Sward structural characteristics and selective foraging behaviour in dairy cows

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We know what we are, but know not what we may be

Shakespeare – Hamlet, Act IV. Sc. 5

ABSTRACT

This thesis sought to further the understanding of foraging behaviour in the context of the manner in which dairy cattle graze in a complex dietary environment, and incorporated an evaluation of the trade-offs cattle make between criteria for selection between alternative patches of vegetation. A series of five experiments at the patch scale were carried out with four trained dairy cows, using a novel methodology of patches arranged in linear sequence. Observations of preferential behaviour (grazing bites, residence time and the mass of herbage removed) were related to choices involving combinations of sward physical, structural and morphological characteristics, and where possible were related to phenomena defining the components of ingestive behaviour, primarily bite depth and bite mass.

Swards in a vegetative phase of growth were offered to animals in Experiment 1, with sward height a stronger patch cue than bulk density, although the relative importance of density within the selection criteria could not be ascertained. Green leaf mass, however, was strongly associated with sward height (Experiments 1 and 2). When sward maturity was added to the heterogeneity of the offered choices, increasing the complexity of decisions the cattle faced, patch reward was no longer always associated with sward height as a cue (Experiments 3 and 4). Cattle then sampled all sward choices in the appraisal phase of foraging to gain information about their potential value. The preferential grazing of the short immature swards in Experiment 3 indicated that the initial approach cue of sward height was strongly conditioned by the information gathered about sward maturity upon patch appraisal. The selective response for short immature swards could not be accounted for by variations in leaf mass or the depth of regrowth, which suggested that the distribution of leaf mass within the canopy, and the intermingling of leaf and stem within the grazed stratum strongly modified patch residence time. The results from Experiment 3 suggested clearly the need to separate out the effects of sward height and maturity on foraging decisions. In Experiment 4, cattle strongly used the handling cue of depth of regrowth rather than sward height as a basis for patch appraisal, and because of the decline in the depth of regrowth with increasing sward height, sward height was negatively associated with patch preference. The strength of the effect of maturity over that of sward height as a selection cue was a particularly significant finding from the programme. The final experiment (Experiment 5) investigated the role of the spatial distribution of patches relative to patch area and sward height on foraging behaviour. When foraging responses were adjusted for per unit area effects, the current patch distance strongly influenced patch selection as measured by the preferential indices of grazing bites and residence time. In this study preference was greater for the short sward treatment but, within sward height treatments, preference was linearly related to sward height. Animals showed strong evidence for the monitoring of patch area.

Analysis of the patch grazing cycle showed an asymptotic relationship between bite depth and bite number (Experiment 4) which indicated a clear adjustment phase where animals increased the depth of penetration as they gained information and appreciated the opportunity value of the patch. The structure and composition of sward strata were found to be important regulators of bite penetration. When the contrast between the stubble and regrowth strata reflecting variations in biting resistance were small (Experiment 2) cattle readily penetrated into the stubble stratum comprising leaf and pseudostem (Experiment 2). At the opposite end of the continuum, when the contrast between the two strata was greater (Experiment 4), the depth of bite penetration was strongly influenced by the vertical position of the regrowth:stubble interface. The response in terms of deeper penetration into the stubble stratum with increasing sward height (Experiment 4) led to the conclusion that the interface was only a partial regulator of bite penetration, although it strongly influenced patch residence time, indicating the relative importance of this structural feature on patch ingestion. The sward combinations used throughout this thesis covered a wide range of sward heights. There was, however, a lack of consistency for the significance of the proportionality concept, a result strongly emphasised when choices comprised controlled variations in the proportions of regrowth and stubble (Experiment 4). This generalised finding raises concerns over the theoretical assumption that bite depth can be modelled as a constant proportion of sward height.

The absence of any consistent relationship for within and between patch behaviour across Experiments 1 to 5, and the absence for evidence of rate of intake control with increasing inter-patch distance (Experiment 5), and increasing number of bites removed per patch (Experiments 4 and 5) calls into question the underlying assumptions and constraints that characterise linear style foraging models such as the marginal value theorem.

The novel methodology used throughout this thesis demonstrated its potential to examine trade-off decisions, but greater effort will need to be focussed on separating many of the naturally confounding sward characteristics and their effects on foraging behaviour.

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There is a potential source of confusion in the description of sward state characteristics, particularly with reference to the tendency to use the terms horizon and stratum interchangeably. Throughout this thesis the terminology as defined below has been adhered to. Accordingly when quoting from published material, the terminology has been changed to maintain this consistency.

Stratum/strata	A depth of sward canopy confined between two distinct lines.
Horizon	A distinct line separating two strata.
Sward height	The average height of the uppermost surface of leaves in an undisturbed sward canopy.
Stubble height	The mean height from ground level of the cut surfaces of tillers following a defoliation or series of defoliations.
Regrowth depth	Depth of a stratum of regrowth. The difference between sward height and stubble height.
Pseudostem height	The height from the base of a tiller to the ligule of the youngest mature leaf.

ONE

INTRODUCTION

The prediction of herbage intake is a core prerequisite in the management of pastoral production systems, but researchers have yet to establish any consistent theory to link the foraging mechanisms used by animals to their functional objectives. There is now comprehensive knowledge of the factors influencing forage intake and, to a lesser extent, dietary choice (eg. morphological characteristics, biochemical compounds, learning through social interactions, experience and post-ingestive mechanisms). However, the inherent weakness lies in the inability to predict the responses to integrated sets of animal, pasture and time based variables in heterogeneous environments. There is limited opportunity for selective grazing in intensive production systems (Taylor, 1993) like New Zealand dairying but, even given the constraints imposed through management practices, animals are continually faced with a series of short-term decisions about what forage to select and where to forage. These decisions are central to the fundamental trade-off between forage quality and quantity, common to all herbivores.

Despite decades of observation of the behaviour of herbivores a reductionist approach largely categorises much of the body of literature (Provenza, 1991; Gordon and Lascano, 1993). By contrast, a mechanistic approach, considering behaviour as a 'process' rather than as an 'event' (Provenza, 1991) will be essential for meeting the objectives of productive and sustainable agricultural systems. Taylor (1993) summarising the session on foraging strategy at the 17th International Grassland Congress, commented that there was a general need for more testing of forage models in complex environments and that models must encompass a wider view of the animals' environment including patch selection behaviour. Since that time there has been active development of foraging theory (eg. Thornley *et al.*, 1994; Ginnett and Demment, 1995; Farnsworth and Illius, 1998; WallisDeVries *et al.*, 1998; Ginnett *et al.*, 1999; Illius *et al.*, 1999), but objective information on the foraging strategy of grazing animals is still limited, particularly with reference to the multiple choice conditions which are characteristic of most foraging environments.

The key objective in this thesis was to develop an understanding of foraging behaviour in dairy cows and in particular to investigate the influence of simultaneous variation in combinations of sward structural characteristics on the decision making process. The studies were based on a field design involving linear sequence of sward patches offering balanced variations in two or three sward variables at a time. Studies were carried out in the context of simple dairy swards, but the methods used are appropriate to the general principals of foraging strategy

TWO

REVIEW OF LITERATURE

2.1 OVERVIEW

The interaction between the herbivore and its food supply is a particularly rich and fruitful field of research. The versatility shown by animals in adapting their behaviour to the environmental conditions encountered is a unique attribute whether through innate or through learned behaviour. Treatment of animals as "intelligent machines" and focusing attention on the variation in behavioural patterns arising from changes in the environment is essentially a mechanistic approach to understanding animal behaviour. The interest in discriminatory behaviour has given rise to a number of models, each focusing on one or two key areas of what can at best be described as a complex and dynamic form of behaviour.

Five conceptual models of preferential behaviour were discussed by Provenza and Balph (1990). These models (i) Euphagia, (ii) Hedyphagia, (iii) Body morphophysiology and size, (iv) Optimal foraging and (v) Learning, were an attempt to provide explanations for 5 identified challenges that environments present to ruminants. Briefly, models (i) and (ii) have been refuted since they do not taken into account the influence of postingestive feedback, for which there is now substantial evidence (see Provenza, 1996a). Models based on morphology and physiology (iii) do hold a place in modelling. However, they ignore the important consideration that animals prefer the familiar to the novel in their diet and this be shaped by experience through learning. Optimal foraging (OFT) (iv) has had wide support in the literature for carnivores whose prey is less variable and distributed within discrete patches, compared to herbivores who are presented with greater ranges in nutritive value but food items distributed continuously. It is only more recently that the theory has been applied to ruminants and of the few published reports there is no clear consensus on the value of OFT to predict selection patterns. Additionally, OFT implies that animals will seek to maximise their intake rate, yet rate maximisation may not be the optimal strategy if the animal is required to learn about its environment, and so this violates the assumptions of complete knowledge. Nonetheless, even in light of criticism, Laca and Demment (1996) argue that OFT offers the strongest base for studying foraging responses. A learning model (v) to some extent avoids many of the limitations associated with the other four models and Provenza and Balph (1990) suggested it was a good framework for further studies into the acquisition of dietary habits, foraging skills and habitat selection patterns by ruminants.

A detailed appraisal on the potential and limitation of the various models now in publication is beyond the scope of this review. The reader is also referred to the papers of Parsons *et al.* (1994b), Thornley *et al.* (1994), Newman *et al.* (1995) and Farnsworth and Illius (1998) for examples of other recently formulated models. Several of the fundamental inputs into models are yet to be extensively studied; for example, the rules and cues animals adopt in discriminating between patches, which extends to the searching strategies employed in spatially heterogeneous environments. Consequently little experimental evidence exists and of that available, most is predominately of descriptive origin and little is analytical in respect to the manner in which animals assess the value of patches and the criteria for trade-off decisions under their natural foraging environment.

In this chapter the concept of cognition is briefly discussed and the implication of scaling up behaviour within active periods of grazing (minutes) to daily intake and longer term nutrient intake are considered. An in-depth examination of discriminatory foraging behaviour follows, focusing on the methods of evaluating choice and on the patch characteristics thought to be involved where both simple and complex choices are offered. Throughout this chapter the focus will primarily be on ruminants, particularly cattle (*Bos taurus*) and indices, but, to illustrate and clarify concepts, appropriate information will be drawn from other species.

2.2 ANIMAL MINDS

The choice of food which meets both quantitative and qualitative needs is one of the most widespread problems faced by animals (Senft *et al.*, 1987). Although cattle are faced with the need to consume abundant quantities of herbage to fulfil their genetic potential they still choose which patches in a sward are most worth consuming. In doing so the tactics they employ suggest at least that simple rules are learned through the cognitive and sensory processes actively involved within a central decision making unit

(Menzel and Wyers, 1981; Griffin, 1992; Ungar, 1996) which ultimately determines which behavioural activity will be performed at any given time.

The concept of animals acquiring decision-making skills has led to the inevitable questions being asked: if animals make decisions, does this mean they can "think", are they conscious of their decisions and how intelligent are they? These terms, "consciousness", "thinking" and "intelligence" have fuelled considerable debate over the later part of this century (Griffin, 1992; Bavidge and Ground, 1994). Griffin has argued strongly for the concept of consciousness based on the premise that animals may think about simple matters of importance to them. However, proposing that animals may be intelligent tells those interested in understanding behavioural mechanisms very little (Pearce, 1986). It is not imperative that animals are conscious of the reasons or causes for the existence of stimulus response relationships (Wittenberger, 1981; Provenza, 1996a), for example the relationship between foods and their gastric consequences (taste-feedback interaction). What is important is association, the ability to remember recurring events, particularly past encounters of failure (Hosoi *et al.*, 1995) so that the diet can be restricted to foods which are not harmful.

While the subject of consciousness clearly stimulates much speculation there is increasingly greater confidence in using the term "cognition" as a means of exploring the capabilities of foraging animals (Menzel and Wyers, 1981; Bavidge and Ground, 1994) without recourse to mentalistic concepts. The "black-box" experimental approach which focuses on investigating cognitive states indirectly (Slater, 1990; Griffin, 1992) assumes that an animal constructs a perceptual world, acquiring some representation that models the external world. Analysing the patterns of behaviour in response to altering the inputs to elicit differing responses and theories of motivation should then, theoretically, assist in the understanding of how animals perceive their environment.

Cognitive mechanisms are involved in the most elementary foraging behavioural processes (Menzel and Wyers, 1981; Pearce, 1986; Griffin, 1992) and identification of three of the key mechanisms (perception, learning and decision making) is a useful framework for conducting studies of foraging behaviour. This general framework will be used in developing the sections that follow.

2.3 FORAGING STRATEGY

2.3.1 The Grazing Process

Alternating periods of grazing, rumination and rest constitute the diurnal activity of livestock. The act of defoliation, occurring over a 6-12 hour period, can be viewed as the sequence of a succession of bites from any one of the primary food groups (grasses, forbes or browse) interrupted or defined by periods of locomotion. Over this short time frame the animal is faced with a series of tactical decisions about which foods to accept and how to move through its habitat, with the complexity reflecting the level of heterogeneity (Gordon and Lascano, 1993).

On grasslands, grazing activity of cattle is initiated when the animal lowers its head in search of food, with a bite removed when the muzzle is inserted into the sward canopy and a series of manipulative jaw movements (with or without protruding tongue sweeps) gathers herbage which is then held between the lower incisors and dental pad and severed with a jerk-swing action of the head (Arnold, 1981; Hodgson, 1986; Laca *et al.*, 1993a). As grass laminae are notch insensitive the biting action of herbivores will not function as a concentrator of stress making the grass easier to break (Vincent, 1983). This explains why large herbivores, such as cattle, do not use the teeth for biting, rather grasping herbage and breaking clumps of grass in tension using the strength of their large muscle mass (Vincent, 1982 and 1983; Wright and Illius, 1995). Upon ingestion material is manipulated for swallowing, and this chewing action calls for the use of shearing force which is considered a more expensive energetic process than the harvesting of material (Wright and Illius, 1995). Since food is harvested in bite size units (Ungar *et al.*, 1992; Demment and Laca, 1993) the principle of any foraging strategy is dependent upon how the animal decides where to remove bites from across the habitat as well as from within the canopy, and this entails a series of complex mechanisms which are yet to be fully and clearly understood.

2.3.2 Harvesting apparatus and body size influences

The harvesting apparatus and body size of animals accounts for much of the variation that exists in selection strategies between species. Cattle have a wide, flat incisor arcade which restricts their ability to be as selective as other species such as the sheep or goat which both have a more narrow, pointed dental arcade (Gordon and Illius, 1988; Nicol and Collins, 1990). This morphological trait has important consequences for the selection of sward components for cattle, particularly at the fine scale of selecting green leaf and avoiding stem or dead material within the same bite (Illius and Gordon, 1990; Demment and Laca, 1993). Nevertheless, larger ruminants such as cattle have greater gut capacities relative to energy requirements (Gordon and Illius, 1988) and also longer rumen retention times (Poppi *et al.*, 1980; Illius and Gordon, 1990), offsetting the reduced selectivity dictated by the dental structure. The above attributes are critical to the survival of cattle for two reasons. Firstly, cattle are better adapted to maintaining intake rate during periods when feed requirements are high but quality feed is in short supply (Gordon and Illius, 1988), hence their name of "rate maintainers" as opposed to sheep termed as "nutrient concentrators" (Hodgson *et al.*, 1994). Secondly, due to the restrictions imposed on the depth of canopy penetration and the poor capture rate of tillers on short swards (Laca *et al.*, 1993a), cattle are better suited to grazing taller swards. Consequently the greater ability of cattle to digest poorer quality forage (associated with low digestibility) is an advantage in view of the fact that taller swards are often associated with concomitant reductions in forage quality (Illius and Gordon, 1987).

2.3.3 Scales in ecology

Foraging behaviour can be described as a series of behaviours nested over several scales of time and space, from the food taken in a single bite to bites within a feeding station through to patches of selected vegetation and across landscape to region (Senft *et al.*, 1987; Wiens, 1989; Stuth, 1991). The terms "fine grained" and "coarse grained" were introduced to ecology by Levins (1968) as a means of explaining that environments of similar heterogeneity could comprise different structures based on variations in contrast and aggregation (Kotliar and Weins, 1990). There has been considerable inconsistency in the use of the term "grain" as discussed by Norton and Lord (1990) and some effort towards re-defining the term has been made by Weins (1990) and Norton and Lord (1990). Nonetheless the scale of observation used, as opposed to the grain, has a greater bearing on the interpretation of observed behavioural patterns and processes (Weins, 1989; Kotliar and Weins, 1990). The hierarchical basis of decision making, leading to certain criteria being more influential in affecting a decision than others, suggests that the relative importance of criteria for selection will vary according to scale (Manly *et al.*, 1993).

Decision rules occur over very short time scales or at small spatial scales (Kotliar and Weins, 1990) and this has aroused concern over scaling-up (Demment *et al.*, 1995). While fine scaled studies provide the opportunity to explore in depth, and reveal considerable detail about the underlying patterns of biological mechanisms for wild herbivores, generalisations are more likely to emerge at broader temporal scales (Weins, 1989). Instantaneous intake rate (bite mass x bite rate) is unlikely to represent intake for any extended period due to the wider variability and greater complexity introduced by additional levels of patchiness as the boundary expands. This is further complicated by foraging costs and risks as well as foraging decisions increasingly involving trade-offs with non-foraging decisions, for example predator avoidance and the seeking of shelter and water (Senft *et al.*, 1987). Where intensive agricultural practices have been adopted the significance of the scaling-up problem is reduced but not eliminated. Both Weins (1989) and Lucas (1990) have emphasised that a more thorough understanding of foraging decisions will only be achieved if the appropriate scales for the subject animal are used and there is a link between scales to erase the concern of interpreting behavioural data from short term observations (Kotliar and Weins, 1990).

One response has been that of Demment and Laca (1993) who proposed an hierarchical approach incorporating 3 spatio-temporal scales: bite, feeding station and large patch. This model concept is built on the assumption that processes take place on an instantaneous basis and that the aggregation of these processes results in larger scale patterns of forage selection and intake. Both Langvatn and Hanley (1993), who concluded that the finer scaled processes of intake and digestion explained patch choice, and Duncan *et al.* (1994), who considered patch selection a reflection of decisions integrated over longer time scales, provide support for applicability of scaling-up proposals.

2.5 DISCRIMINATION

2.5.1 Terminology

The terms “choice”, “preference”, “palatability” and “selection” describe animal behavioural actions when confronted with a variety of foods (see Lascano *et al.*, 1985; Illius *et al.*, 1992; Cosgrove *et al.*, 1995). The use of single words to describe complex processes has inevitably led to poor interpretation and much confusion. Even though a listing of definitions was published (Hodgson, 1979) in response to the need for greater clarification and these have generally been well acknowledged, often terms have been poorly adhered to in the literature when authors observe preference and infer palatability and likewise observe selection and infer preference (see Newman *et al.*, 1992; Davis, 1993; Semiadi *et al.*, 1995). Interpretation has been further hindered with the emergence of deviations, for example, *apparent palatability* (Petersen *et al.*, 1958) and *intensive selection* (Clark and Harris, 1985) each of which attach un-defined baggage to the original terms.

Correctly defined, diet selection is a function of the preferences which would be exhibited under complete freedom of choice, modified by the opportunity for selection (Hodgson, 1979) and the animals’ morphological constraints (Gordon and Illius, 1988). Palatability is defined as “pleasant to taste” and often confused with or even at worst considered synonymous and used interchangeably with preference (Marten, 1978; Skiles, 1984; Lascano *et al.*, 1985), particularly in plant breeding programmes (Petersen *et al.*, 1958; Buckner and Burrus, 1961).

Preference is used in this thesis to describe the selective response of animals offered choices between patches of vegetation varying in morphological characteristics (see Hodgson, 1979).

2.5.2 Assessment

Preference can be assessed from estimates of the changes in the choices on offer (quantity ingested) and from estimates emanating directly from the grazing animal (bite number, grazing time and animal presence). During the 1960’s the continuous recording of animal movements was not a common procedure owing to the time and cost of automatic recording equipment (Hunt and Hay, 1990). Also, Hughes and Reid (1951) advised that observations at regular intervals (they recommended 4 minutes) would equally suffice. Technological advances have now seen the use of automated recording equipment become more widespread (Hunt and Hay, 1990; Duncan *et al*., 1994; Parsons *et al*., 1994a). This allows for a complete record of animal movements and counteracts problems with the length of the grazing period, allowing the point to be ascertained at which preference switches due to diminished supply of the most preferred food type (Cowlishaw and Alder, 1960; Hunt and Hay, 1990). Various observations can be obtained from records and/or recorded manually as a backup in the event of automatic recording failure. The material covered in the following sections is not exhaustive, but will serve to indicate the range of assessment and methodologies used in preference studies

2.5.2.1 Quantity ingested

For sward conditions, herbage sampling before and after grazing assesses the quantity removed and is usually expressed as a proportion of available herbage (Ivins, 1952; Uwe, 1956; Petersen *et al*., 1958; Cowlishaw and Alder, 1960; Hedges *et al*., 1978; Lascano *et al*., 1985). The reliability of estimates and the subsequent correlation with observed behaviour poses problems, particularly on a small scale (see Peterson *et al*., 1958). Nonetheless if the error is consistent across foods, relative comparisons within a study should hold (Cowlishaw and Alder, 1960), but comparison between studies requires caution. Visual assessment of the intensity of grazing has also been used to assess preference and is commonly expressed as a percentage of material removed (Cowlishaw and Alder, 1960; Powell and Box, 1966), percentage of grazed plants using a pace transect (Dwyer *et al*., 1964) or as a numerical rating (Buckner and Burrus, 1961; van Saten, 1992; Ganskopp *et al*., 1996; Shewmaker *et al*., 1997). Langvatn and Hanley (1993) recorded visual assessments, which were later adjusted as part of a double sampling technique.

Estimates of the quantity ingested derived from either herbage cuts or visual appraisal can compare (Buckner and Burrus, 1961; Shewmaker *et al*., 1997), although visual appraisal can over-estimate herbage removed on lightly grazed patches (Buckner and Burrus, 1961). However, whilst visual scoring may involve less time (Shewmaker *et al*., 1997) and particularly that involved with processing herbage samples and avoid destruction of pregraze sward conditions, these advantages need to be balanced against the fact that a numerical rating only allows for comparison within a single study where as absolute values of herbage removed (assuming they are accurate) provide the opportunity for comparison across studies. Further, the length of the grazing period can also largely influence the outcome on utilisation ranking and animal-based observations should be recorded as a useful check (Cowlishaw and Alder, 1960).

For indoor experiments, the quantity consumed is derived from the difference in food mass before and after each test period (Kenney and Black, 1984; Illius *et al.*, 1992; Mizuno *et al.*, 1993). Preference for one food is expressed as a proportion of total intake (Kenney and Black, 1984; Colebrook *et al.*, 1990; Illius *et al.*, 1992), on an absolute basis (Hutson and van Mourik, 1981) or where the difference in percentage of intake from one specie to a control specie constitutes preference (Mizuno *et al.*, 1993).

2.5.2.2 Bite number and grazing time

Bite number, expressed as either the total number of bites from each choice or as the proportion of total bites, is the most recent parameter to be used as a preference criterion (Marinier and Alexander, 1991; Illius *et al.*, 1992; Newman *et al.*, 1992; Demment *et al.*, 1993; Wallis de Vries and Daleboudt, 1994; Ganskopp *et al.*, 1996; Laws *et al.*, 1996). However, given the generally well established inverse relationship between bite number and bite mass (see Allden and Whittaker, 1970), bite number itself may not correlate with the quantity of herbage ingested as a criterion of preference.

Grazing time has been an extremely popular method of assessing preference. It is commonly expressed as the proportion of test time spent eating each choice (Uwe, 1956; Petersen *et al.*, 1958; Black and Kenney, 1984; Davis, 1993; Duncan *et al.*, 1994; Parsons *et al.*, 1994a; Wilmshurst *et al.*, 1995; Dumont *et al.*, 1995b) but absolute values (Archer, 1973; Hutson and van Mourik, 1981), or a selectivity ratio (Demment *et al.*, 1993), are other forms.

