 45 ± 0.3 %, $P < 0.10$) than lambs grazing on Yorkshire fog swards, but liveweight gain (131 vs. 121 ± 9 g day^{-1}) and wool yield (79 vs. 79 ± 1.1 %) did not differ significantly. The stocking rate maintained on ryegrass plots was 25% greater than on Yorkshire fog plots.

Similar low concentrations of CT were recorded in the diets of ryegrass and Yorkshire fog swards (≤ 0.2% on a DM basis). These results were confirmed by measurements of NH_3 concentration in the rumen fluid. The low levels of CT had no significant effects on diet selection, herbage intake, grazing behaviour patterns or lamb performance. However, the lambs grazing on Yorkshire fog swards showed small and non-persistent responses to CT in terms of faecal egg counts, wool growth and liveweight gain.

In conclusion, the results of this study indicate that: (i) under high fertility conditions and intensive management, perennial ryegrass/white clover swards appear to have higher feeding value than Yorkshire fog/white clover swards for lamb production and (ii) the low CT concentrations (≤ 0.2% on a DM) observed in both swards did not influence lamb performance significantly. The new evidence on the presence of CT in perennial ryegrass may require a re-appraisal of the feeding value of this grass for animal production.

Keywords: *Lolium perenne* (perennial ryegrass); *Holcus lanatus* (Yorkshire fog); *Trifolium repens* (White clover); Polyethylene glycol (PEG); Condensed tannins (CT); herbage intake; diet selection; grazing behaviour and lamb production.

4.2 INTRODUCTION

The results of the initial grazing experiment (Chapter 3) showed some advantages in favour of ryegrass swards over Yorkshire fog swards in terms of herbage quality, herbage intake and animal performance. However, these effects were not conclusive, and need to be investigated in animals of higher production potential and nutrient demand over a greater range of seasons.

Laboratory analyses of extrusa samples (Section 3.4.2.1, Chapter 3) established the presence of limited concentrations of condensed tannins in both swards. These low concentrations of condensed tannins in *Holcus lanatus* (Yorkshire fog) have been related to probable nutritional benefits in animal production (Terrill *et al.*, 1992a,b) and potential effects on lamb parasitism (Niezen *et al.*, 1993b). However, more experimental work is needed to establish the effect of CT level on animal performance (Barry, 1989; Terrill *et al.*, 1992a,b; Montossi *et al.*, 1994) to delineate an optimum range, and further grazing experiments are needed with sheep in different physiological states to further define production responses to dietary CT (Montossi *et al.*, 1994; Wang *et al.*, 1994). There is no definitive information on the effects of *Holcus lanatus* CT concentrations on lamb production.

The experiment described in this chapter was designed to explore aspects of the plant-animal interface with particular reference to the effects of low concentrations of condensed tannins in *Holcus* and in perennial ryegrass on this interactive process, involving comparative evaluations of its effects on wool growth, liveweight gain, and carcass weight in lambs grazing summer swards.

4.3 MATERIALS AND METHODS

The experimental procedures in the present trial were similar to those employed in Experiment 1 (Chapter 3). Only those techniques not used in Experiment 1 are described here.

4.3.1 Site preparation and management

The experiment was conducted at Massey University (latitude 41^{0} 10'S) Palmerston North, New Zealand, from December 1992 to March 1993. The swards used in Experiment 1 were used again, and managed under the same conditions in the present study. Further details of experimental site and sward and animal management are described in Chapter 3.

Weather data of the experimental site was assumed to be similar to that of the Crown Pastoral Research Institute (CRI) Meteorological Station, approximately 2 km distance. The monthly rainfall for December 1992, January, February and March 1993 was 167, 54, 44, 80 mm respectively, compared with respective averages of 94, 79, 67, and 69 mm. Mean soil temperatures (10 cm depth) for December-January-February-March were 15.6, 16.4, 16.5, and 14.5ºC, compared with respective averages of 17.5, 18.5, 18.1, and 16.3º C. The summer 1992/1993 was considerably wetter than that of long-run rainfall data averages (especially December), while soil temperatures were not as high as those observed in long-run averages.

Nitrogen and phosphate fertilisers (50 kg of urea and 300 kg of superphosphate ha^{-1} respectively) were applied to the experimental area in April 1992. Two additional applications of urea of 50 kg ha^{-1} each were made, one before the trial began, and the other in the second week of January.

4.3.2 Experimental design

The trial was conducted on four 0.2 ha paddocks for each sward mixture (Yorkshire fog/white clover and perennial ryegrass/white clover). These paddocks correspond to those used in the initial grazing experiment. Two spare paddocks, one for each sward mixture, were used to maintain ruminal fistulated sheep during rumen metabolism measurements. Both experimental and spare swards were maintained at approximately 6 cm height under variable continuous stocking management.

Sixty four, four month old weaned, mixed-sex Suffolk × Romney lambs (mean weight 28.3 ± 2 kg) were used in the present study. The 64 lambs selected, were divided into balanced sets of 8 lambs according to fasted liveweight and sex; four to graze Yorkshire fog/white clover and four to graze perennial ryegrass/white clover swards. Eight lambs grazed each plot (2 female and 6 castrated male). Experimental animals grazed the spare plots for two weeks before measurements commenced. Additional spare adult sheep were used, mainly in ryegrass plots, to maintain the desired sward height (6 cm).

The effects of CT on rumen metabolism and animal production were assessed by twice daily oral administration (0730 and 1730 hours) of polyethylene glycol (PEG; MW 4,000) for 16 weeks to half of the lambs (n = 4) in each plot. PEG binds CT and forms a stable complex, and can be used to either prevent protein reacting with CT or to displace protein from pre-formed CT:protein complexes (Barry, 1989). It is assumed that the inert PEG:CT complex is excreted in the animal faeces. A minimum of 1.8 g of PEG/g CT is required to reverse the effects of CT (Barry and Forss, 1983). Based on previous experience by Terrill *et al.* (1992a,b) of CT concentrations in *Holcus lanatus*, a daily dose of PEG of 40 g in 80 ml of water per lamb was used for both ryegrass and Yorkshire fog treatments.

4.3.3 Sward measurements

Herbage mass and its botanical composition were estimated monthly by cutting ten 0.1m^2 quadrats to ground level, with an electric shearing handpiece, in each plot. The herbage samples were processed as described in Chapter 3 (Section 3.3.3).

Forty sward surface height (SSH) readings were recorded twice per week in each plot, using a sward stick (Birchman, 1981; Barthram, 1986). These sward height estimates were used to adjust animal numbers. Five readings were also made inside each quadrat when herbage mass samples were collected, giving 50 readings for each plot. The bulk density of the swards was calculated, by dividing the herbage mass estimated for each quadrat cut, by the corresponding SSH average (mean of 5 readings).

The vertical distribution of plant tissue within the sward canopy was measured monthly using an inclined point quadrat (Warren Wilson, 1963) set at 32.5º to the horizontal. At least 100 contacts were recorded in each plot every month. Contacts were recorded for species, morphology (leaf, stem, petiole), and state (live and dead). Point quadrat observations were expressed as the number of contacts per 2 cm of sward height and were set out graphically by a computer programme to illustrate the vertical distribution of the various herbage components within the sward profiles.

4.3.4 Animal measurements

4.3.4.1 *Liveweight gain, carcass weight, dressing out percentage and GR measurements*

Unfasted lamb liveweight was recorded weekly between 3 December 1992 to 10 March 1993. At the end of the trial on 11 March 1993 all the lambs were slaughtered and fasted liveweight (24 hours) was recorded prior to slaughter. Hot carcass weight (HCW) was obtained immediately after slaughter. Dressing out percentage was calculated as HCW divided by fasted liveweight (x 100). The total tissue thickness (GR) between the surface of a lamb carcass and the rib at a point 11 cm from the midline, in the region of the 12th rib (Kirton, 1989), was measured on both sides of the hot carcass.

4.3.4.2 *Midside wool growth*

Wool growth was estimated at 6 week intervals by clipping 10 × 10 cm patches to skin level on the right midside of all the animals while they lay on a flat surface (Bigham, 1974). All the comparisons of wool growth were made on the basis of wool weight on a 1 cm^2 patch of skin area in the centre of each clipped area for each sampling period (Short and Chapman, 1965). Immediately after sampling, wool samples were stored in untied plastic bags for further analysis.

The weight of each greasy midside sample was recorded after conditioning at 20º C and 65% relative humidity for 48 hours, then samples were conditioned and scoured using the method described by Morris (1992). Clean wool weight and yield (expressed as the ratio of clean to greasy weight) were subsequently recorded.

4.3.4.3 *Diet selection and extrusa analyses*

During two-week periods in December and January two pairs of castrated male sheep fistulated at the oesophagus, were rotated between plots on a daily basis, and one extrusa sample was collected from each animal from each plot using the procedure described in Chapter 3 (Section 3.3.4). Further laboratory analyses of extrusa samples were undertaken for CT, OM digestibility, total N, hemicellulose, cellulose, and lignin. Laboratory analyses for those plant components are reported in Chapter 3 (Section 3.3.4).

The botanical composition of the diet selected was assessed by suspending sub-samples of extrusa in water in a gridded tray and identifying the proportions of sward components (as a percentage of total contacts) recorded at grid intersections (Clark and Hodgson, 1986).

4.3.4.4 *Dry matter intake and grazing behaviour*

Herbage organic matter intake measurements and grazing behaviour studies were undertaken simultaneously in two periods (December and January) according to procedures described in Chapter 3 (Section 3.3.4).

The chromic oxide release rates were determined from capsules recovered from 16 lambs (4 per treatment) slaughtered at the end of the trial. Additionally, chromic oxide release rates in December and January were obtained from ruminal fistulated wethers, which grazed in spare plots of both swards (3 per treatment).

PEG administration (40 g/day) was deducted from faecal output values prior to calculating organic matter intakes, on the assumption that PEG is indigestible (Barry and Duncan, 1984).

4.3.4.5 *Faecal egg counts (FEC)*

Experimental lambs, fistulated sheep, and spare wethers were drenched at the beginning of the experiment and at 28 day intervals with Levamisol (Nilverm, Coopers-Pitman-Moore, New Zealand Ltd). Faecal egg counts (FEC) were made on day 28 or day 14 after drenching during the entire experiment. FEC counts were made using a Modified McMaster technique as described by Williamson *et al.* (1994).

4.3.4.6 *Rumen metabolism evaluation*

Rumen ammonia (NH_3) concentration indicates the effectiveness of PEG in binding condensed tannins (Waghorn *et al.*, 1987a). Between the 15th and 16th of January a 24 hour evaluation of rumen ammonia concentration was carried out, sampling rumen contents at 4 hour intervals (0500, 0900, 1300, 1700, 2100, 0100 hours), using 12 wethers fistulated in the rumen (3 per treatment). Ruminal fistulated wethers were drenched daily (40 g/wether) with PEG or water for 10 days before the sampling day commenced. The rumen fluid samples (20 ml each) collected in the field were refrigerated (+4º C), subsequently centrifuged at 3000 *g* for 15 minutes, and then the residue was frozen until analyzed. Rumen ammonia concentration was determined according to the method described by Waghorn *et al.* (1987a). In addition to rumen ammonia evaluations, two field pH determinations were carried out at the 0500 and 1700 hours sampling.

4.3.5 Statistical analyses

The pasture and animal data were analyzed using the statistical package SAS (SAS, 1990), based on a Split-Split-Plot Design using 4 blocks, with swards (Yorkshire fog or perennial ryegrass) as the main plot, PEG (CT inactivated or operating) as the split-plot factor, and sex (female or male) as the split-split-plot factor. Means are presented with their standard errors (SEM). A point quadrat package (Butler, 1991) was used in the analysis of inclined point quadrat data. All data were initially tested for normality and homogeneity of variance. In cases where these assumptions were not valid, data were appropriately transformed.

Liveweight gain and wool growth were adjusted by co-variance, for initial weight and for initial wool removal from the midside area of each animal respectively. An additional group of 10 lambs was slaughtered at the commencement of the trial, and their carcass weights, dressing out percentages and GR measurements were used as co-variates for statistical analyses of the

64 test lambs. Animal and sward results generated from sequential sampling were analyzed using the 'repeated measures' option of the SAS general linear models procedure.

4.4 RESULTS

Most of the interactions amongst swards, PEG supplementation, and sex were not significant for sward or animal variables. Therefore, the presentation of plant and animal results is concentrated principally on main effects.

4.4.1 Sward measurements

4.4.1.1 *Herbage mass, sward surface height and sward bulk density*

Both swards were maintained close to the designated sward height (6 cm) (Figure 4.1) throughout the measurement period, with the exception of the start of the trial, where the SSH of ryegrass plots were significantly higher than that of Yorkshire fog plots. It was necessary to keep spare animals in ryegrass plots from December to February to achieve the desired sward height, which resulted in a 25% higher stocking rate overall for the ryegrass treatment.

Mean values for herbage mass and bulk density, and their green and dead components are presented in Table 4.1.

At the commencement of the trial in December, ryegrass swards had significantly higher total herbage and dead herbage masses than Yorkshire fog swards, while there were no significant differences in green herbage mass or sward bulk density between swards. In January, there were no significant differences between swards in any of the sward variables studied. However, in February, Yorkshire fog total herbage mass was higher than that of ryegrass, reflecting the fact that dead herbage mass of Yorkshire fog was almost double that of ryegrass. Green mass was also higher for ryegrass.

Table 4.1. The effect of sward species on herbage mass (kg DM ha^{-1}) and on sward bulk density (Kg DM ha^{-1} cm^{-1}) from December to February.

Sward components	DECEMBER				JANUARY				FEBRUARY			
	Ryegrass	Fog	SEM‡	Sig§.	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig.
Herbage mass	2770	2210	189	*	3790	3530	202	NS	2460	3100	220	*
Green herbage mass	1750	1560	127	NS	2550	2260	132	NS	1430	1080	98	*
Dead herbage mass	1020	650	68	**	1240	1270	82	NS	1030	2020	130	**
Herbage bulk density	380	370	24	NS	580	670	31	NS	560	730	49	*
Green herbage bulk density	240	260	16	NS	390	430	21	NS	350	240	22	**

SEM‡ = Standard error of the mean
Sig§. = * $P < 0.05$, ** $P < 0.01$, and NS (not significant).
Number of observations contributing to the mean each month (n = 40).

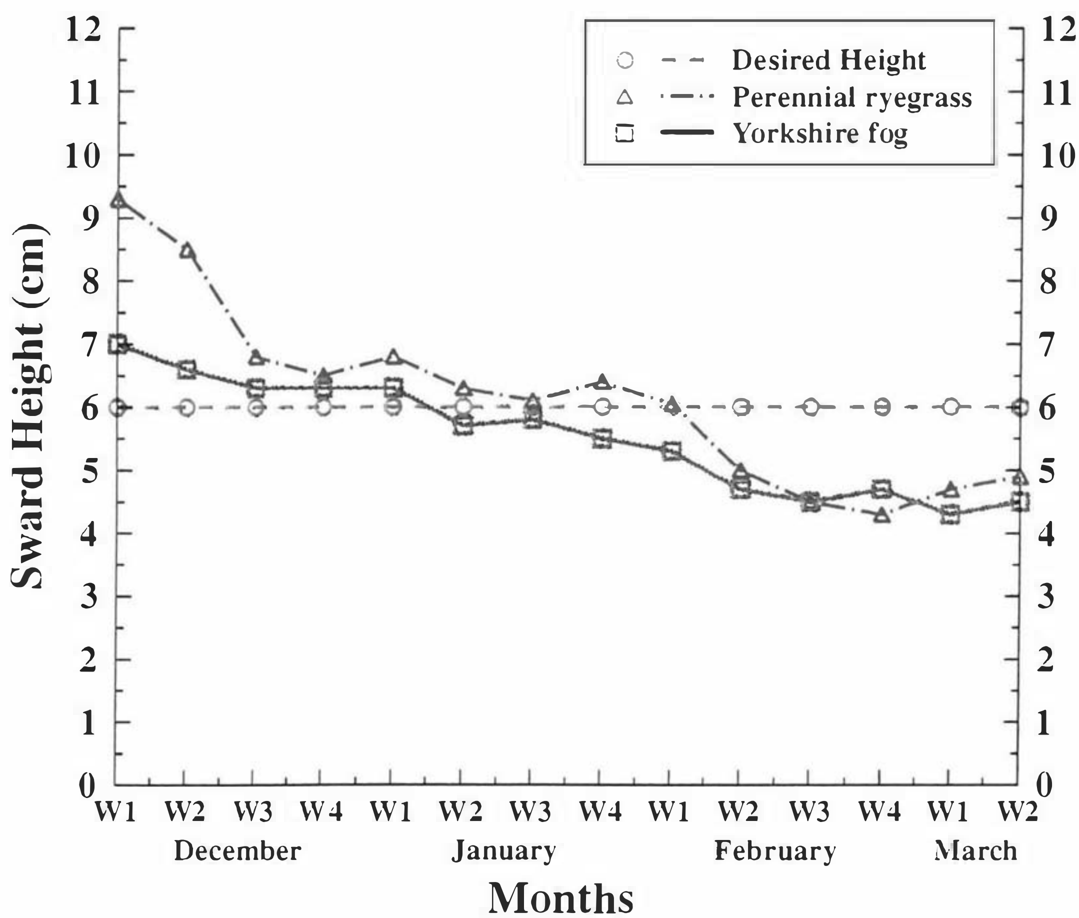


Figure 4.1. Weekly variation of average pasture heights for perennial ryegrass and Yorkshire fog swards when continuously grazed by lambs to a desired height of 6 cm during December, January, February, and March.

For January and February, in Yorkshire fog swards there was a trend for higher dead material accumulation and higher bulk densities in comparison with ryegrass swards.

4.4.1.2 *Sward composition*

Details of the botanical composition of swards derived from hand separated samples are given in Table 4.2. Sown grasses formed the major components of both Yorkshire fog and ryegrass swards throughout the experiment, although there was an important contribution of ryegrass and other grasses in *Holcus* swards. The proportion of white clover did not differ amongst swards or sampling periods. There was a higher content of grass leaf in ryegrass swards than in *Holcus* swards, while the dead material proportion was higher in *Holcus* in January and February. Weeds (principally docks) were a minor component and did not differ significantly between swards.

4.4.1.3 *Canopy structure*

Comparisons of point quadrat data (Figures 4.2, 4.3 and Appendix Figure 4.1) indicated that proportions of sown grasses, clover, and *Poa* spp were always higher in ryegrass/white clover pastures than in Yorkshire fog/white clover pastures, but the proportion of dead material was higher in Yorkshire fog/white clover pastures. Contacts with weed species were negligible in both swards. The changes in the composition of the swards over time from December to February showed that dead material increased in both swards, with corresponding decrease in live components, in particular the leaf component (Appendix Figure 4.1). Clover contacts were slightly higher in ryegrass swards than in Yorkshire fog swards.

Table 4.2. The proportions of components of ryegrass and Yorkshire fog swards estimated from hand separation (DM basis) from December to February.

Sward components (%)	DECEMBER				JANUARY				FEBRUARY			
	Ryegrass	Fog	SEM‡	Sig§.	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig .
Main grass stem	16	15	2.5	NS	23	13	1.4	*	15	9.0	1.7	NS
Main grass leaf	32	29	4.0	NS	31	18	2.0	*	27	13	2.7	*
Main grass plant	48	44	5.8	NS	54	31	3.0	*	42	22	4.1	*
Clover petiole	3.0	4.7	1.5	NS	1.5	2.7	0.4	NS	1.5	1.3	0.2	NS
Clover leaf	4.2	4.1	1.4	NS	2.5	5.7	0.8	NS	3.5	2.7	0.4	NS
Clover plant	7.2	8.8	2.8	NS	4.0	8.4	1.2	NS	5.0	4.0	0.5	NS
Companion grass[1] (C)	0.3	12	3.6	NS	0.2	21	4.0	*	0.1	5.7	0.5	**
Other grasses (O)	8.2	7.0	3.5	NS	6.9	3.9	1.3	NS	4.2	1.8	1.6	NS
C + O	8.5	19	6.2	NS	7.1	25	2.8	*	4.3	7.5	2.0	NS
Weeds	0.6	0.2	0.4	NS	2.1	0.0	1.4	NS	7.7	0.2	5.3	NS
Green material	64	71	3.3	NS	67	64	3.4	NS	59	34	3.3	*
Dead material	36	29	3.3	NS	33	36	3.4	NS	41	66	3.3	*

[1] The companion grasses are Yorkshire fog and ryegrass, for ryegrass and Yorkshire fog swards respectively.
SEM‡ = Standard error of the mean
Sig§. = * $P < 0.05$, ** $P < 0.01$, and NS (not significant).
Number of observations contributing to the mean each month ($n = 8$).

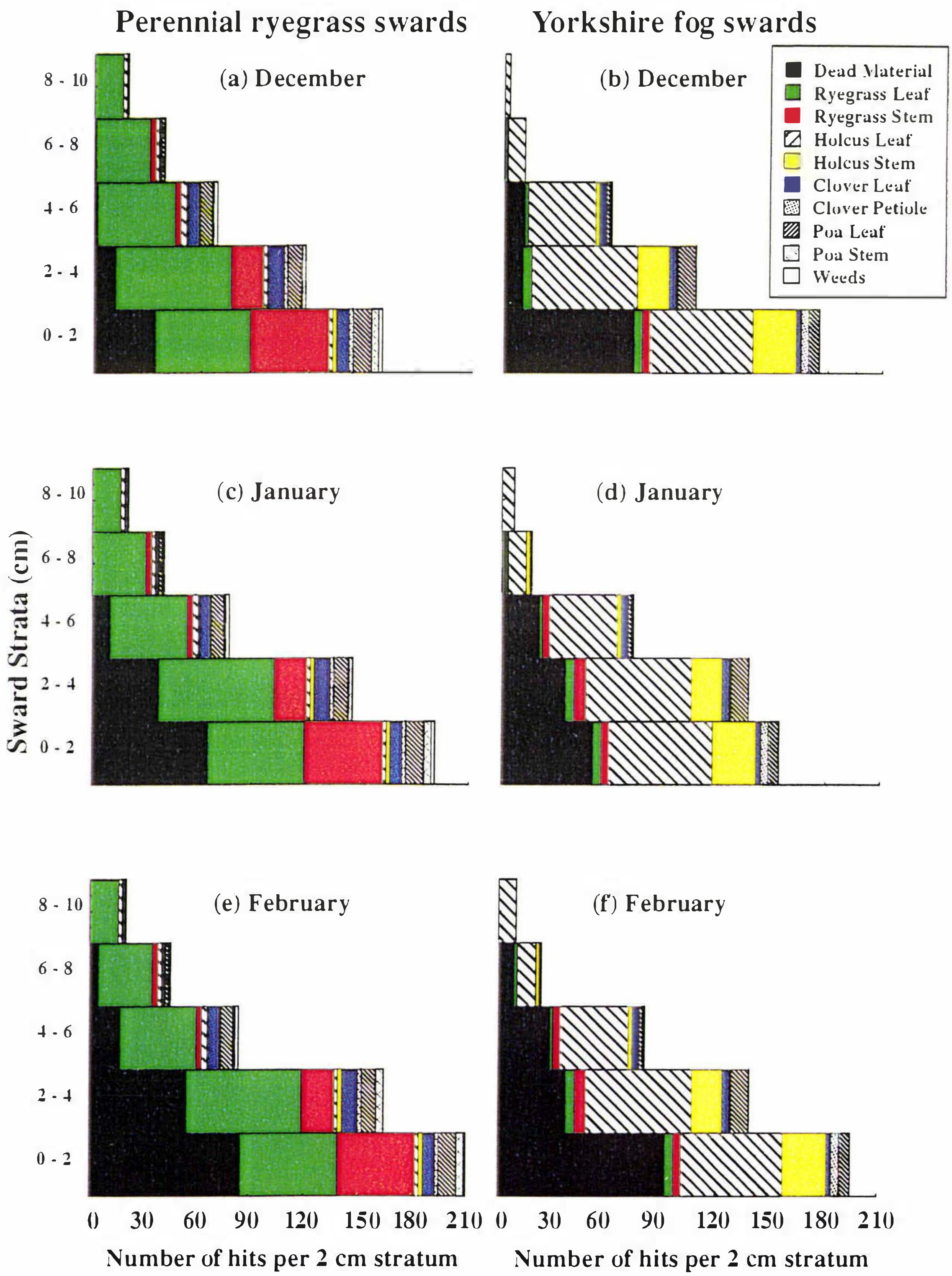


Figure 4.2. Proportional distribution of plant species and morphology for ryegrass and Yorkshire fog swards during December, January, and February determined from inclined point quadrat contacts.

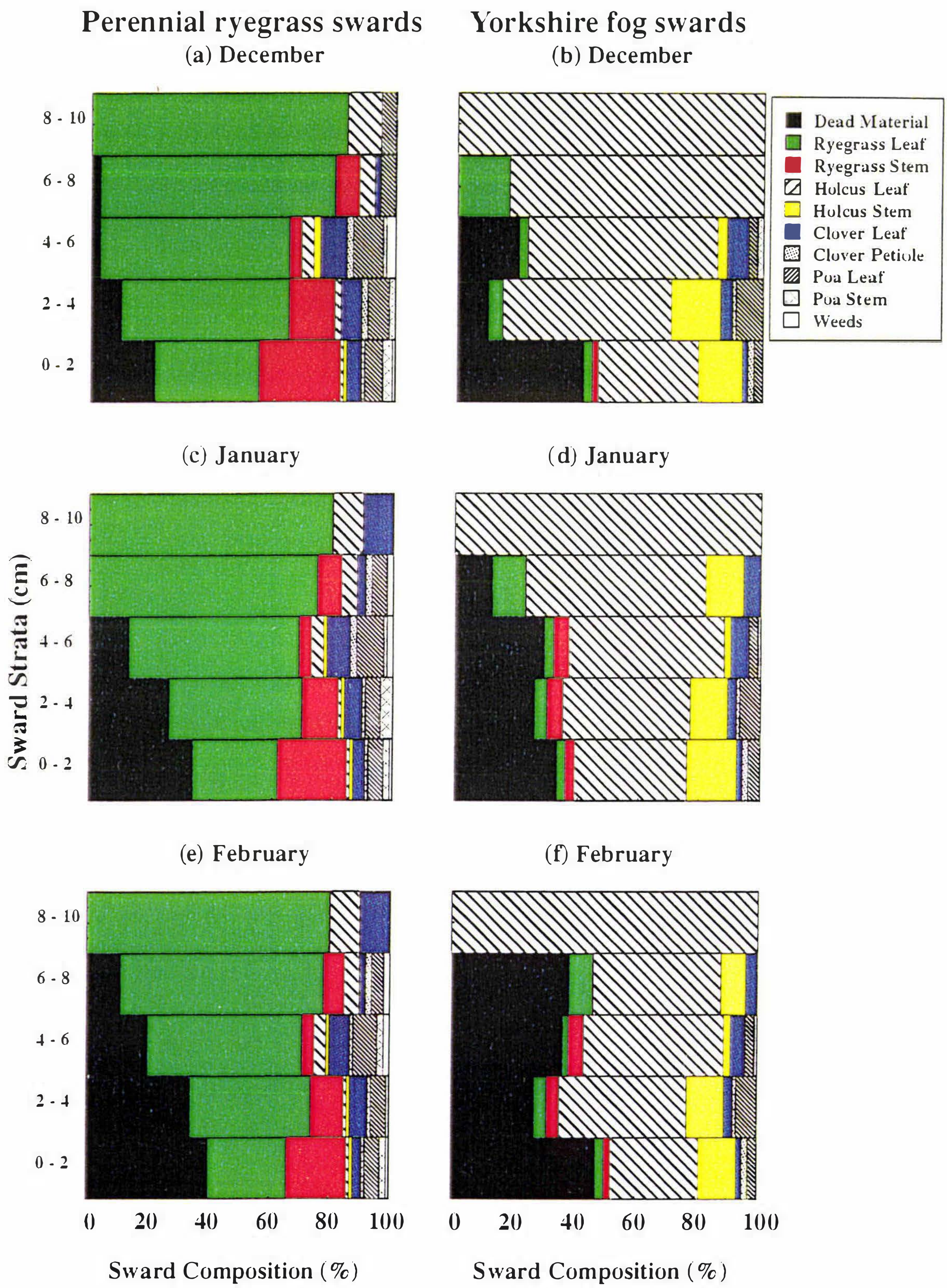


Figure 4.3. Variation in the canopy structures of ryegrass and Yorkshire fog swards during December, January, and February.

The vertical distribution of the recorded hits of both sward components and their proportion in the sward canopy are reported and compared for December, January, and February in Figures 4.2 and 4.3 respectively. In both swards, herbage mass was mainly concentrated at the base of the swards (from 0 to 4 cm height). Live leaf lamina was the major component of the uppermost layers (from 4 to 10 cm height) of both swards, particularly in ryegrass swards. However, stem frequency increased substantially from the top to the bottom in both sward profiles. Dead material was distributed throughout most strata in both ryegrass and Yorkshire fog swards, but it was principally concentrated at the base of both sward canopies (from 0 to 4 cm height). In general, dead material was distributed lower in the canopy of ryegrass swards than Yorkshire fog swards. In both swards, dead material was distributed higher in the sward canopy in February than in December, with transitional values in January. White clover was distributed higher in the sward canopy of ryegrass pastures than Yorkshire fog pastures. Changes in the vertical distribution of white clover in the sward canopy of both swards were similar over time. *Poa* spp were positioned at greater heights in ryegrass swards than in Yorkshire fog swards. A similar tendency was observed for weeds.

4.4.2 Animal measurements

4.4.2.1 *Botanical and chemical composition of the diet selected*

Table 4.3(a) shows the botanical composition of the diet selected by oesophageal fistulated wethers (OF) for ryegrass and Yorkshire fog swards during December and January. Separate identification of grass species in extrusa samples was difficult, so the results are based on comparisons of grasses versus white clover proportions and of live material versus dead material proportions. Leaf and pseudostems, and leaf lamina and sheath were not distinguished. Weeds were not observed in ingesta samples for either sward. In both December and January, grasses and live material were the main constituents of the diet selected in both swards. In both sampling periods, OF ingesta samples contained

Table 4.3. Botanical (a) and chemical (b) composition of the diet selected from ryegrass and Yorkshire fog swards in December and January.

Diet proportions (a)	DECEMBER				JANUARY			
	Ryegrass	Fog	SEM‡	Sig§.	Ryegrass	Fog	SEM	Sig.
White clover (%)	7	4	0.7	**	4	2	0.5	**
Green material (%)	94	89	1.0	**	89	91	1.0	NS

Diet proportions (b)	DECEMBER				JANUARY			
Concentration (% DM) of:	Ryegrass	Fog	SEM	Sig.	Ryegrass	Fog	SEM	Sig.
OM Digestibility	0.81	0.78	0.04	**	0.80	0.79	0.05	NS
N	3.69	3.73	0.06	NS	3.74	3.99	0.04	*
NDF[1]	35.1	35.1	–	–	41.48	37.30	–	–
ADF[1]	17.1	17.0	–	–	20.68	16.83	–	–
Lignin[1]	1.3	1.5	–	–	2.45	1.54	–	–
Free tannin	0.056	0.059	0.006	NS	0.072	0.065	0.010	NS
Protein-bound tannin	0.088	0.102	0.018	NS	0.120	0.082	0.008	NS
Fibre-bound tannin	0.021	0.025	0.001	NS	0.061	0.026	0.010	NS
Total condensed tannin	0.166	0.186	0.024	NS	0.265	0.174	0.030	NS

SEM‡ = Standard error of the mean
Sig§. = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
[1] = Bulked samples: no analysis of variance possible.
Number of observations contributing to the mean each month (n = 16).

significantly higher proportions of grasses and white clover than both swards on offer. In December OF samples from Yorkshire fog swards contained significantly less live material and more dead material than those from perennial ryegrass swards, but in January the proportions of dead and live material were similar for each sward.

Comparisons of the chemical composition of the diet selected for both swards in December and January are given in Table 4.3(b). In December, the OMD of the diet selected by OFs was 3% units higher in ryegrass swards than in Yorkshire fog swards, but in January there was no significant difference between diets. In January, the N content of the ingesta samples collected in Yorkshire fog swards was significantly higher than that of ryegrass swards, but no significant differences between swards were found in December.

Analyses of fibre components were made on bulked samples and no analysis of variance was possible; the results are shown for comparative purposes only.

The total, free, protein-bound and fibre-bound condensed tannins in the diet selected from ryegrass and Yorkshire fog swards did not differ significantly between swards or sampling periods (Table 4.3(b)). However, the values in Yorkshire fog samples tended to be higher in December and lower in January in comparison with those of ryegrass.

4.4.2.2 *Rumen metabolism*

Rumen ammonia concentration (Appendix Table 4.1 and Figure 4.4) was always higher in ruminal fistulated wethers (RF) grazing on ryegrass than on Yorkshire fog. Rumen ammonia values tended to increase by PEG administration in both swards, particularly 5 - 6 hours after PEG supplementation, and this effect attained significance at $P < 0.05$ at 0100 h and at $P < 0.10$ at 1700h and 2100h

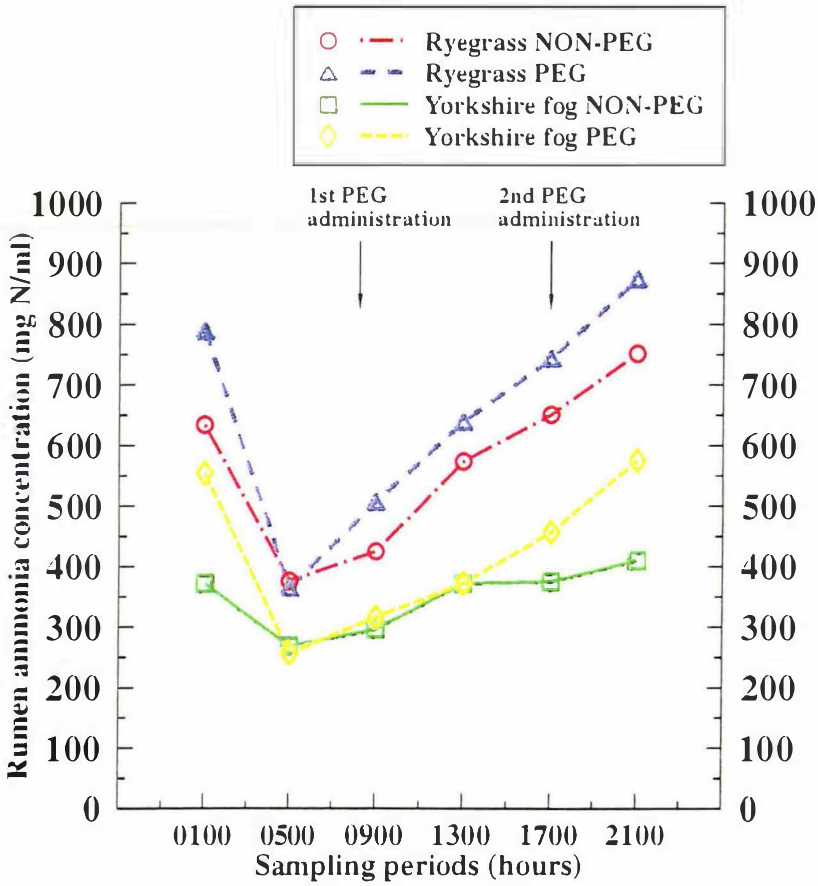


Figure 4.4. Variation in rumen ammonia concentration (mg N/ml) during 24 hours in rumen fistulated wethers grazing on Perennial ryegrass and Yorkshire fog swards treated with zero or 40 g/wether/day of polyethylene glycol (PEG; MW 4,000).

(Appendix Table 4.1). There was no significant interaction between swards and PEG supplementation.

Rumen fluid pH values were higher on Yorkshire fog swards than ryegrass swards on both sampling occasions, but to a greater extent at 0500 h ($P < 0.05$) (Table 4.4). PEG administration had no effect on rumen pH in either sward. The pH values of the samples taken at 1700 h tended to be higher than those taken at 0500 h for all treatment combinations.

4.4.2.3 *Herbage intake and ingestive behaviour*

The results of two 24 hours grazing behaviour studies, and evaluations of bite size measured by OF corresponding to the months of December and January are shown in Table 4.5. Animals were off the plots for 127 minutes (December) or 90 minutes (January) each day for PEG drenching and faecal sampling.

Mean bite size on Yorkshire fog swards tended to be higher than on ryegrass swards in both sampling periods, but differences were not significant in December. Rates of biting were significantly affected by sward species in December, being higher in Yorkshire fog than in ryegrass. However, the opposite was the case in January. Grazing, ruminating, and resting times were not significantly different between swards in both sampling periods. For both sward species, most of the daily grazing activity (between 78 and 83%) occurred during daylight (from 0600 to 2000 hours), though, in January, lambs on Yorkshire fog swards spent more time grazing (21 % versus 18 %) during the night (from 2000 to 0600 hours) than those on ryegrass swards. Resting time was mainly concentrated in the night period for both swards (between 88 and 93%). However, in January, lambs tended to have higher resting time during daylight on Yorkshire fog swards than on ryegrass swards (10% versus 7%). Ruminating times were similarly distributed in both swards, but the distribution between

Table 4.4. Variation in pH values in two sampling periods (0500 and 1700 hours) in rumen fistulated wethers grazing on Yorkshire fog and perennial ryegrass swards treated with zero or 40 g sheep^{-1} day^{-1} of polyethylene glycol (PEG; MW 4,000).

TIME	Species (SPP)			Oral PEG supplementation			SPP × PEG					Significance[§] of the main effects and interaction		
							RYEGRASS		YORKSHIRE FOG					
Hours	R[1]	Fog[2]	SEM[‡]	Without	With	SEM	NONPEG	PEG	NONPEG	PEG	SEM	SPP	PEG	SPP×PEG
0500	5.9	6.4	0.06	6.2	6.1	0.10	5.8	5.9	6.5	6.2	0.15	*	NS	NS
1700	6.5	6.9	0.11	6.6	6.8	0.12	6.3	6.6	6.8	6.9	0.16	NS	NS	NS

R[1] = Perennial ryegrass
Fog[2] = Yorkshire fog
SEM[‡] = Standard error of the mean
Sig. [§] = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean in each sampling time for main effects (n = 6) and interactions (n = 3).

Table 4.5. Effects of sward species on intake per bite (mg OM $bite^{-1}$), rate of biting (bites $minute^{-1}$), grazing, ruminating and resting times (minutes).

Behavioural Components		DECEMBER				JANUARY			
		Ryegrass	Fog	SEM[‡]	Sig[§].	Ryegrass	Fog	SEM	Sig.
Mean bite size (mg OM $bite^{-1}$)		80	95	5.0	NS	85	111	5.3	**
Rate of biting (bites min^{-1})	Morning (M)	66	76	1.3	**	65	61	1.2	*
	Afternoon (A)	68	70	0.8	*	64	62	1.0	NS
	M + A	67	73	0.8	**	64	61	1.0	*
Grazing time (min)	Daylight[1]	520	494	21	NS	521	511	10	NS
	Night[2]	96	102	3	NS	113	134	4	*
	24 hr[3]	616	596	25	NS	634	645	11	NS
Ruminating time (min)	Daylight	126	130	11	NS	158	164	8	NS
	Night	102	94	6	NS	299	294	6	NS
	24 hr	228	224	16	NS	457	458	8	NS
Resting time (min)	Daylight	53	73	11	NS	18	24	2	NS
	Night	416	420	7	NS	241	223	8	NS
	24 hr	469	493	17	NS	259	247	10	NS
Grazing time	(% in Daylight)	83	82	0.5	NS	82	79	0.5	*
Ruminating time	(% in Daylight)	63	66	2.3	NS	34	35	1.4	NS
Resting time	(% in Daylight)	11	15	2.0	NS	7	10	0.6	*

Daylight[1] = Between 0600 - 2000 hours; Night[2] = Between 2000 - 0600 hours; 24 hr[3] = Daylight + Night.
SEM[‡] = Standard error of the mean.
Sig[§]. = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean each month (n = 32).

daylight and night activity differed between sampling periods.

Mean release rates of chromic sesquioxide (Cr_2O_3) capsules (mg day^{-1}) were evaluated with rumen-fistulated (RF) wethers and experimental lambs in January after slaughtering (Appendix Table 4.2). When the assessment was made by RF, release rates of Cr_2O_3 were higher for Yorkshire fog swards than for ryegrass swards, but unaffected by PEG supplementation. However, no significant effects of sward species or PEG supplementation were found on the release rates of Cr_2O_3 in slaughtered lambs. Therefore, a common release rate of 188.5 mg Cr_2O_3 day^{-1} was used amongst treatments and periods. A larger coefficient of variation was observed with the RF sampling procedure in comparison to the use of intact lambs (16% versus 8% respectively).

In both sampling periods, herbage intakes on ryegrass swards were higher than those on Yorkshire fog swards, but the difference was only significant in December (Table 4.6). There were no significant differences in herbage intakes due to PEG supplementation or sex effects (Table 4.6), or their interactions (Appendix Table 4.3).

4.4.2.4 *FEC measurements*

The effects of sward species, PEG supplementation, and sex on lamb FECs are presented in Table 4.7. Lambs on Yorkshire fog had lower FEC in times T1 and T3 than those on ryegrass; though the opposite tendency was found in times T2 and T4, but none of these differences were significant. There was no significant difference in FECs amongst PEG supplementation and sex treatments. However, a significant interaction between sward species and PEG supplementation was found 28 days after the commencement of the trial (T1), where the NON-PEG lambs grazing on Yorkshire fog swards had lower FEC than the rest of the treatments, but these effects disappeared in the following sampling periods (T2, T3, and T4).

Table 4.6. Effects of sward species, oral PEG supplementation and sex of lamb on herbage intake (HI; g OM $lamb^{-1}$ day^{-1} or g OM kg $LW^{0.73}$ day^{-1}) for December and January.

PERIODS	Species (SPP)				Oral PEG supplementation				SEX			
	Ryegrass	Fog	SEM[‡]	Sig[§]	Without	With	SEM	Sig	Female	Male	SEM	Sig
DECEMBER												
Herbage intake/head	990	800	40	*	900	880	20	NS	900	880	30	NS
Herbage intake/kg $LW^{0.73}$	82	70	2.8	*	76	75	1.7	NS	78	74	2.0	NS
JANUARY												
Herbage intake/head	1370	1190	60	NS	1300	1260	60	NS	1320	1240	70	NS
Herbage intake/kg $LW^{0.73}$	98	85	3.5	NS	90	93	4.0	NS	94	90	4.5	NS

SEM[‡] = Standard error of the mean
Sig.[§] = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and sex of lamb (male = 48; female = 16).

Table 4.7. Effects of sward species and PEG supplemetation on lamb mean faecal egg count (eggs g fresh faeces^{-1}).

TIME[4]	Species (SPP)			Oral PEG supplementation			SPP × PEG				
							Ryegrass		Fog		
	R[1]	Fog[2]	SEM[‡]	Without	With	SEM	NONPEG	PEG	NONPEG	PEG	SEM
1	579 (22)	430 (19)[5]	2.6	503 (20)	506 (21)	2.0	733[b3] (25)	425[ab] (18)	273[a] (15)	578[b] (24)	2.8
2	52 (5)	72 (7)	1.7	62 (5)	61 (6)	1.0	46 (4)	58 (6)	79 (6)	65 (7)	1.3
3	192 (11)	88 (7)	4.1	134 (9)	146 (9)	1.4	177 (9)	206 (11)	92 (8)	85 (7)	1.9
4	110 (8)	175 (11)	2.3	123 (9)	162 (11)	1.0	71 (6)	150 (10)	175 (11)	175 (12)	1.4

Significance[§] of the main effects and their interactions	TIMES 1	2	3	4
SPP	NS	NS	NS	NS
PEG	NS	NS	NS	NS
SEX	NS	NS	NS	NS
SPP×PEG	*	NS	NS	NS
SEX×PEG	NS	NS	NS	NS
SPP×SEX	NS	NS	NS	NS
SPP×PEG×SEX	NS	NS	NS	NS

R[1] = Perennial ryegrass
Fog[2] = Yorkshire fog
[3] Means within rows for interactions with letters in common are not significantly different at the P < 0.05.
SEM[‡] = Standard error of the mean
Sig.[§] = * P < 0.05, ** P < 0.01 and NS (not significant).
TIME[4] = T1 (12/1), T2 (28/1), T3 (12/2), T4 (12/3). For T1, T3 and T4 measurements were made 28 days after drenching, and for T2 14 days after drenching.
[5] Faecal egg count data was normalized by square root transformation plus 0.5 prior to analysis (values In brackets).

Number of observations contributing to the mean each month for main effects (n = 32) and interactions (n = 16).

4.4.2.5 *Wool growth and wool yield*

Table 4.8 shows the effects of sward species, PEG supplementation and sex on wool growth (greasy and clean) and wool yield. There was no significant influence of sward species on clean and greasy wool growth. However, lambs on ryegrass swards tended to have higher wool growth from midside areas (between 5 and 8%, $P < 0.10$) than those on Yorkshire fog swards in both sampling periods. For the two periods of evaluation, there was no effect of PEG supplementation or sex on clean and greasy wool growth. However, in the period December-January, a significant sward species × PEG supplementation interaction showed that the wool growth of NON-PEG lambs on ryegrass swards was higher than those of the rest of sward × PEG supplementation combinations (Appendix Table 4.4(a,b)). No effects of treatments on wool yield were evident in all the comparisons (Table 4.8 and Appendix Table 4.4(a,b)).

4.4.2.6 Liveweight gain, carcass weight and yield, and carcass GR measurements

For the entire experimental period, lambs grazing ryegrass swards tended to have greater rates of liveweight gain (8%) than lambs grazing Yorkshire fog swards (Table 4.9, Appendix Table 4.5(a,b), Figure 4.5), with the difference attaining significance at $P < 0.10$ in December, when lambs grazing on ryegrass swards grew 28% faster than those grazing on Yorkshire fog swards. PEG supplementation had no effect upon liveweight gain. Female lambs had significantly greater liveweight gains than castrated male lambs.

Table 4.8. Effects of sward species, oral PEG supplementation and sex of lamb on greasy and clean wool growth from midside areas (μg cm^{-2} day^{-1}) and on wool yield (%).

PERIODS		Species (SPP)				Oral PEG supplementation				Sex			
		Ryegrass	Fog	SEM‡	Sig.§	Without	With	SEM	Sig.	Female	Male	SEM	Sig.
DECEMBER - JANUARY (54 days)	Greasy wool growth	1340	1260	30	NS	1270	1330	41	NS	1340	1260	49	NS
	Clean wool growth	1030	970	15	NS	970	1030	17	NS	1040	970	32	NS
	Wool yield	78	77	1.1	NS	78	78	0.34	NS	78	77	0.81	NS
FEBRUARY - MARCH (41 days)	Greasy wool growth	1610	1500	45	NS	1600	1500	45	NS	1590	1510	50	NS
	Clean wool growth	1260	1200	15	NS	1190	1260	33	NS	1250	1210	38	NS
	Wool yield	79	80	1.1	NS	80	79	0.88	NS	79	80	0.86	NS

SEM‡ = Standard error of the mean
Sig.§ = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and sex of lamb (male = 48; female = 16).

Table 4.9. Effects of sward species, oral PEG supplementation and sex of lamb on lamb liveweight gain (g/day) from December to March assessed in three different periods and overall.

TIME	Species (SPP)				Oral PEG supplementation				SEX			
	Ryegrass	Fog	SEM[‡]	Sig.[§]	Without	With	SEM	Sig.	Female	Male	SEM	Sig.
08/12 - 18/01	165	129	10	NS	136	158	15	NS	141	153	11	NS
18/01 - 06/02	190	208	28	NS	190	207	16	NS	186	211	12	NS
06/02 - 15/03	64	68	10	NS	72	60	10	NS	86	47	8	**
Overall	131	121	9	NS	122	130	7	NS	134	119	4.4	*

Table 4.10. Effects of sward species, oral PEG supplementation and sex of lamb on carcass weight (kg), GR (mean value of left and right sides, mm) and dressing out (%).

Carcass quality measurements	Species (SPP)				Oral PEG supplementation				SEX			
	Ryegrass	Fog	SEM[‡]	Sig.	Without	With	SEM	Sig.	Female	Male	SEM	Sig.
Carcass weight	17.5	16.3	0.22	*	16.8	17.0	0.36	NS	16.6	17.1	0.48	NS
GR[1]	6.7	5.4	0.59	NS	6.2	5.9	0.72	NS	7.4	4.8	0.58	**
Dressing out	46.2	45.4	0.31	NS	45.2	46.4	0.41	NS	46.5	45.1	0.43	**

SEM[‡] = Standard error of the mean.
Sig.[§] = * P < 0.05, ** P < 0.01 and NS (not significant).
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and sex of lamb (male = 48; female = 16).
GR[1] = Mean value of left and right sides.

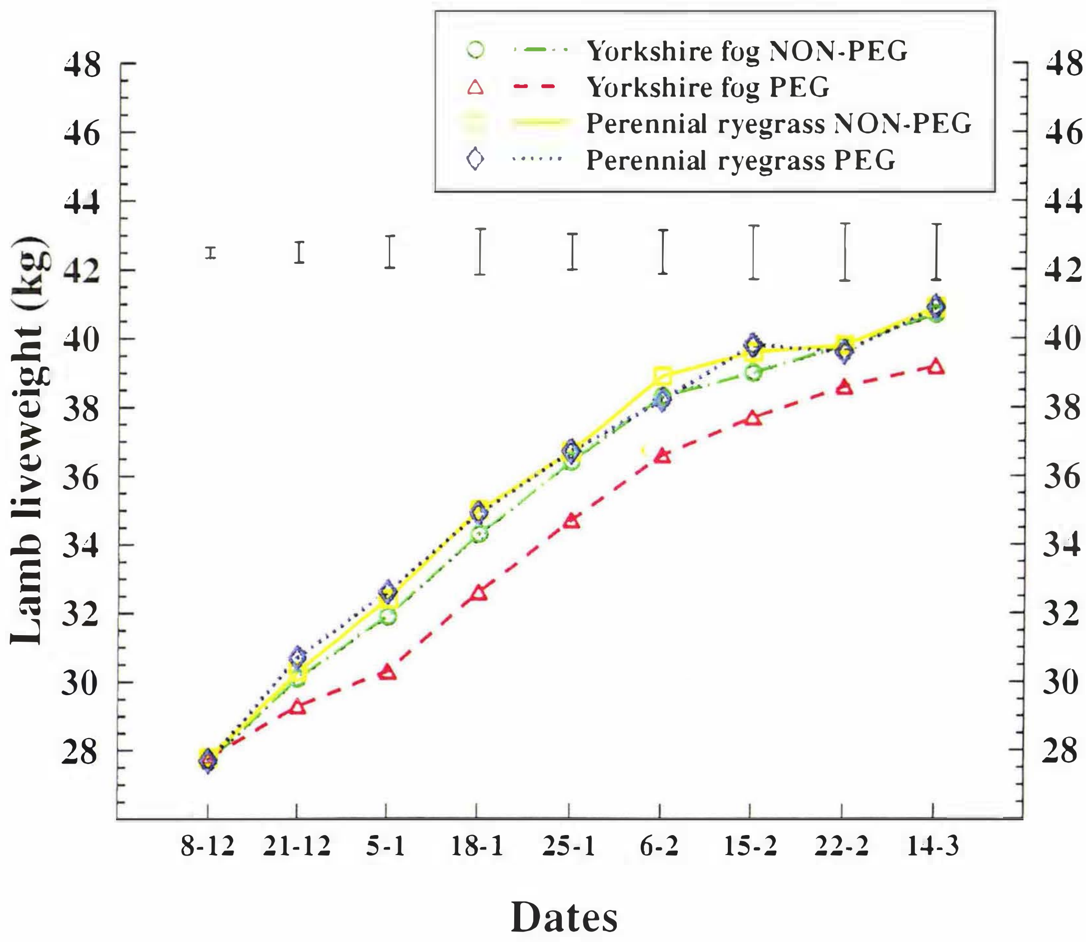


Figure 4.5. Liveweight gain of lambs grazing on Yorkshire fog or perennial ryegrass swards treated with zero or 40g/lamb/day of polyethylene glycol (PEG; MW 4,000) from December to March. Vertical lines indicate the standard error of the mean.

Results of the effects of sward species, PEG supplementation, and sex on carcass weight, dressing out percentage, GR measurements are given in Table 4.10 and Appendix Table 4.6(a,b). Carcass weight, dressing out percentage, GR values tended to be higher for lambs grazing on ryegrass swards than those on Yorkshire fog, but only the difference in carcass weight attained significance ($P < 0.05$). PEG supplementation had no effect on those variables. Female lambs had significantly higher values of GR and greater dressing out percentage than castrated male lambs. There was no significant difference in carcass weight between sexes.

4.5 DISCUSSION

4.5.1 Evaluation of sward results

4.5.1.1 *Herbage mass, surface sward height, sward bulk density, and sward composition*

After the first two weeks of the experiment, both swards were maintained within the limit of 6.5 and 4.5 cm surface height throughout the experiment, close to the desired sward height (6 cm) (Figure 4.1). From December to mid-February, despite the higher stocking rates maintained in ryegrass swards in comparison to those of Yorkshire fog (40 lambs + 10 adult wethers/ha versus 40 lambs/ha respectively), swards heights of ryegrass plots tended to be slightly, but consistently, higher than those of Yorkshire fog plots. In the last four weeks of the trial, sward heights of both swards slowly declined below 5 cm and stocking rates were reduced in both swards, but to a greater extent in ryegrass plots. These findings are consistent with the observations of Niezen *et al.* (1993b). The higher stocking rate capacity of ryegrass swards, in contrast to Yorkshire fog swards, taken together with the higher herbage intakes observed on ryegrass plots, is evidence of higher pasture growth of ryegrass swards. The moderate to high fertility status of the experimental site (Chapter 3) and the favourable climatic conditions at the beginning of the experiment (Section 4.3.1) probably contributed to this difference in growth. In other comparative studies ryegrass has been found present study, showed a greater accumulation of protein-bound and fibre bound CT in Yorkshire fog with increasing leaf age. Therefore, these authors concluded that CT may be associated with slow rates of decomposition in Yorkshire fog dominated grassland.

The botanical composition observed in both swards differed markedly in relation to the sampling procedure utilized (hand separation or point quadrat contacts). With the exception of January, the trend in the variation of the proportion of dead material between swards tended to be similar over time for both techniques, but consistently higher proportions of dead material for both swards were recorded by hand separation. The results of Hodgson (1981) and of Grant *et al.* (1985) confirm these findings. Grant *et al.* (1985) suggested that the inclined point quadrat (set at 32.5º to the horizontal) tends to underestimate only the proportion of dead material in the lower horizons of the sward, because this component is too dense to record precisely. However, it is unlikely that this technique led to an erroneous interpretation of the results (Hodgson, 1981).

Weeds were a minor component of both swards. The proportions of white clover did not differ amongst swards and periods, probably reflecting the previous conventional grazing management applied in the experimental area (Watkin *et al.*, 1974). These results are in accordance with the information reported in the initial experiment during late autumn (Section 3.5.1, Chapter 3).

The finding of higher proportions of unsown species in Yorkshire fog plots (Table 4.2 and Appendix Figure 4.1) coincide with other published results (Watkin and Robinson, 1974; Harvey *et al.*, 1984; Smith and Allcock; Watt, 1987; Morton *et al.*, 1992) where 'Massey Basyn' *Holcus lanatus* was more prone than perennial ryegrass to invasion by unsown species (Watt, 1987), but disagrees with the results of Niezen *et al.* (1993) and with those of Experiment 1 (Section 3.5.2, Chapter 3).

The discrepancies between these studies may be partially explained by the differences in the grazing management and fertilization policy of the experimental site. Close and frequent defoliation reduces the DM production and the proportion of *Holcus lanatus* to a much greater extent than that of *Lolium perenne* whether the species are grown in monoculture or mixture (Haggar, 1976).

4.5.2 Evaluation of animal results

4.5.2.1 *Botanical and chemical composition of the diet selected and canopy structure*

With the exception of the information gathered from the initial experiment (Chapter 3), there are no data available in the literature describing the sward structure of Yorkshire fog swards and diet selection on those swards.

The discussion and interpretation of the results of diet selection in this section are based on the assumption that mature oesophageal fistulated wethers provide samples representative of the diet selected by lambs. Experimental evidence comparing the diet selected by mature or immature animals in sheep (Hughes *et al.*, 1984) and in cattle (Hodgson and Jamieson, 1981) supports the above assumption.

Leaf and pseudostem components could not be distinguished in extrusa samples, but visual appraisal suggested that green leaf was the main component of the diet selected amongst swards and sampling periods (Tables 4.2 and 4.3(a)). In both sampling periods, on average, green material (principally grass leaf) formed a high proportion of the diet selected by OF sheep in all swards (above 90%) in comparison to its presence in the whole sward profile (from 34 to 36% and from 30 to 38% for perennial ryegrass and Yorkshire fog swards respectively, measured by hand separation procedure) (Table 4.2). However, in both swards the proportion of dead material in the herbage mass of both swards was substantially higher than that found in the diet (Tables 4.2 and 4.3(a,b)).

In Yorkshire fog swards in both sampling periods, white clover was harvested by oesophageal fistulated sheep in a lower proportion than its presence in the total sward (8 to 9% vs 2 to 4%). But in the case of ryegrass swards the proportions were similar (Tables 4.2 and 4.3(a)). Weed species were not detected in extrusa. It has been clearly documented that the diet eaten by grazing animals contains higher proportions of leaf and green material, and lower proportions of stem and dead tissue, than are found in the sward on offer (Van Dyne, 1980; Arnold, 1981; Clark *et al.*, 1982; Hodgson, 1982, 1985b, 1990; L´Huillier *et al.*, 1984; and Bootsman *et al.,* 1990).

When diet and sward comparisons are based on the composition of the upper layers of both swards (above 4 cm), rather than on the sward on offer, the differences become much smaller (Table 4.11). In temperate swards, there is evidence suggesting that the diet of oesophageally fistulated animals clearly reflects the composition of the top strata of the sward, indicating substantially unselective grazing (Milne *et al.*, 1982; Barthram and Grant, 1984; Illius *et al.*, 1992; Clark, 1993; Montossi *et al.,* 1994). In both swards, the important contribution of green grass leaf in the diet selected is probably related to its high vertical distribution in the sward canopy, increasing the opportunity to be selected by sheep, and due to its ease of prehension related to its low structural strength (Hodgson and Grant, 1982; Poppi *et al.*, 1987) (Figures 4.2 and 4.3).

Dead material may be rejected because of low acceptability (Clark *et al.*, 1982; Kenny and Black, 1984) or its inaccessibility in the base of the sward (Clark *et al.*, 1982; Poppi *et al.*, 1987). In this study, dead material appeared in the extrusa samples collected from both swards, in December and January, but to a greater extent in Yorkshire fog samples. This may be explained by the high proportion of this component in the whole sward profile, but particularly in the surface layers of the sward canopy of Yorkshire fog. The presence of dead leaf and sheath material is reputed to reduce the acceptability of *Holcus lanatus* to sheep (Cameron, 1979).

Table 4.11. Relationships between the proportions of sward components in the upper layers (between 4 to 10 cm) of the ryegrass and Yorkshire fog sward canopies and the composition of the diet selected during December and January.

Components	DECEMBER				JANUARY			
	Ryegrass		Yorkshire fog		Ryegrass		Yorkshire fog	
	Sward	Diet	Sward	Diet	Sward	Diet	Sward	Diet
Grasses(%)	94	93	94	96	91	96	92	98
White clover (%)	6	7	6	4	9	4	8	2
Green Material (%)	98	94	84	89	93	90	76	91
Dead Material (%)	2	6	16	11	7	10	24	9

The higher vertical distribution of white clover in the sward canopy of perennial ryegrass than of Yorkshire fog, providing greater accessibility for the grazing sheep, may explain the higher proportion of clover in ryegrass extrusa samples. Additionally, the much higher proportion of dead material dispersed in the intermediate and upper layers of the canopy of Yorkshire fog swards, in a high degree of aggregation with white clover, may have reduced the ability of sheep to select clover from fog swards. These results disagree with those found in Experiment 1, where the proportion of white clover in the diet was higher in Yorkshire fog swards than in ryegrass swards. This difference may be related to the higher distribution of white clover in the Yorkshire fog sward canopy than in ryegrass in the initial grazing experiment, and to the lower position of dead material in the sward canopy (Hu, 1993) compared with the present summer comparison.

The results of white clover selection in ryegrass swards are not in accord with the summer observations of Bootsman *et al.* (1990), using weaned red deer stags, where clover was subjected to a severity of defoliation which was at least equal to that of the grasses, despite its lower position in the sward profile. This discrepancy can be related to the higher vertical distribution of white clover in the upper strata (above 4 cm) in this study (9%) compared with the records (5%) of Bootsman *et al.* (1990), giving better opportunity for its selection by the sheep. In addition, this result is in agreement with the suggestions of Bootsman *et al.* (1990) that in comparable circumstances sheep would be less selective for clover than deer.

The low concentration of CT in extrusa samples were not expected to affect *in vitro* digestibility, and hence prediction of the *in vivo* digestibility (T.N. Barry, personal communication). In December, OF animals selected a diet 3 units more digestible on ryegrass swards than on Yorkshire fog swards (Table 4.3(b)). This observed difference is in agreement with the results of the initial experiment (Section 3.5.4, Chapter 3) and of Morton *et al.* (1992). However, this result is not supported by other published reports (Harvey *et al.*, 1984; Watt, 1987), where pasture samples were taken by sward cutting techniques. The higher OMD recorded in ryegrass swards may reflect the important contribution of green grass leaf and white clover, and the lower proportion of dead material in the extrusa samples of ryegrass swards compared with those taken in Yorkshire fog swards. In January, the OMD values of the diet on ryegrass plots tended to be higher by one unit, than those on Yorkshire fog plots, and the difference was not significant. This result is probably the consequence of the increase in dead material and the decrease in white clover contents which occurred in ryegrass diet samples. Although no statistical comparisons were possible, the high values of ADF, NDF, and lignin in January for ryegrass samples, substantiate the lower OMD values in comparison with those recorded in December (Table 4.3(b)).

The higher N content recorded in the extrusa boluses of Yorkshire fog swards compared with ryegrass swards, particularly in January, is consistent with the reports of other researchers (Jacques *et al.*, 1974; Haggar, 1976; Frame, 1982; and Harvey *et al.*, 1984).

The presence of low concentrations of CT (< 0.2% on a DM basis) in *Lolium perenne* has been confirmed in the present study, supporting the evidence obtained in Experiment 1 and in the trials of Liu *et al.* (unpublished data). The low CT concentrations in *Holcus lanatus* are in accordance with the results of other research reports (Terrill *et al.*, 1992a,b; Douglas *et al.*, 1993; Montossi *et al.* 1994; Iason *et al.*, 1995; Liu *et al.*, unpublished data). In both sampling periods, the total CT and their different forms did not differ significantly between sward species. These results disagree with the observations reported in Experiment 1, where *Holcus lanatus* contained more total CT and protein-bound CT than *Lolium perenne*. Possible explanations for this discrepancy may be related to the probable presence of Yorkshire fog in ryegrass plots, which may have biased the concentration of CT in ryegrass diets, or due to variations in the growing conditions between species prior to sampling.

The experiments of Iason *et al.* (1995) and of Douglas *et al.* (1993) indicated that the CT concentration of *Holcus* green leaf is approximately twice that of green stem. However, probably green grass leaf was the predominant component in the diet selected in *Holcus* swards. Additional evaluations, using the information provided by Iason *et al.* (1995) of the CT concentration of the components of *Holcus* swards indicate similar values of CT between the diet selected and the sward on offer. Therefore, it is unlikely that the low CT concentration of *Holcus* swards, influenced the selective patterns of the oesophageal fistulated sheep in those swards. This evidence is supported by the experiments of Jones and Mangan (1977) and of Waghorn and Jones (1989) who worked with plants of higher CT content than Yorkshire fog or perennial ryegrass (sainfoin and dock respectively). For temperate swards, Waghom *et al.* (1990) suggested that palatability is unlikely to be influenced by the presence of CT.

4.5.2.2 *Rumen metabolism*

The rumen NH_3 concentrations observed in both swards, suggests that PEG would preferentially bind CT and prevent the binding of proteins, which would then be rapidly degraded to ammonia (Table 4.4). This increase in rumen NH_3 concentration in RF sheep with PEG administration provides additional evidence of the presence of CT in both ryegrass and Yorkshire fog swards, and is consistent with a reduced de-amination of plant proteins when CT are present (Waghorn *et al.*, 1987b). Terrill *et al.* (1992b) also found that PEG administration resulted in increased rumen ammonia concentration in the diet of RF with low concentration of CT (0.47 % on a DM basis). The higher NH_3 values recorded for ryegrass could be explained if protein solubility in the rumen of animals (70%; Ulyatt *et al.*, 1975) was higher for ryegrass than for Yorkshire fog. However, this assumption is somewhat speculative because no experimental evidence is available to support it, and more investigation is needed.

The high rumen HN_3 values recorded for both swards are probably related to the application of nitrogen fertiliser (50 kg ha^{-1} of urea) to the experimental plots four days before the rumen metabolism observations. The variation observed in rumen NH_3 concentration amongst sampling periods in both swards indicated that twice daily PEG supplementation, may not have completely eliminated binding of plant proteins to CT in the rumen for a full 24 hr period. This result is in agreement with the findings of Terrill *et al.* (1992b) with once daily PEG supplementation.

The lower rumen pH values observed in ryegrass rumen fluid samples in comparison with those of Yorkshire fog are most likely due to its higher OM digestibility (Table 4.3b), resulting in greater volatile fatty acid concentrations, which in tum lowered pH (T.N. Barry, personal communication). The oral administration of PEG had no effect on rumen pH in RF sheep grazing on ryegrass and Yorkshire fog swards, which corresponds to the results given by Terrill *et al.* (1992b). The pH values recorded from both swards (5.8 to 6.9) fall into the indicated optimum pH range for the formation of stable and insoluble CT-protein complexes (Jones and Mangan, 1977).

4.5.2.3 *Grazing behaviour and herbage intake*

The higher mean bite weight of OF animals grazing on Yorkshire fog than on ryegrass swards, particularly in January (Table 4.5), is in agreement with the results of Montossi *et al.* (1994)(Chapter 3) and with further evidence from Liu *et al.* (unpublished data). Possible explanations for the higher mean bite weight achieved by OF animals on Yorkshire fog swards are either their higher bulk density, particularly of the green components of the sward in this experiment (Table 4.1) (Section 3.5.5, Chapter 3) or the lower tensile strength of *Holcus lanatus* 'Massey Basyn' leaves in comparison with those of perennial ryegrass (Evans, 1967; Jacques *et al.*, 1974), Although no direct estimations of leaf strength were made in this study, Evans (1967) found that leaves of perennial ryegrass had significantly greater strength and cellulose content than those of Yorkshire fog and *Poa trivialis*, an important component of Yorkshire fog swards in this experiment, particularly in January. In the study of Evans (1967), the magnitude of the differences in leaf strength and cellulose content between grass species was higher in favour of Yorkshire fog in the summer comparison than in other seasons. Increases in bulk density (Burlinson *et al.*, 1991; Laca *et al.*, 1992) and decreases in leaf shear breaking load (Poppi *et al.*, 1987) have been positively correlated with bite weight.

In January, a compensatory response to the lower intake per bite found in ryegrass was observed, with a higher rate of biting in ryegrass swards than in Yorkshire fog swards, and with grazing, ruminating, and resting times being similar for both swards. Similar grazing behaviour patterns were observed in December, with the exception of the higher rate of biting recorded in fog swards. The time spent in grazing in this experiment is higher than that reported previously by Penning *et al.* (1991) for non-lactacting ewes on perennial ryegrass swards grazed at a constant surface sward height of 6 cm during summer, though, the higher growth potential and nutrient demand of the lambs of the present trial could explain this difference. These results confirm that, within grazing behaviour components, intake per bite is the most sensitive response to variations in sward characteristics of the sward canopy (Hodgson, 1985b, 1990).

Although no statistical analyses were possible, field observations suggest that there was no evidence of any effect of PEG supplementation on the behaviour patterns of the lambs grazing on both swards.

The high coefficient of variation in the mean release rate of Cr_2O_3 observed in rumen-fistulated sheep compared with non-fistulated sheep (Appendix Table 4.2) is in accordance with the results of Parker *et al.* (1990), who suggested that the difference in the Cr_2O_3 release rates between fistulated and non-fistulated animals, can probably be attributed to temperature fluctuations associated with the removal of the capsule from the rumen for measurements and to different gaseous conditions between intact and fistulated rumens. The findings of Parker *et al.* (1990) support the decision to use the rate of Cr_2O_3 release from intact lambs to calculate herbage intake in the present study.

In December, lambs grazing on ryegrass swards had higher herbage intakes than those grazing on Yorkshire fog swards (Table 4.6). This result is in agreement with those observed previously for adult sheep in an autumn comparison (Section 3.5.5, Chapter 3), where the evidence suggested that the most important limits were nutritional rather than behavioural in origin, and reflected differences in diet digestibility rather than in bite weight. This explanation also fits the results for January, where herbage intakes from both swards were similar, reflecting the similar OM digestibilities observed in both diets (Table 4.3b), despite the higher intake per bite recorded in Yorkshire fog swards (Table 4.5). When expressed per unit of metabolic weight (Table 4.6), lamb intakes were similar to those recorded previously by Jamieson and Hodgson (1979) for comparable lambs grazing ryegrass swards of similar digestibility, under continuous stocking management, and lower than those observed on ryegrass swards in summer with ewes by L'Huillier *et al.* (1986). The latter discrepancy in intake may reflect the lower dietary OMD reported by L'Huillier *et al.* (1986) in comparison with the present study.

Coinciding with the results of Terrill *et al.* (1992b), in both grass species, there was no evidence that low dietary CT concentrations (CT $< 0.2\%$ on a DM basis) affected lamb herbage intake (Table 4.6 and Appendix Table 4.3).

4.5.2.4 *Internal parasites*

There were no consistent treatment effects on FEC values. However, 28 days after the first drenching, a significant interaction was observed, where NON-PEG lambs grazing on Yorkshire fog swards had the lowest FEC (Table 4.7). The trials of Niezen *et al.* (1993b, 1995) showed that lambs grazing on Yorkshire fog swards had lower production losses due to parasitism than those grazing on perennial ryegrass swards. The short response in lamb FEC on Yorkshire fog swards may be attributable to the presence of CT in this grass. Similar observations have been reported by Niezen *et al.* (1993a) and Niezen *et al.* (1994), which showed that the effect of CT on FEC in lambs grazing *Lotus* spp and *Hedysarium coronarium* (Sulla), persisted for a short period (21 - 42 days). It has been suggested that feeding plants containing CT might reduce the effect of parasitism by increasing the post ruminal availability of dietary protein, and as a result affect the establishment or persistence of gastrointestinal nematodes (Niezen *et al.*, 1993a).

4.5.2.5 *Lamb performance*

4.5.2.5.1 Effects of sward species and sex

Lamb performance results showed a general tendency in favour of ryegrass swards, where lambs had higher wool growth (5 to 8%), liveweight gain (8%), higher carcass weight (7%), and higher GR values (18 - 24%) than lambs from Yorkshire fog swards. However, not all of these differences attained significance (Tables 4.8, 4.9, 4.10, Appendix Tables 4.4, 4.5, 4.6, and Figure 4.5). Wool yields were similar for both swards.

The lamb liveweight gain results of Morton *et al.* (1992) in an autumn comparison, and of the trials carried out during summer by Niezen *et al.* (1993b) and Niezen (1995), comparing perennial ryegrass, Yorkshire fog, tall fescue, and browntop swards grazed to a constant sward height of 5 cm, and of Chestnutt

(1992) observed previously for comparable animals at 6 cm sward height under continuous stocking management, are in agreement with the results of this experiment. In contrast, the above results are not consistent with the findings of other research (Watkin and Robinson, 1974). In the latter experiments, ryegrass and Yorkshire fog swards had similar quality. In this study, the superior intake of lambs grazing on ryegrass swards, particularly at the beginning of the trial, is more likely to be due to the higher dietary OMD found in ryegrass than in Yorkshire fog swards, resulting in a greater liveweight gain. In addition to the better individual lamb performance on ryegrass swards, the stocking rates maintained on ryegrass swards until March were 25% superior to those on Yorkshire fog, suggesting a greater lamb weight gain per hectare for ryegrass swards. The results of Niezen *et al.* (1993b) and Niezen (1995) also support this finding under continuous stocking management.

The information in the literature comparing wool growth of lambs grazing on ryegrass or Yorkshire fog swards appears to be limited to the results of Watkin and Robinson (1974), who found greater fleece weights (5%) in favour of the ryegrass treatment, although differences were not statistically significant.

Lamb sex had no effect on FEC measurements, wool growth and carcass weight, but female lambs had significantly higher liveweight gains, dressing out percentages and GR values than castrated male lambs. This liveweight effect does not follow the expected higher performance in favour of castrated male lambs (Kirton and Morris, 1989). The discrepancy may be related to the unbalanced sex distribution of the group of lambs slaughtered in the final phase of the experiment (March). However, the higher GR values in favour of female lambs are in accordance with the suggestions of Kirton and Morris (1989).

4.5.2.5.2 *Condensed tannins and PEG effects*

Comparative information on the effects of low concentrations of condensed tannins of temperate grasses (< 1% on a DM basis) on lamb performance appears to be restricted to the recent trial published by Terrill *et al.* (1992a).

In general, PEG supplementation had no effect on the animal performance parameters studied. However, after the start of the trial, transitory effects (4 to 5 weeks) of CT on lamb performance were observed in comparisons between PEG and NON-PEG lambs grazing on Yorkshire fog swards. Data for wool growth, liveweight gain, and FEC (Tables 4.7, 4.9 Appendix Table 4.4, and Figure 4.5) all illustrate this effect, but suggest that the low CT concentrations present in the diet of lambs grazing on ryegrass and Yorkshire fog swards were not enough to increase lamb performance in the longer term. Other researchers (Barry, 1985; Lowther and Barry, 1985) observed partial CT adaptation of sheep fed on *Lotus pedunculatus*. Furthermore, Robbins *et al.* (1987b) found some buffering effects of sheep´s saliva against high dietary concentrations of CT. More research is warranted in this area before attempting to draw any general conclusion.

In the December to January period, the unexpected higher wool growth of PEG lambs on ryegrass swards (Appendix Table 4.4) is in agreement with the results of Liu *et al.* (unpublished data). Recently evidence of Niezen *et al.* (1993a) showed significant improvement in body growth rates resulting from PEG administration in lambs grazing on ryegrass swards. These results suggest that there may be an unknown stimulating effect of PEG supplementation to sheep feeding on ryegrass swards and indicates that further investigation is needed to improve our knowledge of the role of PEG in sheep performance.

In contrast with the results of the present experiment, the spring trial of Terrill *et al.* (1992b) indicated that low levels of CT increased lamb liveweight gain (29%) and wool growth (18%). However, the dietary levels of CT reported by Terrill *et al.* (1992b) were higher than those of the present study (0.47% versus 0.2% on a DM basis respectively). The results of this study also imply some degree of superior CT effectiveness in favour of Yorkshire fog, but the higher protein-bound CT values of Yorkshire fog swards in December and the greater protein-bound CT values of ryegrass in January (both NS)(Table 4.3b) do not support this hypothesis. These results are not in agreement with the significantly and consistently higher protein-bound CT percentages found in the initial experiment in favour of Yorkshire fog swards (Section 3.4.2.1, Chapter 3). All the CT concentrations were relatively low, and close to the lower limits of estimation (Terrill *et al.*, 1992a), therefore increasing the probability of lack of repeatability between samples during laboratory analyses. More research is needed in this area to confirm these findings.

The accumulated experimental evidence from this Centre (Experiments 1 and 2, and Liu *et al.*, unpublished data) confirmed the presence of low CT concentrations in perennial ryegrass and proved that this grass is not suitable as a "negative control species" for testing the effect of CT on animal performance. The results of other previously published research in this area, where ryegrass was used as a control treatment without testing the effect of its low CT concentration, must be interpreted with care. The results of the present studies from this Centre, indicate that for future research in this area, it will be necessary to consider the effect of CT in ryegrass on animal performance in order to provide a firmer basis of comparison, and indicate the need for further developmental work to improve definition of causative relationships. Finally, despite the similar concentrations of CT found in the diets of animals on both swards, animal performance data indicate that the relatively small and non-persistent responses to CT appear in some degree to be more consistent in *Holcus* swards than in perennial ryegrass. This effect suggests a possible higher protein-binding capacity of CT in *Holcus* than that of perennial ryegrass, and deserves further study.

4.6 CONCLUSIONS

The better sward structure, sward quality, herbage intake and lamb performance achieved on perennial ryegrass/white clover swards compared with Yorkshire fog/white clover swards in the conditions of the present study appear to indicate that perennial ryegrass/white clover swards growing under high fertility conditions and intensive grazing management have higher feeding value in terms of lamb production and higher stocking rate capacity than Yorkshire fog/white clover swards. However, the moderate difference found in lamb production in favour of perennial ryegrass swards and in the light of recent experimental evidence (Morton *et al.*, 1992) comparing both swards indicate the potential value of Yorkshire fog swards for poorer environments (e.g. in Hill Country Grasslands).

The diet selected by oesophageal fistulated sheep consistently reflected the composition of the upper layers (above 4 cm) of both sward canopies, suggesting that differences in canopy height between legumes and grasses determined their selection by sheep within the sward canopy.

No evidence was found to suggest that the low CT concentrations (≤ 0.2% on a DM basis) of perennial ryegrass and Yorkshire fog species have any influence on the degree of discrimination exhibited by the grazing animal for, or against, plant species or plant components. Further information from this trial provides evidence that these low CT levels have no effect on herbage intake or on grazing behaviour patterns.

The generally small and non persistent effects of CT on animal responses observed in the present study show that CT dietary concentrations of 0.2% on a dry matter basis do not have any direct nutritional benefits to lamb production. More research is necessary to define the minimal effective CT concentration in forage diets to improve ruminant production.

Given the traditional economic relevance of perennial ryegrass to New Zealand farming, this trial poses questions about the importance of CT in perennial ryegrass and the potential for improving the nutritional characteristics and ruminant production potential of the grass by up-grading the levels of CT by either conventional plant breeding techniques or by genetic engineering.

CHAPTER 5

EXPERIMENT 3: A COMPARATIVE STUDY OF HERBAGE INTAKE, INGESTIVE BEHAVIOUR AND DIET SELECTION, AND EFFECTS OF CONDENSED TANNINS UPON BODY AND WOOL GROWTH IN LAMBS GRAZING *HOLCUS LANATUS/TRIFOLIUM REPENS* AND *LOLIUM MULTIFLORUM/TRIFOLIUM REPENS* SWARDS WITH PRESENCE OR ABSENCE OF *LOTUS CORNICULATUS*.

5.1 ABSTRACT

An experiment was carried out from August to early November 1994 to examine differences in diet selection, herbage intake, grazing behaviour, and animal performance between *Lolium multiflorum* (annual ryegrass)/*Trifolium repens* (white clover) and *Holcus lanatus* (Yorkshire fog)/*Trifolium repens* (white clover) swards both with presence or absence of *Lotus comiculatus* (Birdsfoot trefoil) rotationally grazed by lambs. The effects of CT on lamb production were assessed by twice daily oral administration of polyethylene glycol (PEG; Molecular weight 4,000) to half the lambs on each sward combination.

Overall estimates of pre-grazing herbage mass and sward surface height (extended and compressed) for the annual ryegrass and Yorkshire fog swards respectively, were 5840 vs 4360 ± 190 kg DM ha^{-1} ($P < 0.001$), 30 vs 23 ± 0.3 cm ($P < 0.001$), and 15 vs 12 ± 0.2 cm ($P < 0.001$). Pre-grazing proportion of green leaf (73 vs 62 ± 1.4%, $P < 0.01$) was greater for Yorkshire fog than for ryegrass, while that of dead material was greater for annual ryegrass (27 vs 22 ± 0.8%, $P < 0.01$).

The OMD of the diet selected and the herbage intake of lambs grazing on Yorkshire fog swards were higher than those on annual ryegrass (78 vs 74 ± 0.8%; $P < 0.05$, and 1070 vs 860 ± 57 g OM lamb^{-1} day^{-1} respectively), reflecting the higher contents in the diet of grass green leaf (98 vs 93 ± 1.4%, $P < 0.05$) and of legume (0.9 vs 0.4 ± 0.2%, $P < 0.13$) and the lower content of dead material (8 vs 11 ± 1.5%, $P < 0.08$) in favour of Yorkshire fog swards. Similar grazing behaviour patterns were observed between swards. Lambs grazing on Yorkshire fog swards had higher clean wool growth (1470 vs 1280 ± 30 μg cm^{-2} day^{-1}, $P < 0.01$), greater fibre diameter (31 vs 29 ± 0.2 μ, $P < 0.001$) and longer fibre length (25 vs 24 ± 0.5 mm, $P < 0.12$), greater liveweight gains (152 vs 108 ± 5.5 g day^{-1}, $P < 0.001$), final weight (42 vs 38 ± 0.5 kg, $P < 0.001$), carcass weight gains (89 vs 69 ± 2.5 g day^{-1}, $P < 0.001$), carcass weight (19 vs 17 ± 0.3 kg, $P < 0.001$), GR values (11 vs 8 ± 0.5, $P < 0.01$), and lower FEC transformed values (11 vs 9.2 ± 0.4 eggs g fresh faeces^{-1}, $P < 0.01$).

Slightly higher condensed tannins (CT) dietary concentrations were recorded in Yorkshire fog swards than in annual ryegrass (0.420 vs 0.365 ± 0.02% on a DM basis, $P < 0.08$). These low CT levels increased clean wool growth (1440 vs 1310 ± 32 μg cm^{-2} day^{-1}, $P < 0.05$), fibre diameter (30.7 vs 29.5 ± 0.21μ , $P < 0.01$), liveweight gains (141 vs 120 ± 4.3 g lamb^{-1} day^{-1}), although differences in carcass measurements were relatively smaller, and tended to reduce FEC transformed values (9.6 vs 11 ± 0.6 eggs g fresh faeces^{-1}, $P < 0.16$). The effects of CT on animal performance were greater in Yorkshire fog swards. CT had no significant effects on diet selection, herbage intake, and grazing behaviour patterns.

The very small effects of lotus on sward composition, sward structure and on lamb performance were explained by its very low contribution to Yorkshire fog and annual ryegrass swards (1.1 vs 0.5 ± 0.2%, $P < 0.05$ respectively). Time trends had a strong effect in most of the sward and animal variables evaluated.

In conclusion, the results of this study indicate that: (i) under low to moderate soil fertility conditions and lax rotational grazing management, Yorkshire fog swards have better composition and structure for lamb production than annual ryegrass, as a consequence of the early reproductive development in annual ryegrass, (ii) low CT concentrations (range 0.36 to 0.42% on a DM basis) may increase wool production, liveweight gains, carcass weight by 10%, 17%, and 2% respectively, particularly in Yorkshire fog swards, (iii) spring grazing management has a strong influence on sward quality and lamb production.

Keywords: *Lolium multiflorum* (annual ryegrass); *Holcus lanatus* (Yorkshire fog); *Trifolium repens* (White clover); *Lotus corniculatus* (Birdsfoot trefoil); polyethylene glycol (PEG); condensed tannins (CT); diet selection; herbage intake; grazing behaviour; lamb production; spring grazing management.

5.2 INTRODUCTION

The results of the first two grazing experiments (Chapters 3 and 4) indicated that under high fertility conditions (pH 5.7; Olsen-P > 25 - 27 μg/ml; exchangeable K > 0.61 - 0.64 meq/100g; SO_4-S > 4 - 5 μg/g), applying either rotational or continuous grazing managements, the herbage intake and performance of sheep was generally higher on perennial ryegrass/white clover swards than on Yorkshire fog/white clover swards. These findings have been recently supported by other research (Morton *et al.*, 1992; Niezen *et al.*, 1993b; Niezen, 1995; Liu *et al.*, unpublished data). However, taking into account the potential value of *Holcus lanatus* for poorer environments (Haggar, 1976; Watt, 1987; Niezen, 1995), and for control of worm parasites (Niezen *et al.*, 1993b; Niezen, 1995), there is a case for more comparative studies of the species covering a wider range of circumstances.

The similar and low dietary concentrations of condensed tannins (CT) found in oesophageal fistulated sheep grazing on Yorkshire fog and perennial ryegrass swards in Experiments 1 and 2 had small and non-persistent effects on sheep production, particularly in the case of ryegrass. However, taken together with evidence from other studies (Waghom *et al.*, 1990; Terrill *et al.*, 1992a), these findings suggest that further moderate increases in the concentration of CT in those swards by the concentrating effects of nutrient-poor habitats (Lowther *et al.*, 1987) or by the inclusion of species containing higher levels of CT (eg *Lotus comiculatus*) might enhance animal performance. In addition, *Holcus lanatus* and *Lotus comiculatus* are of particular interest for the Basaltic soils in Uruguay. However, there is little quantitative information on herbage intake, diet selection, grazing behaviour and performance of lambs grazing those species.

The trial described in this chapter was conducted in Uruguay, in a low soil fertility location, to evaluate herbage intake, ingestive behaviour, diet selection, internal parasites and animal performance in lambs grazing on *Lolium multiflorum*/white clover or *Holcus lanatus*/white clover swards with presence or absence of *Lotus corniculatus*, with particular reference to the effects of low concentrations of CT on those animal variables between sward combinations.

5.3 MATERIALS AND METHODS

The experimental procedures in the present trial were similar to those used in Experiments 1 and 2 (Chapters 3 and 4 respectively). Only those techniques not used in Experiments 1 and 2 are described in detail here.

5.3.1 Site preparation and management

From August to November 1994, an experiment was conducted at Glencoe Research Unit (latitude 32^0 01' 32" S, 57^0 00' 39" W) of the INIA-Tacuarembó Research Station (INIA), Paysandú State, in an extensive region of basaltic soils in central-north Uruguay, South America.

The mixed swards were sown in April 1994 with annual ryegrass (*Lolium multiflorum* L. cv. 'INIA Estanzuela 284') or Yorkshire fog (*Holcus lanatus* L. cv. 'INIA La Magnolia') both combined with white clover (*Trifolium repens* L. cv. 'INIA Estanzuela Zapicán') with presence or absence of lotus (*Lotus corniculatus* L. cv. 'INIA Estanzuela San Gabriel') in plots of 0.175 ha. The sowing rates were 17, 8, 3.6, 8.4 kg ha^{-1} for ryegrass, Yorkshire fog, white clover and lotus respectively. Pastures were sown on mixed ryegrass-oat stubble cultivated in the previous year for green feed and grain purposes. The predominant soil types on the experimental site were silty clay loam (Typic brown-reddish and black Litosoles), shallower than 50 cm with stone content and slopes ranging from 10 to 25% and 1 to 3% respectively. These soils have low water holding capacity with high drought risk (E.J. Berreta, personal communication).

A soil fertility test performed on the experimental site in March 1993 showed that the original phosphorus status was very low (1.75 ± 0.5 µm/g Resinas-P), with medium to high values of organic carbon (C) and exchangeable potassium (K) (2.9 ± 0.16 g/100g soil and 0.97 ± 0.17 meq/100g soil respectively). The area received an application of 380 kg of Phosphate of Ammonia (18-46-46-0) ha^{-1} in April 1994.

In early June, white clover and lotus species were reseeded at the same rates described above in all sward combinations due to the poor initial legume establishment achieved. Also during June, all sward combinations were grazed down to approximately 5 cm by drenched adult sheep for two days, then left to accumulate herbage.

Annual mean rainfall, evaporation, and temperature records for the Basaltic Region are 1200 mm, 850 mm, and 19ºC respectively, increasing to the north, the mean temperature of the warmest month (January) being 27ºC and for the coldest month (July) being 14ºC (Corsi, 1975). Weather data of the experimental site was assumed to be similar to that of Glencoe Experimental Unit (INIA-Tacuarembó), approximately 1 km distant. The monthly rainfall for the months of August, September, October, and November 1994 was 90, 126, 161, 66 mm respectively, compared with respective averages (6 years) of 77, 77, 96, and 92 mm. The late winter-spring 1994 was considerably wetter than that of long-run rainfall data averages (with the exception of November).

Experimental animals grazed treatment plots for one week before measurements commenced. Additional spare drenched wether sheep were employed principally in ryegrass plots to maintain similar sward surface height and herbage mass between treatments. All animals received orally 5 ml of a phosphorus and magnesium mineral supplement (P-20; Blas Ltd, Uruguay) and water was freely available in each sub-plot during the entire experiment.

5.3.2 Experimental design

The trial was conducted on four 0.7 ha blocks, where each block was divided into four 0.175 ha plots by electric nets (Plate 5.1). The four sward mixtures (ryegrass/white clover/lotus, ryegrass/white clover, Yorkshire fog/white clover/lotus, and Yorkshire fog/white clover) were randomly allocated per block, giving a complete randomised block design (CRB) with four replicates. Plots were further sub-divided into four 438 m^2 sub-plots, which were grazed for periods of 7 days in sequence, resulting in a rotation length of 28 days throughout the experimental period.

Plate 5.1. General view of the experimental area (background) surrounded by the native vegetation of the Basaltic region of Uruguay.

Ninety six castrated Corriedale lambs, approximately 10 months old and mean liveweight 29 ± 3.9 kg at the start of the experiment, were used. The 96 selected lambs were divided randomly into balanced groups of 6 lambs according to fasted initial liveweight and then assigned to the four sward treatments in each block (n = 4). At plot level, six lambs grazed in each sward combination at an equivalent stocking rate of approximately 35 lambs ha^{-1}. Half (n = 3) of the lambs that grazed each plot received a twice daily oral administration (0730 and 1730 hours) of polyethylene glycol (PEG; MW 4,000), whilst the remaining lambs (n = 3) received oral administration of water at the same time. The design of the experiment is shown in Table 5.1.

Table 5.1. Experimental design of the trial.

FACTORS	LEVELS
Grasses/white clover	**Ryegrass/white clover** **Yorkshire fog/white clover**
Lotus presence or absence	**+ Lotus** **- Lotus**
PEG supplementation	**+ PEG** **- PEG**

Based on the previous experience of Terrill *et al.* (1992a,b) of CT concentrations in *Holcus lanatus* and *Lotus corniculatus* and of CT concentration in ryegrass (Experiments 1 and 2), daily doses of PEG of 60 g in 120 ml water and of 20 g in 40 ml water per lamb were used for ryegrass and Yorkshire fog/white clover/lotus treatments and for ryegrass and Yorkshire fog/white clover treatments respectively. An equivalent volume of water was used with control lambs.

5.3.3 Sward measurements

5.3.3.1 *Herbage mass, sward height, and herbage bulk density*

Herbage mass and its botanical composition were estimated monthly by cutting quadrats before and after grazing. Ten 0.1m^2 randomly selected quadrats in each plot were randomly cut to ground level using an electric shearing handpiece. The herbage samples were handled as described in Chapter 3 (Section 3.3.3).

Thirty sward surface height (SSH) readings were recorded before and after grazing in each plot using a common ruler and a Ellinbank rising plate meter (RPM; Earle and McGowan, 1979). Sward surface height measurements were made by taking random sample points in a zig-zag line cross in each experimental plot. These sward height estimates were used to adjust animal numbers. Five readings were also made inside each quadrat when herbage mass samples were collected, giving 50 readings for each plot. The bulk density of the swards before and after grazing was calculated by dividing the herbage mass estimated for each quadrat cut by the corresponding SSH average (mean of 5 readings).

5.3.3.2 *Sward structure*

During September and October, before and after grazing, the vertical distribution of plant tissue within the sward canopy was measured using an inclined point quadrat (Warren Wilson, 1963) set at 32.5º to the horizontal; at least 100 contacts were recorded in each plot every month. Contacts were recorded for species, morphology (leaf, stem, petiole), and state (live and dead). Point quadrat observations were expressed as the number of contacts per 5 cm of sward height and were set out graphically by a computer programme to illustrate the vertical distribution of the various herbage components within the sward profiles.

5.3.3.3 *Tiller population and tiller dissection*

In September, ten tiller cores (diameter = 53 mm) were collected in each plot before grazing. The cores were hand separated into categories of species (ryegrass, Yorkshire fog, white clover, lotus, weeds), the number of units (tillers or nodes) of each group of species was calculated, and the results were expressed as units m^{-2}. In addition, ten tillers were sub-sampled from each of the 10 quadrat cuts taken in each plot during September. These tillers were hand separated into pseudo-stem and grass leaf. The materials in each category were measured (length for grass leaf and grass pseudostem, number of leaves per tiller), dried for 48 hours at 100ºC and then weighed.

5.3.4 Animal measurements

5.3.4.1 *Liveweight gain, carcass weight, dressing out percentage and GR measurements*

Unfasted lamb liveweight was recorded at the commencement of the trial and at the end of each subsequent week. Ten lambs were slaughtered at the commencement of the trial to provide information on carcass characteristics used for further analyses of the carcass measurements of the experimental lambs. At the end of the trial all the lambs were slaughtered and fasted liveweight (24 hours) was recorded prior to slaughter. Hot carcass weight (HCW) was obtained immediately after slaughter. Dressing out percentage was calculated as HCW divided by fasted liveweight (x 100). The total tissue thickness (GR) between the surface of a lamb carcass on the rib at a point 11 cm from the midline in the region of the 12th rib (Kirton, 1989) was measured on both sides of the hot carcass.

5.3.4.2 *Midside wool growth and yield, fibre diameter and length*

Wool growth was estimated as described in Chapter 4 (Section 4.3.4.2). Immediately after sampling, wool samples were store in untied plastic bags for further analysis.