Early material (Reid, 1951) was critical of grazing time being considered as reliable as estimates of ingestion/utilisation but Parsons *et al.* (1994a) found good correlations between the proportion of grazing time and intake from each choice, though intake estimates were derived from pure swards outside the preference trial.

2.5.2.3 Animal presence and frequency

The frequency of grazing on each choice has been used to assess preference (Petersen *et al*., 1958; Lascano *et al*., 1985; Semiadi *et al*., 1995; Ganskopp *et al*., 1996) but a greater number of studies have used the percentage of available animals on each food type at a defined time, with the food receiving the most use considered the preferred food type (Ivins, 1952; Uwe, 1956; Cowlishaw and Alder, 1960; Hunt and Hay, 1990; Edwards *et al*., 1993; Clarke *et al*., 1995). Procedures which infer choice from grazing position and leave no room for misinterpretation with flexibility (Rosenzweig, 1990), involve testing individuals singularly indoors (Kenney and Black 1984; Marinier and Alexander, 1991; Illius *et al*., 1992), observing the location of individual animals within each group (Duncan *et al*., 1994; Cosgrove *et al*., 1995), or the location of one focal animal of the group (Bazely, 1988; Newman *et al*., 1994; Parsons *et al*., 1994a; Penning *et al*., 1997) in the field, given that the behaviour of the remaining animals in a group is not independent (Rook and Penning, 1991).

2.5.2.4 Summary

Most studies now use a combination of vegetation and animal estimates while also filming the entire preference test. Films can be analysed for grazing time records (see Duncan *et al*., 1994) or used to supplement intake data, for example, to ascertain which pasture the animal commenced eating and whether pasture types on offer were grazed before one was selected as the most preferred, in addition to recording grazing time (Black and Kenney, 1984), or act as a backup for cross-reference checking to data collected in the field.

2.5.3 Methodology

2.5.3.1 Laboratory based methodologies

Operant conditioning procedures have been used for a number of years for testing discrimination between stimuli and has allowed for the strength of choice to be evaluated through manipulation of ratio and interval schedules, though Marinier and Alexander (1991) adopted other procedures for assessing strength of choice. However, operant tests have had limited application to forage preference assessments (but see Arave *et al.*, 1988) because of (a) poorer motivation for animals to eat forages as opposed to concentrates, (b) greater difficulty encountered in procedures to handle bulky forages and (c) longer sessions are required before a reliable database is obtained as forages are less nutrient dense (Arave, 1996).

Alternatively, food can be presented in troughs (Mizuno *et al.*, 1993), as paired foods in separate bins at the front of metabolism crates (Kenney and Black, 1984), or in a pile on the pen floor (Longhurst *et al.*, 1979). In the latter study (Longhurst *et al.*, 1979) animals tended to eat one specie before beginning consumption of the other two choices. It was therefore possible to add another choice after consumption of the first preferred choice so that the animal always had three choices. Marinier and Alexander (1991) chose the "two-hand" method, in which horses were confined to stalls and samples of one plant specie was held in each hand up against the nostrils of the horse so that test foods made equal contact with the horses' sense organs. Nonetheless, methods using freshly cut material, where nutritive value can change rapidly following harvest, or dried forages, invariably mask the prehension effects animals experience in the field.

Using the hand-constructed sward board technique they pioneered, Black and Kenney (1984) created boards of artificial pasture by threading tillers of kikuyu grass through different size holes to simulate variation in sward density at two levels of height. Swards were paired and fed to penned sheep by bolting the boards to the pen floor. Trays have also been used as the presentation medium with seedling swards, using paired trays pushed together at one end of the pen with swards clearly delimited by the 1 cm plastic lip on each tray (Illius *et al.*, 1992), or using turves cut from the field and anchored in trays by a fine gauge wire mesh (Newman *et al.*, 1992). Trays in the latter study were offered to animals with one specie placed on either side of the pen to accommodate a 40 cm space between species.

2.5.3.2 Field methodologies

The use of sward strips for measuring discriminatory behaviour was reported by Cowlishaw and Alder (1960) who sowed a range of species in strips and later divided the area at right angles for replication. Dumont *et al.* (1995a and 1995b) also used strips to offer choices between mature and vegetative swards of cocksfoot, created through leaving alternate strips to mature while other strips were maintained at a vegetative stage of development by successive mowing. The use of sown patches is the common method used in the field (Buckner and Burrus, 1961; Hunt and Hay, 1990; van Saten, 1992; Demment *et al.*, 1993; Langvatn and Hanley, 1993; Wilmshurst *et al.*, 1995; Cosgrove *et al.*, 1995) with patch size varying from 0.6 x 0.6 m (Demment *et al.*, 1993) to 1 hectare areas of each species (Cosgrove *et al.*, 1995). A more recent method for testing species effects has been the use of individual spaced plants as reported by Ganskopp *et al.* (1996).

Studies by Bazely (1988) and Duncan *et al.* (1994) looked at preference for ryegrass patches of higher nutritional content created by transplanting turves into the background of an existing sward (Bazely, 1988) or creating patches varying in nutritional content *in situ* within a heather mosaic (Duncan *et al.*, 1994). The idea of presenting choices in a background matrix has also been used by Clark *et al.* (unpublished, see Illius and Gordon, 1990) and Semiadi *et al.* (1995). Clarke *et al.* (1995) looked at how preferences for heather and grass altered according to whether the grass was presented in large plots or as small plots surrounded by heather.

2.5.3.3 Summary

To summarise, it is evident that uniformity and control over experimental conditions has been the influential reason amongst researchers for using laboratory based methodologies in evaluating the finer elements of discriminatory behaviour. Many authors have questioned the application of results from studies conducted over small scales of time to long term preferences, nutrient and energy intake and performance of grazing animals, whether comparisons are made between observations in the field (Newman *et al.*, 1992; Parsons *et al.*, 1994a; Dumont *et al.*, 1995a; Newman *et al.*, 1995; Penning *et al.*, 1995;) or by extrapolation of inferences from indoor work to the field (Gong *et al.*, 1996a). Confusion has been provoked by Dumont and Petit's (1995) findings of a good correlation between results from an indoor technique (preference for good and poor hay) with those from field conditions (preference for vegetative and reproductive patches), and the suggestion that it is possible to infer general rules on the way animals forage at a pasture from indoor procedures but not from short duration experiments. Yet Bailey (1995) found little change in preferences recorded between the first exposure to patch types and behaviour 6 hours later.

Nonetheless, laboratory procedures can only demonstrate the simplest case of choice: that is, where animals are offered one food and preference is exhibited between components, or when two foods are offered and one is preferred to the other. Although work like that of Black and Kenney (1984) allowed for responses to single factors to be evaluated in an unconfounded manner, it has limited application to the field context because sward boards lack the normal skewness in vertical biomass distribution, and also because handling and searching components are of immense importance to time and energy budgets of grazing animals. Past studies have concentrated on what animals "choose to eat" and whilst there is scope to further this understanding there is increasingly greater focus on understanding "choosing" behaviour. When food patches are scattered in the environment, representing a more complex level of choice, subsequent decisions in respect of trade-offs between sward components and patch types cannot be understood by piecing together data from indoor studies. Even though Illius *et al.* (1992) commented on patterns occurring in grazing style between swards, a more rigorous test of the manner in which animals perceive their environment can only be obtained through the use of field studies.

2.6 SENSORY WORLD

Foraging choices are mediated by the sensory perception of the animal. The senses sight and smell operate as peripheral sensations, whereas taste and touch are important at the time of ingestion (Illius and Gordon, 1993).

2.6.1 Vision

Ungulates have a wide visual field due to the positioning of the eyes on the side of the head and the horizontal, rectangular pupil (Prince, 1956). Cattle have 330^0 panoramic vision but, as with sheep and goats, their sight is most acute in the frontal $25\text{-}50^0$ visual field (Entsu *et al.*, 1992). Animals respond quickly to visual stimuli, a result of the brain merging the visual recognition and the emotional and behavioural response mechanisms, though speed of recognition and accuracy of visual identification work as the inverse of one another and speed of response often over-rides visual accuracy (Kendrick, 1990). Surprisingly only minimal attention has been given in the literature to work on acuity (resolution of detail) and sensitivity (detection of stimuli) thresholds. In an early study, Seitz (1951) found that ewes made choices at between 1 and 3 m from the objects, but goats failed to discriminate between objects at distances greater than 2 m (Blakeman and Friend, 1986). For cattle Enstu *et al.* (1992) found a slightly higher threshold of 4.3 m. Few studies have attempted to define the threshold for size discrimination and of those reported, artificial conditioning paradigms have been used, making generalisations to choices in the field difficult. For example, Seitz (1951) concluded that symbols had to differ in size by 25 % before ewes could discriminate successfully, and heifers in a more recent study had trouble discriminating a gap width on a landolt ring finer than 15 mm (Entsu *et al.*, 1992). Using plant material, it was believed, for a number of years, that sheep could discriminate between clover varieties based on leaf mark polymorphism (Cahn and Harper, 1976), which indicated selection at a very fine scale. However, since sheep switched preference over time, Hodgson *et al.* (1989) argued that selection possibly reflected the vertical position of morphs within the canopy and postulated that physical characteristics, for example leaf size may have influenced selection more than did the leaf mark. It is suggested that animals have poor static acuity (Piggins, 1992), and this reflects the fact that animals must engage in searching for food, head down, giving the impression of apparent movement (Kendrick, 1992) if they are to discriminate between patches varying in physical parameters, for example height, assuming the contrasts are significantly large.

Arnold (1966a) concluded that temporary covering of the eyes did not interfere with preference by sheep for herbage species, although impairment of vision extensively modified bite selection in the vertical plane on tall swards, suggesting that vision contributes towards recognising plant material and primarily serves to orient the animal in space. Several researchers (Bazely, 1988; Hodgson *et al.*, 1994) have urged caution in the application of conclusions drawn from blinkered animals as in Arnold's study. In contrast to Arnold (1966a), Edwards *et al.* (1997) controlled the cue and reward without direct impairment of the senses, and found strong evidence that preconsumption cues play an important role in foraging decisions. Sheep were observed to exhibit species preferences between white clover and ryegrass without the need to sample, though it was not possible to define whether vision or olfaction was the dominant cue.

There has been a series of works aimed at assessing whether animals have colour vision (Tribe and Gordon, 1949; Soffie *et al.*, 1980; Gilbert and Arave, 1986; Riol *et al.*, 1989), based on the knowledge that the retinae of both sheep and cattle comprise cones which are the photoreceptor cells associated with colour vision (Jacobs, 1981; Arave, 1996). However, a strong case can be argued against the need for animals to have colour vision across a range of hues, particularly those grazing on sown grasslands, when vegetation encountered only varies in shades of green to yellow. The exception is the need to select and avoid plant fruits from a uniform green background, of particular importance to browsing ungulates. The review by Arave (1996) on operant conditioning studies involving colour vision showed that cattle consistently had difficulty discriminating between the colours green and yellow.

Bazely (1988) first suggested that variations in visual appearance of the sward (green-yellow) may be perceived as alternatives based on brightness, the amount of incoming radiation reflected from an object (Jacobs, 1981). Although it has been considered that animals are unable to respond to chemical parameters such as nitrogen, since this compound does not exist at the molecular level in the plant (Arnold and Hill, 1972; Arnold, 1981), many studies have reported animals preferentially selecting swards higher in nitrogen content than control patches (see Bazely, 1988; Duncan *et al.*, 1994) suggesting brightness as a possible cue for location of swards of high nutritional content. This hypothesis was the basis of the study by Bazely and Ensor (1989), who used conditioning techniques to show that sheep could discriminate between cards of 41% and 77% reflection. However when cards of the same hue were offered, discrimination was poor. Piggins (1992), in his review of vision in farm animals, was quick to add that the lack of discrimination between hues may have been due to the wide wavelength bands used, that is, spectrally the green and yellow stimuli were more similar than thought. Future studies will need to equate the spectral reflectance of the stimuli (peak wavelength and waveband) with that of the vegetation to enable clarification of whether such patterns occur as a result of hue or brightness judgement. Nonetheless, Kendrick (1990) also added that sheep seek out dark green lush grass in preference to normal light green grass, and sheep can be observed to track lines of clover sown within a field of grass. Although no experimental evidence was presented, this does suggest that visual cues operating in the appraisal of foods are potentially important.

2.6.2 Olfaction

During grazing cattle are considered to 'sniff' the herbage (Van Dyne *et al.*, 1980) en route to finding a preferred patch to graze, but the exact mechanisms of how the sense of smell operates in selective behaviour are not well understood (Arnold, 1981). Bulbectomy has been used to study the influence of olfactory impairment on feeding behaviour (Baldwin *et al.*, 1977; Milne *et al.*, 1982) but, like vision, the results can be criticised with respect to the unsettled behaviour of test subjects. Both Arnold (1966b) using sheep in a controlled study, and Longhurst *et al.* (1979) reporting on visual observations on deer, reported that animals used the sense of smell as an initial cue in the selection of species. However, the strength of olfactory cues may vary between feeding niches. Longhurst *et al.* (1979) found the sense of smell was not as clearly defined for sheep as that for deer, possibly a reflection of the browsing ability of deer as intermediate feeders. Also, in both of these studies the influence of vision was not controlled. Based on more recent evidence (Kendrick, 1992; Edwards *et al.*, 1997) it is probable that even though odour cues are active in selection, familiar plants are also likely to be recognised by sight. Consequently evidence suggests that, even allowing for different methods of producing anosmia, discrimination between foods is not limited by individuals being anosmic (Krueger *et al.*, 1974; Baldwin *et al.*, 1977; Milne *et al.*, 1982).

The emission of volatile compounds from the external glands of plants, some of which may be detected by olfaction, has been recorded in the literature although few studies have been able to cross correlate volatile aromas with preference studies (see Mayland *et al.*, 1997). The classic case has been the aversion of sheep, but not cattle, to indole alkaloids in reed canarygrass which produce an offensive odour that parallels with the compound skatole found in faeces (Marten, 1978). Rejection of fouled forage is widely recognised (Arnold, 1981; Forbes and Hodgson, 1985b; Lutge *et al.*, 1995), with cattle observed to take deep inhalations as the muzzle passes over dung patches, but immediately after an infected area has been passed inhalations cease (Arnold, 1981). Herbage treated with slurry injected 5 cm deep into the sward is more acceptable to cattle than that treated by surface application although the rejection of the latter herbage can be lessened with the addition of water at the time of application (Laws *et al.*, 1996).

2.6.3 Taste

The most important sense is without doubt that of taste (Kreuger *et al*., 1974), providing the ultimate basis upon which the animal forms a decision as to whether the material is highly preferred, merely tolerated, or completely rejected, but other information, particularly visual cues, can be learned as secondary reinforcers and used as the primary cue at the following food encounter. This relationship is tenable because the evidence suggests that the senses operate independently of each other, and this appears to be true for sight and smell (Kendrick, 1992) and smell and taste (Forbes, 1995). However, this cannot be said of sight and taste because sight-responding cells have been found to also react to the ingestion properties of food (Kendrick and Baldwin, 1986). This prompted Kendrick (1992) to comment that when an animal sees a preferred food it probably simultaneously experiences the satisfaction that subsequent taste, ingestion and digestion of the substance will bring before it actually eats it. This implies that the learned association between sight and taste is a potentially powerful cue to the animal, which sheep could retain for at least a month after the first encounter (Kendrick, 1990). Decision making about pellet consumption, without sampling, when standing directly over patches was shown by Edwards *et al.* (1994), although in this case the possibility that different pellet types had distinctive odours which were being used at short range as affirmative cues cannot be ruled out. Further, it is difficult to explain how sheep would have visually recognised preferred pellets from within a mix of uniform size and shape pellets, and the association with either the subsequent taste or the value of reward from a previous encounter.

Consumption of particular food types, whether familiar or novel, can cease at any time and is reflected in the switching of preference. Preference in this sense is strongly related to aversion, which can occur within minutes of eating or build-up over time. The taste-feedback interaction is the mechanism which triggers the termination of feeding in this case, and the strength of the aversion will be positively related to the feedback signals (Provenza, 1996a). It is clear that animals acquire aversions and form associations between visual cues, taste receptors and previous encounters (memory recall). Horses rejected unadulterated bread for several days after consumption of bread laced with quinine in a study by Marinier and Alexander (1991). Also, Provenza (1996b) quoted the work of Launchbaugh and Provenza where lambs receiving a toxin dose after eating cinnamon-flavoured rice no longer preferred cinnamon flavoured wheat, though they still showed a strong preference for wheat, which indicated that the lambs formed an associated aversion to the flavour cinnamon. Taste-feedback interactions have also been shown, more recently, in the ability of animals to regulate nutrient intake, demonstrating the importance of the ratio of protein to energy in the diet of ruminants. Examples are the preference by lambs for a high protein diet of alfalfa after eating a high energy diet of grain (Provenza, 1996a), and the selection by lambs of a diet higher in crude protein relative to energy, from an array of choices, compared to a control group which were fed a base diet comprising the same ingredients (Görgülü *et al.*, 1996). There have been other studies investigating the influence of aversions and the associated taste-feedback interactions, but further detail of these are beyond the scope of this review and the reader is referred to the recent review on this subject by Provenza (1996a).

2.6.4 Touch

As grazing animals typically lower their muzzle into the canopy of swards while searching, preferential feeding on plants by wild ungulates may be related to the avoidance of physical properties acting as plant defence mechanisms, for example, hairiness and spines (Vallentine, 1990; Belovsky and Schmitz, 1991).

2.6.5 Summary

To summarise, although of relatively recent origin, there is now a greater appreciation of the use of visual, olfactory and gustatory cues on discriminatory behaviour. Whilst there have been significant advances in defining mechanisms and cases of postingestive feedback interactions, the same cannot be said of the separation of preingestion cues. There appears little doubt that animals use vision and/or smell to recognise plant material (see Edwards *et al.*, 1997) but most of the evidence exists for discrimination between vegetation types, for example ryegrass and white clover, and in this sense supports literature from controlled shape discrimination studies (see Baldwin, 1981). Beyond this there is little knowledge on the relative value animals place on cues. Sward height variation, within a monospecific sward is an obvious cue and one where cue value may not necessitate high patch rewards, but it has had little attention because of methodology constraints. Further investigation on the use of "brightness" as a cue is a classic case of highlighting current methodology constraints. It is difficult to define the cues to which animals respond in specific situations, and predict their effects on selective behaviour, but progress in this area will be essential if the nature of trade-off decisions in grazed pastures are to be predicted.

2.7 FORAGING MOVEMENTS

2.7.1 Introduction

The information and illustrated studies that are presented in the following two sections, though perhaps brief and simplifying what is indeed a very complex area, amply demonstrate the inconclusive evidence for optimality theory in grazing animals and raises issues surrounding partial preferences and the possible link with sampling for reinforcement.

2.7.2 Patch use – dwell time and departure rules

The location of a series of potential bites while the animal's forelegs are stationary is known as a feeding station (Ruyle and Dwyer, 1985) and occupies the semi-circular area in front of, and to each side of the animal. Using these boundaries, the largest area accessible to mature steers within a single feeding station is 0.5 m^2 (Ungar, 1996). Sets of several feeding stations constitute a patch, with patch activity terminated when the animal re-orientates to another location (Jiang and Hudson, 1993).

Optimality theory provides the framework within which attempts are made to model and describe foraging behaviour within complex environments. The classical model for the optimal exploitation of patches is the marginal value theorem (MVT) of Charnov (1976), the main feature being that foragers experience diminishing marginal returns; that is, they should depart from a patch when the net gain from staying drops to the expected gain from travelling to and beginning at a new patch. This assumes a patchy environment where patches are clumped together to the extent that no food is found between patches and in this sense is a special case of the arbitrary distribution model (Kacelnik and Bernstein, 1988). Patchiness is organism-defined, (Weins, 1976) so the perceptual capability of animals will shape patch profitability. Recently Focardi *et al.* (1996) claimed that animals evaluate food thresholds on very small scales and do not need to be aware of a patch, suggesting that the perception of patches is anthropomorphism by man. Many model derivations with changes in assumptions (see Focardi *et al.*, 1996) are surfacing in the literature as the knowledge base expands, but models will yield predictions which are only as good as the quality of their underlying assumptions and equations.

Ruminants respond to patch depletion, rarely depleting a patch fully before leaving it for another (Demment *et al.*, 1995; Focardi *et al.*, 1996). This is a reflection of the stratum* grazing style where the number and size of potential bites, and thus rewards, decline as the animal moves vertically down the sward (Ungar *et al.*, 1992; Demment and Laca, 1993). Tests of optimality by Bazely (1988) who varied the number of good patches and/or hobbled sheep to limit movement, and Laca *et al.* (1993b) using steers and manipulated patches and distances *in situ* in the field, confirmed that increasing inter-patch distance increased residence time for both species. However, according to the gain functions used by Bazely (1988), sheep exploited patches for longer periods than model predictions and so must have experienced some reduction in ingestion rate. The longer residence times implies that sheep had little prior knowledge of the location and quality of patches, which conflicts with the assumptions of linear models suggesting that wrong assumptions can give rise to accurate predictions for some scenarios. Jiang and Hudson (1993) discussed how the cropping rate of wapiti within a feeding station, compared to the average cropping rate, influenced departure rules. However, it appears they took no account of travel time between patches, thus assuming constant marginal costs, which violates the assumptions of the marginal value theorem. These authors suggested that wapiti may have made the patch departure decision at the second to last feeding station through learning, but there is little evidence to separate out their suggestion which is intermingled with the effects of declining rewards on the patch. Focardi *et al.* (1996), using a new model based on minimising foraging time, concluded that departure rules for deer were based on a critical biomass threshold. A threshold of this nature would not allow for the physical properties of food to influence selective behaviour unless preference was absolute (ie. animals exhibit a zero-one acceptance rule).

The spatial distribution of "rich" and "poor" patches will also influence the degree of depletion and thus the residence time on any patch, in addition to the

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* Refer to the terminology section

characteristics of the individual patches (Demment and Laca, 1993) influencing the handling components (Stuth, 1991). Periscopic foragers, a name given to foragers who sense numerous patches simultaneously (Mitchell, 1989), are likely to exploit intermediate or even poorer patches, in terms of profitability, according to their position amongst rich patches on the assumption that the patch can be picked up with little extra foraging cost. These points were illustrated with the data of Clarke *et al.* (1995) where in a small patch mosaic sheep were willing to exploit less profitable dividing areas of heather en route to the next grass patch, particularly at lower stocking densities. Currently models only take account of a cost function for travel time and so the relationship between anticipated patch travel time and the expected average patch depletion rate is possibly oversimplified. A simulation model (Wallis deVries, 1996) has shown that although travel costs account for only a small percentage of daily energy intake, their influence should not be underestimated in formulating foraging decisions. Further, Shipley *et al.* (1996) postulate that dwell time per patch may be governed by the dynamics of foraging velocity, therefore the time and energy losses from deceleration to stopping to select a bite and then acceleration from the patch may be important contributing determinants of dwell time.

The assumption of complete knowledge of the environment has become a concern (Packard *et al.*, 1990). Given that cattle are not thought to exhibit long range detection of food choices it is difficult to rationalise how ruminants are able to compare one patch to the expectation of another patch under the law of diminishing marginal returns. What ever the case is, patch perception implies an active and conscious memory system which constantly processes information formulating decision rules on residence time and depletion on the current patch. Future studies need to address the extent of patch information carry-over effects within a foraging path.

2.7.3 Information retention - partial preference and sampling for reinforcement

The classical model predicts that animals either accept or reject foods: that is, animals will not graze from any choice other than the one offering the highest intake rate. However this clearly is not the case as illustrated by the partial preferences demonstrated in response to simple grass:legume contrasts (Illius *et al.*, 1992; Parsons *et al.*, 1994a, Cosgrove *et al.*, 1995) and grass:heather contrasts (Clarke *et al.*, 1995).

The pattern of partial preference as opposed to absolute preference has been put down to discrimination errors. These discrimination errors apparent in selection are attributed a) to the need to continually sample to acquire knowledge of food choices and in doing so tracking fluctuations in the environment and b) poor identification of optimal patches through the lack of clear visual cues, with both error types reducing the impact of discrimination (Hodgson *et al.*, 1994).