The weight of each greasy midside sample was recorded after conditioning at 20º ± 2 ºC and 65 ± 2 % relative humidity for 48 hours, then samples were scoured using the method described by the Laboratory of S.U.L, Uruguay (personal communication)(Table 5.2).

Table 5.2. Wool scouring procedure (as described by SUL, personal communication).

Bath	Detergent (ml)	Temperature (ºC) ± SEM	Time (min)
1	160	64 ± 3	3
2	90	60 ± 3	3
3	60	55 ± 3	3
4	Cold rinse	50 ± 3	3

During scouring each sample was kept in a terylene mesh bag and passed sequentially through four baths (70 litres each) of inorganic detergents at 29%, remaining 3 minutes in each bath, and squeeze rollers removed excess liquid between bath transfers. After the final bath, samples were oven dried at 105 ºC, and conditioned to standard atmosphere at 20º ± 2 ºC and 65 ± 2 % relative humidity for 48 hours to establish correct moisture regain, and then weighed. The wool yield (%) was calculated as initial wool weight divided by conditioned wool weight multiplied by both 100 and the regain factor (16%), where regain factor is equal to 116 divided by the term 100 + regain (Wet wool weight × 100/Dry wool weight). Clean weight of wool tested was calculated as the product of greasy weight and the yield recorded on a sub-sample of wool from the same midside area (Morris, 1992).

Mean fibre diameter (μm) was estimated on the scoured samples using the Air Flow IWTO 6 technique (S.U.L., personal communication). Ten fibres were taken randomly from each scoured sample to estimate fibre length (mm) using a millimetre ruler (S.U.L., personal communication).

5.3.4.3 *Diet selection and extrusa analyses*

Ten castrated male Corriedale wethers (6 tooth) were fistulated at the oesophagus (OF) in March 1994, and then trained. Only the best eight were used in the present study.

During two-week periods in September and October, four pairs of OF sheep were rotated between blocks and plots on a daily basis in a balanced sequence. One extrusa sample was collected from each animal from each plot using the procedure described in Chapter 3 (Section 3.3.4), so plot and animal effects could be isolated in subsequent analysis of variance. Laboratory analyses of extrusa samples were undertaken for CT and their fractions, OM digestibility (OMD), total N, hemicellulose, cellulose, and lignin. The laboratory procedures were the same as those used in Chapter 3 (Section 3.3.4). Due to the lack of facilities for freeze drying, extrusa samples were oven dried at 50ºC until constant weight.

The botanical composition of the diet selected was assessed by suspending extrusa samples in water in a gridded tray and identifying the proportions of sward components (as a percentage of total contacts) recorded at grid intersections (Clark and Hodgson, 1986).

5.3.4.4 *Organic matter intake and grazing behaviour*

In two-week periods during September and October, organic matter intake (OMI) measurements and grazing behaviour studies were undertaken simultaneously.

Levels of OMI were calculated from estimates of total faecal output and herbage digestibility (obtained from extrusa samples collected from OF sheep) according to procedures described in Chapter 3 (Section 3.3.4). Faecal output was estimated indirectly by the use of intra-ruminal chromium controlled release capsules (65% Cr_2O_3 matrix, CAPTEC New Zealand Ltd, Auckland) as described by Parker *et al.* (1990). Chromium release rates were determined from capsules recovered from 32 lambs (8 per treatment) slaughtered at the end of the trial. Field faecal sampling and chromium laboratory analysis procedures are reported in Chapter 3 (Section 3.3.4). PEG administration (60 or 20 g/day) was deducted from faecal output values prior to calculating OMI, on the assumption that PEG is indigestible by ruminants (Barry and Duncan, 1984).

Bite weight was estimated with OF animals using the technique of Stobbs (1973a,b) in each plot in the middle of each grazing period during OMI measurements. Two grazing behaviour studies during daylight hours (defined as 0630 to 2030 hours) were carried out on intact lambs during each faecal collection period and during each study estimates of rate of biting were made using the 20-bite technique (Jamieson and Hodgson, 1979) at daybreak, and after morning and afternoon PEG dosing. Further detailed information of the grazing behaviour techniques used in the present study are provided in Chapter 3 (Section 3.3.4). Only two blocks per treatment were observed in each grazing behaviour study, given the constraints of recording more than 32 lambs by one observer each 15 minute interval and of visual difficulties related to the topography of the experimental site.

5.3.4.5 *Faecal egg counts (FEC) and abomasal and intestinal worm burdens measurements*

Before the start of the experiment, all experimental lambs, OF sheep, and spare animals were drenched with Ivermectin (Ivomec, Agroventas Ltd) at 1 ml/4 kg LW to control internal parasites. Faecal egg counts (FEC) were made fortnightly on two lambs per treatment in each plot using a modified McMaster technique (Williamson *et al.*, 1994). It was intended to establish a drenching criterion, when the average FEC of 50% of lambs rose above 1000 eggs per gram in any group (A. Mederos, personal communication).

After slaughter, a parasitic autopsy from 4 lambs per each grass treatment was carried out. Ligatures were made in the abomasum, small intestine, and caecum. After separation of the organs, the abomasum was cut along the great curvature, the contents collected and washed thoroughly in a 5 ℓ container filled with water. A 500 ml sample was taken from the container and a few drops of 10% formalin were added. The same procedure was followed for the small and large intestines (A. Mederos, personal communication). Larvae were classified and counted under stereoscope microscope as described by Ueno *et al.* (1983).

5.3.5 Statistical analyses

The pasture and animal data were analyzed using the statistical package SAS (SAS Institute Inc., 1985), based on a Split-Split-Plot in time design using 4 blocks, with swards as the main plot arranged in a 2 $\times$ 2 factorial structure, grasses (ryegrass/white clover or Yorkshire fog/white clover) being one factor and lotus (presence or absence) the other factor. PEG (CT inactivated or activated) was treated as the split-plot factor, while time was used as the split-split-plot factor. Means are presented with their standard errors (SEM). All data were initially tested for normality and homogeneity of variance. In cases where these assumptions were not valid, data were appropriately transformed.

Liveweight gain and wool data (growth, yield, fibre diameter, fibre length) were adjusted by covariance for initial weight and for initial wool data removed from the midside area of each animal, respectively. An additional group of 10 lambs was slaughtered at the commencement of the trial, and their carcass weights, dressing out percentages and GR measurements were used as a co-variate to further statistically analyse these variables in the 96 test lambs. A point quadrat package (Butler, 1991) was used in the analysis of inclined point quadrat data.

5.4 RESULTS

5.4.1 Soil fertility

A soil fertility test was performed in the experimental area in April 1994 after the initial fertilizer application (Appendix Table 5.1). The levels of the soil fertility parameters evaluated were similar between treatments, with the exception of the higher values of Resinas-P in ryegrass swards than in Yorkshire fog swards. The Olsen-P ($NaHCO_3$; MW 0.5; pH 8.5) method is not recommended for Uruguayan conditions due to significant reduction in the activity of Ca caused by the ion CO_3, releasing part of the phosphate bound to Ca. In general, results from Uruguay show that the Olsen-P gives lower values than Resinas-P or Bray-P methods (A. Moron, personal communication).

5.4.2 Sward measurements

5.4.2.1 *Herbage mass, sward surface height, and herbage bulk density*

The results of estimates of herbage mass, sward height (measured inside quadrat cuts) and sward bulk density are given in Figure 5.1(a,b,c) and Appendix Table 5.2.

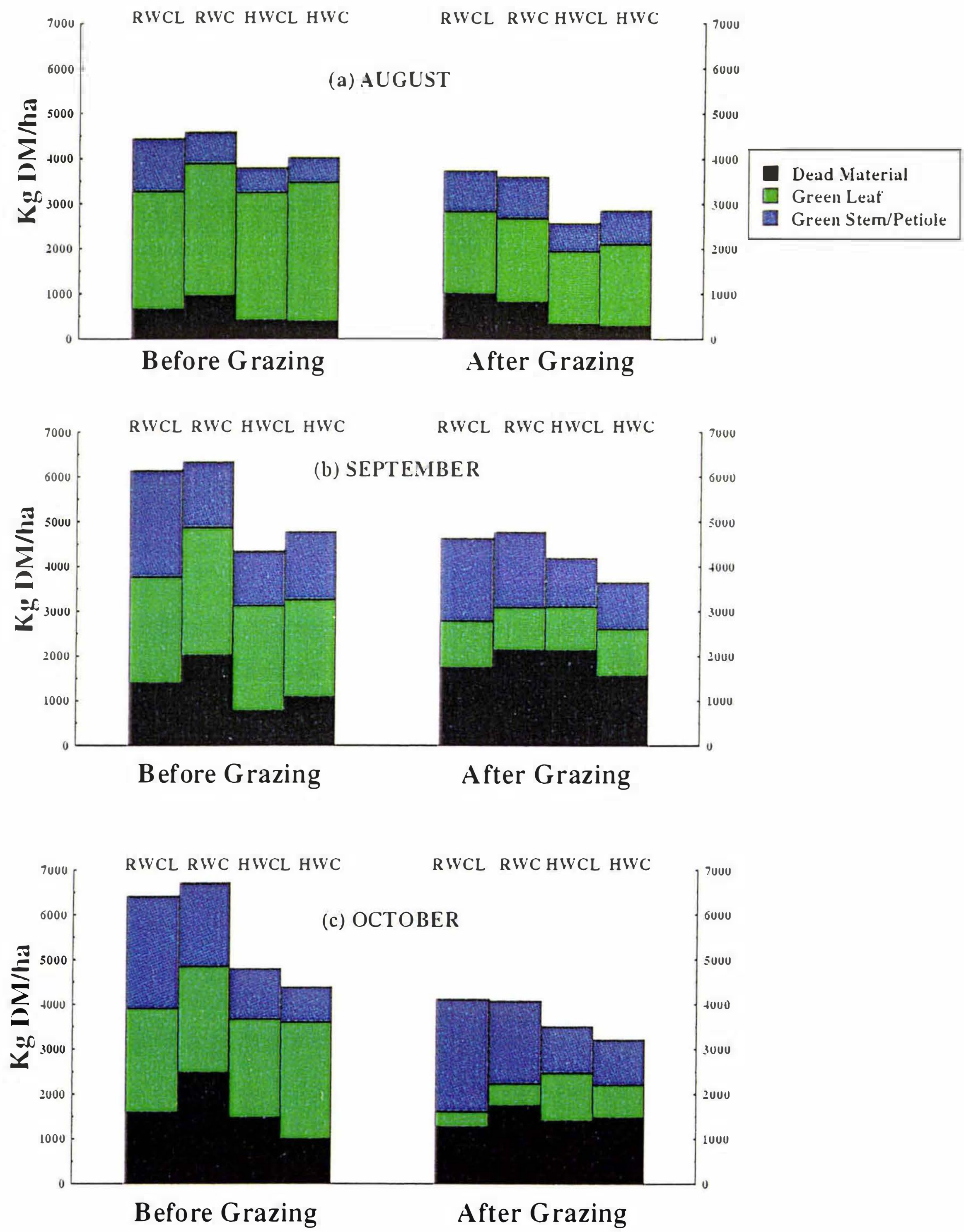


Figure 5.1. Partition of herbage mass into dead material, green leaf and green stem/petiole components for ryegrass and Yorkshire fog swards during August, September, and October before and after grazing.
NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover

The overall herbage mass and sward height inside quadrat cuts, using ruler and rising plate meter, were significantly higher for ryegrass treatments than for Yorkshire fog treatments before and after grazing, while lotus treatments did not have any effect in those sward variables. The pre- and post-grazing herbage mass and sward height inside quadrat cuts for August were significantly lower than those for September and October, which were similar. Pre- and post-grazing sward surface heights measured at plot level by ruler and rising plate meter were higher in August than in September or October (Figure 5.2(a,b) and Appendix Table 5.3). The difference in sward height measured at plot level between grass treatments followed the same trend observed for herbage mass and for sward height measured inside quadrat cuts. Comparing the grass treatments, 30%, 26%, and 13% of the pre-grazing herbage mass of Yorkshire fog treatments was removed during grazing for August, September and October respectively, compared with 8%, 28%, and 35% from ryegrass treatments.

Pre- and post-grazing dead herbage mass was significantly lower for August than for September and October (Appendix Table 5.2). Overall pre-grazing dead herbage mass was significantly greater in ryegrass treatments than in Yorkshire fog treatments, and increased during grazing, in particular, for the Yorkshire fog treatments. As a result, similar post-grazing dead herbage masses were observed in both grass treatments, particularly during September and October. There was no difference in the proportion and amount of dead material between lotus treatments.

Pre- and post-grazing green herbage mass of ryegrass treatments were significantly greater than those of Yorkshire fog treatments. Comparing the grass treatments, 31%, 58%, and 58% of the pre-grazing green herbage mass of Yorkshire fog treatments was removed during grazing for August, September and October respectively, compared with 26%, 40%, and 39% from ryegrass treatments.

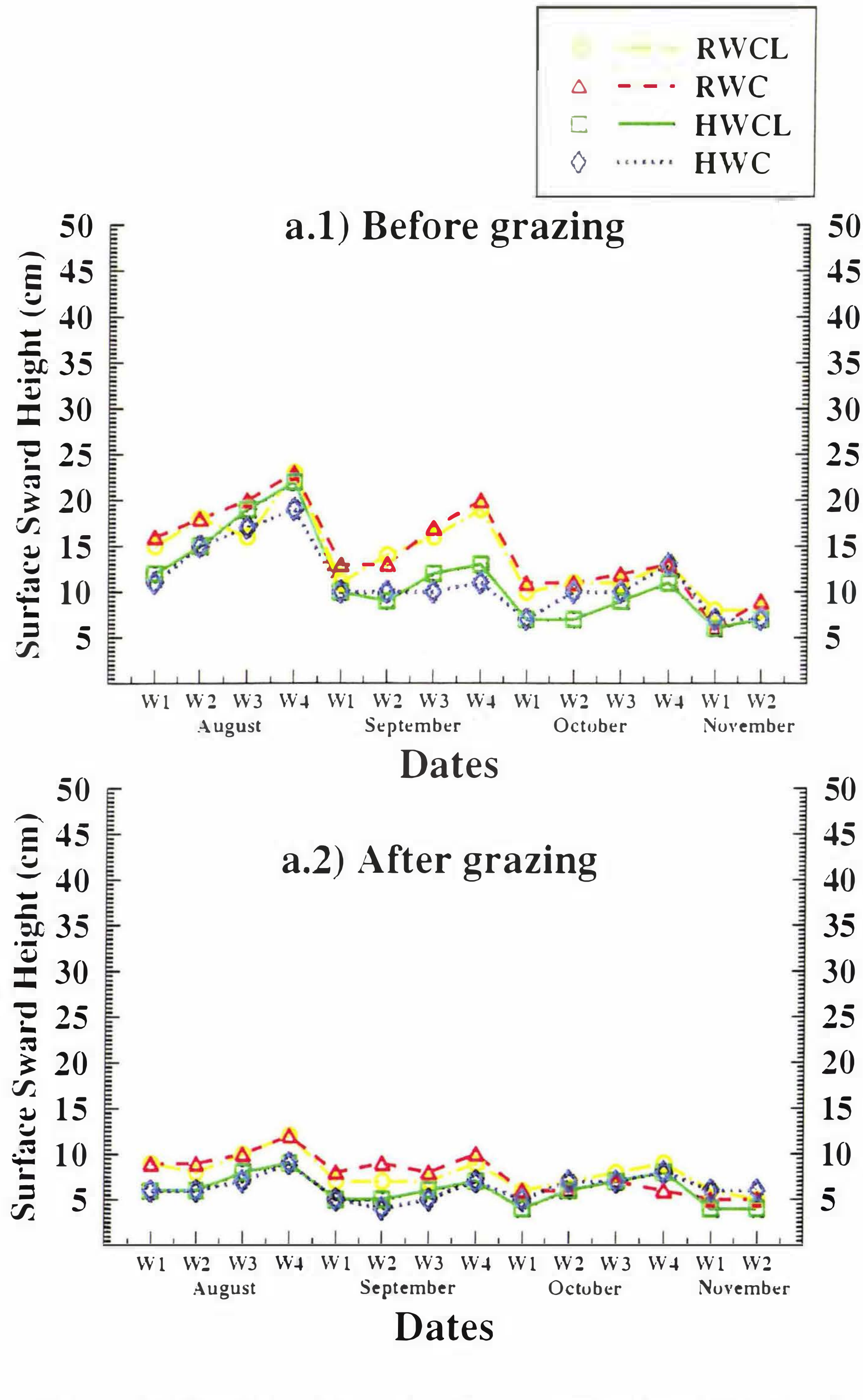


Figure 5.2a. Weekly variation of average sward surface heights (cm) estimated by rising plate meter (RPM) for Yorkshire fog or ryegrass swards before (a.1) and after (a.2) grazing from August to early November.

NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover

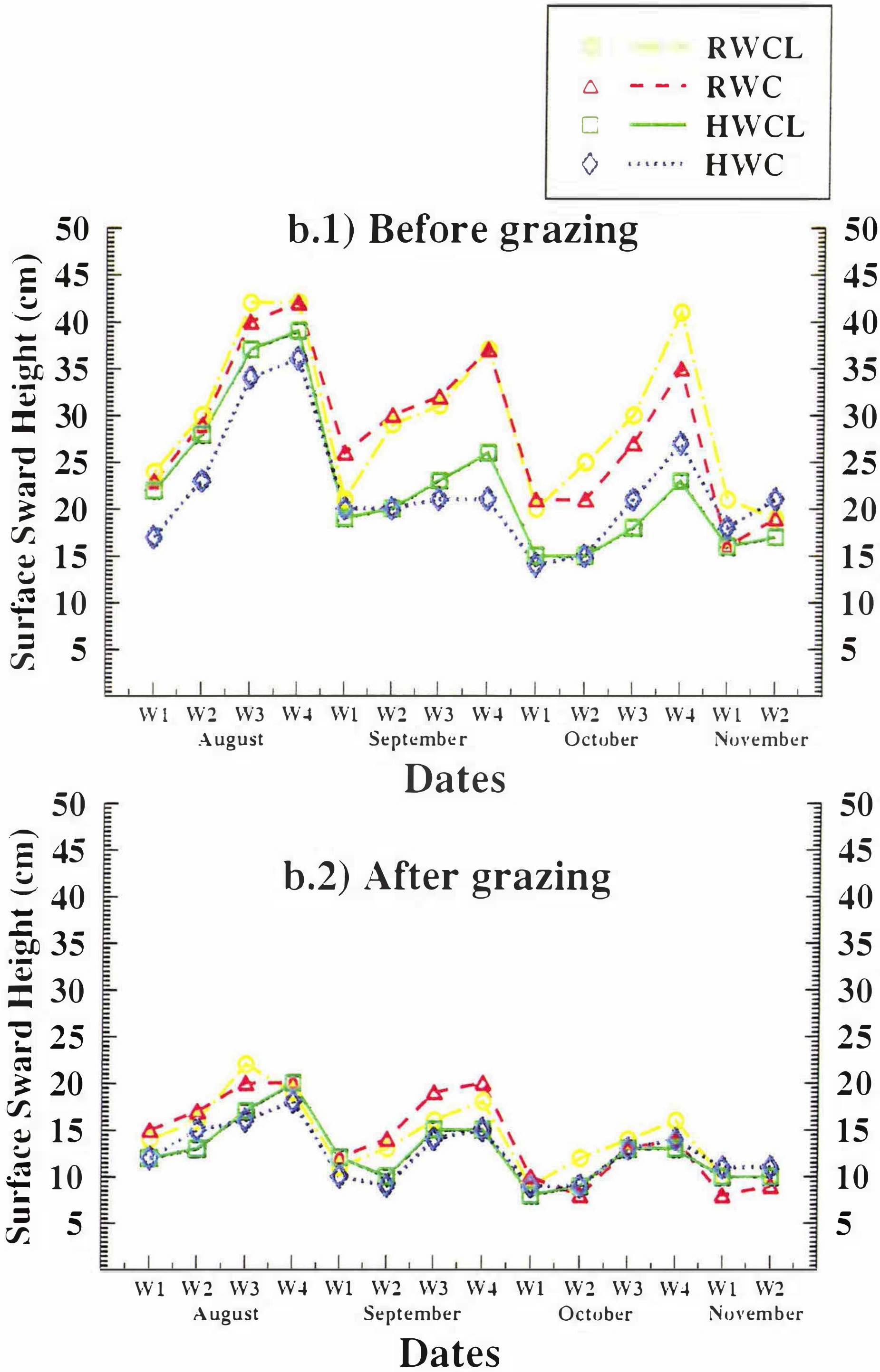


Figure 5.2b. Weekly variation of average sward surface heights (cm) estimated by ruler for Yorkshire fog or ryegrass swards before (b.1) and after (b.2) grazing from August to early November.

NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover

In general, sward and green herbage bulk densities increased over time before and during grazing. Greater pre- and post-grazing sward and green bulk densities were observed in Yorkshire fog swards than in ryegrass swards, either using a ruler or rising plate meter for estimation. However, these differences were much greater for rising plate meter calculations than for ruler estimates. There was no significant differences in either bulk densities between lotus treatments.

5.4.2.2 *Sward components*

Hand separation estimates of the botanical composition of the experimental swards are presented in Table 5.3. Sown grasses formed the major component of both grass treatments before and after grazing. No Yorkshire fog plants appeared in the samples of ryegrass treatments, but ryegrass made a substantial contribution to Yorkshire fog swards. Before and after grazing, the contribution of ryegrass plants to ryegrass and Yorkshire fog swards was greater in August than in September or October, while the contribution of Yorkshire fog plants to Yorkshire fog treatments remained almost constant over time. Sown grass proportions were not significantly affected by the overall effect of lotus treatments.

White clover and lotus proportions were always low. Before and after grazing, there was no significant difference in the proportion of white clover amongst grass and lotus treatments. White clover proportion decreased during grazing in all treatment combinations. Over time, the highest pre-grazing proportion of white clover was recorded in September, and similar proportions were recorded between August and October. The proportion after grazing decreased significantly over time, but to a greater extent in Yorkshire fog swards.

The overall pre-grazing proportion of lotus plants was significantly higher for Yorkshire fog swards than for ryegrass swards, but after grazing there was no significant difference between swards.

	BEFORE GRAZING										AFTER GRAZING									
MONTHS	GRASS × LOTUS					OVERALL EFFECTS					GRASS × LOTUS					OVERALL EFFECTS				
AUGUST	Ryegrass		Yorkshire fog			GRASS					Ryegrass		Yorkshire fog			GRASS				
	+ L[1]	- L	+ L	- L	SEM[‡]	Ryegrass	Yorkshire fog	SEM	Sig.[§]		+ L	- L	+ L	- L	SEM	Ryegrass	Yorkshire fog	SEM	Sig.	
Ryegrass	83	74	40	31	4.0	69	25	1.8	***		72	77	40	24	5.6	65	25	2.8	***	
Yorkshire fog	0	0	40	55	3.0	0	46	1.6	***		0	0	39	61	3.9	0	37	1.5	***	
White clover	1	1	1	3	1.5	2.4	3	1.1	NS		0.3	0.8	1.8	3	0.5	0.2	0.2	0.3	NS	
Lotus	0.5	0	6	0	0.8	0.5	1.1	0.2	*		0.3	0	3.2	0	0.3	0.1	0.7	0.2	NS	
Weeds	0	4	2	2	1.2	0.6	1.5	0.4	NS		0.3	0	3	2.5	0.8	0	1.5	0.3	*	
Dead material	15	21	11	10	2.7	27	22	0.8	**		27	23	13	10	4.5	34	34	2.3	NS	
Green leaf	69	81	84	85	5.0	62	73	1.4	**		35	67	72	71	5.4	40	56	2.6	**	
SEPTEMBER	Ryegrass		Yorkshire fog			LOTUS					Ryegrass		Yorkshire fog			LOTUS				
	+ L	- L	+ L	- L	SEM	+ L	- L	SEM	Sig.		+ L	- L	+ L	- L	SEM	+ L	- L	SEM	Sig.	
Ryegrass	62	66	30	27	4.0	49	46	1.8	NS		61	55	13	25	5.6	46	44	2.8	NS	
Yorkshire fog	0	0	48	38	3.0	24	23	1.6	NS		0	0	35	29	3.9	18	19	1.5	NS	
White clover	5	2	2	9	1.5	2.4	3	1.1	NS		0.3	0	0.3	0.3	0.5	0.6	0.8	0.3	NS	
Lotus	1	0	0.5	0	0.8	1.6	0	0.2	***		0.3	0	0.3	0	0.3	0.8	0	0.2	*	
Weeds	0	0	1	2	1.2	0.9	1.2	0.4	NS		0	0	0.3	2.8	0.8	0.6	0.9	0.3	NS	
Dead material	23	32	18	23	2.7	22	24	0.8	NS		38	45	51	43	4.5	33	35	2.3	NS	
Green leaf	50	66	66	59	5.0	64	67	1.4	NS		36	36	47	50	5.4	48	48	2.6	NS	
OCTOBER	Ryegrass		Yorkshire fog			INTERACTIONS					Ryegrass		Yorkshire fog			INTERACTIONS				
	+ L	- L	+ L	- L	SEM	G×L	T	T×G	T×L	T×G×L	+ L	- L	+ L	- L	SEM	G×L	T[2]	T×G	T×L	T×G×L
Ryegrass	68	63	11	13	4.0	NS	***	*	NS	NS	69	57	24	27	5.6	NS	**	NS	NS	*
Yorkshire fog	0	0	55	42	3.0	NS	NS	NS	**	**	0	0	36	27	3.9	NS	**	**	*	*
White clover	5	0	0.5	3	1.5	NS	*	NS	NS	NS	0	0	1	0.8	0.5	NS	**	NS	NS	NS
Lotus	2	0	0.5	0	0.8	*	*	**	*	**	0.3	0	0	0	0.3	NS	**	**	**	**
Weeds	0	0	2	0	1.2	NS	NS	NS	NS	NS	0	0	0	0.3	0.8	NS	NS	NS	NS	NS
Dead material	25	37	31	23	2.7	NS	***	***	NS	NS	31	43	40	46	4.5	NS	***	**	NS	NS
Green leaf	48	56	66	77	5.0	***	**	**	NS	NS	12	21	51	42	5.5	NS	***	NS	NS	NS

SEM[‡] = Standard error of the mean.
Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1]L = Lotus.
[2]T = Time.
Number of observations contributing to the mean for main effects (n = 16), and interactions (n = 8).

AUGUST

MONTHS	BEFORE GRAZING: GRASS × LOTUS, Ryegrass + L[1]	- L	Yorkshire fog + L	- L	SEM[‡]	OVERALL EFFECTS: GRASS, Ryegrass	Yorkshire fog	SEM	Sig.[§]	AFTER GRAZING: GRASS × LOTUS, Ryegrass + L	- L	Yorkshire fog + L	- L	SEM	OVERALL EFFECTS: GRASS, Ryegrass	Yorkshire fog	SEM	Sig.
Ryegrass	83	74	40	31	4.0	69	25	1.8	***	72	77	40	24	5.6	65	25	2.8	***
Yorkshire fog	0	0	40	55	3.0	0	46	1.6	***	0	0	39	61	3.9	0	37	1.5	***
White clover	1	1	1	3	1.5	2.4	3	1.1	NS	0.3	0.8	1.8	3	0.5	0.2	0.2	0.3	NS
Lotus	0.5	0	6	0	0.8	0.5	1.1	0.2	*	0.3	0	3.2	0	0.3	0.1	0.7	0.2	NS
Weeds	0	4	2	2	1.2	0.6	1.5	0.4	NS	0.3	0	3	2.5	0.8	0	1.5	0.3	*
Dead material	15	21	11	10	2.7	27	22	0.8	**	27	23	13	10	4.5	34	34	2.3	NS
Green leaf	69	81	84	85	5.0	62	73	1.4	**	35	67	72	71	5.4	40	56	2.6	**

SEPTEMBER

MONTHS	BEFORE GRAZING: GRASS × LOTUS, Ryegrass + L	- L	Yorkshire fog + L	- L	SEM	OVERALL EFFECTS: LOTUS, + L	- L	SEM	Sig.	AFTER GRAZING: GRASS × LOTUS, Ryegrass + L	- L	Yorkshire fog + L	- L	SEM	OVERALL EFFECTS: LOTUS, + L	- L	SEM	Sig.
Ryegrass	62	66	30	27	4.0	49	46	1.8	NS	61	55	13	25	5.6	46	44	2.8	NS
Yorkshire fog	0	0	48	38	3.0	24	23	1.6	NS	0	0	35	29	3.9	18	19	1.5	NS
White clover	5	2	2	9	1.5	2.4	3	1.1	NS	0.3	0	0.3	0.3	0.5	0.6	0.8	0.3	NS
Lotus	1	0	0.5	0	0.8	1.6	0	0.2	***	0.3	0	0.3	0	0.3	0.8	0	0.2	*
Weeds	0	0	1	2	1.2	0.9	1.2	0.4	NS	0	0	0.3	2.8	0.8	0.6	0.9	0.3	NS
Dead material	23	32	18	23	2.7	22	24	0.8	NS	38	45	51	43	4.5	33	35	2.3	NS
Green leaf	50	66	66	59	5.0	64	67	1.4	NS	36	36	47	50	5.4	48	48	2.6	NS

OCTOBER

MONTHS	BEFORE GRAZING: GRASS × LOTUS, Ryegrass + L	- L	Yorkshire fog + L	- L	SEM	INTERACTIONS: G×L	T	T×G	T×L	T×G×L	AFTER GRAZING: GRASS × LOTUS, Ryegrass + L	- L	Yorkshire fog + L	- L	SEM	INTERACTIONS: G×L	T[2]	T×G	T×L	T×G×L
Ryegrass	68	63	11	13	4.0	NS	***	*	NS	NS	69	57	24	27	5.6	NS	**	NS	NS	*
Yorkshire fog	0	0	55	42	3.0	NS	NS	NS	**	**	0	0	36	27	3.9	NS	**	**	*	*
White clover	5	0	0.5	3	1.5	NS	*	NS	NS	NS	0	0	1	0.8	0.5	NS	**	NS	NS	NS
Lotus	2	0	0.5	0	0.8	*	*	**	*	**	0.3	0	0	0	0.3	NS	**	**	**	**
Weeds	0	0	2	0	1.2	NS	NS	NS	NS	NS	0	0	0	0.3	0.8	NS	NS	NS	NS	NS
Dead material	25	37	31	23	2.7	NS	***	***	NS	NS	31	43	40	46	4.5	NS	***	**	NS	NS
Green leaf	48	56	66	77	5.0	***	**	**	NS	NS	12	21	51	42	5.5	NS	***	NS	NS	NS

SEM[‡] = Standard error of the mean.
Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1]L = Lotus.
[2]T = Time.
Number of observations contributing to the mean for main effects (n = 16), and interactions (n = 8).

There were no lotus plants in the experimental sward before and after grazing in - lotus treatments. In both grass treatments, the presence of lotus decreased during grazing, but to a greater extent in + lotus Yorkshire fog treatment, particularly during September and October.

Weeds were a minor component of the experimental swards, and before grazing they were not significantly affected by grass or lotus treatments. However, after grazing the proportion of weeds was higher in Yorkshire fog treatments than in ryegrass treatments, and remained constant for lotus treatments.

Overall, before grazing, ryegrass swards had significantly higher proportions of dead material than Yorkshire fog swards. Dead material increased during grazing and also tended to increase over time in all treatment combinations, but to a greater extent in the case of Yorkshire fog swards.

Before and after grazing, the proportion of green leaf was significantly greater for Yorkshire fog swards than for ryegrass swards. This component decreased over time in ryegrass treatments, while small changes occurred for Yorkshire fog treatments before and after grazing (Table 5.3 and Figure 5.1), whereas the proportion of green stem was always higher for ryegrass swards before and after grazing. Lotus treatments did not have a significant effect on this component.

5.4.2.3 *Tiller dissection and tiller population*

Pre-grazing results of tiller population density estimates carried out in September 1994 indicate that tiller density of ryegrass in ryegrass swards was higher than that of Yorkshire fog in Yorkshire fog swards. Ryegrass tillers made an important contribution to the population of Yorkshire fog swards (Appendix Table 5.4), but the contribution of Yorkshire fog tillers in ryegrass swards was insignificant. There was no significant difference in ryegrass tillers between lotus treatments. However, Yorkshire fog tiller density was significantly higher in - lotus treatment than in + lotus treatment. White clover nodes contributed similarly to Yorkshire fog and ryegrass swards and to + lotus and - lotus swards. Lotus nodes maintained a similar population density in both grass treatments, while lotus nodes were absent in - lotus treatment. The population density of weeds in Yorkshire fog swards and - lotus treatment tended to be higher than in ryegrass swards ($P < 0.08$) and + lotus treatment respectively. Total unit populations in grass treatments were very similar. However, the total population density of tillers and nodes was significantly higher in the + lotus treatment than in the - lotus treatment.

In September 1994, pre-grazing data of tiller dissection showed that mean ryegrass pseudostem length per tiller tended to be greater than that of Yorkshire fog ($P < 0.06$; Appendix Table 5.5), while stem weight per tiller did not differ significantly between grass treatments. Yorkshire fog tillers tended to have higher leaf number per tiller ($P < 0.06$) than ryegrass tillers. Leaf weight and leaf length per leaf was similar for both grass treatments. Tiller and node dissection results were similar for + lotus and - lotus treatments.

5.4.2.4 *Sward structure*

The results of estimates of the botanical composition of the swards made by point quadrat measurements indicate that sown grasses formed the major components of both Yorkshire fog and ryegrass swards, although there was an important contribution of ryegrass in *Holcus* swards. In September and October, the proportions of green material, green leaf, white clover, lotus and weeds were all higher in Yorkshire fog swards than in ryegrass swards before and after grazing, while the proportion of dead material and green stem were higher in ryegrass swards (Appendix Figures 5.1 and 5.2). In September, ryegrass contributed in greater proportion to the green component in Yorkshire fog swards, particularly before grazing. However, in October, after grazing, ryegrass made a similar contribution to dead and green components in Yorkshire fog swards. Dead stem contributed to the whole sward profile in a greater proportion in ryegrass swards than in Yorkshire fog swards, in particular after grazing and during October.

Details of the vertical distribution of plant components and their proportions in the sward profiles derived from point quadrat studies during September and October are given in Figures 5.3, 5.4, and in Figures 5.5 and 5.6 respectively. In both swards, recorded hits were concentrated at the base of the swards (below 20 cm height), where most of the dead material and green stem were located. However, higher numbers of hits of dead material and green stem above 20 cm height were recorded in ryegrass swards than in Yorkshire fog swards during September and October, but to a greater extent in October. Live leaf lamina was the major component of the uppermost layers (from 20 to 65 cm) of both grass swards, particularly in Yorkshire fog swards. In general, stem frequency increased substantially from the top to the bottom in both sward canopies, but higher proportions of dead and green stems were recorded in the uppermost layers of ryegrass swards than in Yorkshire fog swards. In September, similar proportions of green ryegrass stem and leaf were recorded in the uppermost layers of Yorkshire fog swards, but in October, recorded hits of green ryegrass stem were higher than those of green ryegrass leaf in the same swards. In both September and October, greater numbers of hits of white clover, lotus, and weeds were recorded in Yorkshire fog swards than in ryegrass swards, and were distributed lower in the canopy of ryegrass swards than Yorkshire fog swards. The proportions of white clover and lotus in the entire sward canopy decreased during grazing in both swards and in both sampling periods, but the reduction was greater in Yorkshire fog swards and in October. Clover petioles and lotus stems were distributed higher in Yorkshire fog swards than in ryegrass swards. No lotus contacts appeared in either grass treatment without the presence of lotus.

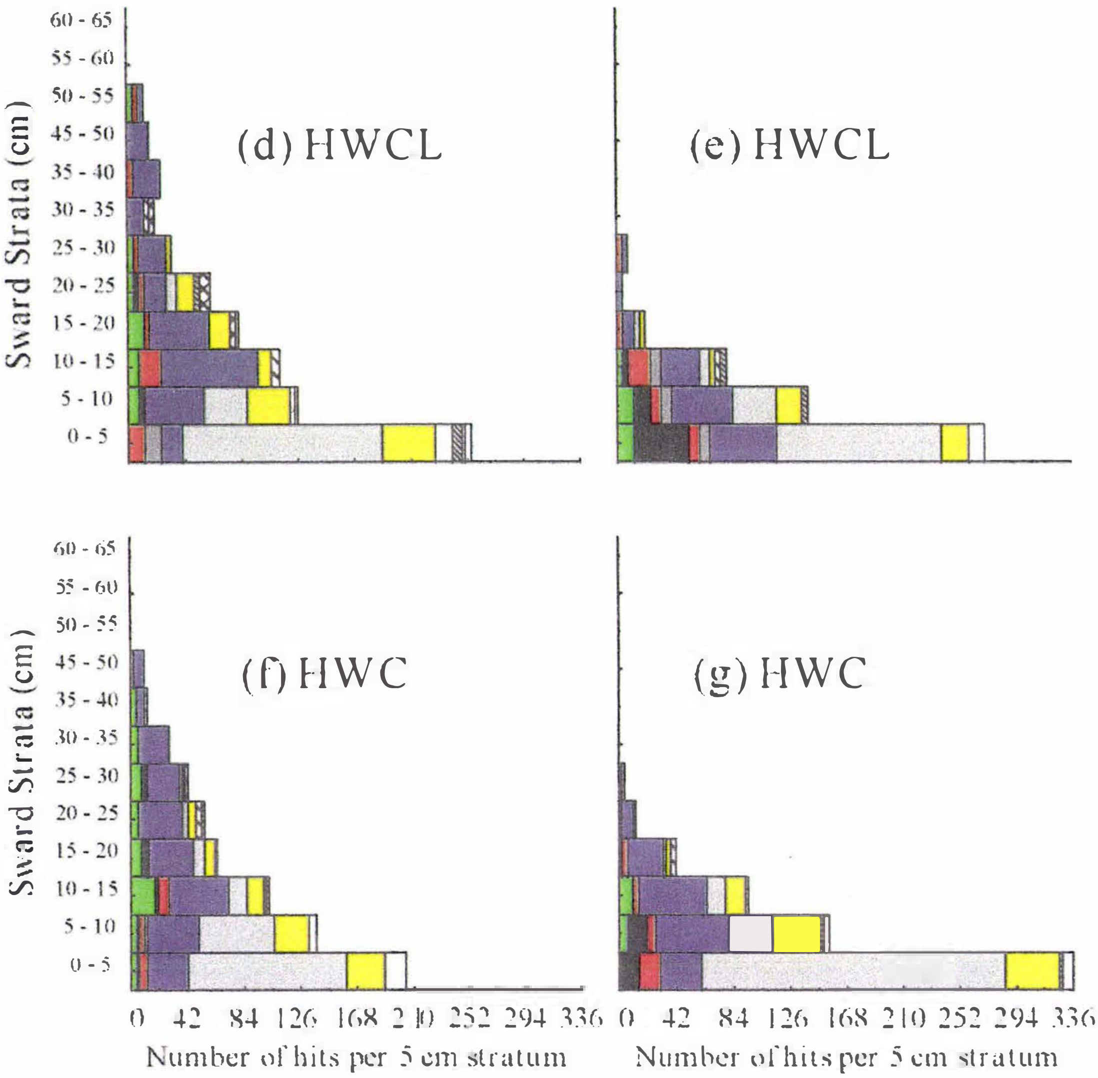
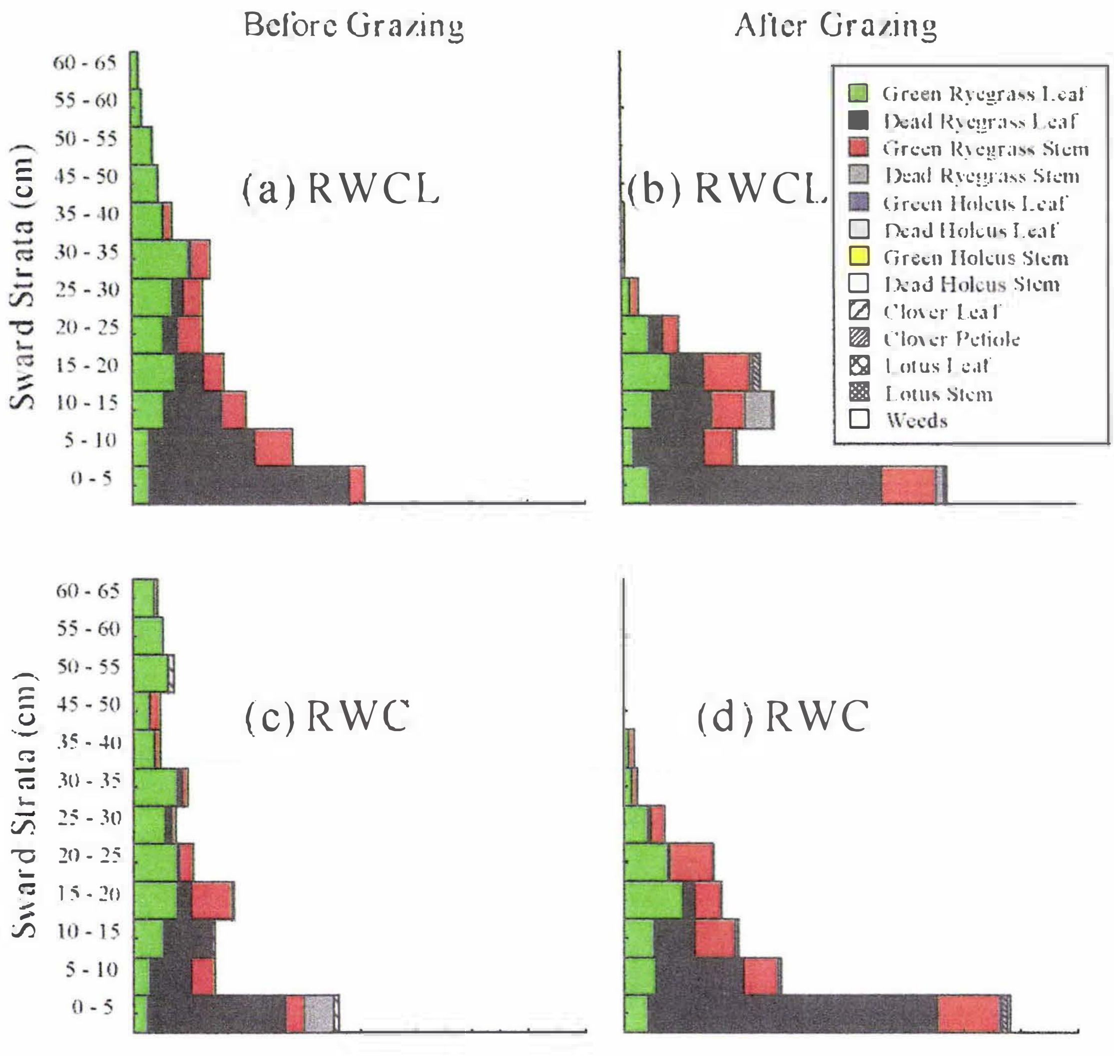


Figure 5.3. Proportional distribution of plant species and morphology for ryegrass and Yorkshire fog swards during September before and after grazing determined from inclined point quadrat contacts.

NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover



Before Grazing
After Grazing
Sward Strata (cm)
60 - 65
55 - 60
50 - 55
45 - 50
35 - 40
30 - 35
25 - 30
20 - 25
15 - 20
10 - 15
5 - 10
0 - 5
(a) RWCL
(b) RWCL
(c) RWC
(d) RWC
Green Ryegrass Leaf
Dead Ryegrass Leaf
Green Ryegrass Stem
Dead Ryegrass Stem
Green Holcus Leaf
Dead Holcus Leaf
Green Holcus Stem
Dead Holcus Stem
Clover Leaf
Clover Petiole
Lotus Leaf
Lotus Stem
Weeds

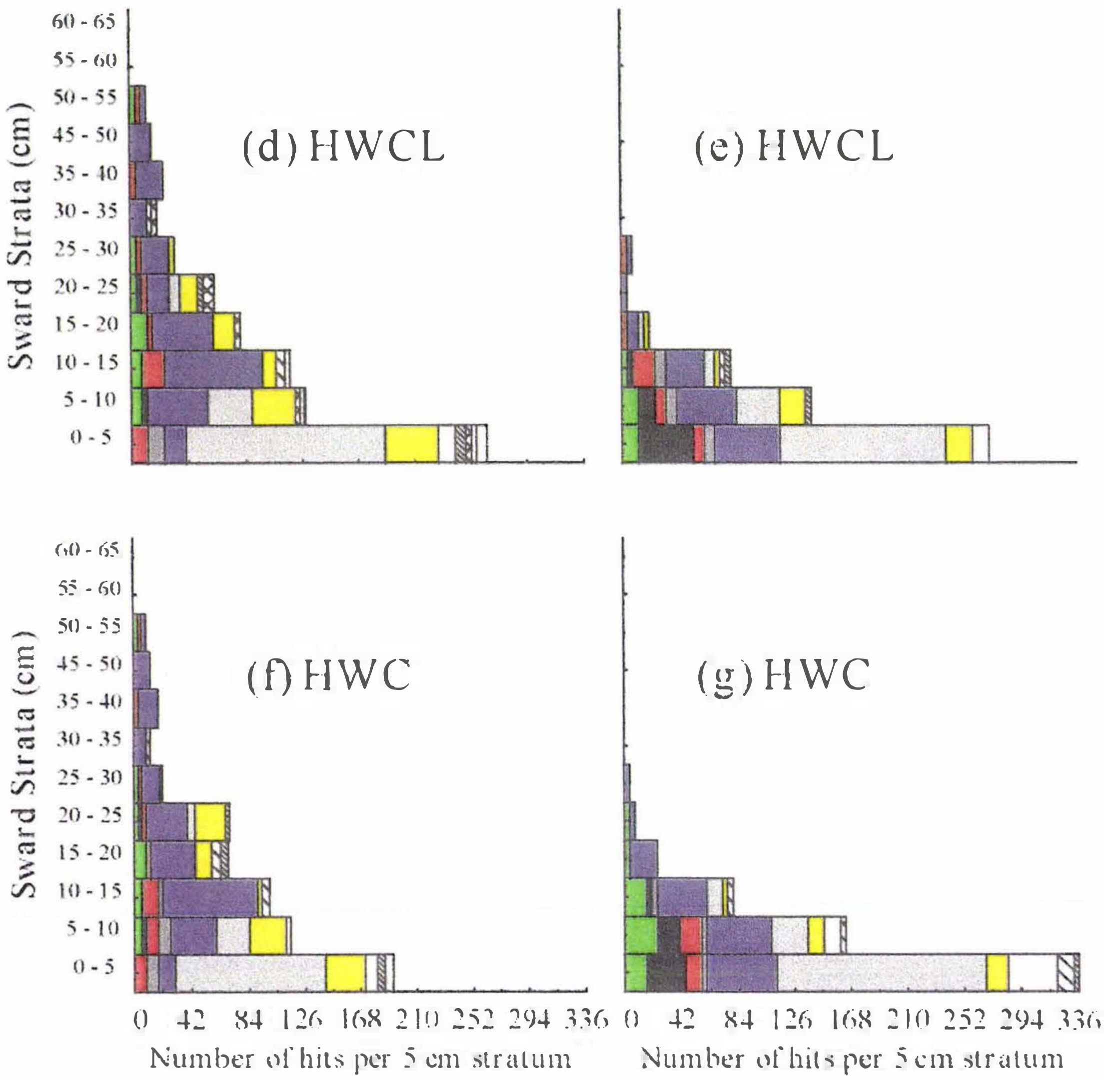
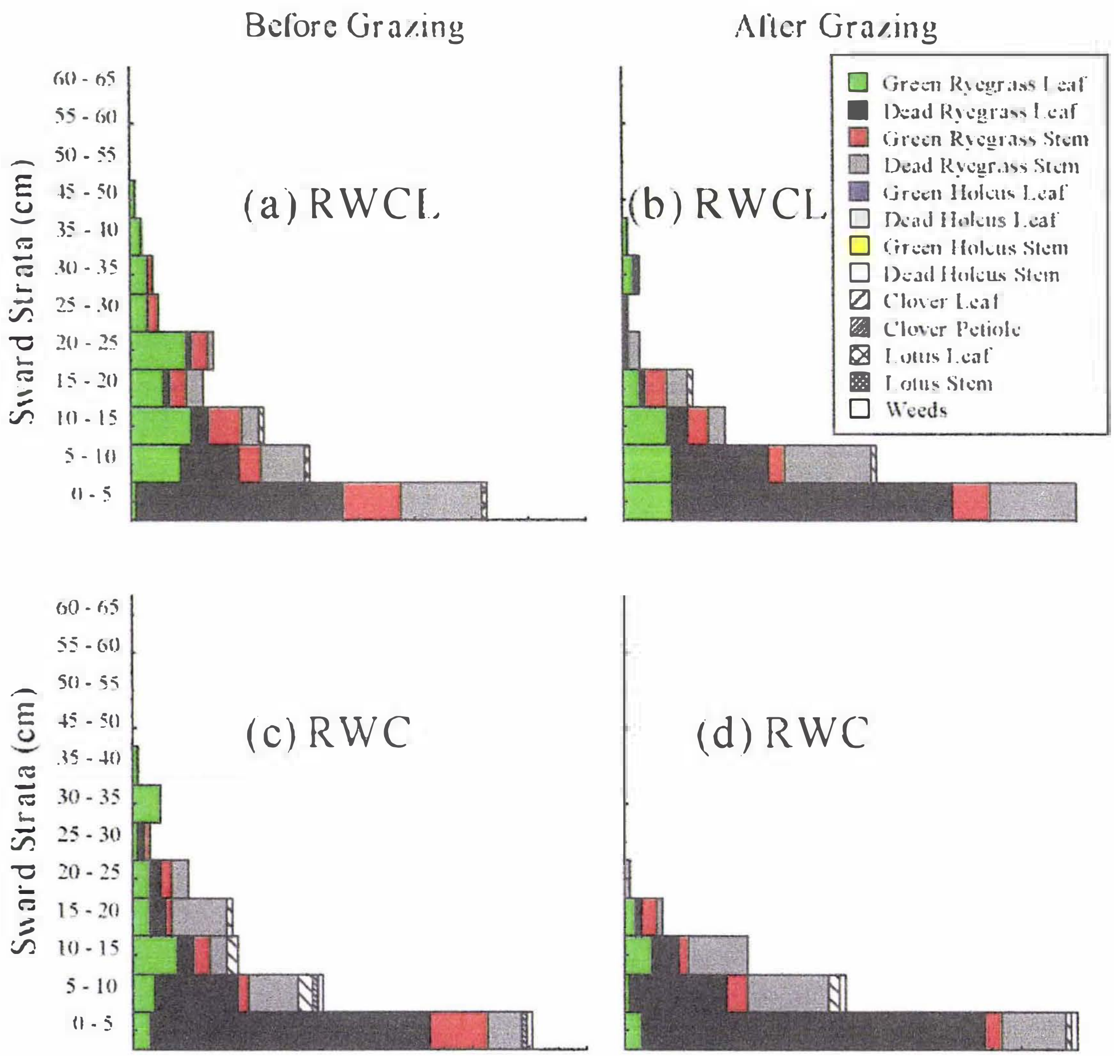


Figure 5.4. Proportional distribution of plant species and morphology for ryegrass and Yorkshire fog swards during October before and after grazing determined from inclined point quadrat contacts.

NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover


Before Grazing
After Grazing
Green Ryegrass Leaf
Dead Ryegrass Leaf
Green Ryegrass Stem
Dead Ryegrass Stem
Green Holcus Leaf
Dead Holcus Leaf
Green Holcus Stem
Dead Holcus Stem
Clover Leaf
Clover Petiole
Lotus Leaf
Lotus Stem
Weeds
Sward Strata (cm)
60 - 65
55 - 60
50 - 55
45 - 50
35 - 40
30 - 35
25 - 30
20 - 25
15 - 20
10 - 15
5 - 10
0 - 5
(a) RWCL
(b) RWCL
(c) RWC
(d) RWC

5.4.3 Animal measurements

5.4.3.1 *Botanical and chemical composition of the diet selected*

Table 5.4 shows the botanical composition of the diet selected by oesophageal fistulated wethers (OF) for ryegrass and Yorkshire fog swards during September and October. As in Trial 2 (Chapter 4) separate identification of grass and legume species was difficult. Leaf lamina and sheath were also not distinguished, so results are compared in terms of green versus dead material, legume versus grass, and green leaf versus green stem.

Grasses made up more than 98% of the diets of OF on both Yorkshire fog and ryegrass swards. The proportion of legume in the ingesta samples of ryegrass treatments tended to be higher than that of Yorkshire fog treatments ($P < 0.13$), the magnitude of this difference being greater in September than in October (Table 5.4). The content of legume was significantly higher in + lotus treatment than - lotus treatment. In both sampling periods, the dead material proportion of ryegrass swards tended to be higher than that of Yorkshire fog swards ($P < 0.08$), while this component was similar between lotus treatments. The botanical composition of extrusa samples also revealed that Yorkshire fog samples were characterised by a significantly smaller proportion of green stem than those of ryegrass swards, while the proportion of green leaf was greater in favour of Yorkshire fog samples. In both sampling periods, similar proportions were observed between lotus treatments in relation to dead material, green stem and green leaf.

Comparisons of the chemical composition of the diet selected in September and October are presented in Table 5.5. The digestibility of the herbage consumed by OF sheep was consistently higher on Yorkshire fog swards than on ryegrass swards, while NDF ($P < 0.07$), ADF, and Lignin were significantly higher on ryegrass swards. Ash content was similar for both grass treatments. Overall total CT ($P < 0.08$) tended to show higher values in the

Table 5.4. Botanical composition of the diet selected by oesophageal fistulated wethers for each sward combination in September, October, and Overall.

MONTHS	GRASS × LOTUS					OVERALL EFFECTS				OVERALL EFFECTS				
SEPTEMBER	Ryegrass		Yorkshire fog			GRASS				INTERACTIONS				
	+ L[1]	- L	+ L	- L	SEM[‡]	Ryegrass	Yorkshire fog	SEM	Sig.[§]	GxL	T[2]	TxG	TxL	TxGxL
Grasses	100	100	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	NS	NS	NS	NS	NS	NS
Legumes	0	0	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	NS	NS	NS	NS	NS	NS
Dead Material	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	[illegible]	NS	NS	NS	NS	NS	NS
Grass green leaf	95	95	99	98.5	2.73	92.8	97.7	1.39	*	NS	*	NS	NS	NS
Grass green stem	5	5	1	1.5	2.73	7.2	2.3	1.39	*	NS	*	NS	NS	NS
OCTOBER	Ryegrass		Yorkshire fog			LOTUS								
	+ L	- L	+ L	- L	SEM	+ L	- L	SEM	Sig.					
Grasses	98.8	99.8	98.2	100	0.78	98.9	99.8	0.22	*					
Legumes	1.2	0.2	1.8	0	0.78	1.1	0.2	0.22	*					
Dead Material	10.7	12.3	9.1	5.7	1.91	10.2	9.5	0.75	NS					
Grass green leaf	92	87.7	95	97.6	2.73	95.4	95.1	1.39	NS					
Grass green stem	8	12.3	5	2.4	2.73	4.6	4.9	1.39	NS					

SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1]L = Lotus.
[2]T = Time.
Number of observations contributing to the mean for main effects (n = 16), and interactions (n = 8).

Table 5.5. Chemical composition (% DM) of the diet selected by oesophageal fistulated wethers for each sward combination in September, October, and Overall.

MONTHS	GRASS × LOTUS					OVERALL EFFECTS				OVERALL EFFECTS				
SEPTEMBER	Ryegrass		Yorkshire fog			GRASS				INTERACTIONS				
	+ L[1]	- L	+ L	- L	SEM[‡]	Ryegrass	Yorkshire fog	SEM	Sig.[§]	G×L	T[2]	T×G	T×L	T×G×L
OM Digestibility	0.76	0.81	0.85	0.77	1.43	0.74	0.78	0.81	*	NS	***	NS	NS	**
NDF	51.4	47.0	45.4	45.5	2.24	49.1	47.0	0.71	NS	NS	NS	NS	NS	NS
ADF	25.0	22.6	19.0	21.3	1.51	24.5	22.8	0.53	*	NS	**	NS	NS	NS
Lignin	2.5	2.5	1.4	1.8	0.21	2.4	1.7	0.10	**	NS	NS	NS	NS	NS
Ash	16.0	15.5	16.2	16.7	0.83	15.6	15.8	0.34	NS	NS	NS	NS	NS	NS
Free tannin	0.088	0.075	0.102	0.095	0.0095	0.082	0.093	0.0054	NS	NS	NS	NS	NS	NS
Protein-bound tannin	0.176	0.143	0.195	0.182	0.0311	0.161	0.198	0.0185	NS	NS	NS	NS	NS	NS
Fibre-bound tannin	0.113	0.120	0.110	0.133	0.0159	0.122	0.129	0.0065	NS	NS	NS	NS	NS	NS
Total condensed tannin	0.377	0.338	0.407	0.410	0.0423	0.365	0.420	0.0206	NS	NS	NS	NS	NS	NS

OCTOBER	Ryegrass		Yorkshire fog			LOTUS			
	+ L	- L	+ L	- L	SEM	+ L	- L	SEM	Sig.
OM Digestibility	0.73	0.68	0.75	0.74	1.43	0.77	0.75	0.81	NS
NDF	47.6	50.5	47.3	50.0	2.24	48.0	48.2	0.71	NS
ADF	25.0	26.3	23.8	27.3	1.51	23.0	24.4	0.53	NS
Lignin	2.3	2.3	1.7	1.8	0.21	2.0	2.1	0.10	NS
Ash	15.5	15.4	15.7	14.8	0.83	15.8	15.6	0.34	NS
Free tannin	0.070	0.095	0.102	0.095	0.0095	0.089	0.085	0.0053	NS
Protein-bound tannin	0.135	0.187	0.192	0.223	0.0311	0.175	0.184	0.0186	NS
Fibre-bound tannin	0.135	0.120	0.143	0.133	0.0159	0.125	0.126	0.0065	NS
Total condensed tannin	0.340	0.402	0.437	0.451	0.0423	0.389	0.395	0.0206	NS

SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1]L = Lotus.
[2]T = Time.
Number of observations contributing to the mean for main effects (n = 16), and interactions (n = 8).

extrusa samples from Yorkshire fog swards than from ryegrass swardsand their fractions, while CT fibre-bound, free tannins and protein-bound tannin were similar between swards. All sward quality variables mentioned above were similar for both lotus treatments. The OMD and ADF values in September were significantly greater than those in October.

5.4.3.2 *Herbage intake and ingestive behaviour*

In December 1993, the effectiveness of the PEG (Salfed Ltd., Uruguay) used in the present trial in binding plant proteins was evaluated in the Nutritional Laboratory of INIA-La Estanzuela (Colonia, Uruguay). Rumen fistulated wethers (n = 3) fed on *Lotus comiculatus* L. 'INIA Estanzuela San Gabriel' receiving three daily oral doses of PEG (20 g each) had a 38% higher concentration of NH_3 in the rumen fluid than those fed on the same legume but without PEG supplementation (110 vs. 71 ± 6 ppm, $P < 0.04$ respectively).

Estimates of herbage intake and mean release rates of Chromium sesquioxide (Cr_2O_3), and results of grazing behaviour studies during September and October are shown in Table 5.6.

Release rates of Cr_2O_3 were very similar in the slaughtered lambs for all treatment combinations. Consequently, a common daily release rate of 187.5 mg Cr_2O_3 was used amongst treatments and periods. In both sampling periods, herbage intakes were significantly higher on Yorkshire fog swards than on ryegrass swards, either expressed as daily intake per lamb ($P < 0.05$) or per unit of metabolic liveweight ($P < 0.07$). The herbage intakes of lambs were not affected by lotus and PEG treatments. Estimates of herbage intake during September were significantly higher than those during October.

Table 5.6. The effects of grass, lotus and PEG administration on the mean release rate of Cr_2O_3 (mg day^{-1}), herbage intake (g OM lamb^{-1} day^{-1} or g OM LW$^{0.73}$ lamb^{-1} day^{-1}), bite weight (mg OM bite^{-1}), rate of biting (bites min^{-1}), grazing time (min), ruminating time (min), and resting time (min) for September, October, and Overall.

GRASS × LOTUS × PEG

SEPTEMBER	Ryegrass + Lotus + PEG	Ryegrass + Lotus - PEG	Ryegrass - Lotus + PEG	Ryegrass - Lotus - PEG	Yorkshire fog + Lotus + PEG	Yorkshire fog + Lotus - PEG	Yorkshire fog - Lotus + PEG	Yorkshire fog - Lotus - PEG	SEM[‡]
Mean Cr_2O_3 release rate	—	—	—	—	—	—	—	—	—
Herbage intake	900	890	1100	1050	1390	1410	1150	1110	118
Herbage intake LW$^{0.73}$	76	71	63	62	78	72	95	96	7.9
Mean bite weight	53		58		59		57		6.1
Rate of biting	72	69	75	78	75	72	78	75	3.0
Grazing time	533	568	535	530	514	542	550	555	23
Ruminating time	173	150	240	245	240	218	220	215	34
Resting time	150	137	80	80	101	96	85	85	18

OCTOBER	Ryegrass + Lotus + PEG	Ryegrass + Lotus - PEG	Ryegrass - Lotus + PEG	Ryegrass - Lotus - PEG	Yorkshire fog + Lotus + PEG	Yorkshire fog + Lotus - PEG	Yorkshire fog - Lotus + PEG	Yorkshire fog - Lotus - PEG	SEM[‡]
Mean Cr_2O_3 release rate[1]	189	191	180	187	188	189	187	188	3.9
Herbage intake	820	790	680	670	910	920	850	840	118
Herbage intake LW$^{0.73}$	45	45	54	54	54	51	57	57	7.9
Mean bite weight[2]	54		48		64		72		6.1
Rate of biting	87	84	90	93	72	81	78	78	3.0
Grazing time[3]	615	631	533	529	518	498	552	492	23
Ruminating time[3]	146	161	195	210	210	238	173	237	34
Resting tima[3]	94	64	128	116	128	120	131	127	18

OVERALL EFFECTS FOR INTERCATIONS	G×L	P×G	P×L	P×G×L	T[4]	T×G	T×L	T×P	T×G×L	T×G×P	T×L×P	T×G×L×P
Mean Cr_2O_3 release rate	NS	NS	NS	NS	—	—	—	—	—	—	—	—
Herbage intake	NS	NS	NS	NS	***	NS	NS	NS	*	NS	NS	NS
Herbage intake LW$^{0.73}$	NS	NS	NS	NS	***	NS	NS	NS	*	NS	NS	
Mean bite weight	NS	—	—	—	NS	NS	NS	—	NS	—	—	—
Rate of biting	NS	NS	NS	NS	***	*	NS	NS	NS	NS	NS	NS
Grazing time	NS	NS	NS	NS	NS	*	NS	NS	NS	NS	NS	NS
Ruminating time	*	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS	NS
Resting time	NS	NS	NS	NS	NS	*	**	NS	*	NS	NS	NS

OVERALL EFFECTS

GRASS	Ryegrass	Yorkshire fog	SEM	Sig.[§]
Mean Cr_2O_3 release rate	187	188	1.9	NS
Herbage intake	860	1070	57	*
Herbage intake LW$^{0.73}$	59	70	3.7	NS
Mean bite weight	53	63	5.5	NS
Rate of biting	81	78	1.8	NS
Grazing time	559	527	19	NS
Ruminating time	190	219	8	NS
Resting time	106	109	14	NS

LOTUS	+ L	- L	SEM	Sig.
Mean Cr_2O_3 release rate	189	186	1.9	NS
Herbage intake	1010	930	57	NS
Herbage intake LW$^{0.73}$	62	67	3.7	NS
Mean bite weight	58	59	5.5	NS
Rate of biting	78	81	1.8	NS
Grazing time	552	534	19	NS
Ruminating time	192	217	8	NS
Resting time	111	104	14	NS

PEG Administration	+ PEG	- PEG	SEM	Sig.
Mean Cr_2O_3 release rate	186	189	2.0	NS
Herbage intake	980	960	12	NS
Herbage intake LW$^{0.73}$	65	63	1.0	NS
Mean bite weight	—	—	—	—
Rate of biting	81	78	0.9	NS
Grazing time	544	543	14	NS
Ruminating time	199	209	13	NS
Resting time	112	103	3	NS

SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
For mean Cr_2O_3 release rate and mean bite weight; main effects (n = 16), and interactions (n = 8). For rate of biting; main effects (n = 24), and interactions (n = 12). For grazing, ruminating, and resting times; main effects (n = 4) and main interactions (n = 2). [1] = Measurements of Cr_2O_3 release rates were taken from 32 lambs slaughtered at the end of the trial (October). [2] = Measurements did not include PEG effects. [3] = Grazing, ruminating and resting activities were recorded during daylight (Between 0630 to 2030 hours). [4]T = Time.

Mean bite weight was greater for Yorkshire fog swards than for ryegrass swards, while there was no significant effect in grazing time and rate of biting between Yorkshire fog and ryegrass swards. No significant differences in any of the grazing behaviour patterns studied were observed between lotus and PEG treatments. Rate of biting and grazing time values were higher in October than in September, but to a greater extent in favour of ryegrass swards. The reverse trend was observed for resting time.

5.4.3.3 *FEC measurements, and abomasal and intestinal worm burdens*

The effects of grass species, lotus and PEG administration on mean FEC values per month are presented in Table 5.7. It was not necessary to drench the lambs in any treatment because FEC values did not reach the described drenching criteria during the entire experiment. The FEC values increased over time, the FEC values of October being significantly higher than those of August or September. Lambs grazing on ryegrass swards had higher overall FEC´s than lambs grazing on Yorkshire fog swards, while FEC´s were similar between lotus treatments. The numbers of eggs recovered from faeces of lambs drenched with water tended to be higher than those drenched with PEG (P < 0.16), and the highest difference between PEG treatments occurred in October.

Abomasal and total worm burdens were significantly higher in lambs grazing on ryegrass swards than on Yorkshire fog swards (Appendix Table 5.6). Most of the abomasal worms in lambs from both swards consisted of *Ostertagia* and *Trichostrongylus* spp., with low numbers of *Haemonchus* spp. Small and large intestinal worm counts also tended to be higher in lambs grazing ryegrass swards compared to those grazing on Yorkshire fog swards. The major small and large intestinal worm species was *Oesophagostomum*, with low numbers of *Trichostrongylus* and *Trichuris* respectively.

Table 5.7. The effects of grass, lotus and PEG administration on mean faecal egg count (FEC; eggs g fresh faeces^{-1}) for August, September, October, and Overall.

GRASS × LOTUS × PEG × MONTHS

MONTHS	Ryegrass				Yorkshire fog				
	+ Lotus		- Lotus		+ Lotus		- Lotus		
	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	SEM‡
AUGUST FEC	75 (8.5)[1]	66 (7.9)	131 (10)	191 (11)	50 (7.1)	106 (8.7)	138 (9.4)	141 (10)	(1.73)
SEPTEMBER FEC	169 (12)	122 (10)	134 (16)	84 (9)	63 (7.7)	59 (7.7)	53 (7.3)	59 (7.5)	(1.73)
OCTOBER FEC	440 (19)	75 (8.5)	325 (10)	272 (15)	256 (13)	225 (13)	147 (11)	59 (7.7)	(1.73)

OVERALL EFFECTS

GRASS	Ryegrass	Yorkshire fog	SEM	Sig.§
FEC	174 (11)	113 (9.2)	(0.4)	**
LOTUS	+ L	- L	SEM	Sig.
FEC	142 (10)	145 (10)	(0.4)	NS
PEG Administration	+ PEG	- PEG	SEM	Sig.
FEC	165 (11)	122 (9.6)	(0.6)	NS

OVERALL EFFECTS FOR INTERACTIONS

	G×L	P×G	P×L	P×G×L	T[2]	T×G	T×L	T×P	T×G×L	T×G×P	T×L×P	T×G×L×P
FEC	NS	NS	NS	NS	***	NS	NS	*	NS	NS	NS	NS

SEM‡ = Standard error of the mean, Sig§. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1] = FEC data was normalized by square root transformation plus 0.5 for analysis (values in brackets).
[2]T = Time.
Number of observationS contributing to the mean each month for main effects (n = 32), and interactions (n = 16).

5.4.3.4 *Greasy and clean wool growth, wool yield, fibre diameter, and fibre length*

Table 5.8 shows the effects of grass, lotus and PEG treatments on wool growth, wool yield, and on fibre diameter and fibre length.

Lambs grazing on Yorkshire fog swards had significantly higher greasy and clean wool growth rates than lambs grazing on ryegrass swards, reflecting a significantly greater fibre diameter ($P < 0.001$) and longer fibre length ($P < 0.12$) in favour of lambs from Yorkshire fog swards, while wool yield was similar for both treatments. All the wool parameters under study tended to be higher for + lotus treatment than for - lotus treatment, but only fibre diameter attained statistical significance ($P < 0.05$). Lambs receiving oral administration of water grew more greasy and clean wool than lambs receiving PEG supplement. This effect in favour of lambs grazing on Yorkshire fog swards was also seen in fibre diameter ($P < 0.01$) and wool yield ($P < 0.09$), but fibre length did not differ significantly between grass treatments. A significant ($P < 0.05$) lotus × PEG interaction reflected the greater greasy and clean wool growth rates from midside areas of NON-PEG lambs grazing + lotus treatment compared to PEG lambs grazing + lotus treatments or compared to PEG and NON-PEG lambs grazing on - lotus treatment. The effect was also observed for fibre diameter. Other significant ($P < 0.05$) grass × lotus × PEG interactions show, in general, that NON-PEG lambs grazing on Yorkshire fog swards with presence of lotus produced more greasy and clean wool growth from midside areas than lambs grazing on the rest of the grass × lotus × PEG combinations. All parameter values were lower in September-October than in August-September, and to a greater extent in the case of NON-PEG lambs grazing on ryegrass swards without presence of lotus.

Table 5.8. The effects of grass, lotus and PEG administration on greasy and clean wool growth from midside areas (μg cm^{-2} day^{-1}), and on wool yield (%), fibre diameter (μ) and fibre length (mm).

PERIODS	GRASS × LOTUS × PEG × MONTHS									OVERALL EFFECTS			
AUG-SEP	Ryegrass				Yorkshire fog					GRASS			
	+ Lotus		- Lotus		+ Lotus		- Lotus						
	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	SEM[‡]	Ryegrass	Yorkshire fog	SEM	Sig.[§]
Greasy wool growth	2060	2160	1920	2000	1970	2420	2270	2320	130	1700	1920	36	**
Clean wool growth	1540	1630	1400	1490	1470	1860	1680	1740	110	1280	1470	30	**
Wool yield	74.3	74.9	73.0	74.8	73.6	76.2	73.9	75.0	1.03	75.8	76.1	0.30	NS
Fibre diameter	28.6	30.4	27.5	28.6	29.4	31.3	28.9	30.4	0.46	29.4	30.8	0.20	***
Fibre length	28.0	32.1	29.7	25.4	28.0	30.1	28.0	31.0	0.93	23.7	24.9	0.50	NS
SEP-OCT	Ryegrass				Yorkshire fog					LOTUS			
	+ Lotus		- Lotus		+ Lotus		- Lotus						
	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	SEM[‡]	+ L	- L	SEM	Sig.
Greasy wool growth	1190	1380	1320	1540	1500	1880	1660	1370	130	1820	1800	36	NS
Clean wool growth	930	1070	1010	1180	1180	1490	1270	1050	110	1400	1350	30	NS
Wool yield	77.7	78.4	76.6	76.9	78.0	78.5	76.7	78.4	1.03	76.4	75.5	0.30	NS
Fibre diameter	29.7	31.1	28.8	30.1	32.3	32.7	30.9	30.8	0.46	30.7	29.5	0.20	**
Fibre length	17.6	20.0	18.3	18.4	20.7	19.9	21.4	19.5	0.93	24.6	23.9	0.50	NS

OVERALL EFFECTS INTERACTIONS	G × L	P × G	P × L	P × G × L	T[1]	T × G	T × L	T × P	T × G × L	T × G × P	T × L × P	T × G × L × P	PEG Administration: + PEG	- PEG	SEM	Sig.
Greasy wool growth	NS	NS	*	*	***	NS	NS	NS	*	NS	NS	NS	1740	1880	38	*
Clean wool growth	NS	NS	*	*	***	NS	NS	NS	*	NS	NS	NS	1310	1440	32	*
Wool yield	NS	NS	NS	NS	***	NS	NS	NS	NS	NS	NS	NS	75.5	76.5	0.37	NS
Fibre diameter	NS	NS	*	NS	***	NS	NS	NS	NS	NS	NS	NS	29.5	30.7	0.21	**
Fibre length	NS	NS	NS	NS	***	NS	NS	NS	NS	**	NS	NS	24.0	24.6	0.45	NS

SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1]T = Time.
Number of observations contributing to the mean each month for main effects (n = 48), and interactions (n = 24).

5.4.3.5 *Liveweight gain and carcass measurements*

Table 5.9 and Figure 5.7 show the liveweight change of the lambs during the entire trial period, while the results of carcass measurements are given in Table 5.10.

Lambs grazing on Yorkshire fog swards grew significantly faster than lambs grazing on ryegrass swards for the entire experimental period ($P < 0.001$) (Appendix Figure 5.3). As a consequence, at the end of the trial, lambs from Yorkshire fog swards were significantly heavier than those from ryegrass swards. These differences were also reflected in heavier carcass weight, higher GR value, and higher carcass gains in favour of lambs grazing on Yorkshire fog swards. Lamb liveweight gains decreased over time in all treatment combinations, resulting in average daily liveweight gains of 212, 112, 70 g day^{-1} for August, September, and October respectively. Dressing out percentages did not differ between swards.

Lamb liveweight change, final liveweight, and all the carcass characteristics measured tended to be higher for + lotus treatment than for - lotus treatment, but none of these differences were significant (Tables 5.9 and 5.10, and Appendix Figure 5.4).

NON-PEG lambs gained significantly more liveweight than PEG lambs during the entire experiment (Tables 5.9 and 5.10, and Appendix Figure 5.5), but the differences being much higher in August and September than in October. There was also a significant ($P < 0.05$) grass $\times$ PEG interaction, which indicated that the difference in lamb liveweight gain between NON-PEG and PEG treatments was greater for Yorkshire fog swards than for ryegrass swards. The same tendency was observed in final liveweight ($P < 0.09$). No significant differences between PEG treatments existed for carcass weight, GR values or dressing out percentages.

Table 5.9. The effects of grass, lotus and PEG administration on lamb liveweight gain (g day^{-1}) in August, September, October, and Overall.

MONTHS	GRASS × LOTUS × PEG × MONTHS								
	Ryegrass				Yorkshire fog				
	+ Lotus		- Lotus		+ Lotus		- Lotus		
	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	SEM[‡]
AUGUST Liveweight gain	170	202	199	164	232	287	197	246	24
SEPTEMBER Liveweight gain	84	113	70	133	112	140	111	133	24
OCTOBER Liveweight gain	50	20	59	34	69	115	87	123	24

OVERALL EFFECTS				
GRASS	Ryegrass	Yorkshire fog	SEM	Sig.[§]
	108	152	5.5	***
LOTUS	+ L	- L	SEM	Sig.
	133	128	5.5	NS
PEG Administration	+ PEG	- PEG	SEM	Sig.
	120	141	4.3	**

OVERALL EFFECTS FOR INTERACTIONS	GxL	PxG	PxL	PxGxL	T[1]	TxG	TxL	TxP	TxGxL	TxGxP	TxLxP	TxGxLxP
Liveweight gain	NS	*	NS	NS	***	NS	NS	NS	NS	NS	NS	NS

SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
[1]T = Time.
Number of observations contributing to the mean each month for main effects (n = 32), and interactions (n = 16).

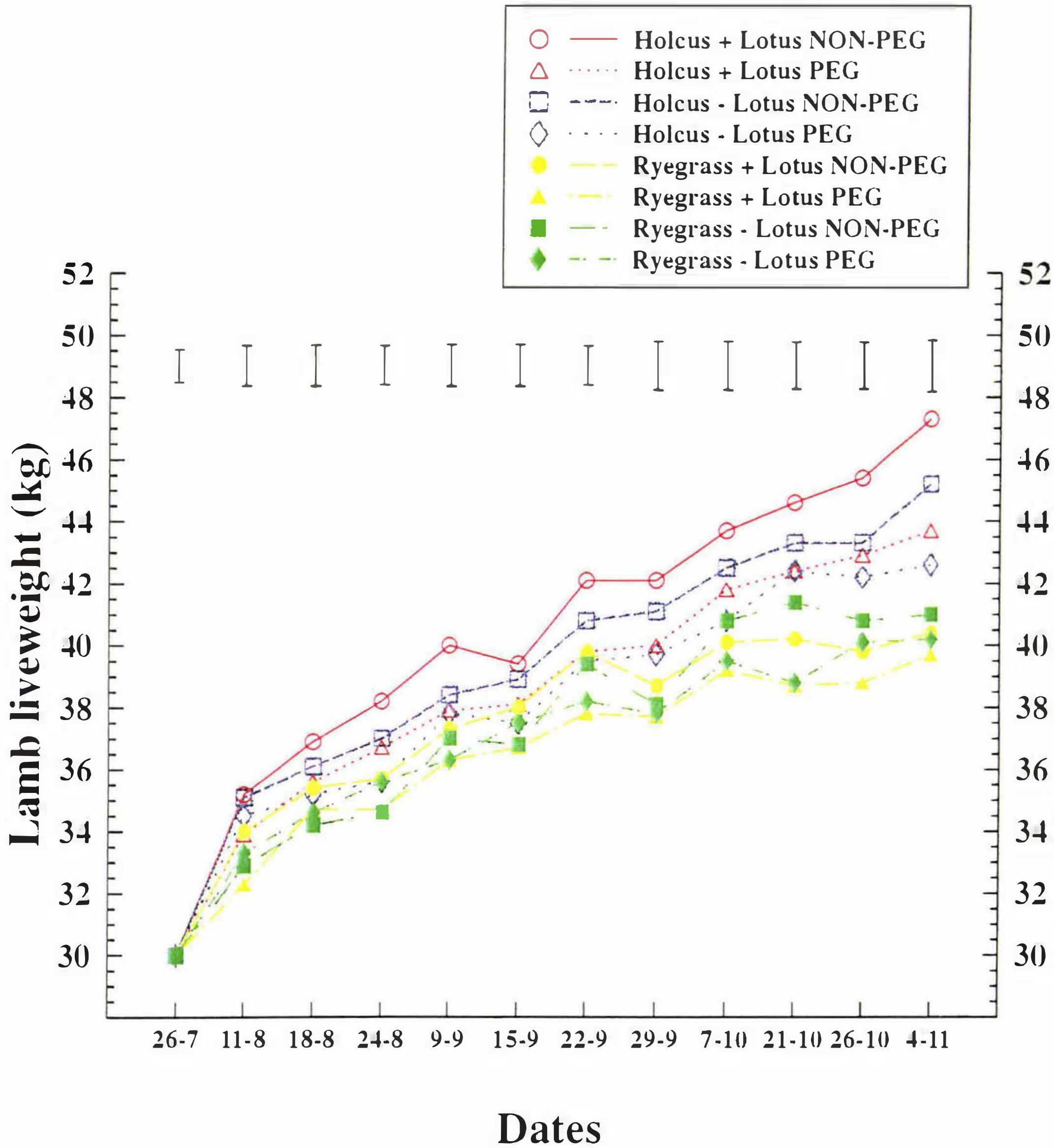


Figure 5.7. The effects of grass species, lotus and PEG administration on lamb liveweight (kg) from August to November. Vertical lines indicate the standard error of the mean.

Table 5.10. The effects of grass, lotus and PEG administration on final liveweight (kg), carcass weight (kg), carcass gain (g lamb^{-1} day^{-1}), GR (mean value of left and right sides, mm), and dressing out (%).

FEATURES	GRASS x LOTUS x PEG									OVERALL EFFECTS			
	Ryegrass				Yorkshire fog					GRASS			
	+ Lotus		- Lotus		+ Lotus		- Lotus						
	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	+ PEG	- PEG	SEM[‡]	Ryegrass	Yorkshire fog	SEM	Sig.[§]
Final weight	37.5	38.8	37.8	38.2	42.5	43.1	41.3	42.8	0.72	38.1	42.4	0.5	***
Carcass weight	16.9	17.5	17.0	16.7	19.2	19.4	18.2	19.2	0.68	17.0	19.0	0.3	***
Carcass gain	67.4	73.0	68.6	66.8	90.6	93.0	81.1	90.4	7.00	68.9	88.8	2.5	***
GR	6.4	9.8	7.6	7.6	12.6	9.7	10.3	10.3	1.20	7.8	10.7	0.5	**
Dressing out	44.7	44.7	45.0	43.8	45.3	45.0	44.2	44.8	1.12	44.6	44.8	0.4	NS

OVERALL EFFECTS FOR INTERACTIONS	G x L	P x G	P x L	G x L x P	LOTUS				PEG Administration			
					+ L	- L	SEM	Sig.	+ PEG	- PEG	SEM	Sig.
Final weight	NS	NS	NS	NS	40.5	40.0	0.5	NS	39.8	40.7	0.4	NS
Carcass weight	NS	NS	NS	NS	18.2	17.8	0.3	NS	17.8	18.2	0.3	NS
Carcass gain	NS	NS	NS	NS	81.0	76.7	2.5	NS	77.0	80.7	3.5	NS
GR	NS	NS	NS	NS	9.6	9.0	0.5	NS	9.2	9.3	0.6	NS
Dressing out	NS	NS	NS	NS	45.0	44.5	0.4	NS	44.8	44.6	0.6	NS

SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).

Number of observations contributing to the mean each month for main effects (n = 48), and interactions (n = 24).

Over the whole experimental period, sheep liveweight output (lamb + spare wethers) per hectare was 28% greater on Yorkshire fog plots than on ryegrass plots (497 vs 389 ± 33 kg ha^{-1}, $P < 0.05$).

5.5 DISCUSSION

There are no comparative studies in the Basaltic region of Uruguay examining sheep performance, herbage intake, and diet selection between *Holcus* and annual ryegrass swards under similar circumstances to the present study. The sole recent report by Bemhaja (1993) was orientated towards sandy soil conditions.

5.5.1 Evaluation of sward results

5.5.1.1 *Herbage mass, surface sward height, sward bulk density, and sward composition*

Estimates of the botanical composition of the experimental swards were derived from hand separation and point quadrat techniques. Although the results from the two sampling procedures are not strictly comparable because (i) point quadrat and hand separation are area and mass based techniques respectively, (ii) point quadrat results were obtained 10 days later than those of hand separation, and (iii) the inclined point quadrat tends to underestimate the proportion of dead material (Hodgson, 1981; Grant *et al.*, 1985), they demonstrated similar patterns of variation between and within treatments (Table 5.3 and Appendix Figures 5.1 and 5.2).

The pre-grazing herbage mass, and its green and dead components were higher for ryegrass swards than for Yorkshire fog swards during the entire experimental period, and in particular during September and October (Figure 5.1 and Appendix Table 5.2). These differences persisted after grazing, but became much smaller, especially in the amount of dead herbage mass. The overall amounts of herbage mass and green herbage mass removed during grazing were higher from ryegrass swards than from Yorkshire fog swards (1660 versus 1020; 1150 versus 780 kg DM ha^{-1} respectively), reflecting the higher stocking rate on the former treatment. However, within the green herbage mass, the pre and post grazing proportions of green leaf were consistently greater for Yorkshire fog swards than for ryegrass (Table 5.3), resulting in similar amounts of green leaf for both swards, with correspondingly greater proportions and amounts of green stem for ryegrass swards. The green leaf removed tended to be higher for Yorkshire fog swards than for ryegrass swards, 585 versus 501 kg DM ha^{-1}, indicating that greater amounts of dead and green stem masses were removed during grazing from ryegrass swards compared to Yorkshire fog swards.

In this study, the higher contents of dead material and green stem in ryegrass swards compared to Yorkshire fog swards are a consequence of the early reproductive development of Italian ryegrass, which normally starts in early October in Uruguay, in contrast to the later reproductive development of *Holcus* tillers in late November and early December (E. Berreta, personal communication). Similar observations on the influence of stage of maturity in annual ryegrass biomass composition have been reported by Hides *et al.* (1983), Ballard *et al.* (1990), Hume (1991), and Jung and Shaffer (1993). These results contrast with those reported in Experiments 1 and 2 (Chapter 3 and 4) when the comparisons were between perennial ryegrass swards and perennial Yorkshire fog swards. The pre- and post-grazing sward surface heights of both swards measured by using a ruler or RPM tended to follow the trend observed for herbage mass (Appendix Tables 5.3 and Figures 5.2(a,b)), with small differences between methods, except for the higher pre-grazing surface heights of ruler measurements during late October. The overall sward surface heights of the two grass swards measured both inside quadrats (Appendix Table 5.2) or at plot level (Appendix Table 5.3) matched very closely. Similar results were obtained by Hu (1993) using the sward stick.

The assessment of the compressed sward surface height by RPM was included in this study because RPM measures the combined effects of sward density and height, and so is more sensitive to differences in bulk density between pastures than other methods (e.g. estimations by ruler or the sward stick).

Coinciding with the results of the first two experiments reported in Chapters 3 and 4, and with those reported by Niezen *et al.* (1993b) and by Niezen (1995), *Holcus* swards had higher total and green bulk densities than ryegrass swards both before and after grazing, in particular when estimations were based on RPM. In Experiments 1 and 2, the dead material content of Yorkshire fog swards made a major contribution to the difference observed in bulk density between swards. However, in this study, the magnitude of the difference in green bulk density between swards was also considerably larger, probably reflecting the higher proportion of leaves in the canopy of Yorkshire fog (Table 5.3 and Figure 5.1). This finding is also supported by the higher number of leaves per tiller of Yorkshire fog compared to those of ryegrass (Appendix Table 5.5). The bulk densities in this trial were generally lower than those in Experiments 1 and 2, probably reflecting the higher average tiller/node population density of perennial ryegrass and *Holcus* than the corresponding annual species (Table 3.3; Chapter 3, and Appendix Table 5.4).

Legumes made minor contributions to herbage mass in both swards. This was a reflection of their poor initial establishment (Appendix Table 5.3 and Table 5.3), even after reseeding, probably reflecting, at least in part, the moderate germination ability of both legumes. Estimates of germination were 67 and 88% for white clover and lotus seeds respectively (C. Rostan, personal communication). Additionally, the initial faster establishment and greater growth of grasses than those of legumes, particularly in ryegrass swards, may have contributed to the low establishment of white clover and lotus. High herbage mass accumulations reduce penetration of light into perennial ryegrass/white clover swards, affecting the growth of white clover plants at the lower strata of the canopy (Curll, 1982). Weeds (principally *Rumex* spp.) made a very low contribution in the experimental swards.

The significant contribution of ryegrass plants in Yorkshire fog swards can probably be related to the presence of ryegrass seed-banks associated with the previous cultivation of this species on the experimental site, and to the rich nitrogen environment given by the high N-fertilizer application at the beginning of the trial, favouring the growth and capacity of competition of ryegrass in relation to Yorkshire fog. This result is similar to that described in Experiment 2 (Chapter 4), and in other works of Haggar (1976), Watt (1987), and Frame (1992). However, the presence of ryegrass plants in Yorkshire fog swards decreased over time (Table 5.3). As a consequence, dead ryegrass tissue made a consistent contribution to dead material in *Holcus* swards. This effect will be discussed in detail in the following section. The loss of ryegrass plants, tillers and leaves with the advance of reproductive development in *Lolium multiflorum* has been well documented by Hume (1991).

5.5.2 Evaluation of animal results

5.5.2.1 *Botanical and chemical composition of the diet selected and canopy structure*

The greater proportion of legume and grass leaf in the samples taken by OF sheep on Yorkshire fog swards (Table 5.4) may be explained by the high proportions of hits of those components in the whole sward profile, but particularly in the surface layers of the canopy of Yorkshire fog compared to ryegrass swards, whereas dead material was distributed higher in the sward canopy of ryegrass swards (Figures 5.3, 5.4, 5.5., 5.6 (a,b,c,d)).

The composition of the diet selected tended to match information on the composition of the uppermost layers of the sward canopies of ryegrass and

Yorkshire fog, in particular above 15 cm height (Table 5.11(a,b)), where most grazing was concentrated. However, some differences were observed between the proportion of legume and in the leaf-stem ratio, suggesting that sheep apparently discriminated in favour of the leaf component, rather than the legume component, and that they probably penetrated in some degree to the lower horizons of both sward canopies (below 15 cm) to increase the selection of leaf material. Sheep appear to graze in horizons where green leaf is the predominant component, irrespective of its vertical position in the sward profile (L'Huillier *et al.*, 1984). The results of point quadrat measurements show that white clover formed most of the legume component dispersed in the upper layers of the canopy of both swards (above 15 cm), with the exception of the presence of lotus in Yorkshire fog swards during October. This result probably suggests that white clover had a greater chance of being be selected than lotus.

The reason why weed species were not detected in extrusa may be explained by their distribution at the base of the swards. The greater contribution of green stem in the diet of both swards in October compared to that in September is principally explained by the enhancement and higher location of this component in the sward canopy, reflecting advanced maturity, particularly in ryegrass swards (Table 5.4). These findings are in contrast to those obtained with perennial ryegrass and Yorkshire fog swards in Experiments 1 and 2 (Chapters 3 and 4), and indicate the importance of the initiation of reproductive development in determining sward composition and structure in annual species, and hence diet selection.

The lower nutritive value of dead material and increased lignification of stalky material probably contributed significantly to the lower digestibility in the extrusa samples from ryegrass swards compared to Yorkshire fog swards (Tables 5.4 and 5.5), the influence on digestibility of the higher legume content in the diet on Yorkshire fog swards is probably of minor importance. In Uruguay, similar results were reported by Bemhaja (1993) in a spring comparison under

Table 5.11. Relationships (%) amongst sward components in the upper layers (above 15 cm) of the ryegrass and Yorkshire fog sward canopies and the composition of the diet selected during September (a) and October (b).

Components (a)	Ryegrass				Yorkshire fog			
	+ Lotus		- Lotus		+ Lotus		- Lotus	
	Sward	Diet	Sward	Diet	Sward	Diet	Sward	Diet
Dead material	13	13	7	10	2	9	10	2
Live material	87	87	93	90	98	91	90	98
Grasses	100	100	98	100	91	99	94	91
Legumes	0	0	2	0	9	1	6	9
Green leaf	75	95	75	95	87	99	89	98
Green Stem	25	5	25	5	13	1	11	2

Components (b)	Ryegrass				Yorkshire fog			
	+ Lotus		- Lotus		+ Lotus		- Lotus	
	Sward	Diet	Sward	Diet	Sward	Diet	Sward	Diet
Dead material	15	11	11	12	5	9	4	6
Live material	85	89	89	88	95	91	96	94
Grasses	100	99	94	100	90	98	93	100
Legumes	0	1	6	0	10	2	7	0
Green leaf	83	92	88	88	87	95	86	98
Green Stem	17	8	12	12	13	5	17	2

sandy soil conditions. The decrease in digestibility in annual ryegrass with increasing maturity of both leaf and stem fractions has been associated with increasing cell wall contents in these fractions, but the digestibility of the leaf fraction usually declines at a slower rate than that of stem (Hides *et al.*, 1983; Ballard *et al.*, 1990; Hume, 1991; Jung and Shaffer, 1993; Fariani *et al.*, 1994). After anthesis in annual ryegrass, the poor digestibility of senescent plant material has a strong influence on whole plant digestibility (Ballard *et al.*, 1990). A probable additional effect on the difference in the OMD of the diet selected from both swards could be related to the lower digestibility of the leaves at the base of the sward compared to those of the uppermost horizons (Ballard *et al.*, 1990; Hodgson, 1990), and to the fact that fistulated sheep may have explored deeper in the lower horizons at the base of the sward canopy, searching for green leaf, in ryegrass swards than in Yorkshire fog swards.

The lower OMD values recorded in the present study (Table 5.5) compared to those of Experiments 1 and 2 (Chapters 3 and 4) can be interpreted partially as a consequence of differences in (i) earlier maturity of annual species (Jung and Shaffer *et al.*, 1993) (Plate 5.2), (ii) the decline in OMD of temperate grasses associated with increasing temperature due to latitude effect (Wilson, 1981), and (iii) the lax grazing management imposed in the present study largely affecting the composition and structure of the experimental swards.

The presence of low concentrations of CT (0.37% on a DM basis) in *Lolium multiflorum* has been established in the present study (Table 5.5). This, together with the evidence obtained in Experiments 1 and 2, and in the trials of Liu *et al.* (unpublished) confirming also their presence in *Lolium perenne*, suggests that the entire *Lolium* genera may contain CT. Horigome and Uchida (1981) also found CT in trace amounts in leaves of annual ryegrass. The CT concentration (0.42% on a DM basis) observed in *Holcus* (Table 5.5) is much higher than that previously reported (Terrill *et al.*, 1992a,b; Montossi *et al.*, 1994; Douglas *et al.*, 1993; Iason, *et al.*, 1995; Liu *et al.*, unpublished; Experiment 2).

Plate 5.2. View of annual ryegrass plot (front) and Yorkshire fog plot (rear) before and after grazing, showing the advanced stage of maturity of ryegrass swards with accumulation of dead material.