Although preferences are partial rather than absolute, animals often still go on to exploit the patch offering the highest rate of food or energy intake as illustrated in the experiments of Illius *et al.* (1992) and Wilmshurst *et al.* (1995). Mitchell (1990) has shown mathematically that the optimal forager does not maximise instantaneous intake rate, and even in the presence of competitors the forager will spend some time as a generalist (rich and poor patches) when it could receive a higher intake rate as a specialist (rich only).

There has been much speculation about the occurrence of partial preferences. Mis-identification has been suggested as a tenable explanation, although in other classes of herbivores it has been found not to account for observed partial preferences (Pyke, 1984). The more recent data of Edwards *et al.* (1997) adds support for this explanation. These authors showed that animals were able to form associations, minimising the need to sample as a means of identifying grass from clover. Another possible explanation is that the variance of food distribution which influences the rate of food intake, although previously ignored, may be more important than once proposed (Pyke, 1984; Focardi *et al.*, 1996). Alternatively, Newman *et al.* (1995) have attributed the diurnal variation in partial preference for grass, which offers lower harvesting rates and greater rumination times for breakdown as compared to legume, to be related to predator attack avoidance. Consumption of grass early in the foraging day would mean a loss of grazing time during daylight hours due to the need to ruminate earlier as a result of the bulkier characteristics of grass. By contrast, grass consumption later in the day means rumination can be maximised when predation risk is at its highest during the night. On a similar note, Clarke *et al.* (1995) noted a tendency for sheep and deer to shift from grass to heather during the night, heather being the least digestible and nutritious specie and so requiring greater rumination. Dumont *et al.* (1995a) also commented that ewes were willing to consume reproductive grass material, as opposed to vegetative material, in late evening, though this behaviour was not observed for the heifers. However, in the latter study the ewes also demonstrated a pattern of consumption of reproductive material early in the morning which does not support the theory being developed from Newman's model. More recently, Provenza (1996a) has offered another possible explanation, which is built around the concept of food aversion. Aversions, amongst other reasons, can result when foods containing toxins or high levels of rapidly digestible nutrients are consumed. Clovers contain toxins in the form of cyanogenic compounds and the breakdown of plant material sees a rapid release of proteins and carbohydrates. In the event of food aversion, Provenza (1996a) argues that animals seek the alternative food type, in this case the less nutritious grass. The explanation put forward certainly assists in explaining why animals prefer the alternative to the previous background diet in the case of Newman *et al.* (1992). However, aversion alone is not sufficient to explain why animals have a period of grazing in the middle of the day, being indifferent to grass or clover, when aversion would suggest the rule should be 'graze grass only'. Needless to say, post-ingestive feedback interactions now add another dimension to what is a complex process and will most certainly need to be incorporated more extensively into models to test whether acquired aversions assist in explaining patterns of behaviour on other specie mixes in addition to those exhibited when animals graze grass:clover mixtures.

Sampling is an integral component of foraging if patch quality is unknown to the forager before it enters patches (Illius *et al.*, 1987). Interpretation, from initial sampling, that the patch is inferior results in animals departing from patches before extensive resource depletion occurs. Even though Kendrick (1990 and 1992) states that sight responding cells will not be activated by food which the animal perceives as non-preferred, the continual sampling of grazed pasture suggests that sight cells are only capable of responding to foods providing clearly recognisable and distinguishable cues, and that subtle changes in food appearance and structure such as vegetation contrasts are not sufficient for activation. This is tenable to the extent that sampling is correlated with the contrasts in choices offered (Stephens and Krebs, 1986), suggesting visual cues and memory of ingestive consequences are of paramount importance. With small differences in visual cues "false alarms" may arise (Illius *et al.*, 1992) from animals responding to novel patches faster than they can process patch identity, even though such differences will undoubtedly influence fitness. However, the continual need to switch between choices for patch reinforcement, even if for only a few minutes, has been interpreted as evidence of poor memory uptake and retention (Clark *et al.* unpublished in Illius and Gordon, 1990). This finding is surprising because sheep and cattle have been found to be adaptive in modifying their behaviour in response to learning and spatial memory (Bailey, 1995; Hosoi *et al.*, 1995; Edwards *et al.*, 1996), holding cognitive or mental maps of preferred foraging areas for up to at least 8 hours since the last period of occupation (Bailey *et al.*, 1989). However, poor information retention may reflect the greater complexity of choice in the field environment where there is often a poor relationship between cue value and food reward (in contrast to the conditions in the study of Edwards *et al.*, 1997) and continual sampling (handling of choices) may be a mechanism to reinforce bite selection. The necessity for switching can decline over time (Dumont *et al.*, 1995b) implying a possible learned association of alternatives with corresponding rewards and support for the role of learning in diet selection (Provenza and Balph, 1990). Further, Dumont *et al.* (1995b) found the act of switching to sample alternatives varies between heifers and ewes, possibly reflecting the selectivity of species. Nevertheless, Provenza (1996a) argues that sampling (or switching) is a means of correcting aversions and varied diets are the result of these acquired aversions, in contrast to sampling being the cause of varied diets.

2.7.2 Summary

To summarise, optimisation is a linear style of thinking which has had limited success in modelling the real environment for a number of reasons, including poor predictions in spatially heterogeneous environments and the assumption of complete knowledge (Packard *et al.*, 1990). Also, given the number of studies reported that observe partial preferences in ruminants and continuous sampling between alternative choices, it is questionable whether it remains appropriate to predict patch departure using the marginal value theorem built around resource depletion. A more synthetic approach for studying ungulate behaviour has been called for (Senft *et al.*, 1987). Assumptions about the level of information animals possess are critical to the development of models of optimal patch departure. In this sense foraging decisions will depend not only on perceptual capabilities but also on the ability of foragers to store information from past experiences in memory and to retrieve this when necessary as well as to associate feedback during grazing. This is the essence of the need for learning to be incorporated into models (Provenza and Balph, 1990). Provenza and Cincotta (1993) have reported on the development of a learning model which is built on the hill-climbing scenario where, although the forager can maximise energy intake and or minimise time spent foraging, it is not assumed that they will necessarily use these routes. Partial preferences are predicted by their learning model. Packard *et al.* (1990) have introduced the concept of artificial intelligence (AI), which is built on four components (perception, action, motivation and learning systems) and links together the linear as well as the synthetic programming styles so that many of the limitations associated with linear programming are overcome. In the past optimality models have been based on encounter rate, but it appears that future models will need to re-address some of these original assumptions, with a change towards models being characterised by information state (Mitchell, 1989) which will reflect the animals' ability to learn and track information as it travels as well as depleting patches according to travel and handling costs.

2.8 PATCH CHARACTERISTICS

2.8.1 Introduction

Grazing animals contribute to the patchiness in the vegetation through selective grazing, further enhancing the level of heterogeneity created through non-grazing activities and dung and urine deposition. Mature and immature patches of vegetation arise from these events, and studies that fail to investigate such levels of heterogeneity inevitably ignore the complexity of grazed pastures. The most important dilemma faced by the herbivore in its acquisition of food is the trade-off between quantity and quality (Senft *et al.*, 1987; Laca and Demment, 1991). Herbage can be organised variously in space, in terms of both (a) the quantity of herbage and (b) the physical and chemical attributes of plant material (Ungar and Noy-Meir, 1988; Ungar *et al.*, 1992). Much of the work prior to the 1990's focused on the relationship between characteristics of the plant community and animal performance, and although efforts were made towards defining relationships between biomass and production, such a simple relationship does little to help understanding of the complexity of the interactions between the herbivore and its environment.

The structural characteristics sward height, herbage density, maturity (leaf:stem ratios and green:dead material ratios) may be important modifiers of decision criteria through their influence on bite depth, the vertical distance animals insert their muzzle into the sward, and bite area, the vertical projection of the area encompassed within a single bite (Hodgson, 1985; L'Huillier *et al.*, 1986; Laca *et al.*, 1994; Hodgson *et al.*, 1994).

2.8.2 Sward height and density

Black and co-workers in Australia working with artificial swards and chopped forages authored a series of papers, summarised by Black (1990). An important inference from these studies was that animals preferred swards that promoted faster rates of consumption, though this inference does not appear to hold true for grass:legume comparisons (see Parsons *et al.*, 1994a; Cosgrove *et al.*, 1995). For monospecific swards, tall swards offer higher rates of intake primarily on the grounds that larger bites are obtainable through greater penetration into the canopy (Black and Kenney, 1984; Mursan *et al.*, 1989; Gordon *et al.*, 1996), and bite mass has the greatest influence on consumption rate (Hodgson, 1986; Arias *et al.*, 1990). The relationship between sward height and potential bite depth was originally formulated as a ramp function (Ungar and Noy-Meir, 1988), but is now generally considered to be a constant proportion of around 35-40% for field studies (Wade *et al.*, 1989) and 50% for laboratory based studies (Mursan *et al.*, 1989; Laca *et al.*, 1992a).

Patch-use studies often only compare paired choices and so behavioural responses have only been charted according to one alternative, but even so there is strong evidence that animals preferentially select the taller sward when given multiple choices between sward patches in the vegetative growth stage, with little variation in chemical composition (Clark *et al.*, unpublished in Illius and Gordon, 1990; Illius *et al.*, 1992; Demment *et al.*, 1993; Mitchell *et al.*, 1993). Nevertheless, height is possibly not used as the sole criterion in choosing which alternative patch to graze in light of the observed constant switching/sampling of alternative choices as a means of learning about patch profitability, particularly bite depth, which is not apparent with vision alone, thus suggesting that handling cues are highly interactive with visual cues (Illius *et al.*, 1992).

A lower limit to acceptable sward height is apparent within studies, although generalisation is difficult due to the pairing of alternatives, and confounding with maturity contrasts. The data of Wilmshurst *et al.* (1995) showed that patches of 2 weeks growth were practically avoided in preference for patches of 4 weeks growth by wapiti. Similarly heifers (in 30 minute tests) spent little time grazing 7 cm vegetative swards when a reproductive sward (sward height unspecified) was the alternative (Dumont *et al.*, 1995b), although this behaviour was not as extreme in another study (Dumont *et al.*, 1995a). Other reports of height comparisons with animals favouring taller patches are evident in studies in a mosaic layout such as those of Bazely (1988) and Jaramillo and Detling (1992) but in these circumstances height is confounded with other nutritional parameters, most notably nitrogen. Clarke *et al.* (1995) were able to test for responses to height variations on patch use by sheep and deer on a mosaic of grass and heather, within their main trial design. They found sward height correlated with patch use by deer only during one period and on one plot when sward height fell below 5 cm. At all other times sward height had little effect on patch choice by deer or sheep, although it is probable that large variations in height were not the intention of the study.

As a result of patch choice studies and investigation of the influence of height on bite dimensions, sward height has been considered the dominant influence on animal choice. However, height and density are usually confounded and whilst Black and Kenney (1984), using sward boards, were the first to tease out the effects of height and density on bite dimensions, few studies have adopted this approach to patch choice under field conditions, obviously due to the difficulty in manipulating variations in density. Demment *et al.* (1993), in a study assessing whether height or density was the dominant cue to patch choice, found selectivity by steers for tall rather than dense patches. Although more importance is attached to height, when steers were given a choice between contrasting densities with height held constant, short dense patches were preferred over short sparse patches. However, the importance of bite mass as a determinant of intake rate and association with preference (see Black and Keneny, 1984) does not always hold. In the study by Demment *et al.* (1993) cattle showed a stronger preference for the choice offering the greater rate of intake, for example tall original density (TOD) over short original density (SOD). However, this occurred because bite rate was faster on TOD rather than greater bite masses obtained from TOD (bite mass was similar for both sward types). Of the other choices in the study by Demment *et al.* (1993) the preference for short dense over short sparse patches occurred even though short dense swards have higher grazing resistance (Coughenour, 1985 cited by Laca *et al.*, 1994), with greater bite forces required to defoliate patches of a high tiller population to a given height (Illius *et al.*, 1995). There is a lack of data pertaining to bite forces. Hughes *et al.* (1991) showed bite force was not a constant, but varied with the potential reward to the animal, suggesting that the choice of short dense swards is a reflection of the counter-balancing act between reward and effort (Hughes *et al.*, 1991; Illius *et al.*, 1995).

2.8.3 Sward structure and morphology

The spatial arrangement of leaf and stem strata and their height relative to total sward height has an important bearing on the parameters bite depth and bite mass for temperate swards (Laca *et al*., 1994), and thus upon the appraisal process. Increasing maturity usually brings about increases in sward height, stem height and total biomass, but reductions in green mass and nutritive value. In section 2.8.2, the important point made was that animals are sensitive to the ease and rate at which they can ingest herbage (Black and Kenney, 1984), and sward height is a useful determinant of this. Theron and Booysen (1966) showed that the tensile properties of grass influencing the ease of prehension were negatively correlated with intake rate, and these properties increase with plant age (Laredo and Minson, 1973). Sward height applies as a suitable criterion only when swards are vegetative, and green leaf mass (L'Huillier *et al*., 1986; Penning *et al*., 1994; Clarke *et al*., 1995; Prache and Petit, 1995), particularly lamina length (Flores *et al*., 1993; Laca *et al*., 1993a) has been found to be a more accurate predictor than sward height of grazing behaviour for temperate swards changing in leaf to stem ratio. There are parallel results for tropical forages (Chacon and Stobbs, 1976).

2.8.3.1 Lamina length, pseudostem height and senescent material

The number and size of potential bites is governed by the leaf and stem strata (Ungar *et al*., 1992), and the importance of these strata has been shown by both Flores *et al*. (1993) and Astigarraga and Peyraud (1995) who found that increased leaf sheath height had a detrimental effect on prehensibility. Flores and co-authors examined these questions in greater depth and confirmed that stem material limited bite depth only when the lamina length was less than half of sward height, as suggested by Laca *et al*. (1992a) and reviewed by Demment and Laca (1993).

Lamina length also influences tiller capture rate, as those tillers with a short length of lamina are likely to escape severance (Laca *et al*., 1993a). Flores *et al*. (1993) found also that bite area could be similar on short and tall swards if animals failed to insert their muzzle below stem height, resulting in the sweeping action bending lamina at ligule height and avoiding capture by the tongue.

Pseudostems have been reported to influence bite depth in sheep (Barthram and Grant, 1984; Edwards *et al*., 1993) and in cattle (Arias *et al*., 1990), suggesting that a pseudostem barrier may be used as a cue or patch departure rule, possibly based on the fact that the force required to fracture pseudostem is three times the force required to fracture leaf in tensile mode (Wright and Illius, 1995; Illius *et al.*, 1995).

Flores *et al.* (1993) have been critical of the cattle work done by Arias *et al.* (1990), in light of their own findings on pseudostem influences which support that of Mursan *et al.* (1989) with steers on ryegrass swards, Laca *et al.* (1992) using steers on lucerne, and Mitchell (1995) with sheep on grass swards. The inference that the pseudostem stratum acted as a barrier to defoliation (Arias *et al.*, 1990; Illius *et al.*, 1995) can be questioned on the grounds that pseudostems were below potential bite depth, the depth to which animals would insert their muzzle if the sward was 100% leaf lamina (Laca *et al.*, 1992a). Laca *et al.* (1993a) have postulated, conceptually, that measured bite depth is not the full depth of insertion into the canopy due to the bowl-shaped configuration of a bite. Such an underestimation of bite depth may explain the discrepancy between observed and measured behavioural parameters with respect to pseudostem constraints. This effect is likely to be greater for grazers than browsers given the differences in incisor arcade breadth. Edwards *et al.* (1993) found that tall fescue and phalaris pseudostems were more "palatable" than those of ryegrass, cocksfoot and prairie, indicating the pseudostem barrier may not be constant across plant species. It is fair to conclude that, based on current evidence, there is no consensus view on the influence of pseudostem on grazing decisions.

The positioning and mixing of senescent material in the sward is also important to the grazing animal (Stuth, 1991). In the studies reported by L'Huillier *et al.* (1986), Black (1990) and Clarke *et al.* (1995), sheep and deer selected against senescent material, preferring young green material regardless of its positioning in the sward (L'Huillier *et al.*, 1986). Even so, sheep encounter difficulty in discriminating between senescent and live components when they are closer than 20 mm (Black, 1990), although more recent work (Edwards *et al.*, 1994) suggested that sheep can discriminate at a fine resolution of a 5 mm cube. This discrepancy between studies may reflect choice between pelleted diets (Edwards *et al.*, 1994) rather than intermingled grass components (Black, 1990). Nonetheless, these selection patterns are aided by a narrow jaw, and may not be as profound with cattle as with sheep. Senescent material positioned high in the sward may call for either the total rejection of a patch by cattle or a decrease in diet quality as a means to maintaining intake rate.

2.8.3.2 Sward maturity

Langvatn and Hanley (1993) working with red deer, Wallis de Vries and Daleboudt (1994) using steers, Wilmshurst *et al.* (1995) with wapiti and Clarke *et al.* (1995) observing deer and sheep have all shown preferential selection of vegetative swards over mature swards in the field. When Dumont *et al.* (1995a and 1995b) offered heifers a tall (18 cm), vegetative patch together with a reproductive patch (sward height unspecified), the vegetative patch was preferentially grazed. Relationships between stage of maturity and cattle preferences have also been reported from a plant breeding programme (van Saten, 1992) and from an indoor cafeteria trial by Mizuno *et al.* (1993). Although in the former study only 56% of the variation could be attributed to stage of maturity, average preference score declined by 0.86 for every unit increase in maturity for a group of medium maturing tall fescue populations. These results highlight the importance of the potential trade-off between biomass and handling and processing constraints, particularly the ease of harvesting and manipulation of material for swallowing.

Dumont *et al.* (1995b) found that reproductive patches (sward height unspecified) were preferred by heifers when the height of the vegetative patches declined to either 11 or 7 cm, on a diminishing scale, reinforcing the view that sward height plays an important role in maintaining intake rate. These authors also found that the preference for reproductive patches, as measured by the time spent grazing on each patch type, increased over three, 10 minute periods, with this effect being greatest at the tallest vegetative patch height (18 cm). These points illustrate one of the problems facing researchers attempting to tease out behavioural responses, as patch maturity and sward height are usually confounded in field experiments. An upper limit on forage maturity was suggested by the results in another paper of the same series by Dumont *et al.* (1995a) where heifer preference for the reproductive sward, when offered as pair with a vegetative sward varying in height, declined as the forage became more mature (approximately 1 week older), even in light of relatively small changes in nutritive value.

The degree of stem maturation, through its influence on stiffness, will also influence the probability that the tiller will spring back, avoiding the clamping movement of the jaws (Laca *et al.*, 1993a). When faced with mature swards dominated by stem material, both sheep (Penning *et al.*, 1994) and cattle (Ruyle *et al.*, 1987) have been observed to alter their feeding strategies, taking a number of bites sideways, termed side bites (Ruyle *et al.*, 1987), whereas top bites were observed only on the previously grazed patches (Ruyle *et al.*, 1987). This tactic is apparently aimed at utilising the new, young growth at the base of the sward and probably reflects the reduction in handling time (Abu-Zanat *et al.*, 1988) and possible slippage of tillers associated with top bites. The effect of stem formation on impact width (see Stuth, 1991) is well illustrated in the study by Ruyle *et al.* (1987). The presence of residual stem acts as a physical impedance to animals but, when previously ungrazed patches are characterised by long (>15 cm) residual stems, and even with stems 10 times greater in abundance than on previously grazed patches, cattle can work their way through the residual stems, pushing them aside to graze the green material at the base of the canopy. Similar behaviour has not been observed with cattle grazing short dense swards where the distance between clumps of stems is likely to be smaller than the width of the muzzle, suggesting it is probable that cattle are physically unable to selectively bite leaf without stem.

Forage maturation, particularly the increasing proportion of sclerenchyma, clearly influences the ease of severance and subsequent digestion of plant material (Wright and Illius 1995). Given that animals cannot sense nitrogen or crude fibre (Arnold, 1966b) these parameters must be related to structural features, yet recent patch use studies (see Langvatn and Hanley, 1993; Wallis de Vries and Daleboudt, 1994; Wilmshurst *et al.*, 1995) have generally overlooked the need for more in-depth sward description, instead opting to relate preferences to nutritive value.

2.8.5 Nutritive value

For many years researchers have attempted to associate preferential behaviour with parameters of plant nutritive value, although with mixed results (Provenza and Balph, 1990). Even where positive correlations are apparent, if ruminants could detect specific nutrients, and it is not thought that they can (Arnold and Hill, 1972) this does not imply that they innately recognise the value of ingesting such compounds (Provenza and Balph, 1990).

Soluble carbohydrate was found to be correlated with preference by Bland and Dent (1964), though the effect was somewhat variable, but not in the studies of Warmke *et al.* (1952), Buckner and Fergus (1960) or Buckner *et al.* (1969). There has been renewed interest in this nutrient (see Dove 1998), with Ciavarella *et al.* (1998) reporting that sheep exhibited a preference for vegetation of higher soluble carbohydrate content.

Positive correlations of preference with crude protein (Nitrogen x 6.25) are apparent in the literature on a dry weight basis (Norman and Green, 1958; Blaser *et al.*, 1960; Keogh, 1973; Bazely, 1988; Day and Detling, 1990; Jaramillo and Detling, 1992; Langvatn and Hanley, 1993; Duncan *et al.*, 1994; Bailey, 1995; Clarke *et al.*, 1995), and also on a fresh weight basis (Longhurst *et al.*, 1979), but the relationship has been discounted by others (Buckner and Fergus, 1960; Buckner *et al.*, 1969; Ganskopp *et al.*, 1996). The selection of patches which differ in structure to the surrounding vegetation, either in the location where animals have previously urinated (Norman and Green, 1958; Keogh, 1973; Lutge *et al.*, 1995) or where this effect has been simulated via the use of nitrogen based fertilisers (Bazely, 1988; Day and Detling, 1990; Jaramillo and Detling, 1992; Duncan *et al.*, 1994) are nearly always associated with higher nitrogen and crude protein concentrations. However, Langvatn and Hanley (1993) were quick to point out that a matching pattern of protein does not imply that ruminants actually made their choices on the basis of digestible protein. Edwards *et al.* (1993) suggest that animals can discriminate the level of nitrogen in grass leaves, though they offered no comment on the mechanism animals used to assess high nitrogen plants (eg. nutrient, brightness, strength properties). Natural or urine simulated patches are often taller than surrounding vegetation due to higher growth rates, therefore permitting a greater bite depth, but the mechanism by which animals discriminate between enriched and surrounding vegetation is unclear (Duncan *et al.*, 1994). One plausible explanation, but for which there is no conclusive evidence, is that the brightness of these patches influences choice (Bazely, 1988; Bazely and Ensor, 1989-refer to section 2.6.1).

When nitrogen is applied to plants there is an increase in the size of the cells without proportionate increases in cell wall material, producing "brighter" more succulent plants whilst reducing, simultaneously, the concentrations of acid detergent fibre (ADF), neutral detergent fibre (NDF) and lignin which subsequently influence digestion rate and passage rate. Consequently a host of factors interact, with studies often reporting a list of compounds that increase and another list which decrease with preference (see Bazely, 1988; Duncan *et al.*, 1994). In few choice studies has the effect of any one compound been isolated while the others are held constant (but see

Ciavarella *et al.*, 1998), a problem which, while it remains extremely difficult to investigate, needs to be resolved before preference can be linked to a single nutrient.