In both sampling periods, the extrusa samples of Yorkshire fog swards tended to contain higher amounts of total CT and protein bound-CT than those of annual ryegrass. This trend was also observed for perennial ryegrass and Yorkshire fog swards in the initial grazing trial (Chapter 3), but not in Experiment 2, suggesting a seasonal variation in the total and fractional concentration of CT. This seasonal variation has also been observed in the results of Liu *et al.* (unpublished), and it is probably related to the seasonal fluctuation in sward composition over the year, in particular the leaf-stem ratio, which in tum may modify the CT concentration of *Holcus* swards (Douglas *et al.*, 1993; lason *et al.*, 1995).

The low fertility conditions of the experimental site in the present study (Appendix Table 5.1) in contrast to those of Experiments 1 and 2 in New Zealand, is probably the most important factor explaining the higher CT concentration in the extrusa samples from *Holcus* swards in this trial. Increased concentrations of CT have been found in CT-containing legumes under environmental stress (Barry and Forss, 1983; Douglas *et al.*, 1993).

As in the first two experiments, it is unlikely that the low CT concentrations of *Holcus* or annual ryegrass swards influenced the selective pattems of the oesophageal fistulated sheep. This conclusion is supported by the results of diet selection in this study, where OF sheep preferred and ate mostly green leaf from both swards, despite the significantly higher CT concentrations in leaves than of stems (Douglas *et al.*, 1993; lason *et al.*, 1995). Similar observations have been made by Jones and Mangan (1977) and by Waghom and Jones (1989) with legumes and weeds containing higher CT concentrations (CT ranged from 2 up to 8% on a DM basis) than those of the grasses used in the present research programme.

The decline in OMD values over time may reflect the changes in sward composition and structure in both swards associated with the advance of the stage of maturity, this effect being more important in ryegrass swards (Table 5.5).

The nutritive value of the experimental swards was not affected by the presence or absence of lotus, probably due to the small contribution of lotus plants to the swards on offer (Table 5.3), and in particular to the diets of both grass treatments associated with its lower position in the sward canopy (Figures 5.3(a), 5.4(d), 5.5(a), and 5.6(d)).

5.5.2.2 *Grazing behaviour and herbage intake*

The general tendency of higher mean bite weight and lower rate of biting and grazing time recorded on Yorkshire fog swards compared to ryegrass swards (Table 5.6) is in agreement with the previous experiments undertaken in New Zealand (Chapters 3 and 4; Liu *et al.*, unpublished). The magnitude of the differences was greater during October, probably reflecting the greater deterioration of sward conditions in ryegrass treatments (Tables 5.3, 5.4, 5.5; Appendix Figures 5.1 and 5.2; Figures 5.3, 5.4, 5.5, and 5.6). As has been mentioned previously in Experiments 1 and 2, the greater leaf bulk density of Yorkshire fog swards compared to that of ryegrass swards could explain the apparent differences in bite weight. The effect of the lower tensile strength of *Holcus* leaves in comparison with that of perennial ryegrass may also account for some of the differences recorded (Evans, 1967; Jacques *et al.*, 1964).

The smaller bite weights recorded in the present study compared to those in Experiments 1 and 2 can be explained by differences in (i) mean size of OF sheep used in Uruguay and New Zealand (hence disparity in mean dental arcade) and (ii) sward composition and structure, specifically differences in tiller population and the proportions of green leaf in the entire sward profile, but in particular in the uppermost horizons.

Confirming the field observations of Experiments 1 and 2, PEG supplementation did not affect the behaviour patterns of the lambs grazing on the experimental swards. There was also no difference in the behaviour of lambs grazing swards with and without lotus (Table 5.6).

The higher herbage intakes of lambs grazing on Yorkshire fog swards than in ryegrass swards of the present study, particularly during October (Table 5.6), differ from the results of Experiments 1 and 2, and of Liu *et al.* (unpublished), where intakes were always greater in favour of perennial ryegrass. Ulyatt (1971) also found better animal performance on annual ryegrass than on perennial ryegrass. This latter difference in intake between studies may reflect the greater proportion of cell wall components of annual ryegrass in comparison with *Holcus* swards, associated with the early reproductive development of annual ryegrass in Uruguayan conditions, resulting in a decline in OMD value and hence intake. Research studies have shown that the intake of leaf fraction is greater than that of the stem fraction of grasses due to the shorter time leaf is retained in the reticulo rumen (Ulyatt, 1971; Poppi *et al.*, 1981a,b). High levels of dead material in the pre-grazing pasture mass affect herbage intake due to its double effect in (i) reducing the digestibility of the herbage harvested (Rattray *et al.*, 1987) and (ii) increasing the animal´s energy expenditure during grazing when searching for highly digestible material (e.g. green leaf) within the sward profile (Birrell, 1989).

When comparisons of intake are expressed in units of metabolic weight ($LW^{0.73}$) (Table 5.6) the intakes observed in this trial are lower than those recorded previously in lambs by Jamieson and Hodgson (1979) or in Experiment 2, and in ewes by L´Huillier *et al.* (1986), probably reflecting the lower nutritive value of the diet selected in the present study.

Confirming the recent results of Terrill *et al.* (1992b) and those of Experiment 2, the herbage intakes of PEG and NON-PEG lambs were similar, suggesting that the higher CT concentrations observed in both swards in this experiment compared with the above studies were not high enough to depress intake. Lamb intakes did not differ in swards with or without lotus, probably reflecting its low contribution to the experimental swards.

5.5.2.3 *Internal parasites*

In general, the levels of FEC recorded in lambs grazing on all sward combinations were low, and it was not necessary to drench to control worm parasites during the entire duration of the trial (Table 5.7). Based on Ueno's classification (1983), low numbers of worms were also observed in the abomasum and in the small and large intestines (Appendix Table 5.6), which supported FEC data (Table 5.7). Despite the high susceptibility of lambs to internal parasites (Familton, 1983), the above results are probably explained by the alternate rotation of crops and pastures in the experimental area in previous years, and by the alternate grazing of sheep and cattle. These latter management practices prevent the establishment of infective larvae populations in pastures (Speedy, 1980; Familton, 1983). Additional factors explaining the low FEC values are (i) lambs were drenched onto plots, and (ii) the short-term period of the trial, resulting in insufficient parasite cycles to build-up infective larvae populations in the experimental swards.

The significantly lower concentrations of FEC and abomasal and total worm burdens (abomasum + small and large intestine; Appendix Table 5.6) in lambs grazing on Yorkshire fog swards than in lambs grazing on ryegrass swards are of greater magnitude than those found in previous reports (Niezen *et al.*, 1993b, 1995; Experiment 2, Chapter 4). There was a slight increase in FEC values in lambs supplemented with PEG, particularly during October when the internal parasite challenge was higher than in previous months (August and September). This small response in lamb FEC to the presence of CT in ryegrass and in *Holcus* supports the findings of other work (Niezen *et al.*, 1993a; 1994; Experiment 2, Chapter 4). In the present study, responses in FEC concentration associated with CT were recorded in both grass treatments, which contrasts with the greater responses in *Holcus* than in ryegrass swards in Experiment 2. However, it should not necessarily be assumed that the greater control of worm parasites in lambs grazing on Yorkshire fog swards is simply a reflection of the presence of CT in this species (Hodgson *et al.*, 1995). Probably other factors are implicated in this effect (e.g. sward canopy structure, leaf surface texture, unknown compounds). More research is required in this area to determine causative relationships.

The modest presence of lotus in Yorkshire fog or ryegrass swards did not affect lamb FEC (Table 5.7).

5.5.2.4 *Wool production*

5.5.2.4.1 Effects of grass species and lotus

Lambs grazing on Yorkshire fog swards had significantly higher midside greasy and clean wool growth rates than lambs grazing on ryegrass swards (13% and 15% respectively), reflecting their greater diameter and length of the fibres (5% and 5% respectively), while wool yield was similar for the two swards (Table 5.8). These findings are not in agreement with those responses obtained in Experiment 2 (Chapter 4, Section 4.4.1.6.1). The differences in wool growth, fibre diameter and length between swards are presumably due, at least in part, to differences in intake of green leaf, resulting in diets of higher quality in favour of Yorkshire fog swards (Tables 5.3, 5.4, and 5.5). As a consequence, based on the equations of Geenty and Rattray (1987), the overall predicted values of metabolisable energy intakes were 12.3 and 9.4 MJ ME day^{-1} for lambs grazing on Yorkshire fog and on ryegrass swards respectively. The reduction in the nutritive value of the swards over time may also explain the decline in wool growth over time in both swards, but particularly in ryegrass swards.

Thompson *et al.* (1994), comparing the effect of stocking rate on wool production from annual ryegrass during spring, showed that more than 74% of the variation in wool growth, fibre diameter and length was accounted for by differences in green herbage mass, the maximum values of wool growth and wool characteristics being achieved in the range of 2000 to 3000 kg green DM ha^{-1} on offer. The nature of the relationship between green feed on offer and wool growth is described best by an asymptotic function (Rattray *et al.*, 1987; Thompson *et al.*, 1994). Similarly, Birrell (1992) found a curvilinear function between OMD and wool growth, where growth rates increase to an apparent optimum around 70% OMD. Above this value inherently highly digestible material could increase the N requirements of rumen microflora. The optimum values of Birrell (1992) were achieved in the diets of both swards in the current study. However, based on previous information (Experiments 1 and 2) and in the advanced stage of maturity of annual ryegrass in the present experiment, it is reasonable to assume that levels of N in the diets of lambs grazing on Yorkshire fog swards were higher than those grazing on ryegrass swards. As a consequence, the higher wool growth in favour of Yorkshire fog swards probably resulted from a better balance between protein and energy, and levels of by-pass protein were probably higher in Yorkshire fog due to its higher CT content (discussed in next section). However, these assumptions are somewhat speculative given the incomplete information on N dietary concentrations and rumen metabolism in the present study.

The greater fibre diameter of lambs grazing on swards with presence of lotus compared with those grazing on swards without lotus (Table 5.8) could be associated, in part, with the interactive effects of (i) slightly higher OMD values of lotus swards (Section 5.4.3.1, Table 5.8), and (ii) random effects.

5.5.2.4.2 PEG supplementation and the effects of CT

PEG administration reduced greasy and clean wool growth rates, and fibre diameter in lambs by 8%, 10%, and 5% compared to their counterparts receiving oral administration of water (Table 5.8). These results matched very closely those of the spring trial of Terrill *et al.* (1992b), where similar CT dietary contents (0.47% on a DM basis) to those of the present study increased wool growth by 18%. Additionally, the higher CT concentrations recorded in this trial compared with those of Experiment 2 (Chapter 4) may explain the higher wool responses obtained in this Uruguayan experiment. The greater wool growth rates of NON-PEG lambs grazing on Yorkshire fog swards within the presence of lotus compared with the rest of the grass × lotus × PEG treatment combinations may reflect the additive effect on wool growth of the higher amounts of CT and CT bound-protein in the diet of the former lambs (Table 5.8).

Limited dietary supply of sulphur amino acids in sheep on forage diets limits wool production (Reis, 1979; Reis *et al.*, 1990). Additionally, the beneficial effect of CT on wool production has been well documented in the literature (Waghom *et al.*, 1990; Lee *et al.*, 1992; Wang *et al.*, 1994). These findings indicate that CT (< 3.5% on a DM basis) increase the availability and absorption of essential amino acids (e.g. methionine and cysteine), resulting in increments in wool production. The greater wool production of NON-PEG lambs is probably a response to improvement in the efficiency of utilization of dietary nitrogen linked to the protective effect of CT.

5.5.2.5 *Liveweight gain and carcass measurements*

5.5.2.5.1 Effects of grass species and lotus

Liveweight gains on Yorkshire fog swards were consistently higher (41%) than those on ryegrass swards for the entire experimental period (Tables 5.9, Figure 5.7, and Appendix Figure 5.3), resulting in significantly greater final weights (11%), carcass gains (12%), carcass weights (29%), and GR values (37%) in favour of the lambs grazing on Yorkshire fog swards (Table 5.10). The lamb production per unit area was also 25% higher for *Holcus* swards in comparison to that of ryegrass. The differences resulted principally from the effects of the higher OMD values and intakes of Yorkshire fog swards compared to those of ryegrass, reflecting the higher proportions in the diet of green leaf and the lower proportions of green stem and dead material in favour of Yorkshire fog swards (Tables 5.4, 5.5, and 5.6), particularly in the uppermost layers of the swards canopies, where most of grazing was concentrated (Table 5.3, Figures 5.1, 5.2, 5.3, 5.4, 5.5, and 5.6). Herbage intake (Poppi *et al.*, 1987; Birrell, 1989), liveweight gain of sheep (Butler and Hoogendoom, 1987; Rattray *et al.*, 1987; Thompson *et al.*, 1994; Fraser, 1994) and milk production (Holmes, 1987; Hoogendoom *et al.*, 1992; Holmes *et al.*, 1992), in particular over late spring and summer, are often better related to leaf allowance than either green or total herbage allowance.

The decline in liveweight gain over time in all treatment combinations was a result of the deterioration of sward conditions linked with the progress of the stage of maturity towards summer (Table 5.9).

The lamb performance results in favour of *Holcus* swards are in agreement with the results of Bemhaja (1993) using heifers in a spring comparison of annual ryegrass and *Holcus lanatus* L. cv. "La Magnolia".

5.5.2.5.2 PEG supplementation and the effects of CT

Liveweight gains and final weights were 18% and 2% greater on NON-PEG lambs than on PEG lambs (Table 5.9 and Appendix Figure 5.5), though differences in carcass characteristics were usually modest and non significant (Tables 5.10). These findings are in accordance with the results of the spring trial with temperate grasses of Terrill *et al.* (1992b) with similar levels of CT in the diet to those of the present experiment. As in Experiment 2 for liveweight gain comparisons and in this study for wool production comparisons, a significant grass × PEG interaction (Table 5.9) indicated that CT in Yorkshire fog was probably more effective than CT in ryegrass in promoting increases in liveweight gain. This latter effect could be related to the slightly higher total CT and protein-bound CT concentrations in extrusa in favour of Yorkshire fog swards (Table 5.5). In addition, due to the fact that extrusa samples were oven dried because of the lack of freeze drying facilities, the actual CT dietary concentrations in both grass swards could be higher than those recorded. Drying tannin-containing plants at 50 or 60ºC in a forced-draught oven (Swain, 1979; Ahn *et al.*, 1989) and grinding of forage samples (Terrill *et al.*, 1990) resulted in variable losses of CT.

5.5.3 Practical implications of the grazing management imposed in the present study

The rotation length and lax grazing intensity adopted previously and during the development of the present study promoted larger pre-grazing herbage masses and lower pasture utilizations than in previous studies (Experiments 1 and 2), particularly in the case of annual ryegrass. This grazing management resulted in a deterioration in sward composition and structure due to the accumulation of dead herbage and an increase in the proportion of reproductive tillers. As a consequence, the quality of the swards were adversely affected, resulting in decreases in lamb performance over time, and affecting, to a greater extent, those lambs grazing on annual ryegrass. Butler and Hoogendoom (1987) suggested that the advantages of generous feeding of livestock due to lax spring grazing may be outweighed by the subsequent combination of reduced leaf accumulation and the effect of increased content of dead herbage on stock performance.

Therefore, in order to maintain a desirable sward composition and quality in annual ryegrass and Yorkshire fog swards from early spring to summer for lamb production on soil of low-moderate fertility of the Basaltic region, shorter rotations and probably more intensive grazing pressure than those used in the present study are required, even accepting the possibility of some immediate reductions in individual performance.

5.6 CONCLUSIONS

The higher dietary nutritive value, and greater herbage intake and lamb performance of Yorkshire fog swards compared with annual ryegrass swards growing under low to moderate fertility conditions was principally explained by differences in sward composition and structure associated with the early reproductive development of annual ryegrass swards. The insignificant effect of lotus on lamb production was a reflection of the poorer establishment and lower contribution of this legume to both swards.

The distribution of green leaf within the canopy of both swards appeared to be the main factor determining selective grazing by sheep.

In agreement with recent research, the parasitism levels of lambs grazing Yorkshire fog swards were consistently lower than lambs grazing annual ryegrass swards, even under the conditions of very light parasite challenge. Despite the presence of CT in this grass, other factors are involved in the latter effect (eg sward canopy structure, leaf surface texture, unknown compounds). More research is required in this area to determine causative relationships.

CT dietary concentrations, (range from 0.36 to 0.42% on a DM basis), increased wool production and liveweight gains in lambs grazing on annual ryegrass and Yorkshire fog swards, but to a greater extent in Yorkshire fog swards. However, the magnitude of the differences in carcass weight were modest. Further information also suggests that the levels of CT in this trial did not influence diet selection, herbage intake or grazing behaviour patterns of the experimental animals.

CHAPTER 6

GENERAL DISCUSSION AND CONCLUSIONS

6.1 INTRODUCTION

The following chapter is divided into five main sections focused on: (6.2) a brief discussion and evaluation of the levels of accuracy achieved with the sward and animal procedures used in the current research program, (6.3) analysis and interpretation of the interrelationships between sward, ingestive behaviour, herbage intake, and animal performance variables, (6.4) a summary and a comparison of the main results drawn from the three experiments related to the effect of CT on animal performance, considering the framework of existing research knowledge in this area, (6.5) the significance of *Holcus lanatus* for grazing systems, reflecting the major findings of this project and those of other research studies, particularly when this grass is compared to perennial ryegrass and tall fescue in terms of animal responses, and finally (6.6) description of the major conclusions drawn from the current research programme.

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

6.2.1 Sward procedures

Measurements of sward traits were associated with moderate to low levels of variability (coefficients of variation (CVs) 5 - 30%), where the complete randomised block design used in Experiments 1, 2, and 3 was partially effective in controlling the between-plot variability intrinsic to large experimental areas like those of Experiment 1 and 2 (1.6 ha) and Experiment 3 (2.8 ha).

Estimates of total, green and dead herbage masses from the three experiments were carried out in this project with satisfactory precision (average CVs ≤ 25%). The average CV values of Experiment 1 were higher than those of Experiments 2 and 3 (30, 25, 21% respectively), probably indicating that more quadrat cuts were required in Experiment 1 to increase the precision of the estimates of herbage mass. Estimates of CVs for dry matter or organic matter mass reported in the reviews of Frame (1981; 1993) and Meijs (1981) range between 10 to 30% for pre- and post-grazing herbage samples.

Pre-grazing and post-grazing sward surface heights were measured both inside quadrat sites and at plot level by various procedures, the HFRO sward stick (Barthram, 1986) being used in Experiments 1 and 2, and a common ruler and Ellinbank rising plate meter (Earle and McGowan, 1979) being used in Experiment 3. Inside quadrat sites, 5 readings were obtained, while at plot level either 30 (Experiment 3) or 40 readings (Experiments 1 and 2) were taken, which corresponded to 120 and 160 readings per treatment, respectively, for each sampling period. The overall CV for pre- and post-grazing sward surface heights at plot level was 17%, this value being much lower than that reported in the literature (Rhodes and Collins, 1993). In Experiment 3, in line with the reports of Rhodes and Collins (1993), the CVs (based on plot means) of rising plate meter measurements were higher than those of common ruler measurements (21 vs 15% respectively). Sward surface heights measured both inside and outside quadrat cuts tended to be similar amongst sward treatments. These results indicate that, when measurements of sward height and herbage mass are conducted together, the average estimate of sward height inside quadrat cuts is a reliable indicator as those taken at a plot level.

Additionally, hand separation and point quadrat (set at 32.5º to the horizontal; Warren Wilson, 1963) techniques tended to describe similar patterns in the botanical composition of the experimental swards during the entire experimental programme. It has been well documented that one of the disadvantages of the point quadrat technique is the loss of accuracy for quantifying and describing the dense lowest stratum of the sward (Grant, 1993), resulting in an underestimation of the proportion of dead material in the sward profile (Hodgson, 1981; Grant *et al.*, 1985). In particular, this tendency was observed in Experiment 2. However, it is unlikely that this technique induces erroneous interpretation of the results (Hodgson, 1981). In the circumstances of the present study, the results derived from hand separation and point quadrat procedures tended to complement one another, so that the ultimate description of the sward was more comprehensive than with either method alone, particularly when the ultimate goal was to describe sward composition and structure to facilitate interpretation of the results of diet selection.

6.2.2 Animal procedures

In the diet selection studies of Experiments 1, 2, and 3 using the point analysis technique (Clark and Hodgson, 1986) to describe diet composition, the levels of variability were associated closely with the component under examination. The CVs of proportions of legume and dead material in the diet reached values up to 100% and 50% respectively (even after transformation), while those of grass and green material were 2% and 6% respectively. These differences may be related to the small and irregular contribution of legumes to the experimental swards throughout the research program, and to the increase in the experimental error in the point analysis technique associated with the presence of dead material in the diet (Clark and Hodgson, 1986). Additional difficulties were observed with the use of the point analysis technique for describing diet composition, namely difficulties in separating the small amounts of pseudostems from leaf, and of sheath from leaf lamina, particularly when the swards on offer were very leafy (Experiments 1 and 2). However, it is unlikely that this difficulty introduced any bias in the conclusions drawn from the diet selection studies. In general, the point quadrat procedure (area based technique), and the hand separation technique (mass based technique) supported the results obtained by the point analysis technique (area based technique).

The discussion and interpretation of the results of diet selection studies in this research project were based on the assumption that mature oesophageal fistulated wethers provide samples representative of the diet selected by lambs. Experimental evidence comparing the diet selected by mature or immature sheep (Hughes *et al.*, 1984), goats (Hughes *et al.*, 1984), and cattle (Hodgson and Jamieson, 1981) supports the above assumption. However, general hypotheses about interactions between the effects of body size, mouth size, animal age and sward conditions upon ingestive behaviour and herbage intake are conflicting and require further critical evaluation (Hodgson, 1985b).

The overall estimates of the OMD of extrusa samples collected by oesophageal fistulated sheep (OF) were very precise (CVs $\leq$ 1.7%) in comparison with the CV values reported by Le Du and Penning (1982) or by Meijs (1981) for *in vitro* digestibility estimations. Potential sources of error were controlled by (i) using well trained OF sheep which were acclimatized to the experimental swards for one week before the commencement of the sampling period, (ii) using experimental cross-over designs in order to remove the individual animal variation between OF sheep (Le Du and Penning, 1982), (iii) discarding extrusa samples with excessive saliva contamination and re-sampling, and (iv) following the suggested protocols of extrusa sample processing (Le Du and Penning, 1982).

The rumen NH_3 concentrations observed in Experiments 1 and 2, suggested that PEG would preferentially bind CT and prevent binding of proteins which would then be rapidly degraded to ammonia. However, the results of Experiment 2 suggest that twice daily PEG supplementation may not have completely eliminated binding of plant proteins to CT in the rumen for a full 24-hr period, which may indicate that the potential effects of low CT concentration on animal performance were not completely evaluated. The rumen metabolism studies carried out in Experiment 2 provided additional evidence of the presence of CT in both perennial ryegrass and Yorkshire fog, and were consistent with the evidence provided by the literature that a reduced deamination of plant proteins occurred when CT were present.

The levels of variability in the analyses of total CT and their fractions were moderate (CVs ≤ 16), considering (i) the low number of replications per treatment used (n = 4) in each evaluation, and (ii) the difficulties of sensitivity of the Butanol-HCl procedure to detect CT at very low concentrations, particularly below 1% on a DM basis (Terrill *et al.*, 1992a).

The absence of any direct assessment of the CT concentrations on the swards on offer in the present study was related to the priority to gather information on CT in the diet ingested, given (i) the importance of knowing the magnitude of this parameter to the objectives of the current research programme and (ii) the constraints on CT analyses needed for the swards on offer and their components. Experimental evidence in the literature related to CT concentrations in leaves and stems of *Holcus lanatus*, perennial ryegrass, and white clover (Terrill *et al.*, 1992a,b; Douglas *et al.*, 1993; Iason *et al.*, 1995) was used to support these findings.

The accuracy of the estimates of herbage intake (CVs ≤ 10%) from the indirect technique using the chromium controlled release capsule (CRC) agrees closely with the common range of variability accepted for the use of this technique (Parker *et al.*, 1990; Morris *et al.*, 1994). Though the CRC have not been tested in a wide enough range of environments (Bums *et al.*, 1994), the results from Experiment 3 were promising for future use of this technique to estimate intake in sheep in Uruguayan conditions. The daily release rates of the CRC´s recorded were, on average, 3% lower than those supplied by the manufacturer (193 mg Cr_2O_3 day^{-1}), being 185.5, 187.5, and 188.5 mg Cr_2O_3 day^{-1} for Experiments 1, 2, and 3 respectively. In Experiment 2, mean release rates measured on mature rumen fistulated wethers were 3.5% higher than those measured on intact lambs (199.8 versus 188.5 mg Cr_2O_3 day^{-1}), the variability being higher for rumen fistulated measurements (CVs of 16% versus 8%). Results of the release rates of Cr_2O_3 from this project confirm the need to avoid bias by (i) evaluation of the release rates of CRC´s for the particular situations of each experiment, and (ii) the use of intact animals rather than rumen-fistulated wethers (Experiment 2).

The magnitude of the variation in the ingestive behaviour parameters studied in the current research programme lay within the ranges of CVs reported by Hodgson (1982) using sheep grazing temperate swards. Bite weight showed the greatest variation across treatments and experiments (CVs between 26 and 34%), while variabilities on biting rate and grazing time were lower (13 and 5%, respectively).

The arithmetic product of IB, RB and GT has been used to predict feed intake. However, Jamieson and Hodgson (1979) showed substantial discrepancies between estimates of herbage intake (HI) calculated in this way and estimates obtained from faeces output and feed OM digestibility. Hodgson (1982) suggested that "it is probably prudent to think of measurements of ingestive behaviour as a means of explaining observed effects on HI rather than as a means of estimating intake itself, and to measure intake independently". In the series of experiments reported here independent measurements were made of HI and each of its components, recognising that the procedures used to measure IB, RB and GT would result in estimates which were individually comparable, but the product of which would not necessarily equate quantitatively to daily intake. In fact, estimates of HI resulting from the product of the components of ingestive behaviour over the three experiments were 2.2 - 3.5 times (mean 2.8) greater than those calculated by faeces output and feed OM digestibility. This disparity can be explained in part by the fact that RB was estimated as a maximum rate measurement rather than a daily average over the recording of GT, and in part, particularly in Experiment 2, by differences in liveweight between fistulated and non-fistulated animals. For these reasons no attempt has been made to present estimates of intake based on the components of ingestive behaviour, or to make comparisons between alternative estimates of intake.

In Experiments 2 and 3, the use of the initial lamb liveweight, carcass weight, and wool weight measured from the midside areas of lambs as covariates for the statistical analyses of those variables resulted in moderate to low CVs (7, 10, and 14% respectively). These values were slightly higher than those reported by Morris *et al.* (1994) for ewes. However, in Experiment 1, a large variability occurred in liveweight gain assessment (CV = 69%), probably reflecting the lack of adjustment by initial weight, the short period of evaluation used, and the low overall rates of gain in the mature ewes. There were also large variations in FEC values (average CV of 52%), even after transformation. With these latter exceptions, the levels of precision attained in the various animal traits provide for confidence in the evaluation of the experimental results.

6.3 INTERRELATIONSHIPS BETWEEN ANIMAL BEHAVIOUR, ANIMAL PERFORMANCE, AND SWARD VARIABLES

6.3.1 Preparation and statistical analysis of the data

In order to investigate further the association between sward characteristics, ingestive behaviour, and animal performance variables in the current study, the data of Experiment 3 were also analyzed by Canonical Correlation Analysis (CCA) and by partial correlations.

Many attempts to relate the quality of the diet to the characteristics of the forage on offer, and animal performance have been made, but the interpretation of these relationships is difficult because forage attributes tend to be correlated (Langlands and Sanson, 1976). The presence of significant correlations between two or more variables within any set of variables may bias the results from univariate analysis (Cooley and Lohnes, 1971), indicating the advantages of using multivariate approaches which provide a more efficient understanding of the issues concerned, in contrast to looking at variables individually (Gong, 1994). The evaluation and quantification of the associations between two sets of variables is an conceptually ideal ground to apply CCA (Matthew *et al.*, 1994; Manly, 1994).

Within the experiments carried out in the present study, the data set of Experiment 3 were chosen to perform a final CCA, because the size and design of this experiment were more closely related to the fundamental postulates suggested by Gittins (1985) in assessing statistical validity of the use of CCA.

A preliminary preparation of the data set was performed prior to analysis. All the data collected for sward and animal variables were averaged for each plot for each main effect (sward type, lotus, and PEG supplementation) and for two sampling periods (September and October). The CCA´s were carried out on a total of 64 observations, 32 observations at each level for each main effect. CCA was performed using a command, "Proc Cancorr" of the SAS package (SAS, 1990).

The interrelationships between sward and animal attributes were examined by CCA in three different ways, analysing the response patterns of: (i) ingestive behaviour variables (bite weight, rate of biting, grazing time, herbage intake) to variation in sward variables (sward mass, dead mass, green leaf mass, sward surface height, and organic matter digestibility, protein-bound condensed tannins, total condensed tannins of the diet selected), (ii) animal performance variables (liveweight gain, clean wool growth, carcass weight, and faecal egg counts) to variation in sward characteristics, and (iii) animal performance variables to variation in ingestive behaviour variables. Some of the variables measured in Experiment 3 were not included in the analysis because of their (i) unimportance to overall effects, (ii) associative effects, and (iii) limited number of observations.

6.3.2 Results and Discussion

The assessment and interpretation of the contribution of the sward and animal variables to the canonical scores through the standardised coefficients and structural coefficients given by SAS were based on the scheme proposed by I.L. Gordon (personal communication). Only the results of the first canonical factor amongst sward variables, behaviour variables, and animal performance variables are presented in the following section, given that they accounted for at least 70% of the multivariate dispersion, and that the rest of the canonical factors produced by SAS were not significant ($P > 0.05$).

Overall partial correlations amongst sward variables, behaviour variables, and animal performance variables were also performed to measure the degree of dependence between two variables after adjusting for the linear effect of one variable or a group of the other variables under study (Afini and Clark, 1984) (Table 6.1). The results of partial correlation analysis show that organic matter digestibility was strongly and positively associated with herbage intake, which in tum was strongly related to animal performance. In general, herbage mass, dead herbage mass, green leaf, and sward height variables were negatively correlated with animal performance variables and herbage intake. Protein-bound CT and total CT were slightly related in a positive manner with behaviour variables, sward variables, and liveweight gain. The canonical correlations amongst the sets of variables were high (ranging from 0.71 to 0.94) and significant, and explained between 0.70 and 0.88 of the multivariate dispersion (Table 6.2). The largest standardised coefficient of the set of sward variables was dietary organic matter digestibility, with less importance attached to sward height, herbage mass, dead mass, protein-bound CT, and total CT, indicating the importance of organic matter digestibility in affecting herbage intake and animal performance. The first canonical variable for the set of behaviour variables, seems to be influenced by

Table 6.1. Overall partial correlation matrices for the relationships between sward variables (n = 7), ingestive behaviour variables (n = 4), and animal performace variables (n = 4).

VARIABLES	LWG	CWG	CW	FEC	MASS	DEAD	LEAF	SH	OMD	PBCT	TCT	BW	RB	GT
CWG	0.20													
CW	0.28	0.24												
FEC	-0.29	-0.24	-0.36											
MASS	-0.05	-0.08	-0.46	0.17										
DEAD	-0.12	-0.12	-0.31	0.21	0.56									
LEAF	-0.18	-0.27	-0.45	0.12	0.54	0.45								
SH	-0.08	-0.08	-0.40	0.17	0.81	0.26	0.50							
OMD	0.18	0.15	0.01	-0.19	-0.04	0.10	0.13	-0.24						
PBCT	0.13	-0.09	-0.08	0.08	0.38	0.33	0.30	0.23	0.13					
TCT	0.16	-0.08	-0.06	0.09	0.38	0.27	0.22	0.28	0.09	0.93				
BW	0.01	-0.08	0.22	0.04	-0.15	0.11	0.13	-0.18	0.10	0.05	0.09			
RB	-0.18	-0.38	-0.08	0.23	0.02	-0.12	0.06	0.26	-0.16	0.12	0.21	-0.10		
GT	-0.30	-0.10	-0.17	0.01	0.08	-0.10	-0.25	0.03	0.06	0.12	0.16	0.10	-0.01	
INT	0.31	0.40	0.23	-0.21	-0.18	0.04	-0.09	-0.30	0.84	0.17	0.12	0.11	-0.10	0.10

Sward variables: MASS (Herbage mass), DEAD (Dead herbage mass), LEAF (Green leaf herbage mass), SH (Sward surface height), OMD (Dietary organic matter digestibility), PBCT (Dietary Protein-bound CT), TCT (Dietary Total CT).
Ingestive behaviour variables: BW (Bite weight), RB (Rate of biting), GT (Grazing time), and INT (Herbage intake).
Animal performance variables: LWG (Liveweight gain), CWG (Clean wool growth), CW (Carcass weight), and FEC (Faecal egg counts).

Table 6.2. Canonical correlation coefficients between the sets of sward variables, behaviour variables, and animal performance variables, standardised coefficients, structural coefficients and summary of important statistics of the first canonical score.

Levels of treatment	OVERALL (No partitioning by main effects)					
Sets of Variables	Standardised	Correlation	Standardised	Correlation	Standardised	Correlation
SWARD SET						
MASS	-0.22	-0.34	-0.09	-0.51		
DEAD	0.14	-0.05	0.05	-0.25		
LEAF	-0.27	-0.39	-0.56	-0.68		
SH	0.18	-0.55	0.07	-0.70		
OMD	0.92	0.97	0.70	0.84		
PBCT	0.38	0.07	0.45	-0.09		
TCT	-0.32	-0.03	-0.50	-0.19		
BEHAVIOUR SET						
BW	-0.04	0.03			-0.13	-0.09
RB	-0.16	-0.52			-0.51	-0.77
GT	-0.04	-0.13			-0.27	-0.38
INT	0.92	0.99			0.60	0.81
ANIMAL PERFORMANCE SET						
LWG			0.19	0.66	0.34	0.72
CWG			0.68	0.91	0.75	0.94
CW			0.31	0.67	0.04	0.49
FEC			-0.08	-0.57	-0.05	-0.52
Canonical correlation	0.94		0.74		0.71	
Proportion of multivariate dispersion explained	0.88		0.70		0.81	
Likelihood ratio	***		***		***	

Sward variables: MASS (Herbage mass), DEAD (Dead herbage mass), LEAF (Green leaf herbage mass), SH (Sward surface height), OMD (Dietary organic matter digestibility), PBCT (Dietary Protein-bound CT), TCT (Dietary Total CT).
Ingestive behaviour variables: BW (Bite weight), RB (Rate of biting), GT (Grazing time), and INT (Herbage intake).
Animal performance variables: LWG (Liveweight gain), CWG (Clean wool growth), CW (Carcass weight), and FEC (Faecal egg counts).
* $P < 0.05$ ** $P < 0.01$ *** $P < 0.001$

herbage intake (+0.9 or +0.6) and rate of biting (-0.16 or -0.51), with most emphasis on herbage intake. Bite weight and grazing time did not contribute much to the first canonical factor. The set of animal performance variables was dominated by clean wool growth, and secondly by liveweight gain and carcass weight, while the standardised coefficients of faecal egg count were nearly zero. These results show the importance of herbage intake on animal performance, in particular on clean wool growth.

The results from canonical correlation analysis and from partial correlations indicate the importance of dietary organic matter digestibility on herbage intake, and of herbage intake on animal performance, in particular clean wool growth. These results confirm the conclusions of Experiment 3, where the variation of animal performance between swards was explained mainly by the nutritive value of the diet and the herbage intake achieved on those swards.

The importance of organic matter digestibility and of organic matter intake in determining wool growth has been well established by Birrell (1989, 1992). When quantitative sward limitations are minimized, a very close relationship between herbage intake and the digestibility of ingested herbage has been observed, over a wide range of conditions (Hodgson, 1977). Given the high herbage allowance offered to the lambs in Experiment 3, nutritional factors (eg digestibility) are likely to be of primary importance in limiting herbage intake, rather than behavioural constraints (Poppi *et al.*, 1987).

The negative associations between green leaf and organic matter digestibility and between green leaf and animal performance can be attributed, at least in part, to the small contrast in diet composition provided by Experiment 3, where, on average, 95% of the diet was constituted by green leaf. The narrow range of sward conditions offered limited scope for variation in selective grazing behaviour.

6.4 OVERALL EVALUATION OF THE EFFECTS OF THE LOW DIETARY CT CONCENTRATION ON SHEEP PERFORMANCE, HERBAGE INTAKE, DIET SELECTION, AND INTERNAL PARASITES

6.4.1 Effects on wool production, liveweight gain, and carcass weight

From the results of several studies conducted mainly in New Zealand during the last two decades, some authors have attempted to define an optimal CT concentration in forage diets with regard to milk, wool and meat production in grazing ruminants. For instance, Barry (1989) in his review, emphasised the need to define the concentration of CT in fresh forage which will improve the efficiency of N utilization without depressing rumen fibre digestion and voluntary intake, and suggested that this concentration appeared to be between 2 and 4% on a DM basis in *Lotus pedunculatus*. Later, Waghorn *et al.* (1990) established that the CT in the herbage eaten should be 2 to 3% of DM to improve ruminant productivity by 10 to 15%. However, at the time this study commenced there was no conclusive evidence related to: (i) the minimal effective CT to improve ruminant production (Terrill *et al.*, 1992b), and (ii) the potential benefits of low CT concentrations on meat and wool production. However, the new information produced in recent publications and the results of the current research project demonstrate the potential of low CT concentrations to improve sheep production.

The following general comments are based on the results summarized in Table 6.3, which is based on the results collected from a series of studies in relation to the effects of a wide range of total dietary CT concentrations (from 0.14 to 9.6% on a DM basis) of diverse CT-containing species on wool production, liveweight gain, and carcass weight. Given the potential inaccuracy and misinterpretation of results by using perennial ryegrass as a control treatment (Chapter 4), the current comparison is confined to the results of studies where the control treatment (CT inactivated) was the administration of PEG (Polyethylene glycol) to the experimental animals.

Table 6.3. Review of the effect of a broad range of dietary condensed tannin concentrations on wool growth and liveweight gain in sheep receiving or not receiving PEG supplementation.

References and main Species	GMg[1]	Type of Animal	Dietary CT (Total) Concentration (% on DM basis)	Wool production ($mg/100 cm^{-2} day^{-1}$ or $g day^{-1}$)				Liveweight gain ($g day^{-1}$)				Carcass weight or carcass gain (kg or $g day^{-1}$)			
				+ PEG	- PEG	Gain(%)	Sign[2]	+ PEG	- PEG	Gain(%)	Sign.	+ PEG	- PEG	Gain(%)	Sign
1. Lucerne	RG	Lambs	0.03	10.2	10.8	+ 6	NS	178	185	+ 4	NS	62.9	67.7	+ 8	NS
2. Tall fescue/White clover	RG	Lambs	0.14	109	113	+ 4	NS	73	80	+ 10	NS	13.9	14.0	+ 1	NS
3. Yorkshire fog/White clover	CG	Lambs	0.18	109	109	0	NS	113	129	+ 14	NS	16.4	16.2	- 1	NS
3. Perennial ryegrass/White clover	CG	Lambs	0.19	121	108	- 12	*	131	130	0	NS	17.6	17.3	- 2	NS
4. Annual ryegrass/White clover/Lotus	RG	Lambs	0.37	122	134	+ 10	*	105	111	+ 6	NS	17.0	17.1	0	NS
4. Yorkshire fog/White clover/ Lotus	RG	Lambs	0.42	140	154	+ 10	*	135	174	+ 29	**	18.7	19.3	+ 3	NS
5. Perennial ryegrass/White clover/Yorkshire fog	RG	Lambs	0.47	97	115	+ 19	*	136	175	+ 27	**	18.3	19.2	+ 5	NS
6. *Lotus corniculatus*	RG	Lambs	3.40	10.9	12.1	+ 11	*	188	203	+ 8	NS	75.2	78.7	+ 5	NS
7. *Hedysarium coronarium* (Sulla)	RG	Lambs	3.64	105	117	+ 11	*	278	233	- 19	*	24.5	24.4	0	NS
8. *Lotus pedunculatus*	RG	Wethers	7.64	9.5	8.5	- 12	*	166	125	- 33	*	—	—	—	—
9. *Lotus pedunculatus*	RG	Lambs	8.85	104	81	- 28	**	70	27	- 59	**	—	—	—	—
10. *Lotus pedunculatus*	RG	Lambs	9.00	8.6	7.4	- 16	*	70	45	- 55	**	—	—	—	—
11. *Acacia aneura* (Mulga)	Pens	Wethers	9.60	45	24	- 88	**	35	-64	-100	**	—	—	—	—

GMg[1] (Grazing management; RG = Rotational grazing, CG = Continuous grazing). Sign[2] (Significance; * $P < 0.05$, ** $P < 0.01$, NS = Not Significant).

REFERENCES: 1. (Douglas *et al.*, 1995); 2. (Liu *et al.*, unpublished data); 3. (Experiment 2); 4. (Experiment 4); 5. (Terrill *et al.*, 1992a); 6. (Douglas *et al.*, 1995); 7. (Terrill *et al.*, 1992a); 8., 9., and 10. (Barry, 1985); 11. (Pritchard *et al.*, 1992).

(1) *Dietary CT concentrations > 4% (on a DM basis) appear to depress wool growth and liveweight gain substantially .*

Possible explanations for this effect have been suggested and confirmed in field experiments by several authors: (i) High concentrations of CT reduce the availability of protein N for microbial use, resulting in reductions in the microbial population of the rumen and lowering the rate of degradation of plant fibre; as a consequence, herbage intake is depressed (Barry, 1985; 1989; Waghom *et al.*, 1987a; Chiquette *et al.*, 1988; Waghorn *et al.*, 1990; Wang *et al.*, 1994), and (ii) reductions in the degradation and absorption of minerals, mainly sulphur (Waghorn *et al.*, 1987a).

(2) *Very low dietary CT concentrations (< 0.5% on a DM basis) produce small increases in sheep performance.*

The findings of Experiment 2 (Chapter 4) with temperate grasses (perennial ryegrass and Yorkshire fog) growing under moderate to high fertility conditions suggest that very low CT concentrations are able to raise bypass protein supply and protein quality in order to increase the levels of wool and meat production, though sheep responses were limited and were not significant. However, from the results of Experiment 3 and those of Terrill *et al.* (1992a), CT concentrations close to 0.5% on a DM basis had significant effects on wool production and liveweight gain, the effects being more substantial on liveweight gain and wool growth than those obtained by Terrill *et al.* (1992a) and Wang *et al.* (1994) with higher dietary CT concentrations (range 3.4 to 3.64% on a DM basis). These results may indicate that minimal effective CT concentrations are required in forage diets to improve lamb production significantly. They also suggest that there is potential for improving the nutritional value of temperate grasses (perennial ryegrass, tall fescue, Yorkshire fog) by up-grading CT levels by either conventional plant breeding techniques or by genetic engineering.

In Experiment 2, after the start of the trial, transitory positive effects of CT on lamb performance lasting 4 to 5 weeks were observed. Other researchers (Barry, 1985; Lowther and Barry, 1985) reported partial adaptation of sheep grazing on *Lotus pedunculatus* over a period of 8 weeks. Additionally, Robbins *et al.* (1987b) confirmed some buffering effects of sheep´s saliva against high dietary CT concentrations. The results of Experiments 2 and 3 also showed that despite the similar CT concentrations found in the extrusa samples from ryegrass and Yorkshire fog swards, lamb performance responses to PEG supplementation tended to be higher in favour of Yorkshire fog swards. This difference could be explained by differences in (i) molecular weights of CT of the two species affecting the capacity for precipitating protein; this effect has been observed by Barry (1989) in comparisons between legumes, and (ii) unknown mechanisms altering the reactiveness of CT with other plant compounds in the digestive processes of ruminants. All these aspects mentioned deserve further study.

(3) *There is a gap in information related to the effects of CT concentrations on sheep production in the range of 1 to 3% (on a DM basis).*

Barry (1989) and Waghorn *et al.* (1990), based upon digestive studies, have predicted that CT concentration in the range of 2 to 4% (on a DM basis) should improve the nutritive value of plants through: (i) reducing degradation of plant proteins, so increasing the quantity of protein passing out of the rumen for digestion in the intestines, and (ii) selective protection of plant proteins rich in essential amino acids. Research studies have shown that CT increases the availability and absorption of methionine and cysteine at the small intestine level (McNabb *et al.*, 1993a,b; Wang *et al.*, 1994a), thereby improving wool production. However, more quantitative evaluation of animal responses is required to define precisely the potential benefits achievable. Using the information of the surveys published by Terrill *et al.* (1992b) and Douglas *et al.*, (1993), only *Lotus corniculatus*, *Lotus tennuis*, *Coronilla varia* (Crownvetch) and *Ornithopus sativus*

(Serradella) appear to fall into the optimal CT (from 2 to 4% on a DM basis) concentration range recommended by Barry (1985), Waghom *et al.* (1990), and Terrill *et al.* (1992b). However, from the species mentioned above, only *Lotus corniculatus* seems to be of major agronomic relevance for New Zealand farming systems. Nevertheless, the potential nutritional benefits of the presence of CT in *Lotus corniculatus* on ruminant productivity has not yet been isolated by research studies. This is clearly an area which requires further investigation.

(4) *In the light of the results of Table 6.3., apparently the minimal and optimal CT concentrations required to increase wool production are higher than those to improve liveweight gain.*

This difference may be related to the factors which are controlling nutrient utilization and partitioning by the different tissues of ruminants, in particular of undegradable protein and essential amino acids. Sulphur-containing amino acids are of particular importance for wool production because both cysteine and methionine are precursors of cysteine, which is the principal amino acid of wool protein (Reis, 1979; Reis *et al.*, 1990). Several research studies revealed the "selective" protective action of CT in the degradation of cysteine and methionine in the rumen, increasing their absorption at the small intestine level (McNabb *et al.*, 1993a,b; Wang *et al.*, 1994). Kempton (1978) suggested that a higher ratio of protein to energy in the diet is required to support maximum wool growth than to support maximum liveweight gain in growing lambs. Therefore, these concepts need to be integrated into the delineation of the objectives of plant breeding programmes orientated to increase the levels of CT in economically important grass and legume species (eg perennial ryegrass, white clover, red clover, tall fescue) for improving wool and meat production.

(5) *Carcass gain and carcass fatness show little response to low CT concentrations.*

In contrast to the results of liveweight gain, the effects of low CT levels on carcass weight or carcass gain were smaller and usually not significant. This trend has also been reported with high CT concentrations (Terrill *et al.*, 1992b). These results may indicate that the positive effects of CT on liveweight gain have been concentrated on non-carcass components (Terrill *et al.*, 1992b). The lack of response in carcass fatness (expressed as GR) in Experiments 2 and 3 is not in agreement with the findings of Purchas and Keogh (1984) and Terrill *et al.*, (1992a), but agrees with the results of Douglas *et al.* (1995). The small response in carcass fatness to low CT concentrations in the current project could be the result of the greater CT concentrations of *Lotus pedunculatus* or *Hedysarum coronarium* (sulla) compared with those of perennial ryegrass, annual ryegrass, and Yorkshire fog. In general, the effects of the nutritive value of the diet on carcass composition have been found to be small compared with genotype differences reported in sheep (Theriez *et al.*, 1981). Further experiments are required to investigate the effects of CT in the range of 1 to 3% (on a DM basis) on carcass gain and carcass fatness.

(6) *Polyethylene glycol (PEG) supplementation appears to have unexpected effects on sheep performance.*

Polyethylene glycol has been used historically to assess the effect of CT on rumen digestion and animal performance given its properties of binding and inactivating CT, and it has generally been assumed to have no other effects on the digestive process (Jones and Mangan, 1977; Barry and Manley, 1986). However, it has been observed in several studies that PEG supplementation increased wool production (Experiment 3 and Liu *et al.*, unpublished) and liveweight gain (Terrill *et al.*, 1992a; and Niezen *et al.*, 1993a) in lambs. This effect appears to be confined to lambs grazing on perennial ryegrass. More research is needed on the role of the actions of PEG on digestive processes in ruminants.

6.4.2 Effects on diet selection, herbage intake, and ingestive behaviour parameters

The results of the current study indicate that low CT concentrations had no influence in the selective diet patterns of sheep. Oesophageal fistulated sheep grazing on Yorkshire fog swards, preferred and ate mostly green grass leaves rather than grass stem or white clover leaves, despite the significantly higher CT concentrations of leaves than that of stems in *Holcus* (Douglas *et al.*, 1993; Iason *et al.*, 1995) or the absence of CT in white clover leaves or petioles (Barry, 1989; Waghorn *et al.*, 1990). Supporting this information, Iason *et al.* (1995) concluded that it is unlikely that the low levels of CT in *Holcus lanatus* have a selectively-advantageous defensive role against herbivores. Even with forages which normally have high CT concentrations in their tissues (sainfoin, sulla, dock, *Lotus pedunculatus, Lotus corniculatus*), sheep consistently selected from the sward on offer those components with high CT concentrations (mainly leaves) rather than those with low CT concentrations (mainly stems) (Jones and Mangan, 1977; Waghorn and Jones, 1989; Terrill *et al.*, 1992a; Douglas *et al.*, 1995). In tropical areas, animal preferences have been negatively associated with the concentration of CT in plants (mainly leaves of trees with very high CT concentrations) (Provenza and Malechek, 1984; Provenza *et al.*, 1990; Distel and Provenza, 1991). However, considering the current evidence for temperate pastures, it is unlikely that CT influences the selection strategies of ruminants, the variation in the physical characteristics of plants and the distribution of components within the sward canopy probably being the most important factors determining animal preferences.

The negative effects of higher CT concentrations (CT ≥ 4% on a DM basis) on herbage intake have been postulated by several authors (Barry, 1989;

Waghorn *et al.*, 1990; Terrill *et al.*, 1992b). However, as found in the present investigation for perennial ryegrass, annual ryegrass, and Yorkshire fog, low CT concentration (≤ 0.42% on a DM basis) did not have any direct effect on herbage intake by sheep. These results are also supported by the similar patterns of grazing behaviour observed in Experiments 2 and 3 between PEG-lambs and NON-PEG lambs.

6.4.3 Effects on internal parasites

Although Experiments 2 and 3 were not specifically designed to measure the effects of CT on internal parasites, the results obtained showed that low CT concentrations had small effects on FEC, the results of Experiment 3 being more consistent than those of Experiment 2, which could be related to the higher CT concentrations reported in annual ryegrass and Yorkshire fog swards in the Uruguayan experiment (Chapter 5). In Experiment 3, the effects of CT on FEC were confirmed by the limited information on adult worm populations in the abomasum, small and large intestines. In a series of experiments evaluating the effect of CT on FEC (Niezen *et al.*, 1993a; Niezen *et al.*, 1994), lambs grazing on CT-containing plants (*Lotus pedunculatus*, *Lotus corniculatus*, and *Hedysarium coronarium*) had lower FEC than those grazing on perennial ryegrass. In some cases the effects of CT persisted for a short period (21 - 42 days), but the effects were not consistent across comparisons. This is a promising area of research and more experimental work needs to be done to isolate nutritional and non-nutritional effects which may be confounded, and to evaluate the effects of CT *per se* within the range of 2 to 4% (recommend as an optimum CT range to promote wool and meat production). FEC may not be a good indicator to test the effects of CT (Niezen *et al.*, 1993b), therefore, complementary information on adult worm populations in the abomasum, small and large intestines is required.

6.5 THE PLACE OF *HOLCUS LANATUS* IN GRAZING SYSTEMS

Holcus lanatus is widely distributed throughout the temperate grasslands of the world (Jacques, 1974; Watt, 1978), and is present in New Zealand pastures over a wide range of soil and climatic conditions (Jacques, 1974; Watkin and Robinson, 1974). Most of the research on this grass have been focused on agronomic aspects (Jacques *et al.*, 1962; Evans, 1967; Jacques, 1974; Haggar *et al.*, 1976; Frame, 1982, 1992; Harvey *et al.*, 1984; Watt, 1987) and genetic aspects (Jacques *et al.*, 1962; Clements and Easton, 1974; Muangthong, 1989), but few attempts have been made to characterize this grass in terms of its potential for animal production (Watkin and Robinson, 1974; Cameron, 1979). However, during the 1990s, there has been renewed interest in *Holcus lanatus* associated with the findings of low CT concentrations in its tissues (Terrill *et al.*, 1992b; Douglas *et al.*, 1993), and indications of its potential to aid in the control of gastro-intestinal parasites in sheep (Niezen *et al.*, 1993b). Now, with the information recently reported in the literature and that provided by the results of the current study, there is a clearer picture of the potential of this grass for sheep production under different grazing managements and environmental conditions. This information is summarized in Table 6.4, ryegrass and tall fescue being used as comparative species, and provides the basis for considerations of the potential role of *Holcus lanatus* for temperate grazing systems.

In general, the comparative studies between perennial ryegrass and Yorkshire fog swards grown mainly under fertile conditions and either under continuous and rotational grazing managements show that the main difference is the higher stocking rate capacity in favour of perennial ryegrass swards (commonly between 20 and 25% higher; Morton *et al.*, 1992; Hodgson *et al.*, 1995; Experiment 2). Possible explanations for this difference are: (i) the higher herbage production of perennial ryegrass swards compared with Yorkshire fog swards under adequate soil nutrient conditions (Haggar, 1976; Watt, 1987; Frame, 1992; Morton *et al.*, 1992) and (ii) a greater loss of ungrazed tissue in

Table 6.4. Summary of comparative grazing studies carried out with *Holcus lanatus* and other species on aspects of sheep performance.

References and Control(s) Species	GMg[1]	Period	Type of Animal	Wool production (mg/100 cm^{-2} day^{-1} or kg of fleece)				Daily or final liveweight gains (g day^{-1} or kg)				Carcass weight (Kg)				SRC[3]
				Control	*Holcus*	Gain(%)	Sig[2]	Control	*Holcus*	Gain(%)	Sig	Control	*Holcus*	Gain(%)	Sig	(%)
1. Perennial ryegrass and White clover	CG	Summer	Lambs	4.1	3.9	- 5	NS	195	199	+ 2	NS	—	—	—	—	—
2. Perennial ryegrass and White clover	RG	Autumn	Ewes	—	—	—	—	52	53	+ 1	NS	—	—	—	—	- 20
3.1 Perennial ryegrass	CG	Summer	Lambs	—	—	—	—	41.1	34.6	- 19	**	—	—	—	—	- 1
3.1 Tall fescue		to						31.6		+ 9	*					- 34
3.1 Browntop		Autumn						32.1		+ 8	*					- 23
3.2 Perennial ryegrass	CG	Summer	Lambs	—	—	—	—	32.7	27.8	- 18	*	—	—	—	—	+ 2
3.2 Tall fescue		to						27.3		+ 1	NS					- 13
3.2 Browntop		Autumn						27.2		+ 1	NS					- 17
4.1 Tall fescue	CG	Summer	Lambs	—	—	—	—	26.3	23.5	- 12	*	—	—	—	—	+ 17
4.2 Tall fescue		to						29.5	25.2	- 17	*					+ 7
4.3 Tall fescue		Autumn						36.9	30.3	- 22	*					+ 18
5. Perennial ryegrass and White clover	CG	Winter	Lambs	85	81	- 5	NS	172	144	- 20	NS	17.1	16.3	- 5	*	—
6. Tall fescue and White clover	RG	Spring	Lambs	111	118	+ 6	*	77	98	+ 27	**	14.0	14.8	+ 5	*	—
7. Tall fescue and White clover	RG	Summer	Lambs	107	112	+ 4	NS	75	77	+ 3	NS	14.1	14.3	+ 1	NS	—
8. Perennial ryegrass and White clover	RG	Autumn	Ewes	168	111	- 51	NS	—	—	—	—	—	—	—	—	—
9. Perennial ryegras and White clover	CG	Summer	Lambs	115	109	- 6	NS	131	121	- 8	NS	17.5	16.3	- 7	*	- 25
10. Annual ryegrass, White clover and Lotus	RG	Spring	Lambs	128	147	+ 15	**	108	152	+ 41	***	17.0	19.0	+ 12	***	+ 28

GMg[1] (Grazing management; RG = Rotational, CG = Continuous). Sig[2] (Significance; * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, NS = Not Significant). SRC[3] (Stocking rate capacity; difference (%) of *Holcus* from control).

REFERENCES: 1. Watkin and Robinson (1974); 2. Morton *et al.* (1992); 3.1. Niezen (1995; Season 91/92); 3.2. Niezen (1995; Season 92/93); 4. Niezen (1995); 5., 6., and 7. Liu *et al.* (unpublished data); 8. Experiment 1 (Chapter 3); 9. Experiment 2 (Chapter 4); and 10. Experiment 3 (Chapter 5).

Holcus swards (Hodgson *et al.*, 1995). In terms of liveweight gain, carcass weight, and wool production, lambs or ewes tended to attain higher performance on perennial ryegrass swards than on Yorkshire fog swards, though, in some experiments, these differences were modest and not significant, or even in some cases in favour of *Holcus.* In those experiments where sheep performance was greater on perennial ryegrass swards than in *Holcus lanatus*, the authors reported higher dietary organic matter digestibility and herbage intakes in favour of sheep grazing on perennial ryegrass (Experiments 1 and 2; Liu *et al.*, unpublished data). However, in Experiment 3, carried out during spring under low to moderate soil fertility conditions in the Basaltic region of Uruguay, Yorkshire fog swards had better nutritive value than annual ryegrass swards, associated principally with the later reproductive development of the former, which in tum resulted in better lamb performance on Yorkshire fog swards.

In contrast, Yorkshire fog swards carried consistently higher numbers of sheep per unit of area or time than tall fescue swards (Niezen, 1995; Hodgson *et al.*, 1995). These findings derived from trials carried out under continuous stocking management during spring and summer, where the production and persistence of tall fescue are severely affected by this management, particularly when the defoliation intensity is severe (Butler and Hodgson, 1993; Tavakoli, 1993). However, differences between swards in wool production, liveweight gains, and carcass weight per animal were equivocal, performance being better on Yorkshire fog swards than on tall fescue swards in the experiments reported by Liu *et al.* (unpublished data), but the opposite result was reported by Niezen (1995).

The potential usefulness of Yorkshire fog swards as an avenue to control internal parasites in sheep has been described by Niezen *et al.* (1993b) and Niezen (1995) under a moderate to high larval challenge. In a series of trials involving evaluations of trigger-drenched (group of lambs treated when they reached 1500 e.p.g) and suppressively-drenched (fortnightly treatment) lambs grazing on Yorkshire fog, tall fescue, browntop, and perennial swards, the authors noticed that the magnitude of the differences in lamb liveweight gains between drenching systems was lower for lambs grazing on Yorkshire fog than for those lambs grazing on other swards. In Experiment 3, even under low larval challenge, lambs grazing on Yorkshire fog had significantly lower FEC values and abomasal-intestinal worm populations than those grazing on annual ryegrass swards. The results of Experiments 2 and 3 indicate that the presence of CT in *Holcus lanatus* could be associated with this negative effect on internal parasites in sheep. However, other characteristics of *Holcus* (eg sward canopy structure, leaf surface texture, presence of unknown compounds) may inhibit larval establishment and/or survival, and therefore reduce lamb worm burdens.

The findings of the present study and other research results show the potential of *Holcus lanatus* for lamb production, as a viable altemative to perennial ryegrass and tall fescue in poorer environments where the production, persistence and grazing management practices of those grasses are limited. They also reveal the potential advantages of *Holcus* in the biological control of worm parasites in sheep. However, more investigations are needed to identify and isolate the relative importance of factors involved in limiting the build up of intemal parasites in lambs grazing Yorkshire fog, before any attempt is made to integrate and implement these findings into farm systems. In addition, the potential benefits for animal production from Yorkshire fog under conditions of limited soil fertility deserves more experimental investigation.

6.6 CONCLUSIONS

The most significant findings arising from the current research programme with respect to the influence of condensed tannins on diet selection, herbage intake, ingestive behaviour, sheep performance, and the potential value of *Holcus lanatus* for animal production are summarized below. Areas in which further research is required are also suggested.

1. Sheep grazing highly fertilized New Zealand perennial ryegrass/white clover swards showed increased production compared to sheep grazing Yorkshire fog/white clover swards. Evidence from Experiment 2 established that perennial ryegrass swards had a higher potential carrying capacity than Yorkshire fog swards.

2. A spring grazing trial (Experiment 3) undertaken in Uruguay under moderate soil nutrient conditions, showed improved lamb performance and a higher potential carrying capacity from Yorkshire fog swards than from annual ryegrass under rotational grazing management. These findings indicate the potential value of Yorkshire fog swards for moderate soil fertility conditions and warrant more experimental investigation.

3. Lower levels of parasitism were recorded in lambs grazing *Holcus lanatus* swards than in lambs grazing on *Lolium* spp. under conditions of high or very light parasite challenge and indicated the potential advantage of *Holcus* in the biological control of worm parasites. More research is needed in this area to determine causative relationships.

4. Herbage intake and ingestive behaviour results suggest that the most important factors limiting intake were nutritional rather than behavioural in origin, reflecting differences in diet digestibility rather than in any ingestive behavioural component.

5. The diet selected by oesophageal fistulated sheep (OF) was principally green grass leaf from both *Holcus lanatus* and *Lolium* spp. swards. The major determinants of the diet selection patterns of OF sheep were the availability and vertical distribution of the sward species and their morphological components within the sward canopy, rather than any inherent deliberate selection behaviour for any plant species or plant component.

6. Evidence of low CT concentrations in *Lolium perenne* were reported in the present study for the first time, and the presence of low CT levels in *Holcus lanatus* was confirmed.

7. The effects of low dietary CT concentrations (≤ 0.2% on a DM basis, Experiment 2) in Yorkshire fog swards on liveweight gain and wool production, measured in terms of response to PEG supplementation, were small and lasted for only 4 - 5 weeks, indicating some degree of adaptation by the sheep. However, further increases in CT levels in annual ryegrass and Yorkshire fog diets (CT ranged from 0.37 to 0.42% on a DM basis) consistently increased body and wool growth, indicating that probably CT concentrations in forage diets close to 0.5% on a DM basis are the minimum needed to significantly improve ruminant production.

8. Similar dietary CT concentrations between *Holcus lanatus* and *Lolium* spp. were reported in the three experiments. However, the liveweight gain, wool growth, carcass gain, and faecal egg count responses to CT tended to be greater in lambs grazing on *Holcus lanatus* swards than in lambs grazing on *Lolium* spp., which may indicate that the CT present in *Holcus* are more efficient in binding plant proteins than those in *Lolium* spp. The reasons for this apparent difference in animal responses to CT between these grasses require further investigation.

9. Further information from this study also suggests that the low CT concentrations reported in *Holcus lanatus* and *Lolium* spp. did not influence diet selection, herbage intake or grazing behaviour pattems of the experimental animals.

10. The results clearly indicate a promising unexplored potential to improve the nutritive value of *Lolium* spp. and *Holcus*, thereby enhancing ruminant production potential by up-grading the CT levels of those grasses either through conventional plant breeding programmes or by genetic engineering.

BIBLIOGRAPHY

Afini, A.A., and Clark, V. 1984. Computer-aided Multivariate Analysis. Lifetime Learning Publications Belmont, California, USA. 458 pp.

Ahn, J.H., Robertson, B.M., Elliot, R., Gutterridge, R.C., and Ford, C.W. 1989. Quality assessment of tropical browse legumes: Tannin content and protein degradation. Animal Feed Science and Technology, 27: 147 - 156.

Allden, W.G., and Whittaker, I.A. 1970. The determination of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. Australian Journal of Agricultural Research, 21: 755 - 766.

Armstrong, R.H., Robertson, E., Lamb, C.S., Gordon, I.J., and Elston, D.A. 1993. Diet selection by lambs in ryegrass-white clover swards differing in the horizontal distribution of clover. Proceedings of the XVII International Grassland Congress, 715 - 716.

Arnold, G.W. 1966a. The special senses in grazing animals. I. Sight and dietary habits in sheep. Australian Journal of Agricultural Research, 17: 521 - 529.

Arnold, G.W. 1966b. The special sense in grazing animals. II. Smell, taste, and touch and dietary habits in sheep. Australian Journal of Agricultural Research, 17: 531 - 542.

Arnold, G.W., and Hill, J.L. 1972. Chemical factors affecting selection of food plants by ruminants. In: Photochemical Ecology: Annual Proceedings of the Photochemical Society, Nº 8. Harborne, J.L., Editor. pp. 71 - 101.

Arnold, G.W., and Maller, R.A. 1977. Effects of nutritional experience in early life and adult life on the performance and dietary habits of sheep. Applied Animal Ecology, 3: 5 - 26.

Arnold, G.W., and Dudzinski, M.L. 1978. Ethology of Free-ranging Domestic Animals. Elsevier, Holland.

Arnold, G.W. 1981. Grazing behaviour. In: World Animal Science Vol. B1: Grazing Animals. Morley, F.H.W., Editor. Elsevier, Holland. pp 289 - 301.

Arnold, G.W. 1987. Influence of the biomass, botanical composition and sward height of annual pastures on foraging behaviour of sheep. Journal of Applied Ecology, 24: 759 - 772.

Bailey, R.W. 1967. Quantitative studies of ruminant digestion. II. Loss of ingested plant carbohydrates from the reticulo-rumen. New Zealand Journal of Agricultural Research, 10: 15 - 32.

Baker, R.D. 1985. Advances in cow grazing systems. In: Grazing. Occasional Symposium Nº 19. British Grassland Society. Frame., J., Editor. pp 155 - 166.

Ballard, R.A., Simpson, R.J., and Pearce, G.R. 1990. Losses of the digestible components of annual ryegrass (*Lolium rigidum* Gaudin) during senescence. Australian Journal of Agricultural Research, 41: 719 - 731.

Barry, T.N. 1981. Protein metabolism in growing lambs fed on fresh ryegrass (*Lolium perenne*)-white clover (*Trifolium repens*) pastures *ad lib.* British Journal of Nutrition, 46: 521 - 532.

Barry, T.N. 1985. The role of condensed tannins in the nutritional value of Lotus pedunculatus for sheep. 3. Rates of body and wool growth. British Journal of Nutrition, 54: 211 - 217.

Barry, T.N. 1989. Condensed tannins: Their role in ruminant nutrition and carbohydrate digestion and possible effects upon rumen ecosystem. In: The roles of Protozoa and Fungi in Ruminant Digestion. Nolan, J.V., Leng, R.A., and Demeyer, I.D., Editors. Penambul Books. Armidale, Australia. pp. 102 - 145.

Barry, T.N., and Blaney, T.R. 1987. Secondary Compounds of Forages. In: The Nutrition of Herbivores. Hacker, J.B., and Ternouth, J.H., Editors. Academic Press. Sydney N.S.W, Australia. pp. 92 - 119.

Barry, T.N., and Duncan, S.J. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 1. Voluntary intake. British Journal of Nutrition, 51: 485 - 491.

Barry, T.N., and Forss, D.A. 1984. The condensed tannins of vegetative *Lotus pedunculatus*, its regulation by fertiliser application, and effects upon protein solubility. Journal of the Science of Food and Agriculture,34:1047-1056.

Barry, T.N., and Manley, T.R. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 2. Quantitative digestion of carbohydrates and proteins. British Journal of Nutrition, 51: 493 - 504.

Barry, T.N., and Manley, T.R. 1986. Interrelationships between the concentrations of total condensed tannins, free condensed tannins and lignin in *Lotus* spp. and their possible consequences in ruminant nutrition. Journal of the Science of Food and Agriculture, 37: 248 - 254.

Barry, T.N., and Manley, T.R., and Duncan, S.J. 1984. The role of condensed tannins in the nutritional value of *Lotus pedunculatus* for sheep. 4. Sites of carbohydrate and protein digestion as influenced by dietary reactive tannin concentration. British Journal of Nutrition, 55: 123 - 137.

Barry, T.N., and Reid, C.S.W. 1984. Nutritional effects attributable to condensed tannins, cyanogenic glycosides and oestrogenic compounds in New Zealand forages. In: Forage Legumes for Energy-efficient Animal Production. Barnes, R.F., Bell, P.R., Brougham, R.W., Marten, G.C., and Minson, D.J., Editors.Springfield, V.A., U.S.A., U.S.D.A, A.R.S.pp 251-259.

Barthram, G.T. 1981. Sward structure and the depth of the grazed horizon. Grass and Forage Science, 36:130-131.

Barthram, G.T. 1986. Experimental techniques: The HFRO sward stick. Biennial Report 1984 - 1985, H.F.O, Penicuik. pp. 29 - 30.

Barthram, G.T., and Grant, S.A. 1984. Defoliation of ryegrass-dominated swards by sheep. Grass and Forage Science, 39: 211-219.

Bazely, D.R. 1989. Discrimination learning in sheep cues varying in brightness and hue. Applied Animal Behaviour Science , 23: 293 - 299.

Bazely, D.R. 1990. Rules and cues used by sheep foraging in monoculture. In: Behavioural Mechanisms of Food Selection. NATO ASI Series, Vol. G 20. Hughes, R.N., Editor. pp. 333 - 367.

Bell, F.R. 1970. The regulation of voluntary feed intake. Proceedings of the Nutrition Society. 30: 103 - 109.

Bemhaja, M. 1993. *Holcus lanatus* L. "La Magnolia". Serie Técnica Nº32. Instituto Nacional de Investigación Agropecuaria (INIA), Uruguay.

Bighmam, M.L. 1974. Effects of shearing interval on fleece weight and wool growth on a delineated midside patch. New Zealand Journal of Agricultural Research, 17: 407 - 410.

Bircham, J.M. 1981. The effects of change in herbage mass on herbage growth, senescence and net production rates in a continuously stocked mixed species swards. In: Wright, C.E., (ed). Plant Physiology and Herbage Production. Occasional Symposium Nº 13, British Grassland Society. pp. 85 - 87.

Bircham, J.M., and Hodgson, J. 1983. The influence of sward conditions on rates of herbage growth and senescence in mixed swards under continuous stocking management. Grass and Forage Science,38:323-331.

Birrell, H.A. 1989. The influence of pasture and animal factors on the consumption of pasture by grazing sheep. Australian Journal of Agricultural Research, 40: 1261 - 1275.

Birrell, H.A. 1992. Factors associated with the rate of growth of clean wool on grazing sheep. Australian Journal of Agricultural Research, 43: 265 - 275.

Black, J.L. 1990. Nutrition of the grazing ruminant. Proceedings of the New Zealand Society of Animal Production, 50: 7 - 27.

Black, J.L., and Kenny, P.A. 1984. Factors affecting diet selection by sheep. II. Height and density of pasture. Australian Journal of Agricultural Research, 35: 565 - 578.

Bootsmam, A., Ataja, A.M., and Hodgson, J. 1990. Diet selection by young deer grazing mixed ryegrass/white clover pastures. Proceedings of the New Zealand Grassland Association, 51: 187 - 190.

Briseño, V.M., and Wilman, D. 1981. Effects of cattle grazing, sheep grazing, cutting and sward height on a grass-white clover sward. Journal of Agricultural Science, Cambridge, 97: 699 - 706.

Broadhurst, R.B., and Jones, W.T. 1978. Analysis of condensed tannins using acidified vanillin. Journal of the Science of Food and Agriculture, 28 : 788 - 794.

Burlison, A.J. 1987. Sward canopy structure and ingestive behaviour in grazing animals. PhD Thesis. University of Edinburgh, Scotland.

Burlison, A.J., and Hodgson, J. 1985. The influence of sward structure on the mechanics of the grazing process in sheep. Animal Production, 40: 530 - 531.

Burlison, A.J., Hodgson, J., and Illius, A.W. 1991. Sward canopy structure and the bite dimensions and bite weight of grazing sheep. Grass and Forage Science, 46: 29 - 38.

Burnham, D.L., Parker, W.J., and Morris, S.T. 1994. The effect of pasture height on herbage intake and ewe production under continuous stocking management during autumn. Proceedings of the New Zealand Society of Animal Production, 54: 75 - 78.

Burns, J.C., Pond, K.D., and Fisher, D.S. 1994. Measurements of forage intake. In: Forage Quality, Evaluation, and Utilization. Fahey, Jr. G. C., Editor. A.S.A., C.S.S.A., S.S.S.A. Madison, Wisconsin, USA. pp. 494 - 532.

Burrit, E.A., and Provenza, F.D. 1989. Food aversion learning: Ability of lambs to distinguish safe from harmful foods. Journal of Animal Science, 67: 1731 - 1739.

Burrit, E.A., and Provenza, F.D. 1991. Ability of lambs to learn with a delay between food ingestion and consequences given meals containing novel and familiar foods. Applied Animal Behaviour Science, 32: 179 - 189.

Butler, B.M. 1991. The packages of tissue turnover analysis and point quadrat analysis. Mimeograph, Massey University, New Zealand.

Butler, B.M., Hoogendoorn, C.J., and Richardson, M.A. 1987. Pasture quality and animal performance over late spring and summer. Proceedings of the New Zealand Society of Animal Production, 47: 31 - 33.

Cahn, M.G., and Harper, J.L. 1976. The biology of the leaf mark polymorphism in *Trifolium repens* L. 2. Evidence for the selection of leaf marks by rumen fistulated sheep. Heredity, 37: 327 - 333.

Cameron, N.E. 1979. A study of the accessibility of *Holcus* spp. to Perendale sheep. Masters Thesis. Massey University, New Zealand. 106 pp.

Chacon, E.A., and Stobbs, T.H. 1976. Influence of progressive defoliation of a grass sward in the eating behaviour of cattle. Australian Journal of Agricultural Research, 27: 709 - 727.

Chacon, E.A., Stobbs, T.H and Dale, M.B. 1978. Influence of sward characteristics on grazing behaviour and growth of Hereford steers grazing tropical pastures. Australian Journal of Agricultural Research, 28: 89 - 102.

Chestnutt, D.M.B. 1992. Effect of sward surface height on the performance of ewes and lambs continuously grazed on grass/clover and nitrogen-fertilized grass swards. Grass and Forage Science, 47: 70 - 80.

Chiquette, J., Cheng, K.J., Costerton, J.W., and Milligan, L.P. 1988. Effects of tannins on the digestibility of two isosynthetic strains of birdsfoot trefoil (*Lotus corniculatus*) using *in vitro* and in sacco techniques. Canadian Journal of Animal Science, 68: 751 - 760.

Clark, D.A., Lambert, M.G., Rolston, M.P., and Dymock, N. 1982. Diet selection by goats and sheep on hill country. Proceedings of the New Zealand Society of Animal Product, 42: 155 - 157.

Clark, D.A., Rolston, M.P., Lambert, M.G., and Budding, P.J. 1984. Pasture composition under mixed sheep and goat grazing on hill country. Proceedings of the New Zealand Grassland Association, 45: 160 - 166.

Clark, D.A., and Harris, P.S. 1985. Composition of the diet of sheep grazing swards of differing white clover content and spatial distribution. New Zealand Journal of Agricultural Research, 28: 233 - 240.

Clark, D.A., and Hodgson, J. 1986. Techniques to estimate botanical composition of diet samples collected from oesophageal fistulates. Mimeograph, DSIR, Palmerston North.

Clark, H. 1993. Influence of sward characteristics on the diet selection by grazing sheep in perennial ryegrass swards maintained at two sward heights. Proceedings of the XVII International Grassland Congress, 728 - 730.

Clausen, T.P; Provenza, F.D., Burrit, E.A., Reichardt, P.B., and Bryant., J.P. 1990. Ecological implications of condensed tannins structure: A case study. Journal of Chemical Ecology, 16(8): 2381 - 2392.

Clements, R.J., and Easton, H.S. 1974. Genetic shifts in a Yorkshire fog population grazed by sheep. Proceedings of the New Zealand Grassland Association, 38: 268 - 277.

Combellas, J., and Hodgson, J. 1979. Herbage intake and milk production by grazing dairy cows. I. The effects of variation in herbage mass and daily herbage allowance in a short-term trial. Grass and Forage Science, 34: 209 - 214.

Cooley, W.W., and Lohnes, P.R. 1971. Multivariate data analysis. John Wiley and Sons, New York. 364 pp.

Cope, W.A., Bell, T.A., and Smart, Jr., W.W.G. 1971. Seasonal changes in an enzyme inhibitor and tannin content in Serica Lespedeza. Crop Science, 11: 893 - 895.

Cope, W.A., and Burns, J.C. 1971. Relationship between tannin levels and nutritive value of Serica. Crop Science, 11: 231 - 233.

Corsi, W. 1975. Clima. In: Pasturas IV. Centro de Investigaciones Agrícolas Alberto Boeger (CIAAB). MAP. Montevideo, Uruguay.

Crawley, M.J., and Krebs, J.R. 1992. Foraging Theory. In: Natural Enemies: The Population Biology of Predators, Parasites and Diseases. Crawley, M.J., Editor. Blackwell Scientific Publications. Oxford, Boston. pp. 90 - 114.

Curll, M.L. 1982. The grass and clover content of pastures grazed by sheep. Herbage Abstracts, 52: 403 - 411.

Dearker, J.M., Young, M.J., Fraser, T.J., and Rowarth, J.S. 1994. Carcass, liver and kidney characteristics of lambs grazing plantain (*Plantago lanceolata*), chicory (*Chichorium intibus*), white clover (*Trifolium repens*) or perennial ryegrass (*Lolium perenne*). Proceedings of the New Zealand Society of Animal Production, 54: 99 - 104.

Demment, M.W., Distel., R.A., Griggs, T.C., Laca, E.A., and Deo, G.P. 1993. Selective behaviour of cattle grazing ryegrass swards with horizontal heterogeneity in patch height and bulk density. Proceedings of the XVII International Grassland Congress, 712 - 714.

Demment, M.W., and Greenwood, G.B. 1988. Forage ingestion: effects of sward characteristics and body size. Journal of Animal Science, 66: 2380 - 2392.

Demment, M.W., and Van Soest, P.J. 1985. A nutritional explanation for body-size patterns of ruminant and non-ruminant herbivores. The American Naturalist, 125: 641 - 672.

Distel, R.A., and Provenza, F.D. 1991. Experience early in life affects voluntary intake of blackbrush by goats. Journal of Chemical Ecology, 17: 431-450.

Dougherty, C.T., Bradley, N.W., Lauriault, L.M; Arias, J.E., and Cornelius, P.L. 1992. Allowance-intake relationships of cattle grazing vegetative tall fescue. Grass and Forage Science, 44: 295 - 342.

Dougherty, C.T., Bradley, N.W., Cornelius, P.L., and Lauriault, L.M. 1989. Ingestive behaviour of beef cattle offered different forms of Lucerne (*Medicago sativa* L.). Grass and Forage Science, 44: 335 - 302.

Douglas, G.B., Donkers, P., Foote, A.G., and Barry, T. 1993. Determination of extractable and bound condensed tannins in forages species. Proceedings of the XVII International Grassland Congress, 204 - 206.

Douglas, G.B., Wang, Y., Waghorn, G.C., Barry, T.N., Purchas, R.W., Foote, A.G., and Wilson, G.F. 1995. Liveweight gain and wool production of sheep grazing *Lotus corniculatus* and lucerne (*Medicago sativa*). New Zealand Journal of Agricultural Research, 38: 95 - 104.

Dudzinski, M.L., and Arnold. W.G. 1973. Comparisons of diet of sheep and cattle grazing together on sown pastures on the southern tablelands of the New South Wales by principal components analysis. Australian Journal of Agricultural Research, 24: 899 - 912.

Earle, D.F., and McGowan, A.A. 1979. Evaluation and calibration of an automated rising plate for estimated dry matter yield of pasture. Australian Journal of Experimental Agriculture and Animal Husbandry, 19: 337 - 343.

Ellis, W.C. 1978. Determinants of grazed forages intake and digestibility. Journal of Dairy Science, 61: 1828 - 1840.

Erlinger, L.L., Tolleson, D.R., and Brown, C.J. 1990. Comparison of bite size, biting rate and grazing time of beef heifers from herds distinguished by mature size and rate of maturity. Journal of Animal Science, 68: 3578 - 3587.

Evans, P.S. 1967. Leaf strength studies of pasture grasses. II. Strength, cellulose content and sclerenchyma tissue proportions of eight grasses grown as single plants. Journal of Agricultural Science, Cambridge, 69: 175 - 181.

Familton, A.S. 1983. Internal parasites and the growth of lambs. In: Lamb growth. Animal industries workshop. Lincoln College, Canterbury, New Zealand.

Fariani, A., Warly, A., Matsui, L., Fujihara, T., and Harumoto, T. 1994. Rumen degradability of Italian ryegrass (*Lolium multiflorum*) harvested at three different growth stages in sheep. Asian Australasian Journal of Animal Science, 7: 41 - 48.

Fennessy, P.F., and Milligan, K.E. 1987. Grazing management of Deer. In: Livestock feeding on pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 111 - 118.

Flores, E.R., Provenza, F.D., and Balph, D.F. 1989a. Relation between plant maturity and foraging experience of lambs grazing Hycrest Crested Wheatgrass. Applied Animal Behaviour Science, 23: 279 - 284.

Flores, E.R., Provenza, F.D., and Balph, D.F. 1989b. The effects of experience on the foraging skill of lambs: Importance of plant form. Applied Animal Behaviour Science, 23: 285 - 291.

Forbes, J.M. 1986. The Voluntary Intake of Farm Animals. Butterworth and Co. Ltd. London, Boston. 206 pp.

Forbes, J.M. 1988a. Researching the plant-animal interface: the investigation of ingestive behaviour in grazing animals. Journal of Animal Science, 66: 2369 - 2379.

Forbes, J.M. 1988b. Metabolic aspects of metabolic regulation of voluntary food intake and appetite. Nutrition Research Reviews, 1: 145 - 168.

Forbes, T.D.A. 1982. Ingestive behaviour and diet selection in grazing cattle and sheep. PhD Thesis. University of Edinburgh, Scotland.

Forbes, T.D.A., and Hodgson, J. 1985. Comparative studies of the influence of sward conditions on the ingestive behaviour of cows and sheep. Grass and Forage Science, 40: 69 - 77.

Frame, J. 1982. Yield and quality response of secondary grasses to fertiliser nitrogen. In: Efficient Grassland Farming. British Grassland Society. Occasional Symposium Nº 14. Corrall, A.J., Editor. pp. 292 - 294.

Frame, J. 1992. Improved Grassland Management. Farming Press Books. Ipswich, United Kingdom. 351 pp.

Frame, J. 1993. Herbage mass. In: Sward Measurement Handbook. 2nd Edition. Davis, A., Baker, R.D., Grant, S.A., and Laidlaw, A.S., Editors. British Grassland Society. University of Reading, UK. pp. 39 - 68.

Fraser, D.L. 1994. Persistence of dryland pasture species in mixed swards in Canterbury. Proceedings of the New Zealand Grassland Association, 56: 77 - 79.

Fraser, D.L., Hamilton, B.K., and Poppi, D.P. 1990. Effect of duodenal infusion of protein or amino acids on nitrogen retention of lambs consuming fresh forage. Proceedings of the New Zealand Society of Animal Production, 50: 43 - 48.

Freedland, W.J., and Janzen, D. 1974. Strategies in herbivory by mammals: The role of plant secondary compounds. The American Naturalist, 108(961): 269 - 289.

Freer, M. 1981. The control of food intake by grazing animals. In: World Animal Science Vol. B1: Grazing Animals. Morley, F.H.W., Editor. Amsterdam, Elsevier. pp 105 - 120. 405 pp.

Garner, F. 1963. The palatability of herbage plants. Journal of the British Grassland Society, 18: 79 - 89.

Geenty, K.G. and Rattray, P.V. 1987. The energy requirements of grazing sheep and cattle. In: Livestock Feeding on Pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 39 - 54. 145 pp.

Gittins, R. 1985. Canonical analysis: a review with applications in ecology. Biomathematics 12. Berlin, Springer Verlag. 351 pp.

Goatcher, W.D., and Church, D.C. 1970a. Taste responses in ruminants. II. Reactions of sheep to acids, quinine, urea and sodium hydroxide. Journal of Animal Science, 30: 784 - 790.

Goatcher, W.D., and Church, D.C. 1970b. Taste responses in ruminants. IV. Reactions of pygmy goats, normal goats, sheep and cattle to acetic acid and quinine hydrochloride. Journal of Animal Science, 31: 373 - 382.

Gong, Y. 1994. Comparatives studies of effects of sward structure on ingestive behaviour of sheep and goats grazing grasses and legumes. PhD Thesis. Massey University, New Zealand. 330 pp.

Gong, Y., Hodgson, J., Lambert, M.G., Chu, A.C.P., and Gordon, I.L. 1993. Comparisons of response patterns of bite weight and bite dimensions between sheep and goats grazing a range of grasses and clovers. Proceedings of the XVII International Grassland Congress, 726 - 727.

Gordon, I.J., and Illius, A.W. 1988. Incisor arcade structure and diet selection in ruminants. Functional Ecology, 2: 15 - 22.

Gordon, I.J., and Lascano, C. 1993. Foraging strategies of ruminant livestock on intensively managed grasslands: potential and constraints. Proceedings of the XVII International Grassland Congress, 681 - 690.

Grant, S.A., Suckling, D.E., Smith, H.K., Torvell, L., Forbes, T.D.A., and Hodgson, J. 1985. Comparative studies of diet selection by sheep and cattle: The hill grasslands. Journal of Ecology, 73: 987 - 1004.

Grant, S.A., Torvell, L., Smith, H.K., Suckling, D.E., Forbes, T.D.A., and Hodgson, J. 1987. Comparative studies of diet selection by sheep and cattle: Blanket bog and Heather moor. Journal of Ecology, 75: 947 - 960.

Grant, S.A. 1993. Resources description: vegetation and sward components. In: Sward Measurement Handbook. 2nd Edition. Davis, A., Baker, R.D., Grant, S.A., and Laidlaw, A.S., Editors. British Grassland Society. pp. 69 - 98. 319 pp.

Greenwood, G.B., and Demment, M.W. 1988. The effect of fasting on short-term cattle grazing behaviour. Grass and Forage Science, 43: 377 - 386.

Hagerman, A.E., and Butler, L.G. 1978. Protein precipitation method for the quantitative determination of tannins. Journal of Agricultural Food Chemistry, 26(4): 809 - 812.

Hagerman, A.E., Robbins, C.T., Weerasuriya, Y., Wilson, T.C., and MacArthur, C. 1992. Tannin chemistry in relation to digestion. Journal of Range Management, 45: 57 - 62.

Haggar, R.J. 1976. The seasonal productivity, quality, and response to nitrogen of four indigenous grasses compared with *Lolium perenne*. Journal of the British Grassland Society, 39: 159 - 166.

Harvey, B.M.R., Crothers, S.H., and Hayes, P. 1984. Dry matter and quality herbage harvested from *Holcus lanatus* and *Lolium perenne* grown in monoculture and in mixtures. Grass and Forage Science, 39: 353 - 361.

Hides, D.H., Lovatt, J.A., and Hayward, M.V. 1983. Influence of the stage of maturity on the nutritive value of Italian ryegrasses. Grass and Forage Science, 38: 33 - 38.

Hodgson, J. 1971. The development of solid food, and the physical form of previous experience of solid food, and the physical form of the diet, on the development of food intake after weaning. Animal Production, 13: 15 - 24.

Hodgson, J. 1977. Factors limiting herbage intake by the grazing animal. Proceedings of International Meeting on Animal Production from Temperate Grassland, Dublin, Ireland. pp 70 - 75.

Hodgson, J., and Milne, J.A. 1978. The influence of weight of herbage per unit of area and per animal upon the grazing behaviour of sheep. In: Proceedings of the 7th Meeting of the European Grassland Federation. Gent, Belgium, (1978). Part II, Session 4: 4.31 - 4.38.

Hodgson, J. 1981. Influence of sward characteristics on diet selection and herbage intake by the grazing animal. In: Nutritional Limits to Animal Production from Pastures, Queensland, Australia. Hacker, J.B., Editor. CAB Publication. pp. 153 - 166.

Hodgson, J., and Jamieson, W.S. 1981. Variations in herbage mass and digestibility, and the grazing behaviour and herbage intake of adult cattle and weaned calves. Grass and Forage Science, 36: 39 - 48.

Hodgson, J. 1982. Ingestive behaviour. In: Herbage Intake Handbook. British Grassland Society. Editor, J.D. Leaver. pp. 113 - 139. 143 pp.

Hodgson, J., and Grant, J.A. 1982. Grazing animals and forages resources in the hills and uplands. In: The Effective Use of Forage and Animal Resources in the Hills and Uplands. Proceedings of Occasional Symposium Nº 12., The British Grassland Society, Edinburgh. Frame, J., Editor. UK. pp. 41 - 57.

Hodgson, J. 1984. Sward conditions, herbage allowance and animal production: an evaluation of research results. Proceedings of the New Zealand Society of Animal Production, 44: 99 - 104.

Hodgson, J. 1985a. The control of herbage intake in the grazing ruminant. Proceedings of the Nutrition Society, 44: 339 - 346.

Hodgson, J. 1985b. Grazing behaviour and herbage intake. In: Grazing. Occasional Symposium Nº 19. British Grassland Society. Frame., J., Editor. pp 51 - 64.

Hodgson, J. 1985c. The significance of sward characteristics in the management of temperate sown pasture. Proceedings of the XVI International Grassland Congress. pp 107 - 128.

Hodgson, J., Clark, D.A., and Wewala, S. 1989. The influence of physical and biochemical characteristics upon selection of white clover by grazing sheep. Proceedings of the XVI International Grassland Congress, 1049 - 1050.

Hodgson, J. 1990. Grazing management - Science into Practice. Longman Handbooks in Agriculture, London, UK. 200 pp.

Hodgson, J. 1993a. Foraging Strategy and Plant Communities. In: International Symposium on Grassland Resources. Abstracts, Inner Mongolia, P. R. China. pp. 4. pp 188.

Hodgson, J. 1993b. What´s new in grazing management research. In: Proceedings of the 1993 Central Districts Sheep & Beef Farmer´s Conference. Palmerston North, New Zealand. 2: 61 - 66.

Hodgson, J., Clark, D.A., and Mitchell, R.J. 1994. Foraging behaviour in grazing animals and its impact on plant communities. In: Forage Quality, Evaluation, and Utilization. Fahey, Jr. G. C., Editor. A.S.A. Inc., C.S.S.A. Inc., S.S.S.A Inc. Madison, Wisconsin, USA pp. 786 - 827. pp. 998.

Hodgson, J., Niezen, J.H., Montossi, F., Liu, F., and Butler, B.M. 1995. Comparative studies on animal performance and parasite infestation in sheep grazing Yorkshire fog, perennial ryegrass, and tall fescue pastures. Proceedings of the New Zealand Grassland Association, 57: (In press).

Holmes, C.W. 1987. Pastures for dairy cattle. In: Livestock Feeding on Pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 133 - 142. 145 pp.

Holmes, C.W., Hoogendoorn, C.J., Ryan, M.P. and Chu, A.C.P. 1992. Some effects of herbage composition, as influenced by previous grazing management, on milk production by cows grazing on ryegrass/white clover pastures. 1. Milk production in early spring: effects of different regrowth intervals during preceding winter period. Grass and Forage Science, 47: 309 - 315.

Holmes, C.W. and Wilson, G.F. 1987. Milk Production from Pastures. Revised Edition. Butterworths (NZ) Ltd. Wellington, New Zealand.

Hoogendoorn, C.J., Holmes, C.W., and Chu, A.C.P. 1992. Some effects of herbage composition, as influenced by previous grazing management, on milk production by cows grazing on ryegrass/white clover pastures. 2. Milk production in late spring/summer: effects of grazing intensity during preceding spring period. Grass and Forage Science, 47: 316 - 325.

Horigome, T, and Uchida, S. 1981. Nutritional quality of leaf protein prepared from crops containing phenolic compounds and polyphenolase. Proceedings of the XIV International Grassland Congress, 362 - 364.

Howarth, R.E; Glopen, B.P., Fesser, A.C., and Brands, S.A. 1978. A possible role of leaf cell rupture in legume pasture bloat. Crop Science,18:129-133.

Hu, Y. 1993. A comparative study of defoliation in *Holcus lanatus* and *Lolium perenne* pastures grazed by sheep. Masters Thesis. Massey University. New Zealand. 86 pp.

Hughes, T.P., Sykes, A.R., and Poppi, D.P. 1984. Diet selection of young ruminants in late spring. Proceedings of the New Zealand of Animal Production, 44: 109 - 112.

Hughes, T.P., Sykes, A.R., Poppi, D.P. and Hodgson, J. 1991. The influence of sward structure on peak bite force and bite weight in sheep. Proceedings of the New Zealand of Animal Production, 50: 153 - 158.

Hume, D.E. 1991. Primary growth and quality characteristics of *Bromus willdenowii* and *Lolium multiflorum*. Grass and Forage Science,46:313-324.

Iason, G.R., Hodgson, J., and Barry, T. 1995. Variation in condensed tannins concentration of a temperate grass (*Holcus lanatus*) in relation to season and reproductive development. Journal of Chemistry Ecology (In press).

Illius, A.W., Clark, D.A., and Hodgson, J. 1992. Discrimination and patch choice by sheep grazing grass-clover swards. Journal of Animal Ecology, 61: 183 - 194.

Illius, A.W. and Gordon, I.J. 1987. The allometry of food intake in grazing ruminants. Journal of Animal Ecology, 56: 989 - 999.

Illius, A.W. and Gordon, I.J. 1990. Constraints on diet selection and foraging behaviour in mammalian herbivores. In: Behavioural Mechanisms of Food Selection. NATO ASI Series, Vol. G 20. Hughes, R.N., Editor.pp. 369-393.

Illius, A.W. and Gordon, I.J. 1993. Diet selection in mammalian herbivores: Constraints and Tactics. In: Diet Selection: An Interdisciplinary Approach to Foraging Behaviour. Hughes, R.N., Editor. Blackwell Scientific Publication, Oxford, Boston. pp. 157 - 181.