The use of indices of dry matter (DM) digestibility and organic matter (OM) digestibility for predicting preference have strongly been discounted (Hardison *et al.*, 1954; Black, 1990), yet such relationships are still widely reported (see Longhurst *et al.*, 1979; Arnold, 1987; Wallis de Vries and Daleboudt, 1994). Whilst the indices protein and DM digestibility can be correlated, Langvatn and Hanley (1993) have suggested that digestible protein is a more sensitive measure of forage nutritive value. Wade and Le Du (1981) concluded that nitrogen concentration was a better predictor than OM digestibility since nitrogen concentration followed the changes in the proportion of live material. Poor relationships between choice of plant species and OM digestibility were reported by Ganskopp *et al.* (1996) whilst a good prediction of grazing time matching digestible organic matter in dry matter (DOMD) was found by Wallis de Vries and Daleboudt (1994). However, a matching pattern of grazing time with DOMD (Wallis de Vries and Daleboudt, 1994) should not be read to infer that animals use digestibility as a cue because it cannot be ruled out that digestibility is merely a secondary consequence of a former decision with respect to the structural integrity which affects the ability to harvest and manipulate material for swallowing (Vincent, 1983). By a similar token, Wilmshurst *et al.* (1995) discussed the influence on selection of the increasing proportion of ADF and lignin content with increasing age of patches, but both of these parameters have been found to be poorly correlated with force to fracture in tensile mode (Wright and Illius, 1995), suggesting that the use of single parameters is of limited value. Further, the use of digestibility as a sole criterion for patch quality is in itself of limited value when patches can vary significantly in their ratio of leaf to stem with only marginal or subtle differences in digestibility (Laredo and Minson, 1973; Minson, 1982). Needless to say, the reliability of any index is also questionable depending on whether the estimates were derived from the grazed stratum or whole sward estimates, the latter method underestimating the quality of grazed material (Ganskopp *et al.*, 1996), and so complete rejection of OM digestibility on this basis would be premature. Spalinger *et al.* (1986) have suggested that selections should be based upon structural characteristics influencing handling time, rather than simply upon DM digestibility or nutritive value, when the offered choices are of acceptable nutritional quality.

Digestible energy and protein are also strongly correlated, but for large herbivores the intake of protein is considered more important than the intake of digestible energy (Senft *et al.*, 1987). Wilmshurst *et al.* (1995) argue that patterns of selection that maximise long term rates of energy intake also maximise short term rates of protein intake. These results only differ from those of Langvatn and Hanley (1993), who matched selection with protein, by the addition of gut fill to the model, thus extending the time span of foraging.

2.8.6 Summary

To summarise, the importance of the canopy structure on discriminatory behaviour cannot be underestimated. Trade-off between criteria for selection is a mechanism ruminants apply as a means of coping with increasing heterogeneity. However, the interactive nature of the decision rules and sward canopy structure and the point at which these rules are enforced is still essentially at a descriptive stage. For example, the review has clearly demonstrated that herbivores prefer short immature swards. This is merely describing an observation, which emphasises that much of the research has focused on describing 'effect'. It is only more recently that causation has become of priority, and to this end, identification of causation will become critical in defining behavioural mechanisms that allow for the prediction of optimal patch departure.

It is increasingly obvious that the chosen foraging strategy, and particularly its simplicity, alters with the complexity of the choices, supporting the notion that the decisions animals make reflect the spatial arrangement of leaf and stem strata and their height relative to sward height. However, studies are rarely supported by information on the vertical distribution of herbage within the sward canopy profile. Instead authors opt for relationships with nutritive value, particularly digestibility, which has limitations since it largely ignores the need to relate behaviour to some physical property of the plant to which the animal is attentive, thereby dismissing the impact of structural characteristics on handling time. Consequently, information on the makeup of leaf and stem, including its position in the sward canopy, and quantitative estimates of tensile strength, or even simple estimates of force to fracture will be important elements of future studies.

2.9 CONCLUSION

There is now general agreement that while significant advances in plant physiological and morphological responses to defoliation have been identified (Lemaire and Chapman, 1996), and there have been parallel advances in herbivore nutrition (Milligan *et al.*, 1995), there has been slower progress in the study of animal foraging behaviour which provides the essential link between these two disciplines. The studies reviewed here on discriminatory behaviour indicate the need for future patch-use studies to make more use of well defined sward descriptions, in addition to information on nutritive value, as a means to teasing out which cues are potentially important in the appraisal program. In nearly all studies, there appear to have been limitations in the range of choices offered, primarily through experimental design, and so the full extent of trade-off comparisons is limited. Additionally, there have been fewer tests of the patterns of within and between patch behaviour and there is little conclusive evidence for how animals perceive and gain knowledge, within the range of heterogeneity in the current environment.

The three hypotheses evaluated in this thesis using a field-based methodology comprising a linear structured sequence of patches were:

a) Cattle would exhibit a trade-off between sward height and maturity, with maturity a stronger patch selection cue than sward height or bulk density, and sward height a stronger cue than bulk density.

b) Patch behaviour would be governed by the number and location of potential bites to the effect that the cryptic structure of the sward should assist in the understanding of the observed behavioural patterns.

c) Foraging decisions between and within patches would be directly related. Decisions about a current patch would reflect information gained from foraging experience and the expectation of the patch value of unexploited patches in sequence.

THREE

EXPERIMENTAL PROCEDURES

3.1 INTRODUCTION

This chapter provides general information on experimental design and sward measurements common to all experiments. In all there were five experiments and in the following chapters, the experiments have been broken into three groups. Experiment 1 (Chapter 4) was concerned with sward physical characteristics, height and bulk density. Chapter 5 covers Experiments 2, 3 and 4 which were concerned with the interactions between the effects of variations in sward structure and morphological characteristics. Experiment 5 (Chapter 6), focuses on spatial distribution and foraging strategy questions in greater detail. For each chapter, treatment details and patch manipulation procedures are described, followed by the sward measurements summarised in table format with any specific deviations from standard procedures reported at this point and then followed by the results section for each experiment. A discussion covering the experiments pertaining to that chapter then follows.

3.2 EXPERIMENTAL DESIGN

3.2.1 Establishment

A series of five experiments covering the period February 1995 to January 1998 were carried out on a 0.1 ha fenced block of land located on the Dairy Cattle Research Unit, Massey University, Palmerston North, New Zealand (latitude, 40^0 23'S; longitude, 175^0 37'E).

The experimental site was established in May 1994 with five 2.4 m wide x 55.0 m long strips reseeded by broadcasting a mixture of perennial ryegrass (*Lolium perenne* L, cultivar Yatsyn) and white clover *(Trifolium repens*, cultivar Pitau) at rates of 30 and

3 kg of seed per hectare respectively into a prepared seedbed in an existing ryegrass/white clover sward. These strips were separated by 3.0 m wide strips of the original sward (Figure 3.1(a)). Emerging creeping Buttercup (*Ranunculus repens*) and Broad-leaved Dock (*Rumex obtusifolius*) seedlings and the clover population were removed in late July using 2,4-DB at a rate of 7 litres/ha. Sward development was encouraged with close grazing by a mob of ewes at regular intervals during October. Reseeded strips had matured and experimental manipulation began in mid November of 1994. Further invasions of Broad-leaved Dock (*Rumex obtusifolius*) and Californian thistle (*Cirsium arvense*) were controlled by hand cutting.

3.2.2 Sequence layout

Four strips were selected for uniformity of growth and purity, with the 5th strip designated a "training" strip. All experiments followed the basic design and procedures explained below.

Each of the 4 strips was divided into a series of 2.4 m x 0.90 m patches (Figure 3.1(a) and (b)), the number required depending upon treatment combinations, and defined by 0.45 m marginal areas mown to approximately 2 cm (Plate 3.1(a)). For all experiments, treatments were assigned to patches, with block replication within a sequence, forming a linear series of contrasting patch choices. Prior to the grazing observations each strip was divided longitudinally into 3 sections using double strand electric fencing, with the cordoned off centre section being an un-grazed sampling zone (0.45 m wide), hereafter referred to as the centre section, leaving a grazing zone either side (Figure 3.1(b) and Plate 3.1(b)). Single patches, hereafter known as grazed patches, were of approximate dimensions 0.90 m x 0.90 m for Experiments 1, 2 and 4 but varied according to treatment for Experiments 3 and 5. Double strand electric fencing, running parallel to the strip on either side, approximately 1.10 m from the edge of the patch provided a 2.0 m raceway where movement was restrained making it difficult for animals to turn around (Figure 3.1(a) and (b); Plate 3.1(b)). In later experiments (4 and 5) the width of the raceway was reduced to 1.8m.

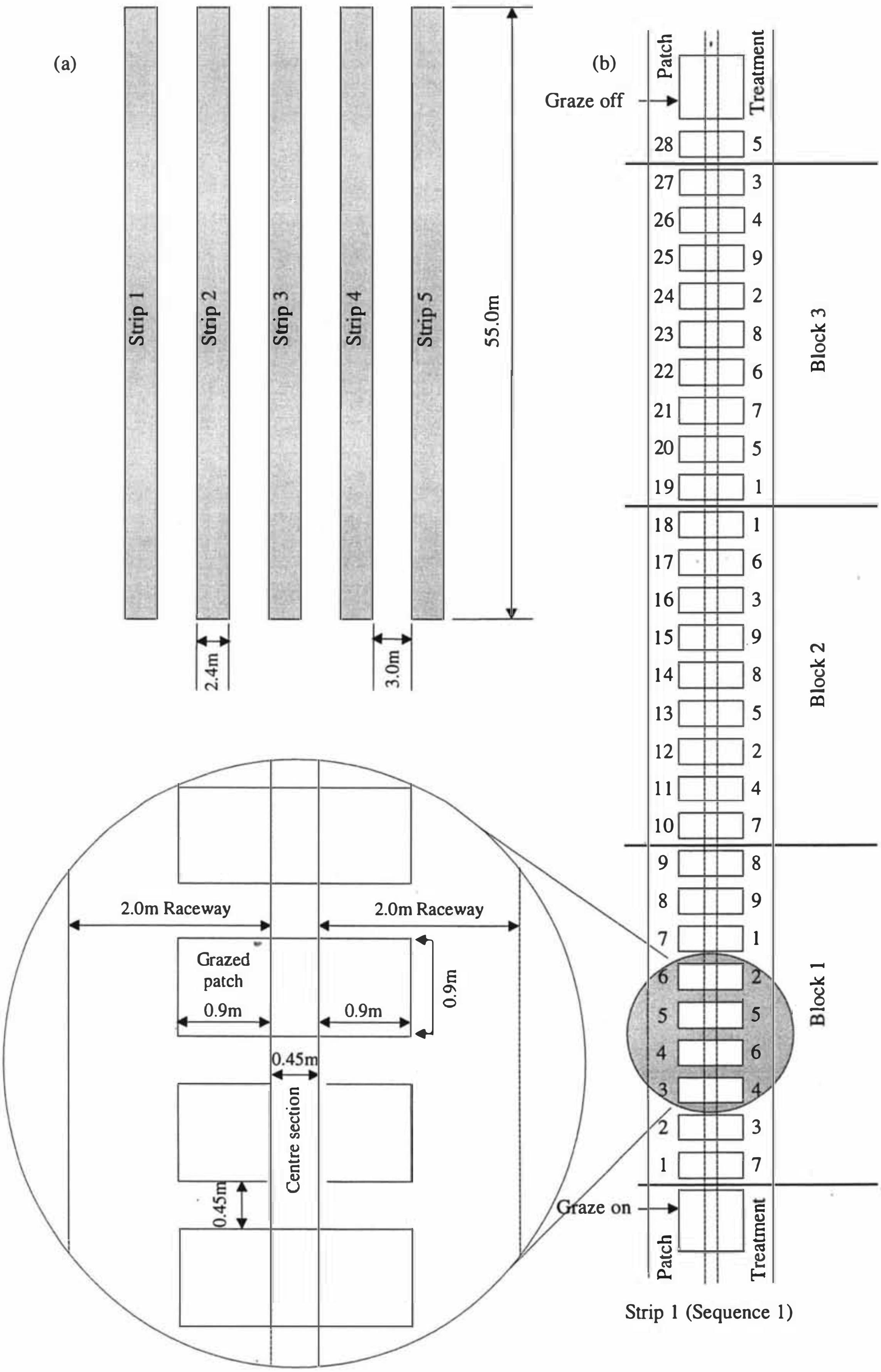

Figure 3.1 (a) Illustration of strip layout and (b) sequence structure for strip 1 in Experiment 1.

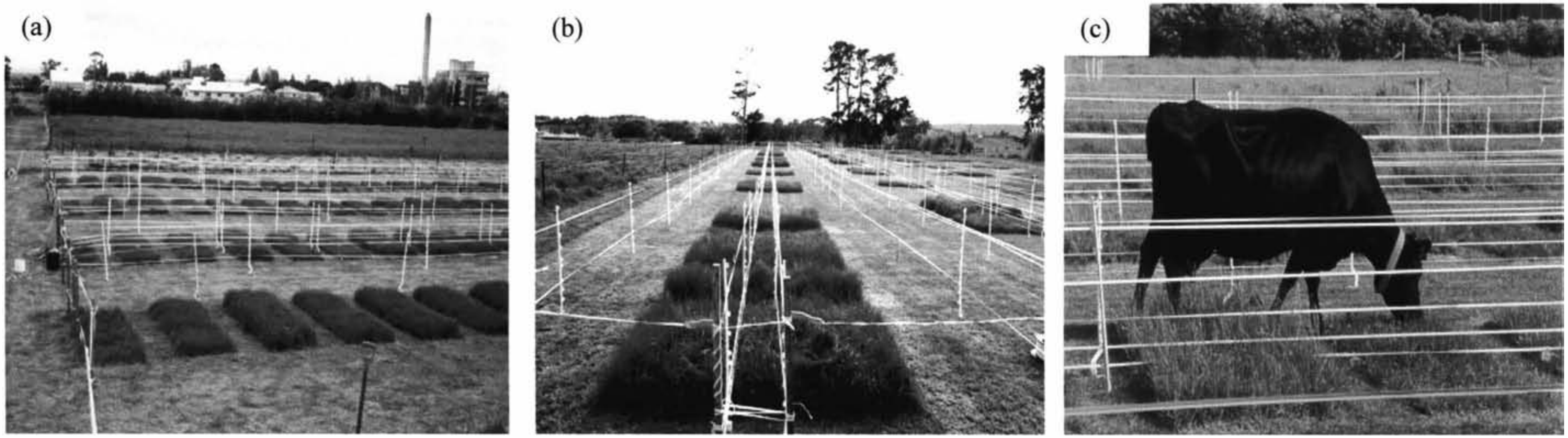

Plate 3.1 Linear patch sequence, (a) patch manipulation (b) sequence layout with one grazing run either side of the centre section and (c) study cow working down the sequence of choices.

For Experiments 1 to 3, a 2-3 m graze-on area was allocated prior to the first patch primarily to ensure animals settled to grazing. These early experiments also examined interactions between adjacent patch effects and so an additional patch (and allocated treatment) was present after the last patch in the last block for this purpose (see 28th patch in Figure 3.1 (b)). For Experiments 4 and 5 a patch was included before the first patch to test for preceding patch effects in addition to succeeding patch effects so that the graze-on area was largely excluded.

3.2.3 Animals

A group of six mature (>4 years, complete dental formation) Friesian and Friesian Jersey cross dairy cows were trained to experimental procedures prior to Experiment 1. An initial training programme, conducted over a month, familiarised all six cows with the narrow raceway and with observers walking parallel with them in close proximity. The training area comprised old ryegrass/white clover pasture but 2 days prior to the grazing runs a rehearsal on strip 5 which had been manipulated to provide gaps between patches and sward height contrasts allowed familiarisation of cows to sward conditions. The rehearsal also enabled the camera crew and observers recording bite number and residence time to adjust their operations and positions according to cow temperament and time to traverse the raceway. Four cows were then chosen as the experimental units. For Experiments 2-5, animals adjusted readily within a week and had no exposure to treatment contrasts prior to the grazing observations. The stage of lactation varied across studies, with Experiment 1 conducted with cows in late lactation, Experiment 2 with dry cows, Experiment 3 used three cows in mid lactation and one dry cow and Experiments 4 and 5 used cows in mid lactation.

The four cows grazed with the herd as per normal but on the morning of experimental sessions they were held back after the morning milking. Initially they were held in a holding bay at the dairy shed and then transferred to a holding bay erected within a paddock adjacent to the experimental site. Existing herbage had been mown to c. 2 cm to avoid grazing. Each animal, in turn, was guided to the beginning of the designated sequence of patches and allowed to graze uninterruptedly (see section 3.2.4). Upon exiting from the last patch in sequence, each cow was herded back and allowed to graze in the adjacent paddock.

3.2.4 Grazing bites and residence time per patch

On trial mornings, grazing observations commenced within 3 hours of morning milking, with cows having had limited opportunity to graze during this period. On any one morning each cow grazed, alone, one sequence of patches and behaviour was monitored in terms of the number of bites removed and residence time on each patch. These parameters were measured directly by two observers walking parallel to each cow, approximately 1.2 m away. Grazing bites were assessed using a combination of visual and sound appraisal, and residence time was measured through clocking entry and exit times from a patch against a running time background on a hand held datalogger (PSION Organiser II). All data was later checked against a video recording made simultaneously by a third attendant.

3.3 GENERAL SWARD MEASUREMENTS

3.3.1 Sward height and Pseudostem height

Sward height prior to grazing was assessed on each of the grazed patches using a sward stick (Barthram, 1986) with between 10 and 30 readings (depending on experiment) taken at the point at which the transparent tongue of the stick first came into contact with live leaf. At the completion of the grazing observations a further set of readings (equal to the number of pregraze readings) were taken, this time only from grazed areas. For the initiation of post-graze readings a minimum of 4 bites was set as the criteria unless otherwise specified.

Pseudostem height was assessed using a sward stick and the sward with the centre section. Pseudostem height was recorded at the point of contact with the upper ligule of the youngest mature leaf on any randomly chosen tiller.

3.3.2 Herbage mass

Herbage in the centre section was considered to be representative of pregraze conditions for each pair of patches. The removal of all herbage remaining on the grazed patches at the completion of the grazing observations constituted postgraze mass estimates. For

Experiments 1 to 3 direct estimates of herbage mass, both pre and postgraze, were made using a variety of techniques from complete removal of herbage using a rotary mower or an electric shearing handpiece to clipping herbage within a 0.1m^2 quadrat to approximately 2 cm above ground level. However reliable estimates of herbage removal, through direct procedures, proved difficult to obtain on small-scale patches and so for later experiments (4 and 5) effort was made to establish relationships between capacitance probe (Crosbie *et al.*, 1987) and dry mass estimates. Samples retrieved were bagged, weighed, subsampled and washed, except for Experiment 1 where washing was not undertaken. All material was dried at 80^{0}C for 24 hours for dry mass.

3.3.3 Botanical composition

One small hand-size sample, approximately 15-20 g for Experiments 1, 2, 3 and 5 and approximately 20-30 g for Experiment 4, was gathered from the centre section for each pair of patches, cutting to approximately 2 cm above ground level. Samples for treatment combinations were either bulked across blocks within sequences, or bulked across treatment combinations within blocks or according to stubble height depending on the experiment. A stratified sampling technique was carried out for Experiment 4. After bulking, samples were sub-sampled and dissected into component categories from the following: ryegrass leaf, ryegrass pseudostem, ryegrass leaf and pseudostem, ryegrass reproductive stem, other species leaf and pseudostem, other species leaf, other species pseudostem, other species reproductive stem, other species, weed and dead. All dissected material was dried at 80^{0}C for 24 hours for dry weight.

3.3.4 Nutritive value

Dried herbage mass samples (pregraze) were bulked on an equal weight basis and all samples were ground using a hammer mill fitted with a 1mm screen. Some variation exists between experiments in bulking procedures and in the methods used for assessment of nutritional parameters. In some cases nitrogen % was assessed by the Kjeldahl method and dry matter digestibility (DMD) and organic matter digestibility (OMD) were measured by the *in vitro* technique of Roughan and Holland (1977).

Alternatively, estimates of protein (N x 6.25), carbohydrate (soluble sugars and starch), lipid, neutral detergent fibre (NDF), acid detergent fibre (ADF), ash, organic matter digestibility (OMD) and metabolisable energy (ME) were determined using Near Infrared Reflectance Spectroscopy (NIRS) (Shenk and Westerhaus, 1994).

3.3.5 Strength properties

Two approaches for assessing strength properties were adopted. Shear strength was assessed in Experiments 2 and 3 using a Warner Bratzler meat shear-test apparatus, but concern over the reliability of data led to the use of an Instron testing apparatus to measure force to fracture in Experiment 4 (see appropriate sections for details).

3.4 STATISTICAL ANALYSIS

Behavioural data for each experiment was analysed using the SAS General Linear Models procedure (SAS Institute, 1995). The statistical model and framework were common to all experiments and the various terms are discussed below.

Base model = Sequence|Cow Block(Sequence x Cow) Treatment Treatment(Sequence x Block)

It was expected there would be variation across sequences, cows and blocks and these sources of variation were removed before consideration of treatment effects. Since the effects of these terms were not related to the objectives of the experiments, no data is presented for these effects throughout the thesis. The exception to this is Experiment 4 where between-cow variation was considered. For each experiment, tables within the main body of the results present data from the analysis of variance for treatment effects (and linear regression effects where applicable) only.

For the initial experiments (Experiments 1 to 3) the focus of interest was on the influence of components of sward structure and the sequence, block and cow effects were structured to avoid confounding the treatment effects. The sequence term was intended to allow for differences between sequences and likewise block and cow terms were added to remove variation across blocks and between cows. Sequences were partially confounded with cows in every experiment. For Experiments 2 and 3, where only 2 sequences were used, the degrees of freedom for the cow term did not equate to n-1 but rather n-2. In these cases, after removal of the sequence effect, a degree of freedom was used for the comparison between pairs of cows on each sequence. In Experiment 4 extra sequences were added at the expense of block replication, providing extra replication of cows and ensuring sufficient degrees of freedom for a between-cow comparison without sacrificing replication of sward effects. The 6 sequences, with 2 sides to each sequence, allowed for each cow to be paired with every other cow for a balanced incomplete block comparison of cows.

Replication of the treatments down a sequence varied between experiments. Treatments were allocated randomly to paired patches (2 sides per sequence) in complete blocks, and the block(sequence x cow) term of the model allowed for these blocks. The exception to this was Experiment 5 where constraints on strip length resulted in 1.5 replicates. In this experiment the four half-replicates joined together to form an extra 2 replicates with the 3 factor interaction confounded, thus across a pair of sequences (1 and 2; 3 and 4) there were three blocks of 8 paired patches.

The sward parameters of interest for each experiment, for example density and herbage mass in Experiment 1, were set up as nominal treatment effects (Model 1). One of the main objectives was to study how sward height influenced grazing decisions and the degree to which other structural variables modified foraging behaviour. Because of this, sward height is considered as a variable which can be fitted as either a conventional nominal treatment variable (Model 1) or as a continuous measurement (alternative models). The latter case assumes a linear regression relationship between a behaviour x and sward height. Many of the statistical effects presented in the tables are highly significant, and comparison on the basis of the relative magnitude of the variation attributable to each effect is also emphasised. Where alternative models have been used extracts from the analysis of variance output for these models are presented for comparison of the magnitude of differences and significance levels with the output from the base model (Model 1). Sums of squares and probability values for sward effects are presented in order of fitting and sed (standard error of the difference) values are shown.

With each sequence being grazed by 2 cows, one either side, there was a pair of patches for each treatment within each sequence. The term treatment(sequence x block) was added after nominal treatment effects and measured the variability between the paired patches of each sequence. The allocation of treatments to paired patches led to the treatment variability being dependent on paired patch variability, and this variance was estimated by the mean square of treatment(sequence x block). Using this as the error term in the analysis was equivalent to using the mean of both sides of a patch as the observation for the analysis of treatments. Consequently for the calculation of the sed, within patches, the variance (s^2) was the mean square error for treatment(sequence x block). For between-patch comparison, where there was only one value obtained from the centre section for every pair of patches, for example shear strength, the variance (s^2) was estimated in the conventional manner as the mean square error.

Further details on models are explained in the results sections for the experiments concerned. Sward descriptive data was analysed under the same framework, utilising the terms from the base model where appropriate.

FOUR

PHYSICAL CHARACTERISTICS

Experiment 1 An assessment of the use of sward height and bulk density as cues on patch selection behaviour using a linear structured field design

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4.1 INTRODUCTION

Foraging behaviour covers multiple scales (Senft *et al.*, 1987; Stuth, 1991), and the animal is faced with a number of strategic decisions at all levels of this hierarchy. The complexity of these decisions is defined by the level of sward heterogeneity (Gordon and Lascano, 1993), the morphology and physiology of the animal concerned (Illius and Gordon, 1987), and involves the fundamental trade-off between forage quality and quantity.

Few studies have examined the effect of sward physical characteristics on the rules governing animal foraging (see Bazely, 1988 and 1990). In one of the few known studies, sward height was a stronger patch selection cue than bulk density, and short dense swards were preferentially grazed over short sparse swards when sward height was held constant (Demment *et al.*, 1993). In general, attempts to understand the mechanisms of herbivore foraging behaviour have utilised laboratory-based methodologies which have provided the opportunity for close control over intra-specific sward conditions and enabled a detailed understanding of the effects of sward height and bulk density on the dimensions of individual bites. However, the simulated foraging environment and low number of choices offered at any one time is very simplified compared to the array of choices and constraints animals' face in their natural ecosystem.

There is increasing interest in the application of optimal foraging theory to herbivore foraging patterns (Bazely, 1988; Laca *et al.*, 1993b). Assumptions about the level of information animals possess and how information gained is incorporated into subsequent decision making is critical to the development of models of optimal foraging. Currently, due to the general lack of knowledge about both the information animals carry with them and the detailed selective responses which emerge, it is premature to define any optimal strategy for herbivores (Illius and Gordon, 1990).

In this initial study the aim was to examine discrimination more objectively. Firstly, through extending the technique of Laca *et al.* (1993b), and testing a controlled field methodology to monitor the decisions animals made about alternative patch choices on offer. Secondly, to investigate the preference and potential trade-off decisions exhibited when dairy cattle were offered a range of sward patches varying in the physical parameters, sward height and bulk density. Thirdly, to assess the influence of conditions of the forthcoming patch in sequence on selection decisions about the current patch.

4.2 PATCH TREATMENTS and MANIPULATION

Sets of 9 combinations derived from 5 sward heights and 3 sward bulk densities (Table 4.1) were created over the period November 1994 to February 1995. Each set of 9 treatments was replicated 3 times down each sequence (blocks) and 4 different sequences were used. Balance across the 4 sequences was achieved by dividing the 9 treatments into 3 groups according to sward height, short (T1, T2, T4), medium (T3, T5, T7) and tall (T6, T8, T9) and randomising with the restriction that each height group followed each other height group with equal frequency. The structure of 5 sward heights and 3 bulk densities was also intended to provide comparability in herbage mass across sward types.

Table 4.1 Experimental treatments for Experiment 1.

Sward height level	Regrowth period (weeks)	Bulk density		
		High	Medium	Low
5	4			Treatment 9
4	3		Treatment 6	Treatment 8
3	2	Treatment 3	Treatment 5	Treatment 7
2	1.5	Treatment 2	Treatment 4	
1	1	Treatment 1		

Sward bulk density contrasts were created by regular trimming to a stubble height of approximately 5 cm at intervals of 3 (high), 2 (medium) or 1 (low) weeks for a period of 9 weeks, and contrasts in sward height were created by synchronising 4, 3, 2, 1.5 and 1 week final periods of regrowth prior to grazing. High, medium and low bulk densities are considered as relative values within the context of the experiment.

4.3 SUMMARISED SWARD MEASUREMENTS

Table 4.2 Summarised sward measurements for Experiment 1.

Measurement	Particulars
Sward height	10 readings pre and post graze.
Herbage mass	Herbage for pregraze and postgraze mass estimates was removed from the designated areas to approximately 2 cm with a rotary mower.
Botanical composition	Samples for each treatment combination were bulked across blocks within sequences, sub-sampled and dissected into the components, ryegrass leaf, ryegrass pseudostem, other species leaf and pseudostem, weed and dead material.

For further details on measurement of sward height refer to section 3.3.1, herbage mass refer to section 3.3.2 and botanical composition refer to section 3.3.3 under "General sward measurements".

4.4 RESULTS

4.4.1 Treatment contrasts

The sward preparation procedures produced patches which varied in height, with approximately 3 cm increments between sward height levels, except for heights 1 and 2 (Table 4.3). Variations in bulk density within levels of density were not consistent and there was no evidence of consistency between estimates of pregraze herbage mass on the diagonal (Table 4.3). As a result, there was a strong trend for both bulk density and herbage mass to increase with increasing sward height. The proposed model for analysing the data was a simple model of nominal bulk density and nominal herbage mass (Model 1).

$$\text{Model} = \text{Bulk density}|\text{Herbage mass} \qquad (1)$$

However, in light of the poor contrasts in bulk density and control over herbage mass within patches, an alternative model using nominal sward height and nominal bulk density nested within nominal sward height was adopted (Model 2).

$$\text{Model} = \text{Sward height Bulk density(Sward height)} \qquad (2)$$

The swards comprised predominantly the sown specie ryegrass. Increases in sward height were associated with an increase in the proportion of ryegrass leaf. The exception to this pattern was at the tallest sward height of 19.6 cm (T9) where ryegrass leaf declined to similar levels to that found on T3, T5 and T7 (Table 4.4). There was indication that pseudostem content was influenced by sward height but this did not attain significance (Table 4.4). The contribution of ryegrass stem to sward composition was less than 3 % DM (Table 4.4) and contamination from invading grass species was also relatively small at less than 4 % DM (Table 4.5). Neither of these components were influenced by sward height. Swards were generally weed free, with any contamination being from broad-leaved dock (*Rumex obtusifolius*). The large value for weed content recorded for T5 led to the significant sward height effect on weed content (Table 4.5). The percentage of dead material present in swards generally declined with increasing sward height (Table 4.5), though again T9 was the exception to the pattern. There was no effect of bulk density on the proportions of any of the botanical components across the 9 treatments.

Table 4.3 Mean values for sward height, bulk density and pregraze mass for the 9 treatments in Experiment 1.

		Sward height (cm)			Bulk density (mg DM cm^{-3})			Pregraze mass (g DM m^{-2})		
		Bulk density			Bulk density			Bulk density		
		1	2	3	1	2	3	1	2	3
Sward Height	5			19.6			1.86			362.5
	4		16.0	16.8		1.67	1.72		266.6	291.8
	3	13.2	13.2	13.5	1.38	1.53	1.43	182.1	202.5	192.4
	2	10.2	10.4		1.23	1.34		125.1	138.1	
	1	8.9			1.37			121.1		
sed		0.40			0.188			19.1		
P value : Sward height[†]		0.0001			0.0022			0.0001		
P value : Bulk density(Sward height)[†]		0.2502			0.9058			0.5053		

[†] Nominal treatment effect

Probability values for the effects of sward height and bulk density are given in sequential order of fitting and derived from analysis using Model 2.

Table 4.4 Mean values for botanical composition (% DM) for the 9 treatments in Experiment 1.

	Ryegrass leaf			Ryegrass pseudostem			Ryegrass stem		
Sward Height	Bulk density 1	2	3	Bulk density 1	2	3	Bulk density 1	2	3
5			72.6			7.9			2.9
4		78.5	77.8		7.6	6.8		0.0	0.5
3	72.5	72.6	73.5	6.5	6.9	6.4	1.6	0.0	0.0
2	71.8	70.5		5.6	6.9		0.4	0.0	
1	64.5			7.1			0.6		

	Ryegrass leaf	Ryegrass pseudostem	Ryegrass stem
sed	3.16	1.31	1.54
P value : Sward height[†]	0.0010	0.6017	0.3186
P value : Bulk density(Sward height)[†]	0.9858	0.8155	0.8088

[†] Nominal treatment effect

Probability values for the effects of sward height and bulk density are given in sequential order of fitting and derived from analysis using Model 2.

Table 4.5 Mean values for botanical composition (% DM) for the 9 treatments in Experiment 1.

	Other grasses			Weed			Dead		
	Bulk density			Bulk density			Bulk density		
Sward Height	1	2	3	1	2	3	1	2	3
5			1.9			0.0			14.7
4		2.4	2.3		0.5	1.3		11.1	11.6
3	2.9	0.3	2.2	1.6	3.5	1.0	15.1	16.6	17.0
2	2.7	0.0		0.0	0.1		19.6	22.6	
1	3.2			0.4			24.2		
sed	2.14			0.95			2.13		
P value : Sward height[†]	0.8847			0.0213			0.0001		
P value : Bulk density(Sward height)[†]	0.5622			0.1178			0.5687		

[†] Nominal treatment effect

Probability values for the effects of sward height and bulk density are given in sequential order of fitting and derived from analysis using Model 2.

Table 4.6 Mean values for bite number, residence time and herbage removed for the 9 treatments in Experiment 1.

		Bite number			Residence time (sec)			Herbage removed (g DM m^{-2})		
	5			53.5			55.3			-14.8
Sward	4		45.5	46.7		42.8	43.1		3.1	50.7
Height	3	31.3	30.8	32.0	27.1	25.7	27.5	-39.9	7.9	-19.7
	2	4.2	4.8		3.2	3.7		-44.7	-18.3	
	1	0.2			0.1			-43.7		
		1	2	3	1	2	3	1	2	3
		Bulk density			Bulk density			Bulk density		

	Bite number	Residence time (sec)	Herbage removed (g DM m^{-2})
sed	2.14	2.02	31.92
P value : Linear effect of sward height	0.0001	0.0001	0.0329
P value : Quadratic effect of sward height	0.0001	0.0001	n/a
P value : Nominal sward height	0.0001	0.0001	0.3012
P value : Nominal bulk density(sward height)	0.9968	0.8725	0.2887

n/a term not used in the model, for further information refer to the text.
Probability values for the effects of sward height and bulk density are given in sequential order of fitting and derived from analysis using Models 3 and 4.

4.4.2 Bite number, residence time and herbage removed

The mean values for the number of bites, residence time and herbage removed per patch are presented in Table 4.6. The initial analysis of behavioural parameters using Model 1 showed strong significant effects of both bulk density and herbage mass (Table 4.7). The analysis of variance using the alternative model (Model 2) showed strong effects of sward height on bite number and little effect of density (Table 4.8) suggesting the strong density effect observed in the output from Model 1 was a reflection of the variation in sward height.

Table 4.7 Extract from the analysis of variance output for bite number using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Bulk density†	2	37420.59	18710.30	277.89	0.0001
Herbage mass†	2	34835.12	17417.56	258.69	0.0001
Bulk density x Herbage mass†	4	5073.60	1268.40	18.84	0.0001

† Nominal treatment effect

Table 4.8 Extract from the analysis of variance output for bite number using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Sward height†	4	77289.10	19322.27	286.98	0.0001
Bulk density(Sward height)†	4	40.22	10.10	0.15	0.9628

† Nominal treatment effect

When sward height was fitted as a continuous variable after nominal treatment parameters the effect of sward height on bite number was strongly significant (P=0.0001). As this effect was an indicator of within treatment variation in sward height, a continuous linear regression effect of sward height was added to the model before the nominal treatment effects (Model 3).

Model = Sward height† Sward height Bulk density(Sward height) (3)

†Linear effect of sward height

The output from the analysis of variance for Model 3 showed a strong linear relationship between bite number and sward height (Table 4.9) and this is reinforced by the values recorded in Table 4.6 with bite number increasing from 0.2 to 53.5 bites with increasing sward height across the range 8.9 to 19.6 cm. The significant nominal sward height effect observed in Table 4.9 suggests a non-linear response pattern. To test whether a curvilinear fit was appropriate for the data set, a quadratic term, continuous sward height squared was fitted after the linear effect of sward height but before the nominal treatment effects (Model 4)

Table 4.9 Extract from the analysis of variance output for bite number using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	71104.52	71104.52	1291.04	0.0001
Nominal sward height	4	7593.05	1898.26	34.47	0.0001
Nominal bulk density(sward height)	4	9.03	2.26	0.04	0.9968

Model = Sward height† (Sward height)^{2‡} Sward height Bulk density(Sward height) (4)

†Linear effect of sward height ‡Quadratic effect of sward height

The quadratic term being significant in Model 4 supported an asymptotic relationship between bite number and sward height (Table 4.10 and Figure 4.1). However, the quadratic term did not account for all the variation and the small residual significance of the nominal sward height term suggested that the 5 treatment heights intrinsically influenced bite number in different ways.

Table 4.10 Extract from the analysis of variance output for bite number using Model 4.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	71104.52	71104.52	1299.58	0.0001
Quadratic effect of sward height	1	3965.51	3965.51	72.48	0.0001
Nominal sward height	4	3689.67	922.42	16.86	0.0001
Nominal bulk density(sward height)	4	8.88	2.22	0.04	0.9968

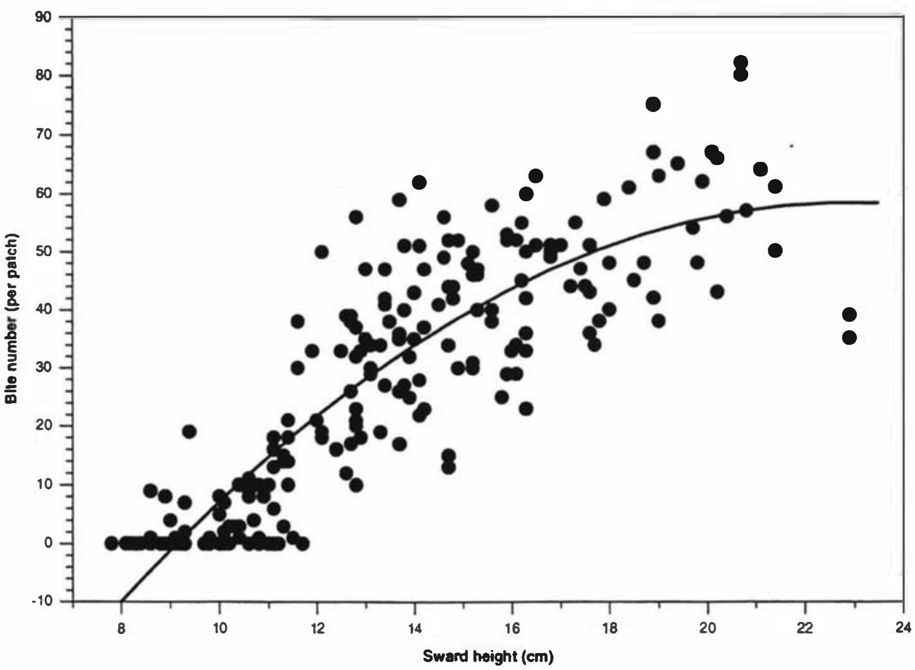

Figure 4.1 Relationship between bite number per patch and sward height for the 9 treatments in Experiment 1. A curvilinear, quadratic function is fitted for T1-T9 (——). Plotted data includes patches where there were no prehended bites and matches the output from the analysis of variance.

In the same way, patch residence time increased, range 0.1 to 55.3 sec, with increasing sward height (Table 4.6). In agreement with bite number, the time spent at each patch also tended towards a maximum as sward height increased. These similar patterns in the two aspects of behaviour shown in Table 4.6 reinforce the very strong correlation between the two behavioural measures (r = 0.99).

There was fluctuation in growth across each sequence to the effect that estimates of herbage mass from the centre section were lower than for the grazed patches either side of this section. Reasons for this effect were unclear but possibly reflected the wheel track marks from sowing. This effect led to a substantial number of negative estimates of herbage removed (Table 4.6), and these discrepancies were also reflected in the very high coefficient of variation for herbage removed per patch (c.v.= 475.7), particularly when compared with bite number (c.v.= 28.3) and patch residence time (c.v.= 29.0). Due to the poor reliability of estimates for herbage removed, and the strong correlation between bite number and patch residence time, further data for this experiment will be presented for bite number only.

Table 4.11 Mean values for bite rate, bite depth and bite depth/sward height for the 9 treatments in Experiment 1.

		Bite rate (bites min^{-1})			Bite depth (cm)			Bite depth/Sward height (%)		
	Bulk density	1	2	3	1	2	3	1	2	3
Sward Height	5			58.5			9.3			47.2
	4		64.3	65.1		8.5	9.0		52.4	53.7
	3	70.3	72.1	71.1	6.8	7.0	7.6	51.1	52.9	55.1
	2	76.5	77.8		4.6	5.0		44.6	48.2	
	1	80.0			4.8			47.5		

	Bite rate	Bite depth	Bite depth/Sward height
sed†	2.44-3.61	0.29-0.43	1.99-2.94
P value : Linear effect of sward height	n/a	0.0001	0.8369
P value : Quadratic effect of sward height	n/a	0.0004	0.0001
P value : Nominal sward height	0.0001	0.0023	0.0046
P value : Nominal bulk density(sward height)	0.9202	0.4894	0.4055

† sed range for T2-T9 only.

n/a term not used in the model, for further information refer to the text.

Probability values for the effects of sward height and bulk density are given in sequential order of fitting and derived from analysis using Models 2 and 4.

4.4.3 Bite rate

Combining the data on bite number and residence time from Table 4.6, and excluding patches where fewer than 4 bites were removed, provided estimates of bite rate. These values are presented in Table 4.11. Within treatment variation in sward height did not influence rate of biting (P=0.6075) and Model 2 was used to analyse the observed patterns. The output from the analysis of variance table showed significant effects of sward height on the number of bites prehended per minute (Table 4.12), with the rate consistently declining from 80 bites min^{-1} to 58.5 bites min^{-1} with increases in sward height over the range 8.9 to 19.6 cm (Table 4.11).

Table 4.12 Extract from the analysis of variance output for rate of biting using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Sward height†	4	6306.49	1576.62	22.05	0.0001
Bulk density(sward height) †	4	65.16	16.29	0.23	0.9220

† Nominal treatment effect

4.4.4 Bite depth

The depth of penetration into the sward, measured by the difference between sward height pre and postgraze, was analysed using Model 3 since there was significant within treatment variation in sward height (P=0.0001). The output from Model 3 showed a strong and positive linear relationship between bite depth and sward height (Table 4.13).

Table 4.13 Extract from the analysis of variance output for bite depth using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	363.77	363.77	359.76	0.0001
Nominal sward height	4	30.71	7.68	7.59	0.0001
Nominal bulk density(sward height)	4	3.69	0.92	0.91	0.4647

However, there was also some minor evidence that nominal sward height influenced bite depth. The fitting of Model 4 with a quadratic term for sward height, whilst itself being significant (Table 4.14) only marginally decreased the effect of nominal sward height on bite depth indicating that there were small treatment effects, unrelated to sward height, influencing the depth of penetration. The relatively small effect of the quadratic term as against the linear sward height term indicated that there was only minor evidence for curvature in the relationship between bite depth and sward height.

Table 4.14 Extract from the analysis of variance output for bite depth using Model 4.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	363.77	363.77	365.19	0.0001
Quadratic effect of sward height	1	13.69	13.69	13.74	0.0004
Nominal sward height	4	18.37	4.59	4.61	0.0023
Nominal bulk density(sward height)	4	3.44	0.86	0.86	0.4894

Whilst the increases in mean bite depth diminished with increasing sward height, when depth of penetration was expressed as a proportion of initial sward height (Table 4.11) there was no significant linear relationship between bite depth and sward height (Table 4.15) indicating that bite depth in this experiment can be considered as a constant proportion, approximately 50 %, of sward height. However, considering the significance of the residual nominal sward height term, Model 4 with the quadratic effect of sward height was run. The results from the analysis of variance (Table 4.16) confirmed that there was evidence for a quadratic response in the proportion of sward height removed with each bite with increasing sward height. However, this effect is largely attributed to the value recorded for T9. When T9 was excluded from the analysis the linear sward height effect became significant (P=0.0003), and the quadratic effect did not attain significance (P=0.1864)

Table 4.15 Extract from the analysis of variance output for bite depth/sward height using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	1.93	1.93	0.04	0.8412
Nominal sward height	4	1320.0	330.00	0.93	0.0001
Nominal bulk density(sward height)	4	202.01	50.50	1.06	0.3825

Table 4.16 Extract from the analysis of variance output for bite depth/sward height using Model 4.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	1.93	1.93	0.04	0.8369
Quadratic effect of sward height	1	784.83	784.83	17.39	0.0001
Nominal sward height	4	745.30	186.33	4.13	0.0046
Nominal bulk density(sward height)	4	183.25	45.81	1.01	0.4055

4.4.5 Adjacent patch effects

The analysis of variance output using Model 2 did not show strong evidence that the sward height of the succeeding patch in sequence influenced the number of bites removed from the current patch, though the effect did approach significance at 0.1 probability (Table 4.17).

Table 4.17 Extract from the analysis of variance output for the influence of succeeding patch height on bites removed from the current patch.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	68042.93	68042.93	1470.88	0.0001
Nominal sward height	4	7004.32	1751.08	37.85	0.0001
Nominal bulk density(sward height)	4	16.10	4.02	0.09	0.9862
†Next patch nominal sward height	4	407.92	101.98	2.20	0.0759

†Next = succeeding patch

4.5 DISCUSSION

This was the initial experiment in a series where the core objective was to quantify discriminatory behaviour of dairy cattle using procedures that offered animals a more diverse range of choices *in situ* than that offered in laboratory-based studies, thereby simulating the complexity of decisions grazing animals face in their natural habitat. Four sequences of 27 patches (nine treatments x three blocks) were manipulated to offer animals contrasts in sward height and bulk density, both parameters considered as factors influencing potential forage intake rate. As the focus in this experiment was on assessing the methodology no data was collected on nutritive value or herbage strength.

4.5.1 Sward height and bulk density effects on preferential grazing behaviour

Demment *et al.* (1993) manipulated patches for variations in sward height and bulk density *in situ* but steers were only offered paired swards such that behavioural responses were only relative to one alternative. While this experiment attempted to provide similar contrasts in sward height and bulk density to those described by Demment *et al.* (1993), but over a wider range of combinations, the attempt to manipulate sward bulk density by control of tiller density met with limited success. The absence of consistent variations in bulk density was reflected in the increasing values recorded for bulk density within levels of density and for herbage mass per patch with increasing sward height for treatments on the diagonal (eg. T1, T4, T7). These conclusions were confirmed using the revised analysis of variance model (Model 2).

In the absence of consistent controlled contrasts in bulk density it was hypothesised that animals would exercise a deliberate choice by removing more bites and increasing residence time on the tall swards in a manner consistent with intake rate maximisation (Black and Kenney, 1984), irrespective of whether rate of intake on a short-term basis was actually used as a decision rule (Illius and Gordon, 1990). This indeed was the case: cattle increased the residence time and removed a greater number of bites per patch with increasing patch height. The preferential selection of taller swards extends and supports the work by Bazely (1990), although the taller patches in Bazely's study were confounded with variations in nutritive value over the shorter patches, and that of Clark and co-workers (reported in Illius and Gordon, 1990), who found that cattle, sheep and goats all preferentially grazed the taller of offered pairs of swards. Nonetheless, the limited influence of bulk density on preferential behaviour, as opposed to the more controlled contrasts in sward height, does not negate the possibility that trade-offs would be observed if strong independent contrasts in bulk density were introduced. Consequently, the limited influence of bulk density in this experiment should be treated with caution.

Although there were difficulties with reliable predictions of herbage mass and subsequently rate of intake, given the depth of existing knowledge from the literature on the influence of sward height on bite mechanics, it follows that the rate of intake potentially increased with increasing patch height. Indirectly supporting this was the strong linear relationship between bite depth and sward height, consistent with the findings by Ungar *et al.* (1991) and Laca *et al.* (1992a) for cattle. Bite mass is commonly described as having an inverse relation with the rate of biting (Forbes and Hodgson, 1985a; Spalinger *et al.*, 1988; Laca *et al.*, 1992a; Wallis de Vries and Daleboudt, 1994; Ginnett and Demment, 1995), whilst bite depth is strongly correlated with both sward height and bite mass (Mitchell *et al.*, 1991; Laca *et al.*, 1992a; Flores *et al.*, 1993; Laca *et al.*, 1994; McGilloway *et al.*, 1997), although there are studies where this relationship does not always prevail (Demment *et al.*, 1993). Even so, the declining rate of biting with increasing bites removed supported the theory of an increasing amount of herbage harvested per bite with increasing sward height. In this context, as herbage mass reflected the variation in sward height and it is rare for the rate of biting to completely compensate for reduced bite mass, the curve constructed in Figure 4.1 fits a typical functional response between intake rate and herbage mass (Spalinger *et al.*, 1988; Demment and Laca, 1994).