Inoue, T., Brookes, I.M., John, A., Barry, T.N., and Hurt, W.F. 1993. Effect of physical resistance in perennial ryegrass leaves on feeding value for sheep. Proceedings of the XIV International Grassland Congress, 570 - 571.

Ivins, J.D. 1955. The palatability of herbage. Herbage Abstracts, 25(2): 75 - 79.

Ivins, J.D. 1952. The relative palatability of herbage plants. Journal of the British Grassland Association, 7: 43 - 54.

Jacques, W.A. 1974. Yorkshire fog (*Holcus lanatus*). Its potential as pasture species. Proceedings of the New Zealand Grassland Association, 35: 249 - 257.

Jacques, W.A., Robinson, B.R., Watkin, B.R., Clements, R.J., Hill, M.J., and Scott, R.S. 1962. The breeding and agronomic performance of improved variety of Yorkshire fog (*Holcus lanatus* L.). Proceedings of the XII International Grassland Congress, 799 - 804.

Jamieson, W.S., and Hodgson, J. 1979. The effect of daily herbage allowance and sward characteristics upon the ingestive behaviour and herbage intake of calves under strip-grazing for grazing dairy cows. Grass and Forage Science, 34: 261 - 271.

Jamieson, W.S., and Hodgson, J. 1981. The effect of variation in sward characteristics upon the ingestive behaviour and herbage intake of calves and lambs under a continuous stocking management. Grass and Forage Science, 34: 273 - 282.

Jansman, A.J.M. 1993. Tannins in feedstuffs for simple-stomach animals. Nutrition Research Reviews, 6: 209 - 236.

John, A., and Lancashire, J.A. 1981. Aspects of feeding value of *Lotus* spp. Proceedings of the New Zealand Grassland Association, 42: 152 - 159.

Jones, W.T., Anderson, L.B., and Ross, M.D. 1973. Bloat in cattle. New Zealand Journal of Agricultural Research, 16: 441 - 446.

Jones. W.T., Broadhurst, R.B., and Lyttleton, J.W. 1976. The condensed tannins of pasture legume species. Phytochemistry, 15: 1407 - 1409.

Jones, W.T., and Lyttleton, J.W. 1971. A survey of legume forages that do and do not produce bloat. New Zealand Journal of Agricultural Research, 14: 101 - 107.

Jones, W.T., and Mangan, J.L. 1977. Complexes of the condensed tannins of sainfoin (*Onobrychis viciifolia Scop*) with fraction 1 leaf protein and with submaxillary mucoprotein, and their reversal by polyethylene glycol and pH. Journal of Science Food Agriculture, 28: 126.

Jung, H.G., and Koong, L.J. 1985. Effects of hunger satiation on diet quality by grazing sheep. Journal of Range Management, 38: 302 - 305.

Jung, H.G., and Shaffer, J.A. 1993. Component yields and quality of binary mixtures of lucerne and perennial, italian or short rotation hybrid ryegrass. Grass and Forage Science, 48: 118 - 125.

Kempton, T.J. 1978. Protein to energy ratio of absorbed nutrients in relation to wool growth. In: Physiological and Environmental Limitations to Wool Growth. Black, J.L., and Reis, P.J., Editors. University of New England Publication Unit. Armidale N.S.W, Australia. pp 34 - 41.

Kenny, P.A., and Black, J.L. 1984. Factors affecting diet selection by sheep. I. Potential intake and acceptability of feed. Australian Journal of Agricultural Research, 35: 551 - 563.

Kirton, A.H. 1989. Principles of classification and grading. In: Meat production and processing. New Zealand Society of Animal Production. Occasional Publication Nº 11. pp 143 - 158. 229 pp.

Kirton, A.H., and Morris, C.A. 1989. The effect of mature size, sex and breed on patterns of change during growth and development. In: Meat production and processing. New Zealand Society of Animal Production. Occasional Publication Nº 11. pp 73 - 86. 229 pp.

Korte, C.J., Chu, A.C.P., and Field, T.R.O. 1987. Pasture production. In: Livestock feeding on pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 7 - 22. 145 pp.

Kumar., R., and Vaithiyanathan, S. 1990. Occurrence, nutritional significance and effect on animal productivity of tannins in tree leaves. Animal Feed Science and Technology, 30: 21 - 38.

L'Huillier, P.J., and Poppi, D.P. 1984. Influence of green leaf distribution on diet selection by sheep and the implications for animal performance. Proceedings of the New Zealand of Animal Production, 44: 105 - 107.

L'Huillier, P.J., Poppi, D.P., and Fraser, T.J. **1986.** Influence of structure and composition of ryegrass and prairie grass-white clover swards on the grazed horizon and diet harvested by sheep. Grass and Forage Science, 41: 259 - 267.

Laca, E., and Demment, M.W. 1990. Modelling intake of a grazing ruminant in a heterogeneous environment. Proceedings of the V International Congress of Ecology, Yokohama, Japan (abstract).

Laca, E., and Demment, M.W. 1991. Herbivory: The dilemma of foraging in a spatially heterogeneous food environment. In: Plant Defense Against Mammalian Herbivory. Palo, R.T., and Robbins, C.T., Editors. CRC Press Incorporated, Boca Raton. pp. 29 - 44.

Laca, E., Distel, R.A., Griggs, T.C., Deo, G., and Demment, M.W. 1993. Field test of optimal foraging with cattle: the marginal value theorem successfully predicts patch selection and utilisation. Proceedings of the XVII International Grassland Congress, 709 - 710.

Laca, E.A., Ungar, E.D., Seligman, N., and Demment, M.W. 1992. Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. Grass and Forage Science, 47: 91 - 102.

Langlands, J.P. 1967. Studies of the nutritive value of the diet selected by grazing sheep. II. Some studies of error when sampling oesophageally fistulated sheep at pasture. Animal Production, 9: 167 - 175.

Langlands, J.P., and Sanson, J. 1976. Factors affecting the nutritive value of the diet and the composition of rumen fluid of grazing sheep and cattle. Australian Journal of Agricultural Research, 27: 691 - 707.

Lascano, C., Hoyos, P., Schultze-Kraft, R., and Amezquita, M.C. 1985. The effect of previous experience of animals on subsequent preference in a palatability grazing trial. Proceedings of the XV International Grassland Congress, 166 - 167.

Leathwick, D.M., and Atkinson, D.S. 1995. Dagginess and flystrike in lambs grazed on *Lotus corniculatus* and ryegrass. Proceedings of the New Zealand Society of Animal Production, 55: (In press).

Leaver, J.D. 1985. Effects of supplements on herbage intake and performance. In: Grazing. Occasional Symposium № 19. British Grassland Society. Frame, J., Editor. pp. 79-88.

Le Du, Y.L.P., Combelas, J., Hodgson, J., and Baker, R.D. 1979. Herbage intake and milk production by grazing dairy cows. 2. The effects of level of winter feeding and daily herbage allowance. Grass and Forage Science, 34: 249 - 260.

Le Du, Y.L.P, and Penning, P.D. 1982. Animal based techniques for estimating herbage intake. In: Herbage Intake Handbook. British Grassland Society. Editor, J.D. Leaver. pp. 37 - 76. 143 pp.

Lee, J., Harris, P.M., Sinclair, B.R., and Treloar, B.P. 1992. The effect of condensed tannin containing diets on whole body amino acid utilisation in Romney sheep: Consequences for wool growth. Proceedings of the New Zealand Society of Animal Production, 52: 243 - 245.

Lees, G.L., Howarth, R.E., Glopen, B.P., and Fesser, A.C. 1981. Mechanical disruption of leaf tissues and cells in some bloat-causing and bloat-safe forage legumes. Crop Science, 21: 444 - 447.

Lowther, W.L., and Barry, T.N. 1985. Nutritional value of ´Grassland Maku´ lotus grown on low fertility soils. Proceedings of the New Zealand Society of Animal Production, 45: 125 - 127.

Lowther, W.L., Manley, T.R., and Barry, T.N. 1987. Condensed tannin concentrations in *Lotus corniculatus* and *L. pedunculatus* cultivars grown under low soil fertility conditions. New Zealand Journal of Agricultural Research, 30: 23 - 25.

Lynch, J.J., Hinch, G.N., and Adams, D.B. 1992. The Behaviour of Sheep: Biological Principles and Implications for Production. CAB International and CSIRO, Australia. 236 pp.

Lynch, J.J., and Bell, A.K. 1987. The transmission from generation to generation in sheep of a learned behaviour for eating grain supplements. Australian Veterinary Journal, 64: 291 - 305.

Mangan, J.L. 1988. Nutritional effects of tannins in animals feeds. Nutrition Research Reviews, 1: 209 - 211.

Malechek, J.C., and Balph, D.F. 1987. Diet selection by grazing and browsing livestock. In: The Nutrition of Herbivores: Second International Symposium on the Nutrition of Herbivores. Hacker, J.B., and Ternouth, J.H., Editors. Academic Press. Sydney, Australia. pp. 199 - 201.

Manly, B.F.J. 1994. Multivariate Statistical Methods: A Primer. Second Edition. London, Chapman and Hall. 215 pp.

Marten, G.C. 1978. The animal-plant complex in forage palatability phenomena. Journal of Animal Science, 46(5): 1470 - 1477.

Marten, G.C., and Andersen, R.N. 1975. Forage nutritive value and palatability of 12 common annual weeds. Crop Science, 15: 821 - 827.

Marten, G.C., and Jordan, R.M. 1974. Significance of palatability differences amongst *Phalaris arundinacea* L., *Bromus Inermis* leyss., and *Dactylis glomerata* L. grazed by sheep. Proceedings of the XII International Grassland Congress, 305 - 312.

Matthew, C., Lawoko, C.R.O., Korte, C.J., and Smith, D. 1994. Application of canonical discriminant analysis, principal component analysis, and canonical correlation analysis as tools for evaluating differences in pasture botanical composition. New Zealand Journal of Agricultural Research, 37: 509 - 520.

McCall, D.G., and Lambert, M.G. 1987. Pasture feeding of goats. In: Livestock feeding on pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 105 - 110. 145 pp.

McClymont, G.L. 1967. Selectivity and intake in grazing animals. In: Handbook of Physiology, Section 6: Alimentary Tract, Vol 1. Control of Food and Water Intake. Code, C.F., and Wegner, H. Washington D.C., Editors. American Physiology Society. pp. 129 - 137.

McNabb, W.C., Waghorn, G.C., Barry, T.N., and Shelton, I.D. 1993a. The effect of condensed tannins in *Lotus pedunculatus* on the digestion and plasma metabolism of methionine and cystine in sheep. Proceedings of the XVII International Grassland Congress, 583 - 585.

McNabb, W.C., Waghorn, G.C., Barry, T.N., and Shelton, I.D. 1993b. The effect of condensed tannins in *Lotus pedunculatus* on the digestion and metabolism of methionine, cystine and inorganic sulphur in sheep. British Journal of Nutrition, 70: 647 - 661.

McLeod, M.N. 1974. Plant tannins: Their role in forage quality. Nutrition Abstracts and Reviews, 44: 803 - 815.

Mehansho, H., Butler, L.G., and Carlson, D.M. 1987. Dietary tannins and salivary proline-rich proteins: Interactions, induction, and defense mechanisms. Annual Review of Nutrition, 7: 423 - 440.

Meijs, J.A.C. 1981. Herbage intake by grazing dairy cows. Agricultural Research Report 909. Center for Agricultural Publishing and Documentation, Wageningen, The Netherlands. 264 pp.

Milne, J. 1991. Diet selection by grazing animals. Proceedings of the Nutrition, 50: 77 - 85.

Milne, J.A., Hodgson, J., Thompson, R., Souter, W.G., and Barthram, G.T. 1982. The diet ingested by sheep grazing swards differing in white clover and perennial ryegrass content. Grass and Forage Science, 27: 209 - 218.

Minson, D.J. 1981. Effects of chemical and physical composition of herbage intake eaten upon intake. In: Nutritional Limits to Animal Production from Pastures. Hacker, J.B., Editor. Publication CAB International, Queensland, Australia. pp. 167 - 182.

Mirza, S.N., and Provenza, F.D. 1990. Preference of the mother affects selection and avoidance of foods by lambs differing in age. Applied Animal Behaviour Science, 28: 255 - 263.

Mirza, S.N., and Provenza, F.D. 1992. Effects of age and conditions of exposure on maternally mediated food selection in lambs. Applied Animal Behaviour Science, 33: 35 - 42 .

Mitchell, R.J., Hodgson, J., and Clark, D.A. 1991. The effect of varying leafy sward height and bulk density on the ingestive behaviour of young deer and sheep. Proceedings of the New Zealand Society of Animal Production, 51: 159 - 165.

Montossi, F.; Hu, Y; Hodgson, J., and Morris, S.T. 1994. Herbage intake, ingestive behaviour and diet selection in sheep grazing *Holcus lanatus* and perennial ryegrass swards. Proceedings of the New Zealand Society of Animal Production, 54: 71 - 74.

Morris, S.T. 1992. A study of out-of-season lamb production in the lower North Island of New Zealand. PhD Thesis. Massey University, NZ. 215 pp.

Morris, S.T., McCutcheon, S.N., and Parker, W.J. 1992. Measurements of the components of grazing behaviour. Herbage Intake Workshop. Massey University, New Zealand.

Morris, S.T., McCutcheon, S.N., Parker, W.J., and Blair, H.T. 1994. Effect of sward surface height on herbage intake and performance of lactating ewes lambed in winter and continuously stocked on pasture. Journal of Agricultural Science, Cambridge, 122: 471 - 482.

Morris, S.T., Parker, W.J., Blair, H.T., and McCutcheon, S.N. 1993a. Effect of sward height during late pregnancy on intake and performance of continuously stocked June and August-lambing ewes. Australian Journal of Agricultural Research , 44: 1635 - 1651.

Morris, S.T., Hirschberg, S.W., Michel, A., Parker, W.J., and McCutcheon, S.N. 1993b. Herbage intake and liveweight gain of bulls and steers continuously stocked at fixed sward heights during autumn and spring. Grass and Forage Science, 48: 109 - 117.

Morton, J.D., Bolton, G.R., and Hodgson, J. 1992. The comparative performance of *Holcus Lanatus* and *Lolium perenne* under sheep grazing in the Scottish Uplands. Grass and Forage Science, 47: 143 - 152.

Moss, R.A., and Vlassoff, A. 1993. Effect of herbage species on gastro-intestinal roundworm populations and their distribution. New Zealand Journal of Agricultural Research, 36: 371 - 375.

Muangthong, T. 1989. Genotypic variability in Yorkshire fog grass (*Holcus lanatus L.*). Masters Thesis. Massey University, New Zealand. 130 pp.

Murdiati, T.B., McSweeney, C.S., and Lowry, J.B. 1992. Metabolism in sheep of gallic acid, tannic acid and hydrolysable tannin from *Terminalia oblongata.* Australian Journal of Agricultural Research, 43: 1307 - 1319.

Newman, J.A., Penning, P.D., Parsons, A.J., Harvey, A., and Orr, R.J. 1994. Fasting affects intake behaviour and diet preferences of grazing sheep. Animal Behaviour, 47: 185 - 193.

Newman, J.A., Parson, A.J., and Harvey, A. 1992. Not all sheep prefer clover: diet selection revisited. Journal of Agricultural Science, Cambridge, 119: 275 - 283.

Nicol, A.M., and Collins, H.A. 1990. Estimation of the pasture horizons grazed by cattle, sheep and goats during single and mixed grazing. Proceedings of the New Zealand Society of Animal Production, 50: 49 - 53.

Nicol, A.M., and Nicoll, G.B. 1987. Pastures for beef cattle. In: Livestock feeding on pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 119 - 120. 145 pp.

Nicol, A.M., Poppi, D.P., Alam, M.R., and Collins, H.A. 1987. Dietary differences between goats and sheep. Proceedings of the New Zealand Grassland Association, 48: 199 - 205.

Niezen, J.H. 1995. Effects of pasture species on parasitism in lambs. Report on Project 91 MT 25/1.1. New Zealand Meat Research and Development Council 1995. Palmerston North, New Zealand. 105 pp.

Niezen, J.H., Charleston, W.A.G., Hodgson, J., and Waghorn, T.S. 1993b. Effect of four grass species on lamb parasitism and growth. Proceedings of the New Zealand Grassland Association, 55: 203 - 206.

Niezen, J.H., Waghorn, T.S., Waghorn, G.C., and Charleston, W.A.G. 1993a. Internal parasites and lamb production - a role for plant containing condensed tannins? Proceedings of the New Zealand Society of Animal Production, 53: 235 - 238.

Niezen, J.H., Waghorn, T.S., Kaufaut, K., Robertson, H.A., and McFarlane, R.G. 1994. Lamb weight gain and faecal egg count when grazing one of seven herbage and dosed with larvae for six weeks. Proceedings of the New Zealand Society of Animal Production, 54: 15 - 18.

Nolte, D.L., Provenza, F.D., and Balph, D.F. 1990. The establishment and persistence of food preference in lambs exposed to selected foods. Journal of Animal Science, 68: 998 - 1002.

Nuñez-Hernandez, G., Wallace, J.D., Holechek, J.L., Galyean, M.L., and Cardenas, M. 1991. Condensed tannins and nutrient utilization by lambs and goats fed low-quality diets. Journal of Animal Science, 69: 1167 - 1177.

Orr, R.J., Parson, A.J., Penning, P.D., and Treacher, T.T. 1990. Sward composition, animal performance and the potential production of grass/white clover swards continuously stocked with sheep. Grass and Forage Science, 45: 325 - 336.

Parker, W.J., and McCutcheon, S.N. 1992. Effects of sward height on herbage intake and production of ewes of different rearing rank during lactation. Journal of Agricultural Science, Cambridge, 118: 383 - 395.

Parker, W.J., McCutcheon, S.N., and Carr, D.H. 1989. Effect of herbage type and level of intake on the release of chromic oxide from intraruminal controlled release capsule in sheep. New Zealand Journal of Agricultural Research, 32: 537 - 546.

Parker, W.J., Morris, S.T., and McCutcheon, S.N 1992. Chromic oxide controlled release capsule for measurement of herbage intake in ruminants. Herbage Intake Workshop. Massey University, New Zealand.

Parker, W.J., Morris, S.T., Garrick, D.J., Vincent, G.L., and McCutcheon, S.N 1990. Intraruminal chromium controlled release capsules for measuring herbage intake in ruminants - a review. Proceedings of the New Zealand Society of Animal Production, 50: 437 - 442.

Penning, P.D. 1986. Some effects of sward conditions on grazing behaviour and intake by sheep. In: Gudmundsson, O. (ed). Grazing research at Northern Latitudes. Proceedings of a NATO Advanced Workshop. Hvanneyri, Iceland. Vol. 108., pp 219 - 226.

Penning, P.D., Orr, R.J., and Treacher, T. 1988. Responses of lactating ewes, offered fresh herbage indoors and when grazing, to supplements containing differing protein concentrations. Animal Production,46:403-415.

Penning, P.D., Parsons, A.J., Orr, R.J., and Treacher, T. 1991. Intake and ingestive behaviour responses by sheep to changes in sward characteristics under continuous stocking. Grass and Forage Science, 46: 15 - 28.

Phillips, C.J.C., and Leaver, J.D. 1985. Seasonal and diurnal variation in grazing behaviour of dairy cows. In: Grazing. Occasional Symposium Nº 19. British Grassland Society. Frame., J., Editor. pp 98 - 104.

Poppi, D.P., Cruickshank, G.J., and Sykes, A.R. 1988. Fish meal and amino acid supplementation of early weaned lambs grazing Roa tall fescue (*Festuca arundinacea*) or Huia white clover (*Trifolium repens*). Animal Production, 46: 491 - 511.

Poppi, D.P., Hughes, T.P. and L'Huillier, P.J. 1987. Intake of pasture for grazing animals. In: Livestock feeding on pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 55 - 64. 145 pp.

Poppi, D.P., Minson, D.J., and Ternouth, J.H. 1981a. Studies of cattle and sheep eating leaf and stem fractions of grasses. I. The voluntary intake, digestibility and retention time in the reticulo-rumen. Australian Journal of Agricultural Research, 32: 99 - 108.

Poppi, D.P., Minson, D.J., and Ternouth, J.H. 1981b. Studies of cattle and sheep eating leaf and stem fractions of grasses. II. Factors controlling the retention of the feed in the reticulo-rumen. Australian Journal of Agricultural Research, 32: 109 - 121.

Pritchard, D.A., Martin, P.R., and O´Rourke, P.K. 1992. The role of condensed tannins in the nutritional value of Mulga (*Acacia aneura*) for sheep. Australian Journal of Agricultural Research, 43: 1739 - 1746.

Provenza, F.D., and Malechek, J.C. 1984. Diet selection by domestic goats in relation to blackbrush twig chemistry. Journal of Applied Ecology, 21: 831 - 841.

Provenza, F.D., and Malechek, J.C. 1986. A comparison of food selection and foraging behaviour in juvenile and adults goats. Applied Animal Behaviour Science, 16: 49 - 61.

Provenza, F.D., and Balph, D.F. 1987. Diet learning by domestic ruminants: Theory, Evidence and Practical implications. Applied Animal Behaviour Science, 18: 211 - 232.

Provenza, F.D., and Balph, D.F. 1988. The development of dietary choice in livestock on rangelands and its implications for management. Journal of Animal Science, 66: 2356 - 2368.

Provenza, F.D., and Balph, D.F. 1990. Applicability of five diet-selection models to various foraging challenges ruminants encounter. In: Behavioural Mechanisms of Food Selection. NATO ASI Series, Vol. G 20. Hughes, R.N., Editor. pp. 423 - 458.

Provenza, F.D., Burrit, E.A., Clausen, T.P., Bryant, J.P., Reichardt, P.B., and Distel, R.A. 1990. Conditioned flavour aversion: A mechanism for goat to avoid condensed tannins in blackbrush. The American Naturalist, 136(6): 810 - 828.

Provenza, F.D., and Burrit, E.A. 1991. Socially induced diet preference ameliorates conditioned food aversion in lambs. Applied Animal Behaviour Science, 31: 229 - 236.

Provenza, F.D., and Cincotta, R.P. 1993. Foraging a self-organizational learning process: Acceptation and adaptability at the expense of predictability. In: Diet Selection: An Interdisciplinary Approach to Foraging Behaviour. Hughes, R.N., Editor. Blackwell Scientific Publication, Oxford, Boston pp. 78 - 101.

Provenza, F.D., Nolan, J.V., and Lynch, J.J. 1993. Temporal contiguity between food ingestion and toxicosis affects the acquisition of food aversions in sheep. Applied Animal Behaviour Science, 38: 269 - 281.

Purchas, R.W., and Keogh, R.G. 1984. Fatness of lambs grazed on 'Grasslands Maku' lotus and 'Grasslands Huia' white clover. Proceedings of the New Zealand Society of Animal Production, 44: 219 - 221.

Ramos, A., and Tennessen, T. 1992. Effect of previous grazing experience on the grazing behaviour of lambs. Applied Animal Behaviour Science, 33: 43 - 52.

Rattray, P.V., Thompson, K.F., Hawker, H., and Summer, R.M.W. 1987. Pastures for sheep production. In: Livestock Feeding on Pasture. New Zealand Society of Animal Production. Occasional Publication № 10. pp 89 - 103. 145 pp.

Reid, C.S.W., Ulyatt, M.J., and Wilson, J.M. 1974. Plant tannins, bloat and nutritive value. Proceedings of the New Zealand Society of Animal Production, 34: 82 - 93.

Reis, P.J. 1979. Effects of amino acids on the growth and properties of wool. In: Physiological and Environmental Limitations to Wool Growth. Black, J.L., and Reis, P.J, Editors. University of New England, Australia. pp. 223-242.

Reis, P.J., Tunks, D.A., and Munro, S.G. 1990. Effects of infusion of amino acids into the abomasum of sheep, with emphasis on the relative value of methionine, cysteine and homocysteine for wool growth. Journal of Agricultural Science, Cambridge, 114: 59 - 68.

Rhodes, I., and Collins, R. 1993. Canopy Structure. In: Sward Measurement Handbook. 2nd Edition. Davis, A., Baker, R.D., Grant, S.A., and Laidlaw, A.S., Editors. British Grassland Society. pp. 139 - 156. 319 pp.

Roades, D.F., and Cates, R.G. 1976. Towards a general theory of plant antiherbivore chemistry. Recent Advanced Phytochemistry, 10: 168 - 213.

Robbins, C.T., Hanley, T.A., Hagerman, A.E., Hjeljord, O., Baker, D.L., Schwartz, C.C., and Mautz. 1987a. Role of tannins in defending plant against ruminants: Reduction in protein availability. Ecology, 68(1):98-107.

Robbins, C.T., Mole, S., Hagerman, A.E., and Hanley, T.A. 1987b. Role of tannins in defending plant against ruminants: Reduction in dry matter digestion. Ecology, 68(6): 1607 - 1615.

Rodriguez Capriles, J.M. 1973 . The herbage intake of young grazing cattle. PhD Thesis. University of Reading, UK.

Rogers, P.J., and Blundell, J.E. 1991. Mechanisms of diet selection: The translation of needs into behaviour. Proceedings of the Nutrition Society, 50: 65 - 70.

Rogers, P.J., Bryant, A.M., and McLeay, M.N. 1979. Silage and dairy cow production. III. Abomasal infusions of casein, methionine, and glucose, and milk yield and composition. New Zealand Journal of Agricultural Research, 22: 533 - 541.

Roughan, P.G., and Holland, R. 1977. Predicting in vitro digestibilities of herbage by exhaustive enzymic hydrolysis of cell walls. Journal of Agricultural Science, Cambridge, 87: 423 -432.

Sarkar, S.K., and Howarth, R.E. 1976. Specificity of the vanillin test for flavanols. Journal of Agricultural Food Technology, 24(2): 317 - 320.

SAS 1985 and 1990. SAS User's Guide: Statistics, Versions 5 and 6 Edition. SAS Inc, Cary, North Carolina, USA.

Short, B.F., and Chapman, R.E. 1965. Techniques for investigating wool growth. In: Field Investigations with Sheep: A Manual of Techniques. Moule, G.R., Editor. CSIRO. Melbourne, Australia. pp 13.1 - 13.23.

Simons, A.B., and Marten, G.C. 1971. Relationship of indole alkaloids to palatability of *Phalaris arundinacea L.* Agronomy Journal, 63: 915 - 919.

Smith, A., and Allcock, P.J. 1985. The influences of species diversity on sward yield and quality. Journal of Applied Ecology, 22: 185 - 198.

Speedy, A.W. 1980. Sheep production: Science into practice. Longman Scientific and Technical Publication. London, UK. 191 pp.

Squibb, R.C., Provenza, F.D., and Balph, D.F. 1990. Effect of age of exposure on consumption of a shrub by sheep. Journal of Animal Science, 68: 987 - 997.

Steel, R.G.D., and Torrie, J.H. 1981. Principles and Procedures of Statistics, a Biometrical Approach. McGraw-Hill, Japan. pp 633.

Stephens, D.W., and Krebs, J.R. 1986. Foraging Theory. Princeton University Press, New Jersey, USA.

Stobbs, T.H. 1973a. I. The effect of plant structure on the intake of tropical pastures. Australian Journal of Agricultural Research, 24: 809 - 819.

Stobbs, T.H. 1973b. II. The effect of plant structure on the intake of tropical pastures. Australian Journal of Agricultural Research, 24: 819 - 829.

Stobbs, T.H. 1974. Rate of biting by Jersey cows as influenced by the yield and maturity of pasture sward. Tropical Grasslands, 8: 81.

Stobbs, T.H. 1975. Factors influencing the nutritional value of grazed tropical pastures for beef and milk production. Tropical Grasslands, 9: 141.

Swain, T. 1979. Tannins and Lignins. In: Herbivores: Their Interaction with Secondary Plant Metabolites. Rosenthal, G.A., and Janzen, D.H., Editors. Academic Press. pp. 657 - 682.

Taylor, J.A. 1993. Foraging strategy. Proceedings of the XVII International Grassland Congress, 739 - 740.

Telek, L. 1989. Determination of condensed tannins in tropical legume forages. Proceedings of the XVI International Grassland Congress, 765 - 766.

Terrill, T.H., Windham, W.R., Hoveland, C.S., and Amos, H.E. 1989. Forage preservation method influences on tannin concentration, intake, and digestibility of Serica Lespedeza by sheep. Agronomy Journal,81: 435-439.

Terrill, T.H., Windham, W.R., Evans, J.J., and Hoveland, C.S. 1990. Condensed tannin concentration in Serica Lespedeza as influenced by preservation method. Crop Science, 30: 219 - 224.

Terrill, T.H., Rowan, A.M., Douglas, G.B., and Barry, T.N. 1992a. Determination of extractable and bound CT concentrations in forage plants, protein concentrate meals and cereal grains. Journal of the Science of Food and Agriculture, 58: 321 - 329.

Terrill, T.H., Douglas, G.B., Foote, A.G., Purchas, R.W.; Wilson, G.F., and Barry, T.N. 1992b. Effect of CT upon body growth, wool growth and rumen metabolism in sheep grazing sulla (*Hedysarum coronarium*) and perennial pasture.Journal of Agricultural Science, Cambridge ,58:312- 329.

Theriez, M., Tissier, M., and Robelin, J. 1981. The chemical composition of the intensively fed lambs. Animal Production, 32: 219 - 224.

Thompson, A.N., Doyle, P.T., and Grimm, M. 1994. Effects of stocking rate in spring on liveweight and wool production of sheep grazing annual pastures. Australian Journal of Agricultural Research, 45: 367 - 389.

Thorhallsdottir, A.G., Provenza., F.D., and Balph, D.F. 1987. Food aversion learning in lambs with or without a mother: discrimination, novelty and persistence. Applied Animal Behaviour Science, 18: 327 - 340.

Thorhallsdottir, A.G., Provenza., F.D., and Balph, D.F. 1990a. Ability of lambs to learn about novel foods while observing or participating with social models. Applied Animal Behaviour Science, 25: 25 - 33.

Thorhallsdottir, A.G., Provenza., F.D., and Balph, D.F. 1990b. The role of the mother in the intake of harmful foods by lambs. Applied Animal Behaviour Science, 25: 35 - 44.

Thorhallsdottir, A.G., Provenza., F.D., and Balph, D.F. 1990c. Social influences on conditioned food aversions in sheep. Applied Animal Behaviour Science, 25: 45 - 50.

Ueno, H, and Gutierrez, V.C. 1983. Manual para diagnóstico das Helmintoses de Rumiantes. Tokio, Japan.

Ulyatt, M.J. 1971. Studies on the causes of the differences in pasture quality between perennial ryegrass, short-rotation ryegrass, and white clover. New Zealand Journal of Agricultural Research, 14: 352 - 367.

Ulyatt, M.J. 1981. The feeding value of temperate pastures. In: Grazing animals. World Animal Science V B1. Morley, F.H.W., Editor. Elsevier. pp 125-139.

Ulyatt, M.J., MacRae, J.C., Clarke, R.T.J., and Pearce, P.D. 1975. Quantitative digestion of fresh herbage by sheep. 4. Protein synthesis in the stomach. Journal of Agricultural Science, Cambridge, 84: 453 - 458.

Van Dyne, G.M., Brockington, M.R., Szozs, Z., Daek, J., and Ribic, C.A. 1980. Large herbivore sub-system. In: Grasslands, Ecosystems, and Man. Bremeyer, A.I., and Van Dyne, G.M., Editors. Cambridge University Press, Cambridge. pp. 269 - 537.

Vallentine, J.F. 1990. Grazing management. Academic Press, Inc. San Diego, California, USA. 533 pp.

Vickery, M.L., and Vickery, B. 1981. Secondary Plant Metabolism. The Macmillan Press Ltd., London. 335 pp.

Waghorn, G.C., and Barry, T.N. 1987. Pasture as a nutrient source. In: Livestock feeding on pasture. New Zealand Society of Animal Production. Occasional Publication Nº 10. pp 21 - 38. 145 pp.

Waghorn, G.C., and Jones, W.T. 1989. Bloat in cattle: 46. Potential of dock (*Rumex obtusifolius*) as an antibloat agent for cattle. New Zealand Journal of Agricultural Research, 32: 227 - 235.

Waghorn, G.C., Jones, W.T., Shelton, I.D, and McNabb., W. 1990. Condensed tannins and the nutritive value of herbage. Proceedings of the New Zealand Grassland Association, 51: 171 - 176.

Waghorn, G.C., John, A., Jones, W.T., and Shelton, I.D. 1987a. Nutritive value of *Lotus corniculatus* L. containing low and medium concentrations of condensed tannins for sheep. Proceedings of the New Zealand Society of Animal Production, 47: 25 - 30.

Waghorn, G.C., Ulyatt, M.J., John, A., and Fisher, M.T. 1987b. The effect of CT on the sites of digestion of amino acids and other nutrients in sheep fed on *Lotus corniculatus* L. British Journal of Nutrition, 57: 115 - 126.

Walton, P.D. 1983. Production and Management of Cultivated Forages. Reston Pub. Co., Reston, Virginia. 336 pp.

Wang, P., and Ueberschar, K.H. 1990. The estimation of vicine, convicine and condensed tannins in 22 varieties of fababeans (*Vicia faba L.*). Animal Feed Science and Technology, 31: 157 - 165.

Wang, Y., Waghorn, G.C., Douglas, G.B., Barry, T.N., and Wilson, G.F. 1994. The effects of condensed tannins in *Lotus corniculatus* upon nutrient metabolism and upon body and wool growth in grazing sheep. Proceedings of the New Zealand Society of Animal Production,54:219-222.

Warren Wilson, J. 1963. Estimation of foliage denseness and foliage angle by inclined point quadrat. Australian Journal of Botany, 11: 95 - 105.

Watkin, B.R., and Robinson, G.S. 1974. Dry matter production of "Massey Basyn" Yorkshire fog. Proceedings of the New Zealand Grassland Association, 55: 278 - 283.

Watt, T.A. 1978. The biology of *Holcus lanatus L.* (Yorkshire fog) and its significance in grassland. Herbage Abstracts, 48(6): 195 - 204.

Watt, T.A., and Haggar, R.J. 1980. The effect of defoliation upon yield, flowering and vegetative spread of *Holcus lanatus* growing with and without *Lolium perenne*, under cutting. Grass and Forage Science, 42: 43 - 48.

Watt, T.A. 1987. A comparison of two cultivars of *Holcus lanatus* with *Lolium perenne*, under cutting. Grass and Forage Science, 42: 43 - 48.

Westoby, M. 1974. An analysis of diet selection by large generalist herbivores. The American Naturalist, 108: 290 - 304.

Westoby, M. 1978. What are the biological bases of varied diets?. The American Naturalist, 112: 627 - 631.

Williams, R.F., Evans, L.T., and Ludwing, J.L. 1964. Estimation of leaf area for clover and Lucerne. Australian Journal of Agricultural Research, 15:231-233.

Williamson, J.F., Blair., H.T., Garrick, D.J., Pomroy, W.E., and Douch, P.G.C. 1994. The relationship between internal parasite burden, faecal egg count, and mucosal mast cells in fleeceweight-selected and control sheep. Proceedings of the New Zealand Society of Animal Production, 54: 9 - 13.

Wilson, R.J. 1981. Environmental and nutritional factors affecting animal production. In: Nutritional Limits to Animal Production from Pastures. Queensland, Australia Hacker, J.B., Editor. CAB Publication. pp. 111 - 131.

Windham, W.R., Fales, S.L., and Hoveland, C.S. 1988. Crop Utilization: Analysis for condensed tannins in Serica Lespedeza by Near Infrared Reflectance Spectroscopy. Crop Science, 28: 705 - 708.

Zucker, W.V. 1983. Tannins: Does structure determine function? An ecological perspective. The American Naturalist, 121(3): 335 - 365.

APPENDICES

Appendix 3.1 (Chapter 3). Preliminary report of Experiment 1 published in the Proceedings of the New Zealand Society of Animal Production.

Proceedings of the New Zealand Society of Animal Production 1994, Vol 54 71

Herbage intake, ingestive behaviour and diet selection in sheep grazing *Holcus lanatus* and perennial ryegrass swards

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ABSTRACT

Grazing behaviour, diet selection, and herbage intake of ewes in mid-pregnancy were studied on perennial ryegrass/white clover and *Holcus lanatus*/white clover swards rotationally grazed at medium and high allowances (6% and 12% of liveweight as herbage dry matter respectively) during late autumn. Estimates of herbage mass and sward height before grazing were similar for the two pasture types.

Animals on both pasture types concentrated grass rather than clover in the diet, and extrusa samples from both showed evidence of limited concentrations of condensed tannins. Herbage intake was 28% higher from ryegrass than from Yorkshire fog swards (1410 vs 1100 ± 29 g DM/day) and 19% greater at high allowance (1370 vs 1150 ± 50 g OM/day). Bite weight was 61% greater for Yorkshire fog than for ryegrass (139 vs 86 ± 7.0 g OM/bite) and 30% lower for medium allowance than for high allowance (90 vs 130 ± 7.0 mg OM/bite). Grazing time was higher on ryegrass swards and for medium allowance (610 vs 500 ± 34 mins and 620 vs 495 ± 27 mins) whereas differences in rate of biting were small. There was a small advantage in the organic matter digestibility of the herbage selected in favour of ryegrass swards (85.7 vs 82.2 ± 0.3%), while no differences were found between herbage allowances.

It is concluded that herbage intake was influenced more by nutritional than by behavioural constraints, but that these effects need to be investigated in animals of higher production potential and nutrient demand.

Keywords: Yorkshire fog; ryegrass; white clover; grazing allowance; sheep; ingestive behaviour; diet selection and herbage intake.

INTRODUCTION

Yorkshire fog (*Holcus lanatus* L.) is an alternative species to perennial ryegrass (*Lolium perenne* L.) for low to moderate soil fertility conditions (Watkin and Robinson, 1974; Harvey *et al.*, 1984; Morton *et al.*, 1992), and there is active interest in the potential value of its condensed tannins in enhancing the efficiency of dietary protein utilisation (Terrill *et al.*, 1992a). However, there is a lack of information on herbage intake, diet selection, and ingestive behaviour of sheep grazing Yorkshire fog. The specific aim of this study was to investigate differences between Yorkshire fog and perennial ryegrass in these variables.

MATERIALS AND METHODS

The trial was conducted on 0.2 ha paddocks of established Yorkshire fog (cv. Massey Basyn) or perennial ryegrass (cv. Grasslands Nui), each grown with white clover (cv. Grasslands Tahora), which had been continuously stocked with sheep for two years. There were four paddocks of each mixture, distributed at random, and each paddock was divided into two parts by electric fences in the ratio 2:1 to give daily herbage allowances of 6% (medium) and 12% (high) of LW on a DM basis. The four replicate paddocks of each species were grazed for periods of 7 days, in sequence, from May to June 1992. The average instantaneous stocking rates were 90 and 45 ewes ha^{-1} for medium and high allowances respectively.

A total of 48 adult Romney ewes in mid-pregnancy (mean weight 64 ± 7.2 SD kg) were used, 24 in the first two periods and 24 in the second two periods of the experiment. The ewes were randomised amongst treatments in groups of six according to fasted liveweight, and grazed spare plots one week before measurements commenced.

Herbage mass was estimated by cutting six 0.1 m^{-2} quadrats to ground level with an electric shearing handpiece in each plot before grazing. Fresh sub-samples were bulked within each replicate and dissected into categories for morphology (leaves, stem, live and dead tissue) and species, then dried and weighed. Sward surface height (SSH) was measured using a sward stick (Barthram, 1986), with 40 random measurements per plot. The vertical distribution of plant tissue within the sward canopy was measured using an inclined point quadrat (Warren Wilson, 1963) set at 32.5° to the horizontal; 100 contacts were recorded in each plot, and identified for species, morphology (leaf, stem, petiole) and state (live and dead).

Initial and final liveweights were recorded for each set of ewes. Faecal output was estimated for all animals using intraruminal controlled release capsules of chromium sesquioxide (CRC; Captec (NZ) Limited, Auckland), according to procedures described by Parker *et al.* (1989). There were two consecutive 5-day periods of faecal sampling in each half of the experiment. The chromic oxide release rates were determined from capsules recovered from 12 ewes (3 per treatment) slaughtered at the end of the trial.

Two pairs of castrated male sheep fistulated at the oesophagus were rotated between sward type and allowance plots on a daily basis to provide one extrusa sample from each animal from each plot. The extrusa samples were stored at

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-20°C before division into two portions. On one portion, the proportions of grass and white clover in the total diet were assessed by suspending a sample in water in a gridded tray and identifying plant material at grid intersections. The other portion was freeze-dried and ground (1 mm diameter sieve) and then analysed for *in vitro* digestibility on individual samples (Roughan & Holland, 1970), and condensed tannins (CT) on samples bulked within periods (Terrill *et al.*, 1992b).

Herbage organic matter intake was estimated as specified by Parker *et al.* (1992) using the above estimates of faecal output and diet digestibility.

One 24 hour grazing behaviour study was carried out in each of the last two grazing periods. Grazing, ruminating or resting activity was manually recorded for each ewe at intervals of 15 minutes. Rate of biting (bites/minute) was obtained using a 20-bites technique (Jamieson & Hodgson, 1979) recorded by stop-watch during grazing periods at dawn, mid-morning, early afternoon and dusk. The weight of herbage in individual bites was determined by counting the number of bites taken by OF sheep during the collection of extrusa samples (Stobbs, 1973).

The pasture and animal data were analysed using the statistical package SAS (SAS Institute Inc., 1985), based on a split-plot design with 4 blocks, taking pasture type as the main plot and grazing allowance as the split-plot factor. Liveweight gains were adjusted by covariance for initial weight.

RESULTS

Interactions between sward type and grazing allowance were not significant for any sward or animal variable, so results are presented as main effects only.

Sward measurements

There were no significant differences in herbage mass or height between sward types before grazing (Table 1).

Proportions of dead material, and of sown grass and clover in the live component, were similar for the two swards (Table 1). In each case the sward was grass-dominant, and the clover was distributed towards the base (Hu, 1993).

TABLE 1: Herbage mass (kg DM/ha), sward height (cm) and species composition (% of DM) of perennial ryegrass and Yorkshire fog swards.

	Sward	
	Perennial ryegrass	Yorkshire fog
Herbage mass (kg DM/ha)	2250 ± 119	2880 ± 119
Sward height (cm)	13.4 ± 0.42	13.0 ± 0.42
Proportion (% total contacts) of:		
Live material	91 ± 1.8	88 ± 1.1
Proportion (% live contacts) of:		
Sown grass	81 ± 3.5	76 ± 2.2
Other grasses	5 ± 0.9	12 ± 1.2
White clover	14 ± 2.5	12 ± 1.4

Animal measurements

Grasses were the main constituents of the diet selected on all treatments, and there were no significant differences in the relative proportions of grasses to white clover selected between swards and allowances (Table 2). Proportions of dead tissue in the extrusa were negligible.

TABLE 2: Botanical and chemical composition of the diet selected from perennial ryegrass and Yorkshire fog swards.

	Sward type			Herbage allowance		
	Perennial ryegrass	Yorkshire fog	SEM	6%	12%	SEM
Proportion (% contacts) of:						
Grass	98.7	98.3	0.32	98.7	98.2	0.33
Clover	1.3	1.7	0.32	1.3	1.8	0.33
OM digestibility (%)	85.7	82.2	0.3*	83.6	84.3	0.1
Concentration (% DM) of:						
Free tannin	.068	.072	.003			
Protein-bound tannin	.135	.148	.001*			
Fibre-bound tannin	.004	.028	.005			
Total condensed tannin	.208	.248	.009			

The concentration of protein-bound CT was consistently higher in extrusa from the Yorkshire fog sward, whereas concentrations of fibre-bound CT and free CT in samples from both swards were variable. All concentrations were relatively low, and close to the lower limits of estimation (Terrill *et al.*, 1992).

There was no significant difference in the release rate of chromic oxide (Cr_2O_3) amongst treatments, therefore a common Cr_2O_3 release rate of 122 mg Cr_2O_3 day^{-1} was used. Organic matter digestibility (OMD) of the diet selected was 4 units higher for ryegrass swards than for Yorkshire fog swards (Table 2), but there was no significant difference between allowances. OM intakes were 28% greater for ryegrass swards than for Yorkshire fog swards and 19% greater for high allowance than for medium allowance (Table 3).

The mean bite weight on Yorkshire fog swards was significantly higher (61%) than on the ryegrass swards (Table 3). On average, the recovery rate of oesophageal boluses for

TABLE 3: Herbage intake, ingestive behaviour and live weight gain of sheep grazing perennial ryegrass and Yorkshire fog swards at medium (6% LW) and high (12% LW) herbage allowance.

	Sward type			Herbage allowance		
	Perennial ryegrass	Yorkshire fog	SEM	6%	12%	SEM
Bite weight (mg OM)	86	139	7.0*	90	130	7.0*
Bite rate (bites/min)	53	48	2.2	52	48	2.5
Grazing time (mins)	612	501	34	618	496	27
Daily herbage intake (g OM/ewe)	1410	1100	29**	1150	1370	50.1*
Live weight gain (g/day)	168	111	18.8	120	159	23.5

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both swards was 89%. Rates of biting did not differ between swards. Grazing time was 22% greater on ryegrass swards than on Yorkshire fog swards, but the difference was not significant. Reduction in herbage allowance from 12% to 6% depressed mean bite weight by 30%, but did not affect rate of biting. Grazing time tended to be higher at medium than at high grazing allowance.

Liveweight gain was 34% ($P < 0.08$) greater on ryegrass swards than on Yorkshire fog swards, and 25% higher (NS) at high allowance than at medium allowance.

DISCUSSION

Comparative studies of herbage intake and sheep performance between perennial ryegrass and Yorkshire fog swards appear to be limited to the earlier experiments of Watkin *et al.* (1974) and to the recent trial published by Morton *et al.* (1992). There is no information comparing these swards in terms of sward structure, diet selection, and ingestive behaviour.

The sheep concentrated grass in the diet to a similar extent on both swards (Tables 1 and 2), reflecting the distribution of clover foliage towards the base of the canopy in both cases (Hu, 1993). The concentration of white clover in the diet selected was only marginally higher at high allowance, despite greater opportunity for selection.

The vertical distribution of the sward components in both canopies was similar to the results reported by Bootsma *et al.* (1990) and L'Huillier *et al.* (1986) in autumn swards, where the greater grazing intensity was confined to the surface horizons mainly consisting of green leaf. Leaf and pseudostem components could not be distinguished in extrusa samples, but visual appraisal suggested that green leaf was the main component of the diet selected.

The *in vitro* digestibility of the diet was not affected by grazing allowance and only to a limited extent by sward species. The significantly lower OMD of extrusa samples taken from Yorkshire fog swards compared to ryegrass swards is in accord with the results of Morton *et al.* (1992), but in contrast to the published evidence of Watt (1987) and Harvey *et al.* (1984) who found no differences in OMD between Yorkshire fog and perennial ryegrass. However, in these experiments pasture samples were taken by sward cutting techniques.