More recently Prache *et al.* (1998) working with sheep found a curvilinear functional response between intake rate and green leaf mass. This has been attributed to green leaf mass being a stronger predictor of bite mass than sward height (Prache, 1997; Prache *et al.*, 1998). However, this is not always a consistent effect. With cattle, Orr *et al.* (1997) found that while intake rate was best explained by green leaf mass, bite mass remained more strongly correlated with sward height. Using the equations given by McGilloway *et al.* (1997) for calculation of bite volume and bulk density of a bite for dairy cows across a range of sward height from 6 to 22 cm, the calculation of bite mass for the current experiment yielded mean estimates across the 5 levels of sward height of 0.44, 0.36, 0.41, 0.43 and 0.69 g DM bite^{-1} respectively. The respective estimates for the 9 treatments for the current experiment are plotted in Figure 4.2 and illustrate a substantially smaller sward height effect than what was indicated from the relationship between grazing bites and bite rate (Table 4.6, Table 4.11 and Figure 4.1). However, McGilloway *et al.* (1997) comment on the importance of the contribution of the leaf lamina fraction in influencing the estimates. The variation in leaf lamina fraction was greater (c. 20 to 80 %) than the leaf percentages recorded in the current experiment (c. 64 to 79% see Table 4.4).

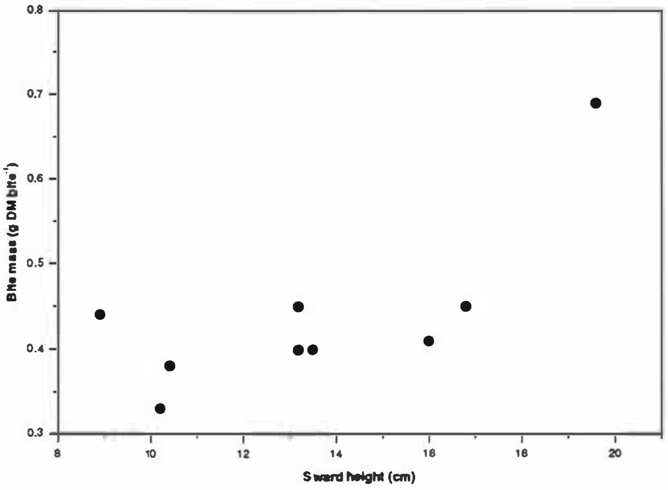

Figure 4.2 Estimates of bite mass for the 9 treatments in Experiment 1 using the equations for bite volume and bulk density given by McGilloway *et al.* (1997).

In the current experiment leaf mass increased with increasing sward height but there was evidence of a stronger curvilinear relationship between bite number and sward height (r^2 = 0.76) than bite number and leaf mass (r^2 = 0.39). Nonetheless, these differences may reflect the inaccuracy of the estimates of herbage mass per patch which were used to calculate leaf mass per patch, and care should be taken with the extrapolation of these values. Further research is required to monitor trade-off responses to independent effects of leaf mass and sward height.

Control over variations in tiller density on a small scale for swards grazed *in situ* is difficult (Bazely, 1988). Greater contrasts might have been achieved had the frequency of cutting been extended (eg. from 3, 2 and 1 week to 6, 3 and 1 week intervals) and over a longer duration (ie. 9 weeks to 12 weeks) but seasonal conditions coming out of winter and moving into summer, and so changing plant phenology, controlled the duration of the manipulative period. There have been varying levels of success in the few studies that have attempted manipulation of density in the field, but in either method the procedures constrain the scale of operation. Demment *et al.* (1993) achieved a high level of success by clipping every other 2.5 cm wide strip of the sparse patches to ground level with grass shears (details given in Distel *et al.*, 1995). Casey *et al.* (1997) achieved variations in tiller and bulk density in the order of 30 to 36 % by hand thinning swards. Even so, the difficulty in manipulating density was exposed in this study as the variation in density between intermediate and low density was minimal (0.99 vs 1.09 and 1.06 g DM m^{-2} mm^{-1} for low, intermediate 1 and intermediate 2 density respectively, although it was not clear from the paper what intermediate 1 and intermediate 2 represented) compared to the contrast between intermediate 1 and high density (1.09 vs 1.54 g DM m^{-2} mm^{-1} respectively). Procedures designed to achieve density contrasts by removing lines or strips of tillers are only applicable to newly reseeded swards and/or while the pasture is uniformly vegetative (eg. Demment *et al*., 1993) and the drill lines are clearly visible. There is no simple answer for the successful manipulation of swards for independent effects of sward height and bulk density *in situ* on a larger scale than a feeding station, where a feeding station is defined as the semi-circular area in front of, and to each side of the animal (Ruyle and Dwyer, 1985). Ungar (1996) commented that an area of 0.50 m^2 constituted a feeding station for a mature steer. Any procedure used for manipulating bulk density is likely to incur a substantial resource time cost.

4.5.2 Bite depth

Depth of penetration was measured on those patches where more than three bites were removed. This benchmark was set because when only one or two bites were removed animals were never observed to decelerate upon entry to a patch, rather 'grabbing' a bite randomly as they walked across the patch, and in this case bites were often shallow and difficult to ascertain accurately. As animals departed from a patch before there was substantial depletion in either the vertical or horizontal plane, bite depth is considered here to be the depth of penetration of a single bite as opposed to the depth of a bite after successive defoliation of a group of tillers in the vertical dimension.

Depth of penetration was linearly related to sward height. The diminishing effect of increasing penetration with increasing sward height followed a similar pattern to the increase in the number of bites removed but on a diminishing scale. While there was no indication that bite depth approached a plateau across the range of sward heights examined in this study (8.9 to 19.6 cm), the similarity in response between grazing bites and bite depth suggests the two aspects of behaviour are linked. Laca *et al*. (1994) have demonstrated that with increasing depletion there is a degree of bite overlap within a grazed stratum. Since the volume of a bite does not have a flat base (Laca *et al*., 1993a), the mean change in bite depth for an incremental increase in sward height could be predicted to increase but on a diminishing scale with increasing depletion. This would hold true if bite penetration is restricted to a single stratum. In absolute terms the proportion of sward height removed with each bite closely approximated 50 %, in general agreement with observations from other studies with cattle (Mursan *et al.*, 1989, 50-57%; Laca *et al.*, 1992a, 48-55%; Flores et al., 60-63%). However, questions about the concept of constant proportionality are raised when T9 is excluded from the analysis. The range in proportionality is small across T3, T5, T6, T7 and T8 (range 51.1 to 55.1 %) where approximately 30 to 45 bites were removed. The three shorter treatments (T1, T2 and T4) recorded lower values of the depth of sward height removed in a bite. This response again indicates an association with the number of bites removed, suggesting the possibility of differentiation between 'sampling' and 'grazing' bites. The significance of the quadratic term in Model 4, although the r square was not particularly strong (r^2 = 0.11), reflected the fact that the proportion of sward height removed in a bite was smaller for the tallest sward height (T9) than for the 13.3 cm (T2, T5 and T8) and 16.4 cm (T6 and T8) swards. Ungar (1996) in his review commented that the pooled data of Curll and Wilkins (1982) exhibited a curvilinear relationship, though a much stronger relationship than presented here, and Laca *et al.* (1992a) demonstrated that the combination of increasing sward height and bulk density had a negative influence on the proportion of sward height removed with each bite. However, the contrast in bulk density within Experiment 1 was not independent of sward height, and furthermore, bulk density was substantially lower than for the swards of Laca *et al.* (1992a). Overall, the results from this experiment do not provide a clear explanation why bite penetration closely approximated 50 % of sward height. Further research targeting this behavioural response is required to define the mechanism operating, animal or plant based.

4.5.3 Bite rate

Absolute estimates of bite rate were higher than observed for cattle in the field based patch study by Demment *et al.* (1993), and where cattle have been subject to long periods of fast (13 hours) (Patterson *et al.*, 1998). However, the faster rates of biting on the shorter swards (T1, T2, T4) were similar to the values recorded by Laca *et al.* (1994)

with cattle grazing hand constructed swards of leaf lamina. The variation in recorded values of bite rate across studies is commonly attributed to estimates representing the beginning of a grazing bout and only incorporating the time taken for a set number or the total number of bites on a patch ie. independent of locomotion (Laca *et al.*, 1992a; Patterson *et al.*, 1998). On a patch basis, caution is urged as there may have been carry-over effects from one patch to another in sequence which was not controlled, although the importance of these effects is constrained by the 1-2 seconds walked between patches and the fact that cattle can bite and chew simultaneously (Laca *et al.*, 1992b). Furthermore, there is danger in comparison of absolute estimates across studies since rate of biting is primarily a response to sward conditions (Hodgson, 1986). The comparison between the estimates from this experiment with the corresponding values given by Orr *et al.* (1997) clearly illustrates this point.

4.5.4 Measures of preference

Cattle took between 8 and 15 minutes to cover a sequence of 27 patches. Patch preference was constant irrespective of whether grazing bites or residence time per patch was used as the definition of preference. How well the contrasts in grazing bites or residence time matched the patch differences in intake rate could not be ascertained in light of difficulties encountered with accurate estimates of the mass of herbage removed. Wallis de Vries and Daleboudt (1994) expressed reservations about the reliability of grazing bites as an indicator of preferential behaviour on the grounds that since bite number is strongly influenced by the size of each harvested bite, the use of this parameter introduces a bias thereby understating the patch value of taller swards in terms of rate of intake. Nonetheless these authors report that bite number was a more sensitive measure of patch choice than was residence time (F = 320.2 vs F = 172.0). Furthermore, while these authors argue that residence time is a more appropriate measure, this does not imply that under short-term studies patch residence time will necessarily reflect the relative differences in rate of intake between alternative patches (Illius *et al.*, 1992).

Additionally, similar patterns in the consistency of preference using bite number, residence time or the mass of herbage removed from each patch as indices were found by Distel *et al.* (1995) over 15 minute periods for cattle grazing swards of ryegrass. More recently a study on feeding station behaviour showed that the mean number of bites removed correlated with residence time per feeding station (Roguet *et al.*, 1998b). In this study less than 5 % of feeding stations exceeded a residence time of 30 seconds, suggesting that for studies of short-term duration (up to at least 15 minutes) bite number can be an equally good criterion as residence time, at least at the patch level.

4.5.5 Sampling behaviour and adjacent patch effects

Sampling is an integral component of patch choice (Illius *et al.*, 1992; Langvatn and Hanley, 1993; Wilmshurst *et al.*, 1995) with animals regularly sampling from all but the shortest of patch types. Illius and Gordon (1990) attributed such responses to poor information uptake and retention, but retrieval of information for decision making is a separate process from the uptake, retention and storage of information (Packard *et al.*, 1990). Ruminants are certainly not constrained in their ability to learn associations between cues and rewards (Edwards *et al.*, 1997) but patch height as a visual cue may not always reflect patch value. While Provenza (1996a) argued that sampling is a mechanism animals use to correct food aversions, its application within a monoculture, particularly where sward patches are at a similar stage of phenology, is rather more limited. Furthermore, in intensive production systems retained information may be of limited value to the animal since animals do not have the freedom of choice. There are rather more studies that suggest that animals in extensive ecosystems use stored information and rapidly modify their behaviour in response to changing conditions once the memory bank has been updated (see Packard *et al.*, 1990). This perhaps suggests that the grazing behaviour of intensively farmed animals reflects the environment that they have evolved in. Differences between animal species in foraging behaviour in response to selection pressures arising from environmental adaptation as well as feeding niche have already been documented with the reports of Grant *et al.* (1985) and Schwartz and Ellis (1981).

There was a lack of clear evidence that sward height alone was responsible for the reluctance to graze T1 (misses n=21 (88 %)) relative to T2 (misses n=11 (46 %)) and T4 (misses n=5 (21 %)) since the contrast in sward height between these three treatments was marginal. The proportion of ryegrass leaf in the sward of T1 was lower than that for T2 and T4 but it is difficult to conceptualise how animals might have recognised and sensed the variation in leaf content without prior ingestion. As with the study of Illius *et al.* (1992) using grass/clover combinations in a paired choice study in a laboratory-based setting, animals exploited the taller patches. This provides supporting evidence that patch selection was strongly influenced by tactile cues, as patch value could only be reinforced by bite selection.

The balancing of patch combinations within and across strips allowed for the magnitude of the potential carry-over effects to be identified. For animals to demonstrate that they calculate when the reward rate within a patch falls below the alternative patches, a critical assumption of optimality theory (Charnov, 1976), one would expect animals to constantly monitor behaviour with past foraging experiences and conditions of forthcoming patches within the perceptive field to make informed decisions on the current patch. There was no strong evidence from this experiment to support the concept that the behaviour on any patch was influenced by the perception of conditions on the succeeding patch in sequence. The sequence and block combinations did not allow for a balanced design in terms of assessing preceding patch effects, but even so there were no strong trends to suggest that patch behaviour reflected the response to the last grazed patch, as suggested by Illius *et al.* (1992). Patch behaviour being independent of other patches in sequence also contrasts with the results of Distel *et al.* (1995) who found that patch behaviour was modified by the alternative patch. While the results from choice studies have been criticised as being highly context dependent (see Lawrence and Illius, 1997), all research falls into that category, and for this reason future research needs to focus on the understanding of the rationale behind the decisions in addition to monitoring patch choice. Greater emphasis was given to these effects in the studies reported in Chapter 5 when contrasts in sward structure and morphology were introduced. Further tests on the effects of adjacent patch conditions on behaviour at the current patch were also carried out in the experiments reported in Chapters 5 and 6.

4.6 CONCLUSION

The objective of this initial experiment was to test a field based methodology as a technique for quantifying discriminatory behaviour. The presentation of sward patches in a linear sequence increased the level of complexity the animal faced in terms of patch characteristics and presented opportunity to determine whether animals would ignore patches offering a low reward in order to concentrate grazing on patches offering a high reward. The procedures described were effective in defining behavioural patterns with a limited land area and number of animals. Animals adapted quickly to the procedures and grazed in a natural manner, without disturbance, over sequences of 27 patches. Sward height largely controlled variations in the depth of penetration and, combined with a slower rate of biting on taller swards, it can be predicted that the taller swards offered a greater rate of intake to which animals responded by increasing the number of grazing bites and residence time with increasing patch height. However, this could not be verified as the limited accuracy of estimates of the mass of herbage removed precluded calculation of rate of intake. Greater control of herbage mass and bulk density between patches would be essential for any assessment of the effect of bulk density on trade-off decisions. There was limited evidence to suggest that animals foraged in a manner in which they used information about the value of the forthcoming patch in sequence to determine the number of grazing bites or residence time on the current patch but further tests of these effects are required. Overall, the consistency in the observed patterns provides confidence in the procedures for monitoring the decisions animals made about alternative patch structures at the patch level.

FIVE

SWARD STRUCTURE and MORPHOLOGY

Experiment 2	Foraging behaviour responses to choices that differ in structural composition.
Experiment 3	Selective response to differences in sward maturity and the role of leaf mass in the decision hierarchy.
Experiment 4	Separation of the effects of structural parameters, sward height and maturity, on foraging decisions.

5.1 INTRODUCTION

Animals are sensitive to the ease with which they can harvest and manipulate ('handling') herbage in preparation for swallowing (Vincent, 1983; Black and Kenney, 1984). They also exercise a pattern of grazing in which the spatial arrangement of the leaf and stem fractions, within and between strata, influences the number and size of potential bites (Ungar *et al.*, 1992) and patch duration. The preference for taller swards in the vegetative phase of growth raises the question of whether similar behavioural patterns will be as profound when maturity is added to the complexity of choice. It therefore is hypothesised that vision alone may not be a primary factor in assessing sward conditions, and handling cues will provide a more reliable assessment of patch value. In this sense, green leaf mass and the depth of the leafy stratum may provide a better description of animal appraisal of sward conditions than sward height (Hodgson *et al.*, 1994), particularly if swards are not of open-sparse structure which permits the lower strata to be grazed preferentially (L'Huillier *et al.*, 1984).

Under these circumstances the consideration of sward height and bulk density alone, as a necessity for calculation of bite mass, may not suffice. Increasing plant age also means that animals are continually faced with the need to balance the trade-off between height, ease of eating and intake rate ie. quantity versus quality. On high mass swards nutrient intake can be maintained by either consuming more total dry matter, which will increase handling time and may also be constrained by grazing time, or selectively grazing the leaf with the latter being a difficult task for cattle. However, one disappointing aspect to date has been the lack of emphasis on manipulating swards in the field as a means of providing choices with pre-determined strata rather than the more favoured contrast of whole sward vegetative and reproductive choices. In the absence of more detailed information on bite location, together with the spatial distribution of components within and between strata, observations of discriminatory behaviour are left open to interpretation.

The results from Experiment 1 suggested very clearly that the developed patch methodology was effective in defining behaviour patterns at the patch level with a limited number of animals and provided scope for adequate control over growing conditions. The main objective of the series of three experiments described in the present chapter was to investigate the association between the effects of sward height and structure on cattle grazing preferences. Experiment 2 was set up to assess the behaviour of cattle in response to variations in maturity. Maturity contrasts were achieved by varying the depth of regrowth perched on differing heights of stubble material at identical and differing sward heights. In Experiment 3, the objective was to separate the influences of sward height and green leaf mass, which was achieved through sward choices which varied in total DM allowance and green DM allowance, across two sward heights. In this study animals preferentially grazed the shorter, leafier sward over the taller and more mature sward. This indicated that the earlier finding of a 'height–preference' relationship on vegetative swards (Experiment 1) was no longer the simple rule. Therefore Experiment 4 focussed on the contrast between sward height and maturity, particularly the opportunity for trade-off decisions between these variables.

In all three experiments, the effects of the characteristics of adjacent patches were tested. Estimates of shear strength or force to fracture were recorded, and in Experiment 4 stratified sampling of the vertical distribution of the sward canopy was undertaken. Also in Experiment 4, the direct estimates of herbage mass were regressed on the capacitance probe and sward height readings in an attempt to provide a more reliable estimate of herbage removed than had been achieved in the earlier studies.

Experiment 2 Foraging behaviour responses to choices that differ in structural composition

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5.2 PATCH TREATMENTS and MANIPULATION

Experiment 2 was conducted over April to June 1995 using 2 sequences, each with 3 replicate blocks of sets of 9 treatment combinations, derived from 4 stubble heights and 3 sward heights. Six of the 9 treatments were classified as non-trimmed ('no-trim') and 3 as trimmed ('trim') as a measure of trimming effects on behavioural responses. Thus treatment pairs 2 and 3; 5 and 6; 8 and 9 were of identical structure but the second treatment of each pair was left untrimmed so that in effect the trim and no-trim treatments were arbitrarily allocated to the same height but actually differed by the depth of extra regrowth (Table 5.1). The three groups of sward height, 8 cm (T1-T3), 12 cm (T4-T6) and 16 cm (T7-T9) were balanced across sequences so that each arbitrary sward height group followed each other with equal frequency.

Patches were of approximate dimensions 0.90 m x 0.90 m. Patch contrasts were created by mowing with a rotary mower to 4 nominal stubble heights (4, 8, 12 and 16 cm) at 10 day intervals over a period of 30 days. A regrowth period of 22 days followed for the 'no-trim' treatments, and 5 days prior to the grazing observations the final trim of the 'trim' swards to their arbitrary sward heights (8, 12 and 16 cm) was carried out

Table 5.1 Treatment structure for Experiment 2.

	Arbitrary Sward height (cm)		
Stubble height (cm)	8	12	16
4	Treatment 1		
8	Treatments 2^T	Treatment 3, 4	
12		Treatments 5^T	Treatment 6, 7
16			Treatments 8^T, 9

T = trimmed prior to grazing observations

5.3 SUMMARISED SWARD MEASUREMENTS

Table 5.2 Summarised sward measurements for Experiment 2.

Measurement	Particulars
Sward height	10 readings pre and post graze.
Herbage mass	Direct estimates of pregraze mass were made by cutting herbage enclosed within a $0.1m^2$ quadrat removed to approximately 2 cm, using an electric handpiece. No estimate of postgraze mass was undertaken.
Botanical composition	Samples for each treatment combination were bulked across blocks within sequences, sub-sampled and dissected into the components, ryegrass leaf, ryegrass pseudostem, other species leaf and pseudostem, weed and dead material.
Nutritive value (whole sward)	Within each sequence and block, samples were bulked according to the 3 nominal sward height groups ie. T1-T3 formed sward height group 1, T4-T6 formed sward height group 2 and T7-T9 formed sward height group 3, and nutritional parameters assessed using NIRS.
Strength properties	Shear strength measured using the Warner Bratzler meat shear-test apparatus.

For further details on measurement of sward height refer to section 3.3.1, herbage mass refer to section 3.3.2 and botanical composition refer to section 3.3.3 under "General sward measurements". For details on measurement of strength properties refer to section 5.3.1 below.

5.3.1 Shear strength

Two samples of 5 tillers each were collected from the centre section for each set of patches and assessed in the laboratory using a Warner Bratzler meat shear-test apparatus (Wright and Vincent, 1996). Approximate actual sward heights were used to gauge the height for tillers to be severed. The "regrowth" and "non-trimmed" swards were treated in a similar manner with one measurement made at the midpoint of the regrowth stratum. The stubble stratum was divided into thirds and 2 measurements made, the exception being treatment 1 where there was only 1 measurement in each of the strata due to the shorter sward height. For the "trimmed" swards, which actually comprised regrowth, no measurements were made in the regrowth stratum. Instead measurements were made at the corresponding point to the midpoint of the regrowth stratum on the "regrowth" swards within each of the 3 groups of final heights. The stubble stratum was treated in the same manner as the "regrowth" and "trimmed" swards. Measurements were therefore made for treatment 1 at 2 cm and 6 cm, treatment 2 at 4 cm and 7 cm, treatment 3 at 2 cm, 5 cm and 11 cm, treatment 4 at 2 cm, 5 cm and 10 cm, treatment 5 at 4 cm, 8 cm and 10 cm, treatment 6 at 4 cm, 8 cm and 15 cm, treatment 7 at 4 cm, 8 cm and 14 cm, treatment 8 at 5 cm, 11 cm and 14 cm, and treatment 9 at 5 cm, 11 cm and 18 cm (Figure 5.1).

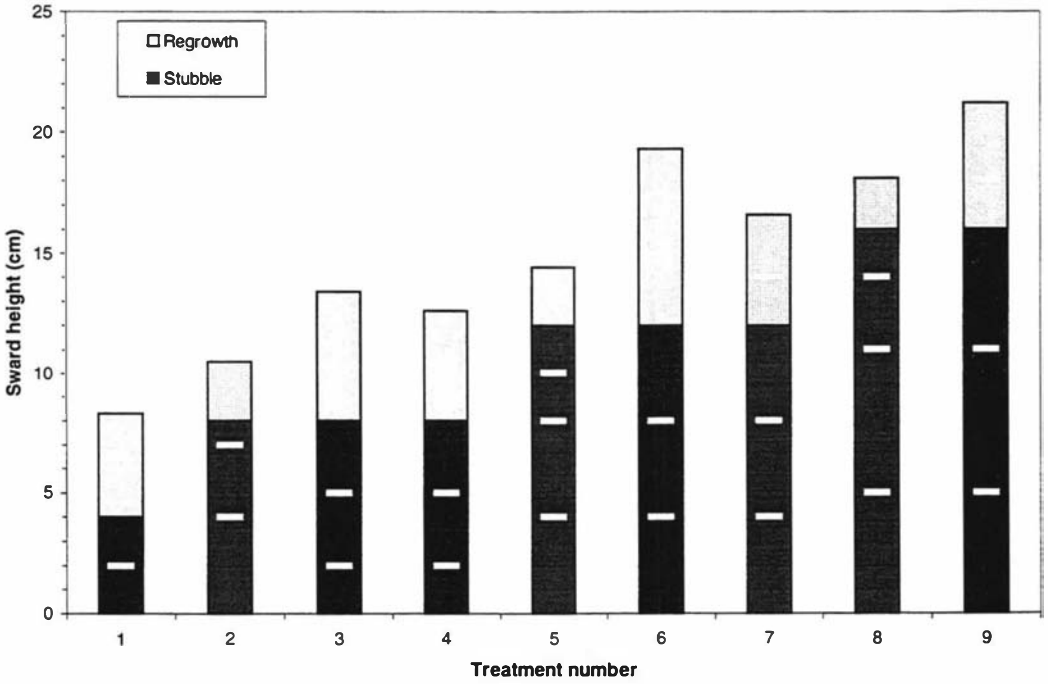

Figure 5.1 Division of strata for estimates of shear strength for Experiment 2. Measurements based on actual heights (white lines represent measurement height).

5.4 RESULTS

5.4.1 Treatment contrasts

The treatment contrasts that resulted from the manipulation procedures were not as planned (Table 5.1), with T2, T5 and T8 comprising regrowth perched on top of the stubble (Figure 5.2). As a result, the data was modelled as nominal sward height and nominal stubble height where T1-T3, T4-T6 and T7-T9 represented the 3 levels of sward height whilst stubble height was grouped according to the regrowth type. T1, T4, T7 represented the 'regrowth swards', T2, T5, T8 represented the 'trimmed swards' and T3, T6, T9 represented the 'extra regrowth swards' (Figure 5.2, Model 1). Using this base model no account was taken of the trimming regime as specified.

$$\text{Model} = \text{Sward height}|\text{Stubble height} \qquad (1)$$

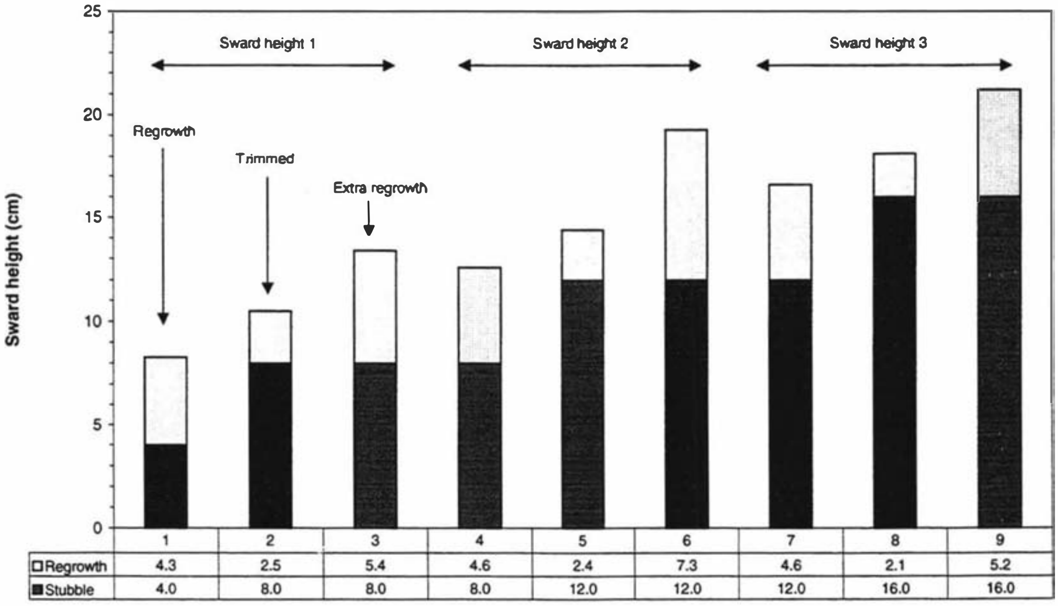

Figure 5.2 Actual regrowth depths (cm), stubble heights (cm) and sward heights (cm) for the 9 treatments in Experiment 2.

The depth of regrowth across treatment height groups followed a pattern, as would be expected under the circumstances, with mean values of 4.5 cm on 'regrowth swards', 2.4 cm on 'trimmed swards' and 6.0 cm on the 'extra regrowth swards' (Table 5.3).

Table 5.3 Mean values for stubble height, regrowth depth, sward height, pregraze mass and bulk density for the 9 treatments in Experiment 2.

Treatment	Stubble height (cm)	Regrowth depth (cm)	Sward height (cm)	Pregraze mass (g DM m^{-2})	Bulk density (mg DM cm^{-3})
1	4.0	4.3	8.3	51.5	0.62
2	8.0	2.5	10.5	124.2	1.19
3	8.0	5.4	13.4	149.8	1.12
4	8.0	4.6	12.6	145.0	1.17
5	12.0	2.4	14.4	199.8	1.39
6	12.0	7.3	19.3	232.5	1.21
7	12.0	4.6	16.6	217.7	1.33
8	16.0	2.2	18.2	249.7	1.38
9	16.0	5.2	21.2	259.0	1.23
sed		0.47	0.47	10.60	0.108
P value : Sward height[†]		0.0119	0.0001	0.0001	0.0001
P value : Stubble height[†]		0.0001	0.0001	0.0001	0.0003
P value : Sward height x Stubble height[†]		0.0092	0.0092	0.0027	0.0032

[†] Nominal treatment effects

Probability values for the effects of sward height and stubble height are given in sequential order of fitting and derived from analysis using Model 1.

Across the levels of sward height, regrowth depth was greater on T4-T6 than on either of the other two groups of sward height (4.1 cm for T1-T3, 4.8 cm for T4-T6, 4.0 cm for T7-T9). Sward height was confounded with stubble height (r = 0.89) as taller stubble heights gave rise to greater sward heights (Table 5.3 and Figure 5.2).

Nominal treatment sward height was the dominant factor influencing pregraze mass (Table 5.3) with mass increasing from 108.5 to 192.4 to 242.1 g DM m^2 across the 3 groups of sward height. The influence of stubble height on pregraze mass most likely reflected the height and the greater density of the stubble component. The dominant effect on bulk density was nominal sward height (Table 5.3), with bulk density increasing across the 3 sward height groups (0.98, 1.25 and 1.31 mg DM cm^{-3}).

There were no significant nominal treatment effects on the percentage of ryegrass leaf, ryegrass pseudostem, other grass leaf and pseudostem, weed or dead matter, across the 9 treatments at the 5 % significance level (Table 5.4). At the 10 % level of significance, nominal sward height influenced the proportion of other grass and the nominal stubble height influenced the percentage of dead matter but the latter effect was largely influenced by the value recorded for T1. There was a strong trend for ryegrass leaf, ryegrass pseudostem and weed content to increase with sward height and other grass leaf and pseudostem to decline with sward height but these effects did not attain significance, with power limited by the number of samples gathered (n=2).

Shear strength in the upper stratum, across treatments, was negatively affected by the nominal stubble height which reflected the depth of regrowth (Table 5.5). Greater values were recorded for T2, T5 and T8, reflecting the fact that these values were taken from the stubble fraction. The height of the stubble fraction had only a marginal effect on the strength of the middle stratum but more strongly influenced the lower stratum, with the significance reflecting the difference in shear strength between the stubble of the regrowth and trimmed swards. Within treatments there was a distinct pattern of increasing strength of herbage down the vertical profile (Table 5.5). Greater contrasts occurred between regrowth material and stubble material than within stubble material (mean regrowth = 29.9 N, mean upper stubble = 62.9 N, mean lower stubble = 74.9 N).

Nominal sward height had a significant effect on crude protein content and strong significant effects on lipid content, acid detergent fibre, neutral detergent fibre, carbohydrate content, organic matter digestibility and metabolisable energy content (Table 5.6). The strong significance arises from the values recorded for T1-T3 compared with those for T4-T9.

Table 5.4 Mean values for botanical composition (% DM) for the 9 treatments in Experiment 2.

Treatment	Ryegrass leaf	Ryegrass pseudostem	Other grass (leaf and pseudostem)	Weed	Dead
1	49.6	13.1	28.1	1.0	8.3
2	28.2	11.4	40.1	2.3	18.1
3	32.2	9.7	40.2	0.2	17.9
4	39.6	10.5	31.9	0.9	17.3
5	39.0	12.2	22.8	3.3	22.9
6	39.1	15.1	25.9	0.0	20.0
7	44.8	14.1	22.7	1.5	17.0
8	43.4	13.8	19.1	1.8	22.0
9	43.7	15.1	19.3	2.6	19.5
sed	6.04	2.80	10.18	1.85	4.59
P value : Sward height†	0.1656	0.2504	0.0749	0.7448	0.1500
P value : Stubble height†	0.1173	0.8633	0.9799	0.3541	0.0785
P value : Sward height x Stubble height†	0.1665	0.4370	0.6095	0.6413	0.8043

†Nominal treatment effects

Probability values for the effects of sward height and stubble height are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.5 Mean values for the force (Newtons) required to sever herbage samples at specified positions within the sward profile for the 9 treatments in Experiment 2. Values given in parenthesis represent the sampling height above ground level, refer to Figure 5.1.

Treatment	Stubble height (cm)	Regrowth depth (cm)	Sward height (cm)	Upper stratum (N)	Middle stratum (N)	Lower stratum (N)
1	4.0	4.3	8.3	31.9 (6 cm)	48.4 (2 cm)	N/A
2	8.0	2.5	10.5	48.1 (7 cm)	59.4 (4 cm)	N/A
3	8.0	5.4	13.4	28.9 (11 cm)	66.0 (5 cm)	76.9 (2 cm)
4	8.0	4.6	12.6	36.7 (10 cm)	55.8 (5 cm)	57.7 (2 cm)
5	12.0	2.4	14.4	56.1 (10 cm)	73.2 (8 cm)	80.4 (4 cm)
6	12.0	7.3	19.3	26.5 (15 cm)	65.4 (8 cm)	76.8 (4 cm)
7	12.0	4.6	16.6	33.3 (14 cm)	65.6 (8 cm)	71.9 (4 cm)
8	16.0	2.2	18.2	60.1 (14 cm)	68.7 (11 cm)	82.8 (5 cm)
9	16.0	5.2	21.2	22.9 (18 cm)	63.4 (11 cm)	74.7 (5 cm)
sed				6.03	7.48	7.24
P value : Sward height†				0.5966	0.1489	0.4588
P value : Stubble height†				0.0001	0.0474	0.0089
P value : Sward height x Stubble height†				0.3292	0.3101	0.2779

†Nominal treatment effects

Probability values for the effects of sward height and stubble height are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.6 Mean values for the content (% DM) of crude protein (CP), lipid, acid detergent fibre (ADF), neutral detergent fibre (NDF), carbohydrates-soluble sugars and starch (CHO), ash, organic matter digestibility (OMD), and metabolisable energy (ME) (MJ ME/kg DM), as determined by Near Infrared Reflectance Spectroscopy (NIRS) for the three sward height groups in Experiment 2.

Treatment	CP	Lipid	ADF	NDF	CHO	Ash	OMD	ME
T1-T3	19.4	3.6	26.5	44.9	8.0	12.4	80.7	12.0
T4-T6	17.4	3.4	29.1	48.3	6.7	12.7	77.4	11.6
T7-T9	17.0	3.3	28.7	48.6	6.9	12.2	77.9	11.6
sed	0.80	0.08	0.73	0.82	0.22	0.19	0.64	0.10
P value : Sward height†	0.0289	0.0088	0.0098	0.0017	0.0004	0.0548	0.0009	0.0015

†Nominal treatment effect

Table 5.7 Mean values for bite number, residence time and bite rate for the 9 treatments in Experiment 2.

Treatment	Stubble height (cm)	Regrowth depth (cm)	Sward height (cm)	Bite number	Residence time (sec)	Bite rate (bites min^{-1})
1	4.0	4.3	8.3	1.1	1.3	45.5
2	8.0	2.5	10.5	13.8	10.8	72.0
3	8.0	5.4	13.4	20.3	17.1	71.6
4	8.0	4.6	12.6	27.1	23.3	68.1
5	12.0	2.4	14.4	25.7	22.4	65.6
6	12.0	7.3	19.3	35.3	32.5	65.7
7	12.0	4.6	16.6	27.8	25.1	66.3
8	16.0	2.2	18.2	32.3	31.7	61.1
9	16.0	5.2	21.2	36.3	33.9	64.0
sed				3.41	3.09	4.17
P value : Linear effect of sward height				0.0001	0.0001	0.0043
P value : Quadratic effect of sward height				0.0024	0.0176	n/a
P value : Linear effect of regrowth depth				0.9616	0.6053	0.0326
P value : Nominal sward height				0.0412	0.0475	0.5490
P value : Nominal stubble height				0.7125	0.9751	0.4425
P value : Nominal sward height x stubble height				0.1175	0.1551	0.8852

Probability values for the effects of sward height, regrowth depth and stubble height are given in sequential order of fitting and derived from analysis using Models 4 and 5.
n/a term not used in the model, for further information refer to the text

5.4.2 Bite number and residence time

Bite number ranged from 1.1 to 36.3 bites with means of 11.7, 29.4 and 32.1 over the 3 sward height groups and means of 18.6, 23.9 and 30.6 bites over the stubble height groups (Table 5.7). Number of bites was initially modelled as nominal sward height and nominal stubble height (refer to 5.4.1 first paragraph) taking into account modifications for the variations in regrowth that occurred (Model 1). The analysis of variance showed strong significant effects of nominal sward height and nominal stubble height on bite number (Table 5.8). There was also evidence of a minor significant interaction between nominal sward height and stubble height.

Table 5.8 Extract from the analysis of variance output for bite number using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Sward height†	2	8797.39	4398.69	59.45	0.0001
Stubble height†	2	2592.06	1296.03	17.52	0.0001
Sward height x stubble height†	4	780.39	195.10	2.64	0.0480

†Nominal treatment effects

As a means of improving Model 1, sward height as a continuous variable was fitted, testing for a linear relationship between sward height and bite number, before the nominal treatment effects (Model 2).

$$\text{Model} = \text{Sward height}^{\dagger}\ \text{Sward height}|\text{Stubble height} \qquad (2)$$

†Linear effect of sward height

The output from the analysis of variance for Model 2 showed that the addition of a linear effect of sward height removed a substantial proportion of nominal sward height sum of squares as well as the majority of the sum of squares associated with nominal stubble height (Table 5.9), which reflected the confounding effect of sward height and stubble height in the sense that taller swards comprised taller stubbles. The use of Model 2 had little effect on the small but significant sward height x stubble height interaction.

Table 5.9 Extract from the analysis of variance output for bite number using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	10618.94	10618.94	153.73	0.0001
Nominal sward height	2	909.60	454.80	6.58	0.0034
Nominal stubble height	2	80.25	40.12	0.58	0.5640
Nominal sward height x stubble height	4	777.89	194.47	2.82	0.0378

Although there was a strong linear relationship between sward height and bite number, the additional significant nominal sward height effect indicated some deviation from linearity. Figure 5.3 illustrates a stronger relationship for T1-T3 than for T4-T6 or T7-T9, a reflection of a large number of patches recording less than 6 bites. A quadratic term, continuous sward height squared, was fitted after the linear effect of sward height but before the nominal treatment effects (Model 3) to test whether a curvilinear fit was appropriate.

$$\text{Model} = \text{Sward height}^{\dagger}\ (\text{Sward height})^{2\ddagger}\ \text{Sward height}|\text{Stubble height} \qquad (3)$$

†Linear effect of sward height ‡Quadratic effect of sward height

The analysis of variance output for Model 3 (Table 5.10) demonstrated a significant curvilinear relationship between bite number and sward height, with no intrinsically important effects of nominal sward height or stubble height.

Table 5.10 Extract from the analysis of variance output for bite number using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	10618.94	10618.94	152.44	0.0001
Quadratic effect of sward height	1	732.46	732.46	10.51	0.0024
Nominal sward height	2	472.20	236.10	3.39	0.0437
Nominal stubble height	2	19.15	9.57	0.14	0.8720
Nominal sward height x stubble height	4	549.19	137.30	1.97	0.1175

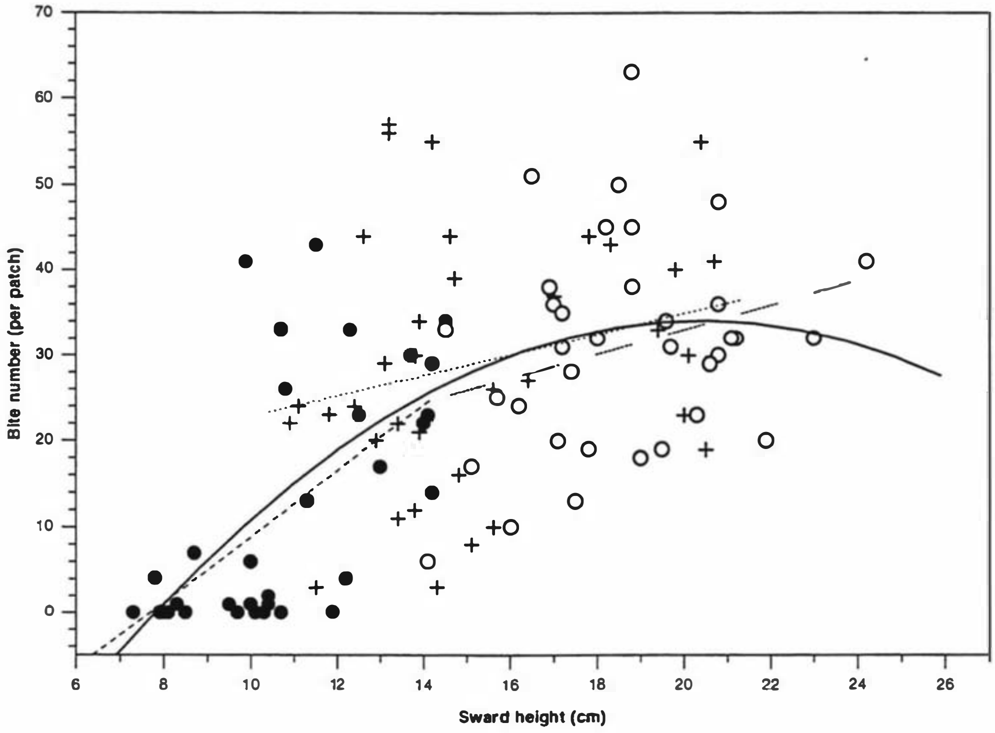

Figure 5.3 Relationship between bite number and sward height for T1-T3 (●), T4-T6 (+) and T7-T9 (O) and linear fits for T1-T3 (– – –), T4-T6 (·······), T7-T9 (···· ····) and a curvilinear, quadratic, fit for T1-T9 (——). Plotted data includes patches where there were no prehended bites and matches the output from the analysis of variance.

An alternative model (Model 4) which fitted regrowth depth as a linear effect after the linear and quadratic sward height effects but before nominal sward height and stubble height effects, was tested to answer the question "Do foraging animals select herbage by using sward height as their cue or does the vertical structure of plant material influence their decisions?"

$$\text{Model} = \text{Sward height}^{\dagger}\ (\text{Sward height})^{2\ddagger}\ \text{Regrowth depth}^{\dagger}\ \text{Sward height}|\text{Stubble height} \qquad (4)$$

†Linear effect of sward height and regrowth depth ‡Quadratic effect of sward height

The fitting of linear regrowth depth was synonymous with fitting a linear stubble height effect since sward height was the sum of the regrowth and stubble fractions, such that fitting any two of these three parameters in the model would result in the same residual sum of squares. There was no linear relationship between bite number and regrowth depth in the main analysis of variance output, and when the order of fit was reversed, the linear regrowth depth effect was relatively small compared to the more dominant effect of linear sward height (Table 5.11). The number of bites removed per patch was therefore strongly related to the height of the patch.

Table 5.11 Extract from the analysis of variance output for bite number using Model 4.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	10618.94	10618.94	152.44	0.0001
Quadratic effect of sward height	1	732.46	732.46	10.51	0.0024
Linear effect of regrowth depth	1	0.16	0.16	0.00	0.9616
Nominal sward height	2	481.58	240.79	3.46	0.0412
Nominal stubble height	1	9.60	9.60	0.14	0.7125
Nominal sward height x stubble height	4	549.19	137.30	1.97	0.1175
Reverse fit					
Linear effect of regrowth depth	1	1078.32	1078.32	15.48	0.0003
Linear effect of sward height	1	9606.47	9606.47	137.91	0.0001
Quadratic effect of sward height	1	666.76	666.76	9.57	0.0036

As in Experiment 1 there was a strong positive correlation between bites removed and residence time (r = 0.99). Further results will be presented for bite number only as the patterns were considered representative of the data for patch residence time. There was no evidence for the influence of nutritive value on bite number.

5.4.3 Bite rate

Model 1 was initially used to test for the influence of nominal treatment effects on bite rate. There were no significant effects of nominal sward height or nominal stubble height on bite rate across treatments. There was however a significant interaction between nominal sward height and stubble height (Table 5.12). From Table 5.7, the comparison between means suggests that the greater contrast in mean values for T1-T3, particularly the value for T1, was the likely cause of the significant interaction. Applying Model 2 had no effect on the significance of a linear relationship between sward height and bite rate (F=0.04, P=0.8445) or on the separate nominal treatment effects. The interaction between nominal sward height and stubble height remained significant as in Model 1. However, fitting Model 3 showed a significant curvilinear relationship between sward height and bite rate (Table 5.13). A plot suggested that 5 extreme outliers (3 assigned to T1, 1 each to T4 and T5) would be obscuring any probable linear relationship. Subsequent removal of these outliers indicated a negative relationship between sward height and bite rate ($r^2 = 0.32$).

Table 5.12 Extract from the analysis of variance output for bite rate using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Sward height†	2	156.61	78.30	0.78	0.4649
Stubble height†	2	113.88	56.94	0.57	0.5712
Sward height x stubble height†	4	2634.91	658.73	6.57	0.0004

†Nominal treatment effects

Table 5.13 Extract from the analysis of variance output for bite rate using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	4.06	4.06	0.04	0.8440
Quadratic effect of sward height	1	772.16	772.16	7.45	0.0095
Nominal sward height	2	427.32	213.66	2.06	0.1411
Nominal stubble height	2	22.78	11.39	0.11	0.8962
Nominal sward height x stubble height	4	1721.21	430.30	4.15	0.0069

Running the analysis excluding T1 showed that nominal sward height had a significant effect on rate of biting and the interaction was no longer significant (Table 5.14). This supports the earlier analysis that T1 was the primary source of the interaction. Fitting a linear sward height regression by using Model 2 confirmed that variations in rate of biting were explained by variations in sward height (Table 5.15).

Table 5.14 Extract from the analysis of variance output, excluding T1, for bite rate using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Sward height†	2	633.89	316.94	6.70	0.0034
Stubble height†	2	183.10	91.55	1.93	0.1596
Sward height x stubble height†	4	35.08	11.69	0.25	0.8628

†Nominal treatment effects

Table 5.15 Extract from the analysis of variance output, excluding T1, for bite rate using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	480.62	480.62	9.34	0.0043
Nominal sward height	2	196.45	98.22	1.91	0.1634
Nominal stubble height	2	152.10	76.05	1.48	0.2420
Nominal sward height x stubble height	3	33.21	11.07	0.22	0.8852

An alternative model (Model 5) fitted linear regression effects of sward height and regrowth depth (in that order), where regrowth depth was synonymous with stubble height, before nominal treatment effects. The output from the analysis of variance indicated significant linear relationships between sward height and rate of biting as well as regrowth depth and rate of biting (Table 5.16). However, reversing the order of the fit of linear regression effects so that regrowth depth was followed by sward height suggested that the rate of biting was determined only by the height of the sward (Table 5.16).

$$\text{Model} = \text{Sward height}^{\dagger}\ \text{Regrowth depth}^{\dagger}\ \text{Sward height}|\text{Stubble height} \qquad (5)$$

†Linear effect of sward height and regrowth depth

Table 5.16 Extract from the analysis of variance output, excluding T1, for bite rate using Model 5.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	480.62	480.62	9.34	0.0043
Linear effect of regrowth depth	1	254.71	254.71	4.95	0.0326
Nominal sward height	2	62.78	31.39	0.61	0.5490
Nominal stubble height	1	31.05	31.05	0.60	0.4425
Nominal sward height x stubble height	3	33.21	11.07	0.22	0.8852
Reverse fit					
Linear effect of regrowth depth	1	21.63	21.63	0.42	0.5210
Linear effect of sward height	1	713.70	713.70	13.87	0.0007

Table 5.17 Mean values for bite depth and bite depth/sward height for the 9 treatments in Experiment 2.