Terrill *et al.* (1992a,b) found that both Yorkshire fog and perennial ryegrass contain trace amounts of CT, the CT values being slightly higher for Yorkshire fog, especially for the CT fraction bound to protein. The results of this experiment confirm these findings. It is unlikely that CT had any influence on animal performance in the conditions of the present experiment because of the low CT concentration in the diet (Table 2), as well as the low bypass-protein requirements of the experimental ewes which were in mid-gestation. There was no indication that the small differences in tannin content influenced discrimination between the grass and legume components of the two swards.

The herbage intake (kg OM ewe^{-1} day-1) and liveweight gain (g ewe^{-1} day^{-1}) achieved were similar to those suggested by Geenty and Rattray (1987) for grazing ewes in mid-pregnancy under New Zealand pasture conditions.

Bite weight was greater from *Holcus* than from ryegrass swards (Table 3). This effect may reflect the greater bulk density of herbage in *Holcus* swards (Hu, 1993) and, taken with the information on diet composition, indicates no particular behavioural constraints on the intake of *Holcus*. In contrast, daily herbage intake was greater from ryegrass than from *Holcus* swards at both allowances (Table 3). To our knowledge, this is the first reported case of an inverse relationship between the two variables. Evidence from the behaviour studies clearly indicates that the advantage to *Holcus* in terms of bite weight was offset by lower bite rate and grazing time. These factors do not explain the inverse relationship between bite weight and daily intake in strict quantitative terms, and there is clearly a need for more detailed work on the components of ingestive behaviour. However, the above contrasts are supported by evidence from a later trial at this laboratory (Montossi, unpublished data).

Reducing the daily herbage allowance from 12 to 6% of LW depressed daily herbage intake by 16%. This decline appears to be related principally to reductions in bite weight. Grazing time increased with declining herbage allowance, though the effect was not completely compensatory, while rate of biting was similar in both allowances. Similar effects of variations in herbage allowance on ingestive behaviour variables have been reported (Hodgson, 1985; Poppi *et al.*, 1987), though intake responses have not usually been observed to such high levels of allowance. Differences between treatments in herbage intake were reflected in differences in weight gain. However, levels of variation were high relative to the low weight increments of the ewes.

CONCLUSIONS

Evidence from this trial confirms the limited concentrations of condensed tannins in Yorkshire fog, and provides further evidence that low concentrations exist in perennial ryegrass. There was no evidence of differences in the degree of discrimination between the grass and legume components in the two swards.

Levels of herbage intake per sheep were substantially lower for Yorkshire fog than for perennial ryegrass swards. Though not conclusive, the evidence suggests that the most important limits were nutritional rather than behavioural in origin, and reflected differences in diet digestibility rather than in bite weight. This evidence requires substantiation for animals with higher growth potential and nutrient demand, and over an expanded range of growing seasons.

ACKNOWLEDGEMENTS

We thank the staff of the Departments of Plant and Animal Science, Massey University, for their support in the field and laboratory work.

The two senior authors were supported by scholarships from the Ministry of External Relations & Trade. FM also received financial support from the Instituto Nacional de Investigacion Agropecuaria (INIA), Uruguay.

Appendix Table 4.1. Variation in rumen ammonia concentration (mg NH_3 ml^{-1} of rumen fluid) during 24 hours in rumen fistulated wethers grazing on Yorkshire fog and perennial ryegrass swards treated with zero or 40 g $sheep^{-1}$ day^{-1} of polyethylene glycol (PEG; MW 4,000).

TIME	Species (SPP)			Oral PEG supplementation			SPP × PEG					Significance[§] of the main effects and interaction		
							RYEGRASS		YORKSHIRE FOG					
Hours	R[1]	Fog[2]	SEM[‡]	Without	With	SEM	NONPEG	PEG	NONPEG	PEG	SEM	SPP	PEG	SPP×PEG
0900	466	306	39	361	411	39	425	506	296	316	56	*	NS	NS
1300	592	390	34	459	524	34	574	639	372	372	48	**	NS	NS
1700	697	417	29	513	600	29	651	743	375	457	41	**	NS	NS
2100	813	493	52	580	724	52	752	874	410	575	73	**	NS	NS
0100	711	463	48	503	671	48	634	788	372	554	67	**	*	NS
0500	370	262	17	321	310	17	376	364	268	256	24	**	NS	NS

R[1] = Perennial ryegrass
Fog[2] = Yorkshire fog
SEM[‡] = Standard error of the mean
Sig. [§] = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean in each sampling time for main effects (n = 6) and interactions (n = 3).

Appendix Table 4.2. Effects of sward species and oral PEG supplementation on the mean release rate of Chromium sesquioxide (Cr_2O_3; mg day^{-1}) measured in rumen-fistulated (RFs) wethers and in intact experimental lambs.

Techniques of evaluation and periods	Species (SPP)				Oral PEG supplementation				SPP × PEG					
									Ryegrass		Yorkshire fog			
	Ryegrass	Fog	SEM[‡]	Sig[§]	Without	With	SEM	Sig	NONPEG	PEG	NONPEG	PEG	SEM	Sig
DECEMBER RFs[1]	189	212	12	NS	207	194	12	NS	165a[2]	212b	222b	200b	17	NS
JANUARY RFs	179	201	4	*	189	190	5	NS	171a	186ab	208b	192b	7	NS
JANUARY Intact lambs	191	186	4	NS	190	188	6	NS	198a	184a	180a	191a	9	NS

[1] Rumen-fistulated wethers.
[2] Means within rows for interactions with letters in common are not significantly different at the $P < 0.05$.
SEM[‡] = Standard error of the mean.
Sig.[§] = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean each month for main effects (January-intact lambs = 32; December and January-RFs = 12) and for interactions (January-intact lambs = 16; December and January-RFs = 6).

Appendix Table 4.3. Effects of sward species, oral PEG supplementation and lamb sex and their interactions on herbage intake (HI; g OM lamb^{-1} day^{-1} or g OM kg LW$^{0.73}$ day^{-1}) for December and January.

PERIODS	SPP × PEG					PEG × SEX					Significance[§] of the main factors and their interactions.			
	Ryegrass		Fog			Female		Male						
	NONPEG	PEG	NONPEG	PEG	SEM	NONPEG	PEG	NONPEG	PEG	SEM	S×P	P×S	SEX×P	S×P×S
DECEMBER														
HI head^{-1}	990	990	820	780	34	900	910	910	860	44	NS	NS	NS	NS
HI kgLW$^{0.73}$	82	82	67	71	2.4	75	81	75	72	3.7	NS	NS	NS	NS
JANUARY														
HI head^{-1}	1350	1390	1240	1130	87	1310	1320	1280	1280	98	NS	NS	NS	NS
HI kgLW$^{0.73}$	100	97	89	80	5.7	93	86	93	94	7.8	NS	NS	NS	NS

SEM[‡] = Standard error of the mean.
Sig.[§] = * P < 0.05, ** P < 0.01 and NS (not significant).
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and lamb sex (male = 48; female = 16).

Appendix Table 4.4. Effects of sward species, oral PEG supplementation and lamb sex on greasy and clean wool growth from midside areas ($\mu g\ cm^{-2}\ day^{-1}$) and on wool yield (%).

(a) PERIODS		Species (SPP)				Oral PEG supplementation				SEX			
		Ryegrass	Fog	SEM[‡]	Sig.[§]	Without	With	SEM	Sign.	Female	Male	SEM	Sign.
DECEMBER - JANUARY (54 days)	Greasy wool growth	1336	1260	27	NS	1268	1329	41	NS	1336	1260	49	NS
	Clean wool growth	1034	973	15	NS	974	1033	17	NS	1035	972	32	NS
	Wool yield	78	77	1.1	NS	77	78	0.3	NS	78	77	0.81	NS
FEBRUARY - MARCH (41 days)	Greasy wool growth	1610	1496	45	NS	1604	1500	45	NS	1592	1514	50	NS
	Clean wool growth	1259	1197	15	NS	1194	1262	33	NS	1248	1208	38	NS
	Wool yield	79	81	1.1	NS	80	79	0.8	NS	79	80	0.86	NS

(b) PERIODS		SPP x PEG						PEG x SEX					
		Ryegrass		Fog				Female		Male			
		NONPEG	PEG	NONPEG	PEG	SEM	Sign.	NONPEG	PEG	NONPEG	PEG	SEM	Sig.
DECEMBER - JANUARY (54 days)	Greasy wool growth	1260a[1]	1440b	1270a	1250a	21	*	1270	1400	1270	1250	69	NS
	Clean wool growth	950a	1110b	990a	950a	24	*	990	1080	960	990	51	NS
	Wool yield	77	79	77	76	0.48	NS	79	77	76	78	1.15	NS
FEBRUARY - MARCH (41 days)	Greasy wool growth	1530	1690	1480	1520	63	NS	1480	1710	1530	1500	70	NS
	Clean wool growth	1210	1310	1180	1210	46	NS	1170	1320	1220	1200	54	NS
	Wool yield	80	78	80	81	1.26	NS	80	79	80	80	1.22	NS

SEM[‡] = Standard error of the mean
Sig.[§] = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
[1] Means within rows for interactions with letters in common are not significantly different at the $P < 0.05$ of probability.
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and lamb sex (male = 48; female = 16).

Appendix Table 4.5. Effects of sward species, oral PEG supplementation and lamb sex on lamb liveweight gain (g day^{-1}) from December to March assessed in three different periods and overall.

(a) TIME	Species (SPP)				Oral PEG supplementation				SEX			
	Ryegrass	Fog	SEM‡	Sig.§	Without	With	SEM	Sig.	Female	Male	SEM	Sig.
08/12 - 18/01	165	129	10	NS	136	158	15	NS	141	153	11	NS
18/01 - 06/02	190	208	28	NS	190	207	16	NS	186	211	12	NS
06/02 - 15/03	64	68	10	NS	72	60	10	NS	86	47	8	**
Overall	131	121	9	NS	122	130	7	NS	134	119	4.4	*

(b) TIME	SPP x PEG						Other interaction factors.		
	Ryegrass		Fog						
	NONPEG	PEG	NONPEG	PEG	SEM	Sig.	SPPxSEX	PEGxSEX	SPPxSEXxPEG
08/12 - 18/01	166	163	149	108	21	NS	NS	NS	NS
18/01 - 06/02	204	175	209	206	22	NS	NS	NS	NS
06/02 - 15/03	53	73	66	70	14	NS	NS	NS	NS
Overall	130	131	129	113	10	NS	NS	NS	NS

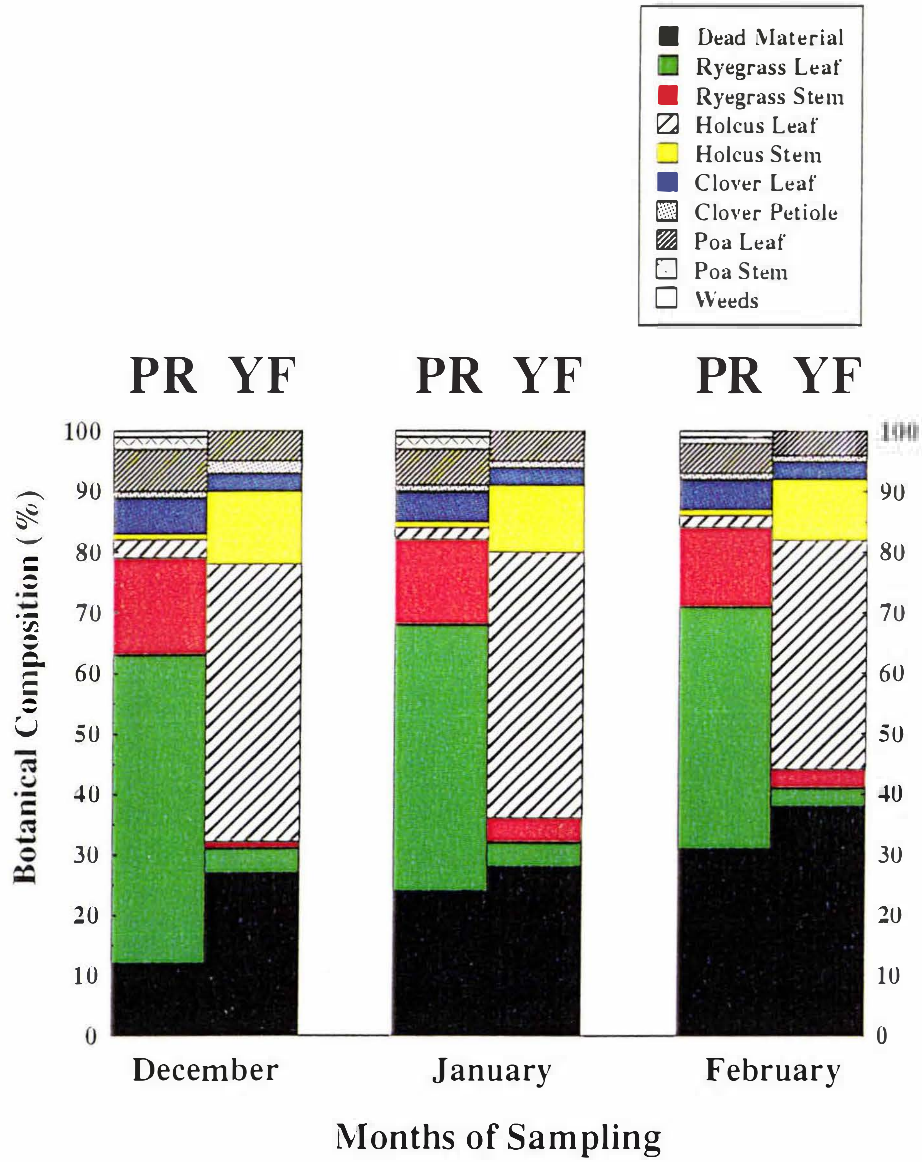
SEM‡ = Standard error of the mean
Sig.§ = * $P < 0.05$, ** $P < 0.01$ and NS (not significant).
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and lamb sex (male = 48; female = 16).

Appendix Table 4.6. Effects of sward species, oral PEG supplementation and lamb sex on carcass weight (kg), GR (mean value of left and right sides, mm) and dressing out (%).

(a) Carcass quality measurements	Species (SPP)			Oral PEG supplementation			Sex		
	Ryegrass	Fog	SEM[‡]	Without	With	SEM	Female	Male	SEM
Carcass weight	17.5	16.3	0.22	16.8	17.0	0.36	16.6	17.1	0.48
GR[1]	6.7	5.4	0.59	6.2	5.9	0.72	7.4	4.8	0.58
Dressing out	46.2	45.4	0.31	45.2	46.4	0.41	46.5	45.1	0.43

(b) Carcass quality measurements	SPP x PEG					Significance[§] of the main factors and their interactions						
	Ryegrass		Fog									
	NONPEG	PEG	NONPEG	PEG	SEM	SPP	PEG	SEX	SPPxPEG	PEGxSEX	SPPxSEX	SPPxPEGxSEX
Carcass weight	17.3	17.6	16.2	16.4	0.52	*	NS	NS	NS	NS	NS	NS
GR	7.0	6.4	5.4	5.4	1.00	NS	NS	**	NS	NS	NS	NS
Dressing out	46	46.4	44.5	46.3	0.64	NS	NS	**	NS	NS	NS	NS

SEM[‡] = Standard error of the mean.
Sig.[§] = * P < 0.05, ** P < 0.01 and NS (not significant).
Number of observations contributing to the mean each month for main effects (n = 32), interactions (n = 16), and lamb sex (male = 48; female = 16).
GR[1] = Mean value of left and right sides.



Appendix Figure 4.1. Botanical composition (%) of perennial ryegrass and Yorkshire fog swards during December, January, and February determined from inclined point quadrat contacts.

NOTE: PR = Perennial ryegrass, YF = Yorkshire fog

Appendix Table 5.1. Levels of pH, Resinas-Phosphorus, Exchangeable Potassium and Carbon of experimental plots measured in April 1993.

FEATURES	GRASS				LOTUS				INTERACTION					
	Ryegrass	Yorkshire fog	SEM[‡]	Sig.[§]	+ L	- L	SEM	Sig.	Ryegrass + L	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM	Sign.
pH	5.4	5.3	0.04	NS	5.3	5.3	0.04	NS	5.4	5.4	5.3	5.3	0.05	NS
Resinas-P (µm/g soil)	8.6	4.5	1.28	*	5.6	7.5	0.06	NS	7.3	10.0	4.0	5.0	1.80	NS
Potassium (meq/100 g soil)	1.1	1.1	0.04	NS	1.1	1.1	0.04	NS	1.2	1.1	1.0	1.2	0.06	NS
Organic Carbon (%/g soil)	2.9	2.9	0.06	NS	3.0	2.8	0.06	NS	3.0	2.8	3.0	2.8	0.09	NS

SEM[‡] = Standard error of the mean.
Sig[§]. = * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ and NS (not significant).
Number of observations contributing to the mean for main effects (n = 8), and interactions (n = 4).

	BEFORE GRAZING									
MONTHS	GRASS x LOTUS x MONTHS					OVERALL EFFECTS				
AUGUST	Ryegrass + L[3]	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM[‡]	GRASS: Ryegrass	Yorkshire fog	SEM	Sig.[§]	
Herbage Mass	4450	4590	3800	4030	280	5820	4360	190	***	
Dead Herbage Mass	670	960	420	400	110	1140	870	57	**	
Sward Height (R[1])	29	27	22	21	1.5	29	21	0.6	***	
Sward Height (RPM[2])	18	21	16	14	1.0	18	12	0.4	***	
Sward Bulk Density R	160	170	180	200	12	201	210	5.2	NS	
Sward Bulk Density RPM	250	220	240	290	20	340	390	11	***	
Green Bulk Density R	130	130	150	170	12	150	170	4.2	*	
Green Bulk Density RPM	210	170	210	260	20	240	300	10	**	
SEPTEMBER	Ryegrass + L	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM	LOTUS: + L	- L	SEM	Sig.	
Herbage Mass	6150	6530	4350	4780	280	5000	5180	190	NS	
Dead Herbage Mass	1410	2090	780	1100	110	1150	1340	57	NS	
Sward Height (R[1])	30	32	23	22	1.5	25	25	0.6	NS	
Sward Height (RPM[2])	17	14	12	11	1.0	15	15	0.4	NS	
Sward Bulk Density R	210	210	200	220	12	200	210	5.1	NS	
Sward Bulk Density RPM	360	360	400	480	20	360	380	11	NS	
Green Bulk Density R	160	140	160	170	12	160	150	4.3	NS	
Green Bulk Density RPM	280	240	320	360	20	280	280	10	NS	
OCTOBER	Ryegrass + L	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM	INTERACTIONS: GxL	T[4]	TxG	TxL	TxGxL
Herbage Mass	6420	6760	4800	4390	280	NS	***	**	NS	NS
Dead Herbage Mass	1600	2500	1490	1010	110	NS	***	***	***	NS
Sward Height (R[1])	28	30	20	20	1.5	NS	NS	NS	NS	NS
Sward Height (RPM[2])	15	17	11	10	1.0	NS	***	NS	NS	NS
Sward Bulk Density R	230	230	240	220	12	NS	***	NS	NS	NS
Sward Bulk Density RPM	440	400	460	440	20	NS	***	NS	NS	NS
Green Bulk Density R	170	140	170	170	12	NS	**	NS	NS	NS
Green Bulk Density RPM	320	260	320	340	20	NS	**	NS	NS	NS

	AFTER GRAZING									
MONTHS	GRASS x LOTUS x MONTHS					OVERALL EFFECTS				
AUGUST	Ryegrass + L	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM	GRASS: Ryegrass	Yorkshire fog	SEM	Sig.	
Herbage Mass	3740	3610	2580	2860	300	4160	3340	125	**	
Dead Herbage Mass	1010	830	340	290	220	1470	1210	123	NS	
Sward Height (R[1])	15	13	11	10	1.3	15	12	0.3	***	
Sward Height (RPM[2])	9	9	6	6	0.9	11	7	0.3	***	
Sward Bulk Density R	260	280	250	320	24	290	310	12	NS	
Sward Bulk Density RPM	440	460	480	520	42	440	560	24	**	
Green Bulk Density R	180	210	200	260	21	190	180	8	NS	
Green Bulk Density RPM	300	320	400	480	38	280	360	14	**	
SEPTEMBER	Ryegrass + L	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM	LOTUS: + L	- L	SEM	Sig.	
Herbage Mass	4640	4780	4200	3655	300	3830	3700	160	NS	
Dead Herbage Mass	1760	2150	2140	1570	220	1320	1340	123	NS	
Sward Height (R[1])	18	20	17	14	1.3	14	13	0.3	NS	
Sward Height (RPM[2])	12	14	10	8	0.9	9	8	0.3	NS	
Sward Bulk Density R	260	240	250	260	24	310	290	12	NS	
Sward Bulk Density RPM	400	360	440	500	42	500	480	24	NS	
Green Bulk Density R	160	133	120	150	21	170	190	7.6	NS	
Green Bulk Density RPM	240	200	200	280	38	300	320	14	NS	
OCTOBER	Ryegrass + L	Ryegrass - L	Yorkshire fog + L	Yorkshire fog - L	SEM	INTERACTIONS: GxL	T	TxG	TxL	TxGxL
Herbage Mass	4130	4090	3520	3230	300	NS	***	NS	NS	NS
Dead Herbage Mass	1280	1760	1410	1490	220	NS	***	NS	NS	NS
Sward Height (R[1])	12	12	19	8	1.3	*	***	NS	NS	NS
Sward Height (RPM[2])	9	10	6	5	0.9	*	***	NS	NS	NS
Sward Bulk Density R	360	330	360	410	24	NS	***	NS	NS	NS
Sward Bulk Density RPM	480	440	640	740	42	NS	***	*	NS	NS
Green Bulk Density R	240	190	110	220	21	*	***	NS	NS	NS
Green Bulk Density RPM	320	240	360	380	38	NS	***	NS	NS	NS

R[1] = Estimates from ruler inside quadrat cuts, RPM[2] = Estimates from Rising Plate Meter inside quadrat cuts, [3]L = Lotus, and [4]T = Time. SEM[‡] = Standard error of the mean, Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant). Number of observations contributing to the mean for main effects (n = 40), main effect-interactions (n = 20).

Appendix Table 5.3. The effect of grass and lotus on sward height at plot level estimated by ruler and Rising Plate Meter (RPM) before and after grazing during August, September, October and Overall.

BEFORE GRAZING

MONTHS	GRASS × LOTUS × MONTHS					OVERALL EFFECTS				
AUGUST	Ryegrass		Yorkshire fog			GRASS				
	+ L[3]	- L	+ L	- L	SEM[‡]	Ryegrass	Yorkshire fog	SEM	Sig.[§]	
Sward Height (R[1])	34	33	31	27	0.9	30	23	0.3	***	
Sward Height (RPM[2])	19	19	17	15	0.6	15	11	0.1	***	
SEPTEMBER	Ryegrass		Yorkshire fog			LOTUS				
	+ L	- L	+ L	- L	SEM	+ L	- L	SEM	Sig.	
Sward Height (R[1])	29	31	22	20	0.9	27	26	0.3	NS	
Sward Height (RPM[2])	15	15	11	10	0.6	14	13	0.1	NS	
OCTOBER	Ryegrass		Yorkshire fog			INTERACTIONS				
	+ L	- L	+ L	- L	SEM	G×L	T[4]	T×G	T×L	T×G×L
Sward Height (R[1])	29	26	18	19	0.9	NS	***	***	NS	**
Sward Height (RPM[2])	11	11	9	9	0.6	NS	***	*	NS	NS

AFTER GRAZING

MONTHS	GRASS × LOTUS × MONTHS					OVERALL EFFECTS				
AUGUST	Ryegrass		Yorkshire fog			GRASS				
	+ L	- L	+ L	- L	SEM	Ryegrass	Yorkshire fog	SEM	Sig.	
Sward Height (R[1])	17	18	15	15	0.7	15	13	0.3	***	
Sward Height (RPM[2])	10	10	7	6	0.4	8	6	0.1	***	
SEPTEMBER	Ryegrass		Yorkshire fog			LOTUS				
	+ L	- L	+ L	- L	SEM	+ L	- L	SEM	Sig.	
Sward Height (R[1])	14	16	13	12	0.7	14	14	0.3	NS	
Sward Height (RPM[2])	7	9	6	5	0.4	7	7	0.1	NS	
OCTOBER	Ryegrass		Yorkshire fog			INTERACTIONS				
	+ L	- L	+ L	- L	SEM	G×L	T	T×G	T×L	T×G×L
Sward Height (R[1])	13	11	10	11	0.7	NS	***	NS	NS	*
Sward Height (RPM[2])	7	6	6	6	0.4	NS	***	**	NS	**

R[1] = Estimates from ruler at plot level.
RPM[2] = Estimates from Rising Plate Meter at plot level.
[3]L = Lotus.
[4]T = Time.
SEM[‡] = Standard error of the mean.
Sig[§]. = * P <0.05, ** P <0.01, *** P <0.001 and NS (not significant).
Number of observations contributing to the mean for main effects (n = 240), main effect-interactions (n = 120).

Appendix Table 5.4. Tiller and node population density in each sward combination (tillers and nodes m^2), data based on tiller and node hand separation measured in September 1993.

FEATURES	GRASS				LOTUS				INTERACTION					
									Ryegrass		Yorkshire fog		SEM	Sign.
	Ryegrass	Yorkshire fog	SEM[†]	Sig.[§]	+ L	- L	SEM	Sig.	+ L[1]	- L	+ L	- L		
Ryegrass tillers	2560	600	117	***	1520	1640	117	NS	2540	2580	500	700	170	NS
Yorkshire fog tillers	3	1720	37	***	720	1010	37	***	0	7	1430	2010	52	***
White clover nodes	40	50	12	NS	30	60	12	NS	37	42	20	80	17	NS
Lotus nodes	40	50	16	NS	0	92	16	**	82	0	100	0	23	NS
Weeds	50	100	16	NS	50	100	16	*	70	35	60	130	23	NS
Total population	2693	2520	112	NS	2320	2902	112	*	2729	2664	2110	2920	159	*

Appendix Table 5.5. Tiller dissection results of ryegrass and Yorkshire fog tillers in each sward combination measured in September 1993.

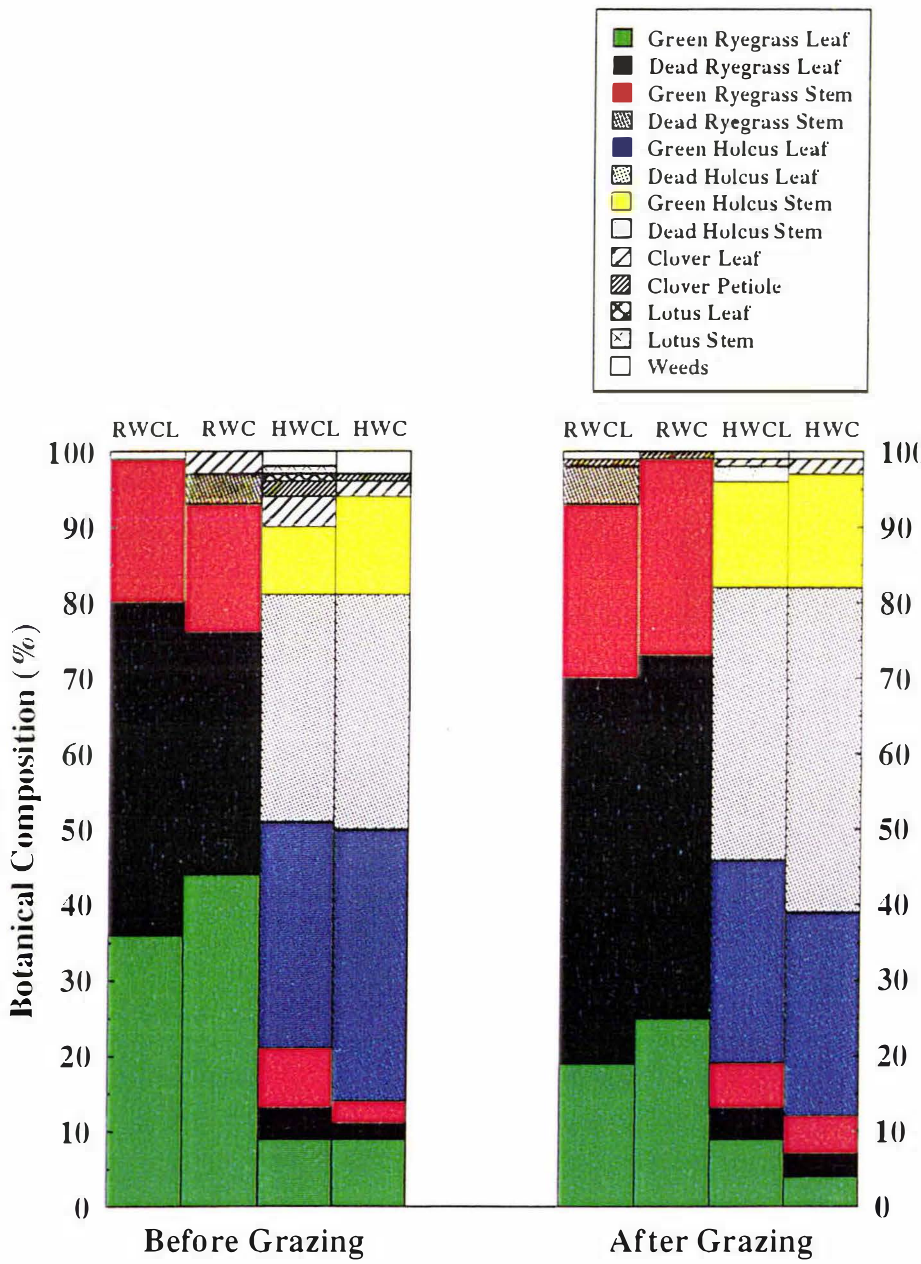
FEATURES	GRASS				LOTUS				INTERACTION					
									Ryegrass		Yorkshire fog		SEM	Sign.
	Ryegrass	Yorkshire fog	SEM[†]	Sig.[§]	+ L	- L	SEM	Sig.	+ L	- L	+ L	- L		
Stem length/per tiller (mm)	187	157	10	NS	181	163	10	NS	191	183	171	143	14	NS
Stem weight/per tiller (mg)	21	16	1.8	NS	21	16	1.8	NS	25	16	16	15	2.6	NS
Leaf number/per tiller	3.5	3.9	0.11	NS	3.8	3.6	0.11	NS	3.7	3.4	3.9	3.9	0.16	NS
Leaf length/per leaf (mm)	160	161	10	NS	172	148	10	NS	172	147	172	150	15	NS
Leaf weight/per leaf (mg)	14	12	1.9	NS	15	11	1.9	NS	18	11	13	12	2.7	NS

SEM[†] = Standard error of the mean. [1]L = Lotus.
Sig[§]. = * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$ and NS (not significant).
Number of observations contributing to the mean for main effects (n = 80), and interactions (n = 40).

Appendix Table 5.6. Mean abomasal, intestinal, and total worm burdens in lambs grazing on Yorkshire fog or on ryegrass swards, which were slaughtered at the end of the trial.

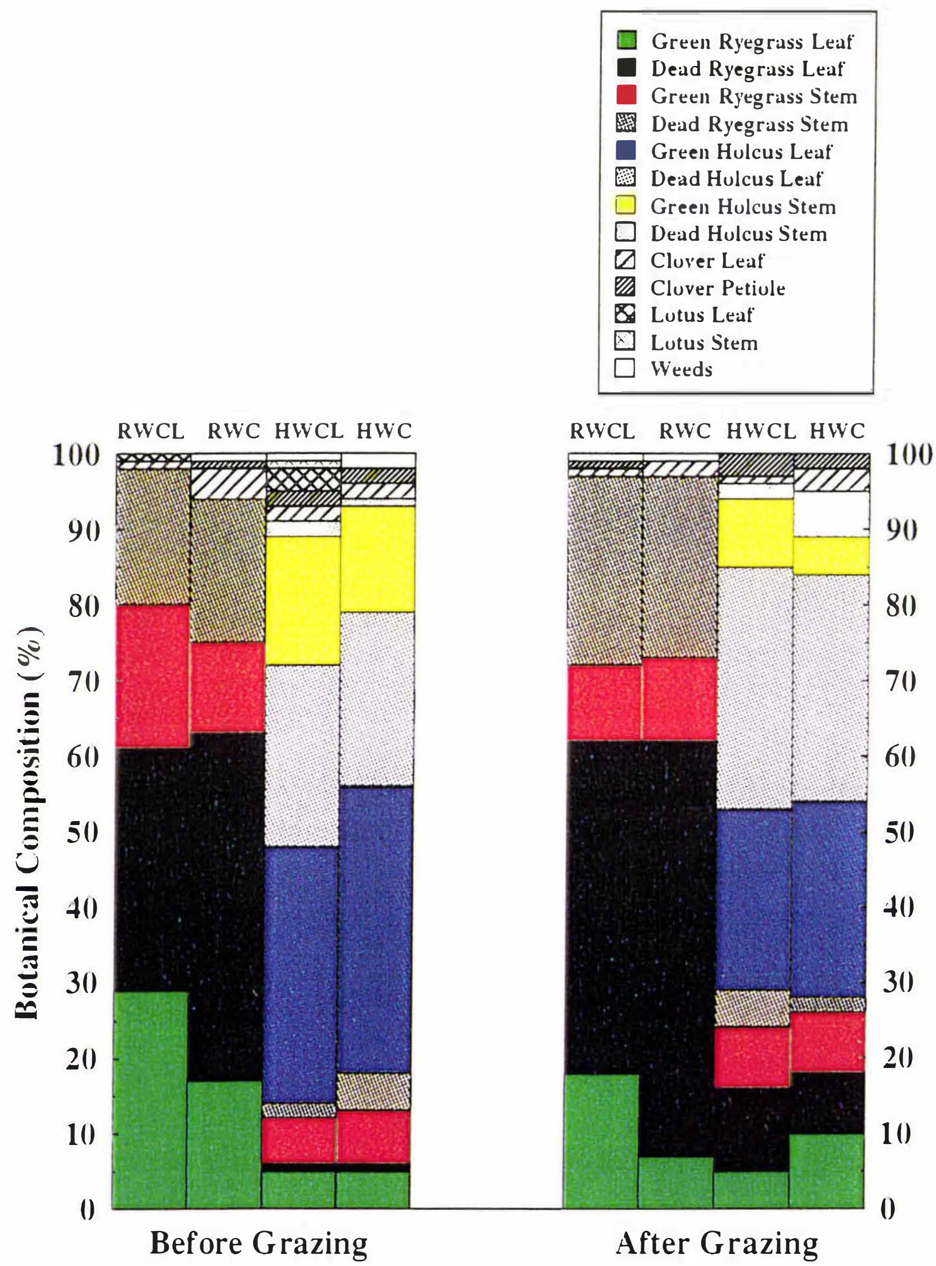
WORMS BURDENS	GRASS			
	Ryegrass	Yorkshire fog	SEM‡	Sig.§
Abomasal population[1]	61 (7.6)[5]	10 (2.8)	(1.00)	*
Small intestinal population[2]	63 (6.8)	10 (2.5)	(2.16)	NS
Large intestinal population[3]	42 (4.9)	11 (3.2)	(1.86)	NS
Total population[4]	166 (12.9)	31 (5.7)	(0.67)	**

[1] = Mainly consisted of *Haemonchus, Ostertagia*, and *Trichostrongylus* spp.
[2] = Only consisted of *Trichostrongylus* spp.
[3] = Mainly consisted of *Oesophagostomum* and *Trichuris* spp.
[4] = Addition of Abomasal and small and large intestinal worm burdens.
[5] = Worm burdens data was normalized by square-root transformation plus 0.5 prior to analysis (values in brackets).
SEM‡ = Standard error of the mean.
Sig§. = * P < 0.05, ** P < 0.01, *** P < 0.001 and NS (not significant).
Number of observations contributing to the mean of grass effect (n = 4).



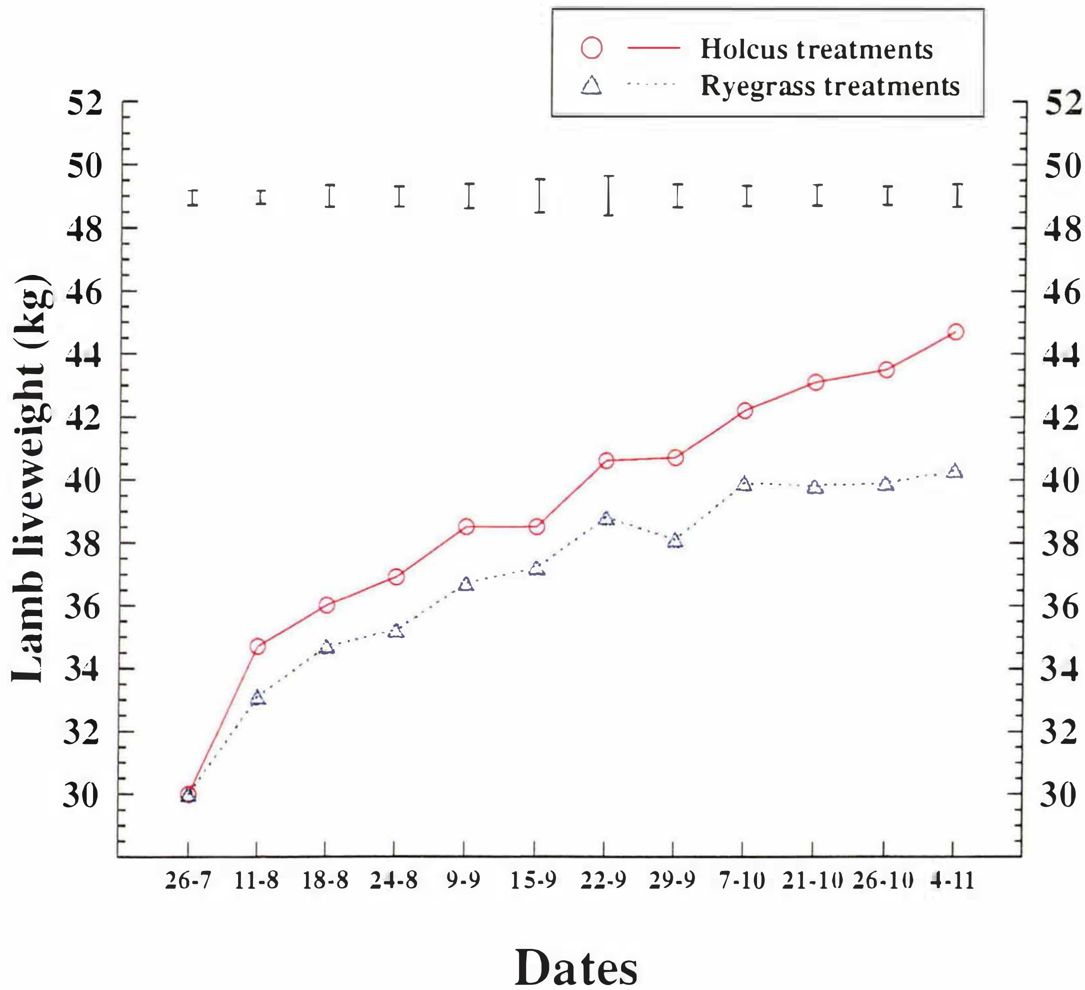
Appendix Figure 5.1. Botanical composition (%) of Perennial ryegrass and Yorkshire fog swards during September determined from inclined point quadrat contacts.

NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover

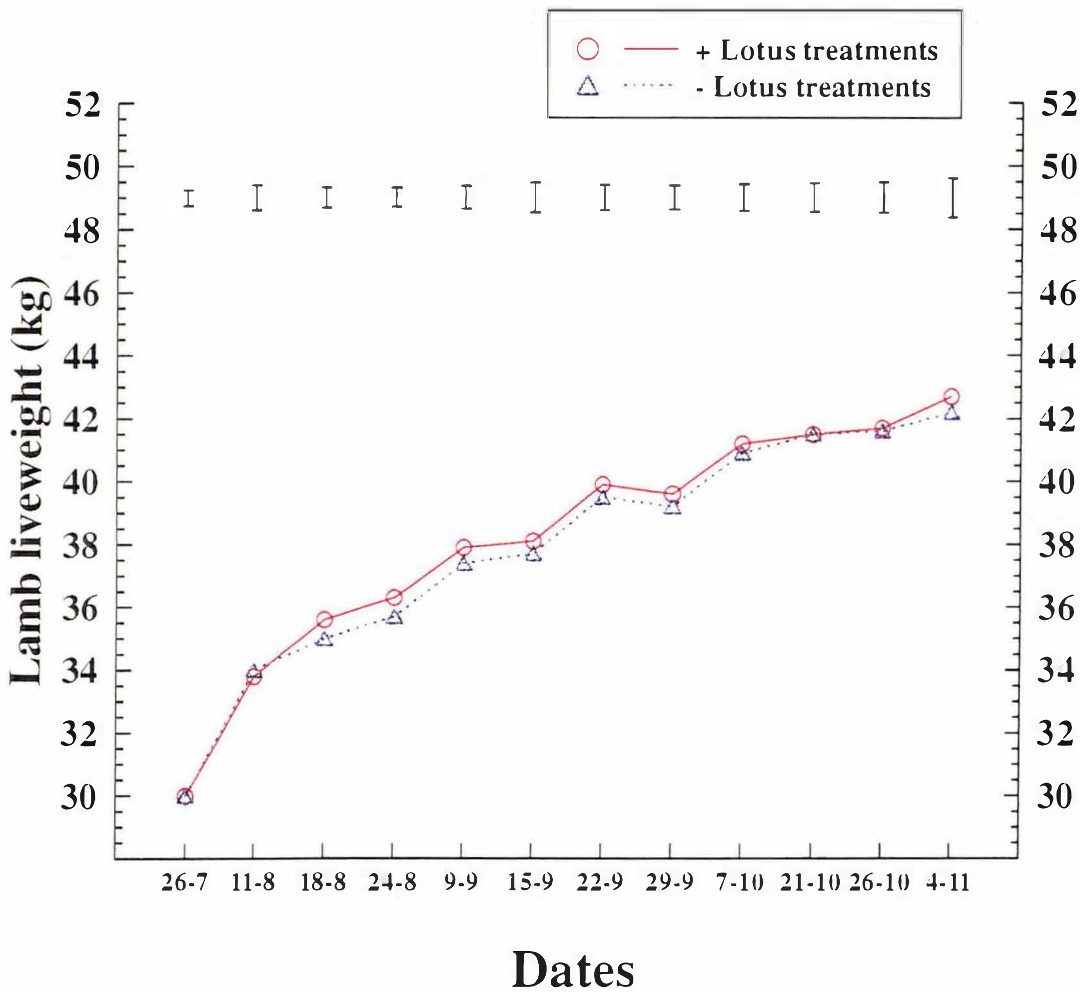


Appendix Figure 5.2. Botanical composition (%) of Perennial ryegrass and Yorkshire fog swards during October determined from inclined point quadrat contacts.

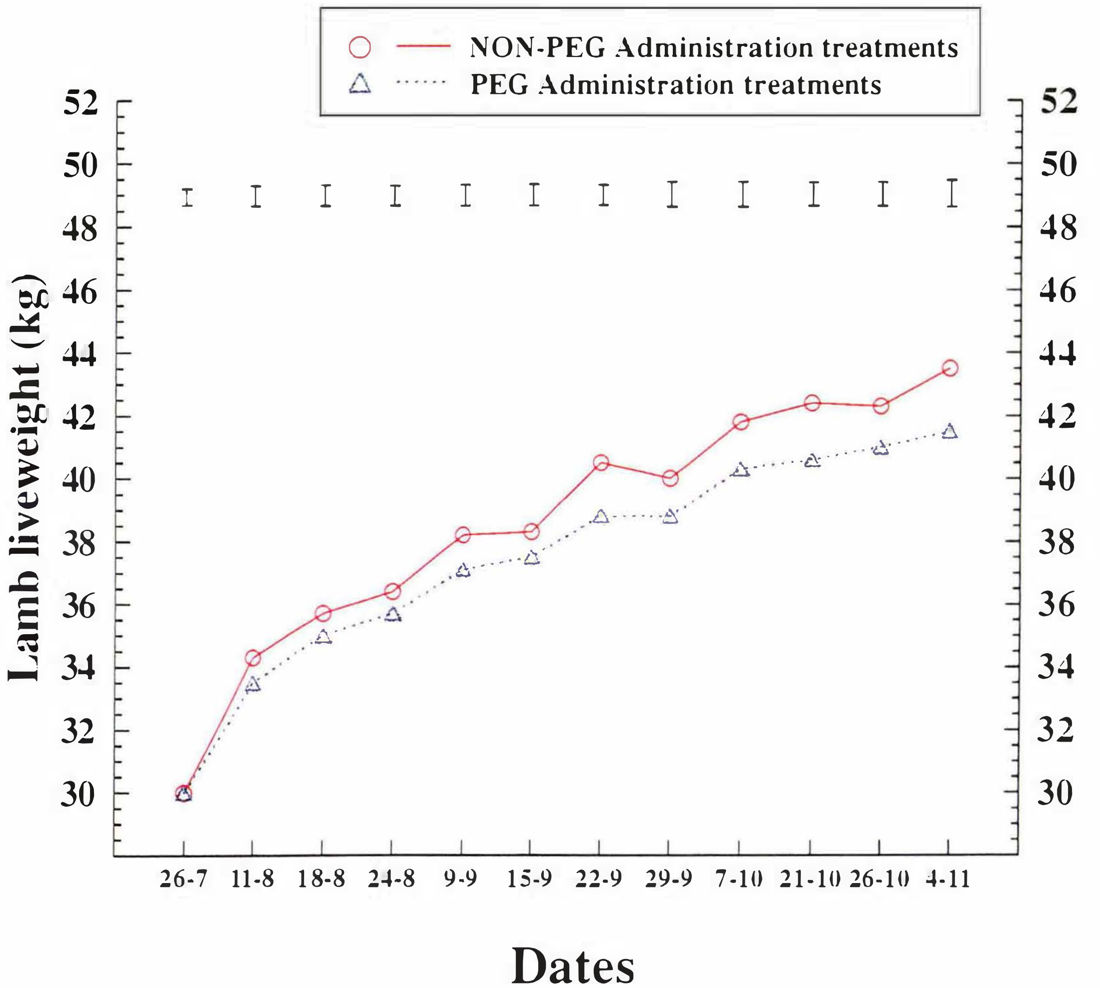
NOTE:
RWCL = Ryegrass + White clover + Lotus
RWC = Ryegrass + White clover
HWCL = Yorkshire fog + White clover + Lotus
HWC = Yorkshire fog + White clover



Appendix Figure 5.3. The effect of grass species on lamb liveweight (kg) from August to November. Vertical lines indicate the standard error of the mean.



Appendix Figure 5.4. The effect of lotus treatments on lamb liveweight (kg) from August to November. Vertical lines indicate the standard error of the mean.



Appendix Figure 5.5. The effect of PEG administration on lamb liveweight (kg) from August to November. Vertical lines indicate the standard error of the mean.

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