Treatment	Stubble height (cm)	Regrowth depth (cm)	Sward height (cm)	Bite depth (cm)	Bite depth / Sward height (%)
1	4.0	4.3	8.3	3.7	44.4
2	8.0	2.5	10.5	5.1	47.8
3	8.0	5.4	13.4	6.6	48.3
4	8.0	4.6	12.6	5.7	45.4
5	12.0	2.4	14.4	6.6	45.9
6	12.0	7.3	19.3	10.6	55.0
7	12.0	4.6	16.6	8.2	49.5
8	16.0	2.2	18.2	8.3	45.5
9	16.0	5.2	21.2	10.4	49.4
sed				0.35^{β}-0.85^{α}	2.33^{β}-5.71^{α}
P value : Linear effect of sward height				0.0001	0.0011
P value : Linear effect of regrowth depth				0.0001	n/a
P value : Nominal sward height				0.3793	0.0072
P value : Nominal stubble height				0.5558	0.0597
P value : Nominal sward height x stubble height				0.2348	0.3184

α n=2, β n=12
n/a term not used in the model, for further information refer to the text
Probability values for the effects of sward height, regrowth depth and stubble height are given in sequential order of fitting and derived from analysis using Models 2 and 5.

5.4.4 Bite depth

Bite depth was computed from patches where three or more bites were removed. The analysis of variance output from Model 1 showed significant effects of both nominal sward height and nominal stubble height and a small significant interaction between these effects on bite depth (Table 5.18). There was a significant linear relationship between sward height and bite depth, and though much smaller, the nominal treatment effects remained significant (Table 5.19). The addition of the quadratic term (Model 3) provided no evidence for a curvilinear relationship between sward height and bite depth (Table 5.20), and the nominal sward height and stubble height effects remained significant.

Table 5.18 Extract from the analysis of variance output for bite depth using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Sward height†	2	114.97	57.48	41.15	0.0001
Stubble height†	2	194.36	97.18	69.56	0.0001
Sward height x stubble height†	4	27.44	6.86	4.91	0.0030

†Nominal treatment effects

Table 5.19 Extract from the analysis of variance output for bite depth using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	357.48	357.48	504.91	0.0001
Nominal sward height	2	12.68	6.34	8.95	0.0007
Nominal stubble height	2	6.00	3.00	4.24	0.0225
Nominal sward height x stubble height	4	4.14	1.03	1.46	0.2348

Table 5.20 Extract from the analysis of variance output for bite depth using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	357.48	357.48	502.10	0.0001
Quadratic effect of sward height	1	0.00	0.00	0.00	0.9581
Nominal sward height	2	13.11	6.55	9.21	0.0006
Nominal stubble height	2	6.69	3.34	4.70	0.0156
Nominal sward height x stubble height	4	3.39	0.85	1.19	0.3326

Fitting Model 5, with linear regression effects of both sward height and regrowth depth (in that order), the output indicated strong significant effects of sward height with some minor but significant influences of regrowth depth on bite depth (Table 5.21). The addition of regrowth depth cancelled out the significant nominal treatment effects observed in the earlier models, confirming a linear and not a curvilinear relationship between sward height and bite depth. The separate effects of sward height and regrowth depth are evident from the data presented in Table 5.17 and Figure 5.4 where bite depth increases with increasing sward height across the sward height groups T1-T3, T4-T6 and T7-T9. For comparison across swards of equal stubble height (comparing T2-T4, T5-T7 and T8-T9), bite depth was always the greatest on the swards with deeper regrowths. Changing the order of the fit of sward height and regrowth depth so that sward height followed regrowth depth showed sward height was the dominant effect on bite depth (Table 5.21).

Table 5.21 Extract from the analysis of variance output for bite depth using Model 5.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	357.48	357.48	504.91	0.0001
Linear effect of regrowth depth	1	17.02	17.02	24.03	0.0001
Nominal sward height	2	1.41	0.71	1.00	0.3793
Nominal stubble height	1	0.25	0.25	0.35	0.5558
Nominal sward height x stubble height	4	4.14	1.03	1.46	0.2348
Reverse fit					
Linear effect of regrowth depth	1	125.93	125.93	177.86	0.0001
Linear effect of sward height	1	248.57	248.57	351.08	0.0001

Taking the analysis a stage further as a means of assisting with the explanation of Table 5.21, sward height was broken down into the separate effects of regrowth depth and stubble height. As the conventional nominal treatment effects were not significant in Model 5, another model (Model 6), which fitted linear effects of regrowth depth and stubble height was applied.

$$\text{Model} = \text{Regrowth depth}^{\dagger}\ \text{Stubble height}^{\dagger} \qquad (6)$$

†Linear effect of regrowth depth and stubble height

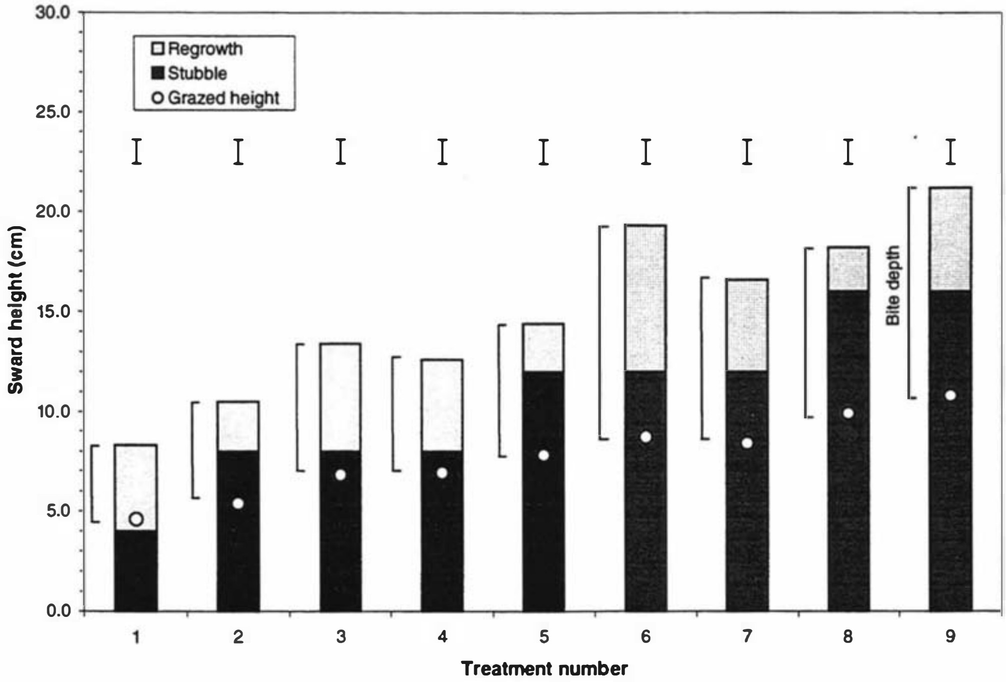

Figure 5.4 Grazed height relative to the interface between the regrowth and stubble strata (vertical bars represent sem).

The sums of squares output from the analysis of variance table using Model 6 (Table 5.22) is identical to the sums of squares for the effects presented for the reverse fit in Table 5.21. This reinforces the point that by fitting any two of the effects of sward height, regrowth depth and stubble height, it is possible to predict the third effect, since the sums of squares were identical regardless of which effect was fitted first. Table 5.22 shows that both regrowth depth and stubble height effects were significant. However, the combined sums of squares for both effects was only marginally greater (374.50 vs 357.48) than for sward height alone (Table 5.21), the difference being the 17.02 recorded as a linear effect of regrowth depth in Table 5.21. These results confirm that the bite depth patterns were largely a reflection of the variations in sward height.

Table 5.22 Extract from the analysis of variance output for bite depth using Model 6.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of regrowth depth	1	125.93	125.93	172.95	0.0001
Linear effect of stubble height	1	248.57	248.57	341.39	0.0001

Dropping the term treatment(sequence x block) from the model allowed for the calculation of the regression of bite depth on sward height (eqn 1):

$$\text{Bite depth (cm)} = -0.86 + 0.58 \pm 0.03(\text{sward height}) \quad r^2=0.84 \qquad \text{(eqn 1)}$$

Expressing bite depth as a function of sward height as the dependant variable, and fitting a linear effect of sward height before nominal treatment effects using Model 2, the analysis of variance output showed a significant linear effect of sward height (Table 5.23). This result indicated that there was no constant proportional relationship between sward height and bite depth, a result which is supported by the range of values (44 to 55 %) recorded in Table 5.17. Nonetheless, T6 had a higher regrowth depth over and above the generalised pattern of regrowth depth across sward heights. It also recorded a higher bite depth/sward height ratio. Subsequent removal of T6 from the analysis removed the significance of the nominal sward height term (P=0.2085) and decreased the significance of the linear effect of sward height to a marginal effect (P=0.0477). However, as the nominal sward height term can be confounded with other patch characteristics it is difficult to clarify with certainty whether T6 alone is the sole cause of the significance of the linear sward height term recorded in Table 5.23.

Table 5.23 Extract from the analysis of variance output for bite depth/sward height using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	414.74	414.74	12.58	0.0011
Nominal sward height	2	376.32	188.16	5.71	0.0072
Nominal stubble height	1	201.69	100.84	3.06	0.0597
Nominal sward height x stubble height	4	161.45	40.36	1.22	0.3184

5.4.5 Adjacent patch effects

The experiment was designed to test the effect of the sward height of the succeeding patch in sequence on the behaviour on the current patch. Two variations of Model 4, with the addition of either nominal sward height of the succeeding patch or a linear sward height effect of the succeeding next patch were tested. The analysis of variance output for the former model is shown in Table 5.24. For both models there was no effect of the adjacent patch sward height on the number of bites removed on the current patch.

Table 5.24 Extract from the analysis of variance output for the influence of the sward height of the succeeding patch in sequence on bites removed using Model 4 in Experiment 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	10871.22	1087.22	166.34	0.0001
Quadratic effect of sward height	1	755.79	755.79	11.38	0.0017
Linear effect of regrowth depth	1	5.82	5.82	0.09	0.7688
Nominal sward height	2	451.02	225.51	3.39	0.0435
Nominal stubble height	1	5.70	5.70	0.09	0.7712
Nominal sward height x stubble height	4	574.16	143.54	2.16	0.0911
†Next patch nominal sward height	1	61.61	61.61	0.93	0.3413

†Next = succeeding patch

Experiment 3 Selective response to differences in sward maturity and the role of leaf mass in the decision hierarchy

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5.5 PATCH TREATMENTS and MANIPULATION

Experiment 3 was conducted over the month December 1995 and involved the products of contrasting pregrazing management (short immature and tall mature patches), superimposed on contrasting patch areas. Sets of four treatment combinations structured from 2 sward heights and 2 patch areas were replicated over 6 blocks within each sequence, and 2 sequences were used. The choice of 4 treatments and 6 replicates allowed for exact balance of treatments across sequences with each pair occurring sequentially 4 times. The balancing of every treatment over the effect of the adjacent patch treatment made it possible to allocate the first and last patches to the same treatment and so the effects of the preceding and of the succeeding patch conditions could be tested. Patch area was adjusted at the end of the regrowth period after measurements from the centre section had been collected and estimates of green leaf mass and total dry mass were calculated (for procedures refer to Table 5.26). Patch area was adjusted for Treatments 2 and 4 so that in total there were 3 contrasts (Table 5.25). Treatments 1 and 4 were intended to provide similar quantities of total herbage per patch at contrasting structures whilst Treatments 2 and 3 were intended to balance the quantity of green herbage per patch given the expectation that the proportion of green herbage would be greater on immature than mature patches. In addition to this there was a third contrast between sward structures (1 and 2 vs 3 and 4).

Table 5.25 Treatment structure for Experiment 3

	Patch area	
Pregraze management	Standard	Adjusted
Short Immature	Treatment 1	Treatment 2
Tall Mature	Treatment 3	Treatment 4

Variations in sward structure (short immature and tall mature swards) were achieved through regular cutting with a rotary mower to either 5 cm or 14 cm at weekly intervals for 6 weeks. A 2 week regrowth period followed and was intended to provide similar depths of regrowth on mature and immature patches with the expectation that the position of the stubble interface might provide answers as to how this influenced grazing decisions. Half of the tall patches (Treatment 4) were reduced in area to 0.47 x 0.90 m to provide a quantity of herbage similar to that provided by the short patches with areas of 0.90 x 0.90 m (Treatment 1).

One week prior to the grazing observations a group of calves invaded the site and it was not feasible to set up contrasting patch areas in the short sward (Treatment 2). The rest of the designed structure was maintained. Two grazing sessions were held over two consecutive mornings, with each sequence grazed by the same cow for both grazing sessions. The objective of the second grazing was to assess whether cattle switched their preferences as the preferred patch type became depleted.

5.6 SUMMARISED SWARD MEASUREMENTS

Table 5.26 Summarised sward measurements for Experiment 3

Measurement	Particulars
Sward height	First grazing session: 15 readings, pre and postgraze, taken from random positions across each grazed patch to represent average sward height conditions. Second grazing session: 15 readings, postgraze, taken from random positions across each grazed patch to represent average sward height conditions.
Herbage mass	Estimates of pregraze mass were obtained by clipping the herbage enclosed within a 0.1m^2 quadrat to approximately 2 cm, using an electric handpiece. No estimate of postgraze mass was undertaken.
Botanical composition	Samples were bulked across blocks within sequences, sub-sampled and dissected into the components, ryegrass leaf and pseudostem, ryegrass reproductive stem, other species leaf and pseudostem, other species reproductive stem, weed and dead material.
Nutritive value (whole sward)	Samples were bulked across blocks within each sequence according to pregrazing management (short immature or tall mature) and nutritional parameters assessed using the Kjeldahl method and *in vitro* standards. As a useful cross-check, remaining dry material was bulked with short immature or tall mature contrasts within blocks and across sequences and nutritional parameters assessed using NIRS.
Strength properties	Shear strength measured using the Warner Bratzler meat shear-test apparatus.

For further details on measurement of sward height refer to section 3.3.1, herbage mass refer to section 3.3.2, botanical composition refer to section 3.3.3 and nutritive value refer to section 3.3.4 under "General sward measurements". For details on measurement of strength properties (shear strength) refer to section 5.6.1 below.

5.6.1 Shear strength

Two samples of 5 tillers each were collected from the centre section for each set of patches and assessed in the laboratory using a Warner Bratzler meat shear-test apparatus (Wright and Vincent, 1996). Approximate mean sward heights of 14 and 21 cm were used to gauge the height for tillers to be severed. Samples were divided into approximate thirds for convenience and 2 measurements taken (Figure 5.5), these being made at 4 cm increments for 14 cm swards (4 and 8 cm from the base) and 7 cm increments for 21 cm swards (7 and 14 cm from the base).

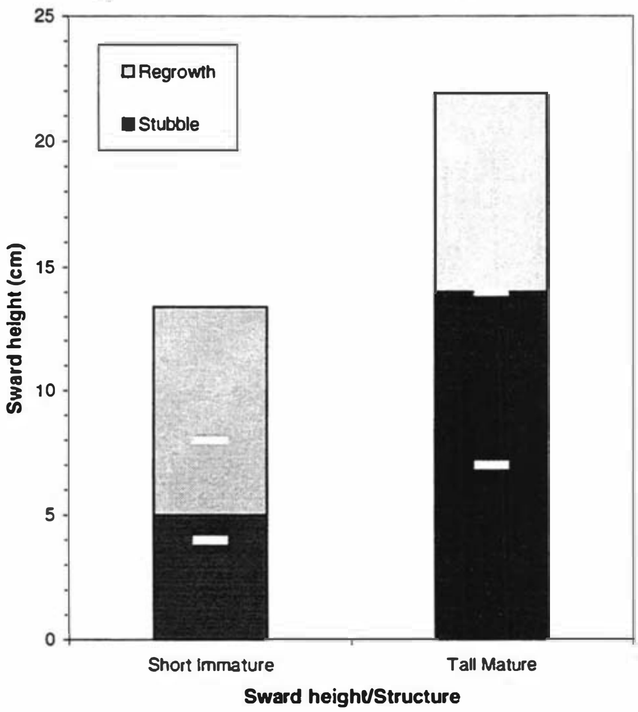

Figure 5.5 Division of strata for estimates of shear strength for Experiment 3 (white lines represent measurement height).

5.7 RESULTS

5.7.1 First grazing session

5.7.1.1 Treatment contrasts

The contrast between short immature [T1 and T2 combined] and tall mature [T3 and T4] was achieved successfully with mean values across sward height categories of 13.4 cm for short immature swards and 21.9 cm for tall mature swards (Table 5.27). After adjustment of patch area for Treatment 4, both T4 and [T1&T2] had similar quantities of herbage per patch (230 g DM per patch and 210 g DM per patch respectively). Patches assigned T3 had a greater quantity of herbage (388 g DM per patch) and the effect of patch area was significant for both sward height and herbage mass per patch for the comparison between T3 and T4 (Table 5.27). Nominal sward height was the dominant factor influencing bulk density (means 1.98 and 2.28 mg DM cm^{-3}) but there were also smaller positive effects of patch area on bulk density (means 2.04 and 2.41 mg DM cm^{-3}) (Table 5.27). However, the difference in bulk density between [T1 & T2] and T3 (a sward height contrast at a constant patch area) was not significant, indicating the strong sward height effect predominately arose from the higher value for T4.

The analysis of variance results testing for the effect of nominal sward height on botanical components were hampered by the small number of samples and only 1 df for the error term. As a consequence the analysis indicated that the effect of sward height did not influence any of the components across the two sward height categories (Table 5.28). Nevertheless, short immature swards comprised a greater percentage of ryegrass leaf (30.2 vs 21.8) and other grass leaf (16.5 vs 7.3) and lower percentages of ryegrass stem (13.7 vs 33.2) and other grass stem (4.9 vs 7.2) (Table 5.28). These values resulted in a higher leaf:stem ratio for the short immature swards (2.55 vs 0.75).

The shear strength of both the top third and middle third of the canopy was significantly greater for tall mature swards than for short immature swards (Table 5.29).

Table 5.27 Mean values for patch area, sward height, pregraze mass and bulk density for the 3 treatments in the first grazing session in Experiment 3.

Analysis	Treatment	Patch area (m^2)	Sward height (cm)	Pregraze Mass (g DM patch)	Pregraze Mass (g DM m^{-2})	Bulk Density (mg DM cm^{-3})
	1 & 2	0.80	13.4	210	265	1.98
	3	0.80	22.5	388	485	2.15
	4	0.45	21.2	230	510	2.41
Main analysis	sed		0.23^{ϕ}–0.32^{χ}	6.9^{ϕ}–9.8^{χ}	10.8^{ϕ}–15.3^{χ}	0.088^{ϕ}–0.125^{χ}
	P value : Sward height†		0.0001	0.0001	0.0001	0.0017
	P value : Patch area†		0.0002	0.0001	0.0979	0.0440
Treatment 3 & 4	sed		0.35^{χ}	9.4^{χ}	15.6^{χ}	0.082^{χ}
	P value : Patch area†		0.0027	0.0001	0.1090	0.0029

†Nominal treatment effects

χ n=24, ϕ n=48

Probability values for the effects of sward height and patch area are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.28 Mean values for botanical composition (% DM) for the two sward height groups in Experiment 3.

Treatment	Sward height (cm)	Ryegrass leaf	Ryegrass stem	Other grass leaf	Other grass stem	Weed	Dead
1&2	13.4	30.2	13.7	16.5	4.9	0.0	34.9
3&4	21.9	21.8	33.2	7.3	7.2	0.2	30.5
sed		3.10	3.35	1.15	0.65	0.15	2.20
P value : Sward height†		0.2251	0.1080	0.0787	0.1718	0.5000	0.2952

†Nominal treatment effect

Table 5.29 Mean values for the shear strength (Newtons) required to sever herbage samples at specified positions within the sward profile for the two sward height groups in Experiment 3.Values determined using the Warner Bratzler meat shear-test apparatus. Values given in parenthesis represent the sampling height above ground level, refer to Figure 5.5.

Treatment	Sward height (cm)	Top third (N)	Middle third (N)
1&2	13.4	55.1 (8 cm)	89.2 (4 cm)
3&4	21.9	96.5 (14 cm)	123.1 (7 cm)
sed		5.10	5.42
P value : Sward height†		0.0001	0.0001

†Nominal treatment effect

There were no significant differences between treatments in the values obtained for crude protein and organic matter digestibility (Table 5.30) from the samples analysed using the Kjeldahl method and *in vitro* standards, a result which in part may have reflected too few samples (n=2). As a cross check, a new set of samples were analysed using NIRS (n=12). The results of this analysis suggested a strong significant effect of nominal sward height on herbage nutritive value, with greater concentrations of crude protein, lipid and ash and lower concentrations of acid detergent fibre, neutral detergent fibre and carbohydrates recorded for short immature swards. The small differences in organic matter digestibility and metabolisable energy content did not attain significance. Crude protein percentage measured by the Kjeldahl method was slightly lower than that of NIRS, while the values for ash concentration and organic matter digestibility measured by the *in vitro* technique were much lower than those of NIRS (Table 5.30).

Table 5.30 Mean values for the content (% DM) of crude protein (CP) lipid, acid detergent fibre (ADF), neutral detergent fibre (NDF), carbohydrate – soluble sugars and starch (CHO), ash, organic matter digestibility (OMD), and metabolisable energy (ME) (MJ ME/kg DM), as determined by Near Infrared Reflectance Spectroscopy (NIRS) and on the content (% DM) of crude protein (CP) as determined by the Kjeldahl method and ash and organic matter digestibility (OMD), as determined using *in vitro* standards for the two sward height groups in Experiment 3.

Analysis Method	Treatment	CP	Lipid	ADF	NDF	CHO	Ash	OMD	ME
NIRS	1&2	12.9	3.1	30.5	54.5	7.9	9.0	75.6	11.3
	3&4	9.4	2.6	31.9	57.2	9.1	8.1	74.8	11.2
	sed	0.32	0.07	0.32	0.49	0.24	0.13	0.90	0.13
	P value : Sward height†	0.0001	0.0001	0.0005	0.0001	0.0002	0.0001	0.3766	0.3674
Kjeldahl method & *in vitro* standards	1&2	11.6	-	-	-	-	8.6	63.8	-
	3&4	8.0	-	-	-	-	6.9	61.7	-
	sed	0.36					0.005	0.82	
	P value : Sward height†	0.0638					0.0001	0.2340	

†Nominal treatment effect

Table 5.31 Mean values for bite number and residence time for the 3 treatments in the first grazing session in Experiment 3.

Analysis	Treatment	Patch area (m^2)	Sward height (cm)	Bite number		Residence time (sec)	
				patch	m^{-2}	patch	m^{-2}
	1&2	0.80	13.4	30.9	39.2	26.8	34.1
	3	0.80	22.5	5.7	7.2	6.5	8.1
	4	0.45	21.2	1.8	4.1	3.5	7.9
Main analysis	sed			1.82^{ϕ}– 2.58^{χ}	2.24^{ϕ}– 3.17^{χ}	1.60^{ϕ}– 2.26^{χ}	1.95^{ϕ}– 2.76^{χ}
	P value : Sward height†			0.0001	0.0001	0.0001	0.0001
	P value : Patch area†			0.1417	0.3382	0.1994	0.9189
Treatment 3 & 4	sed			1.19^{χ}	1.44^{χ}	1.07^{χ}	1.45^{χ}
	P value : Patch area†			0.0076	0.0559	0.0187	0.8489

†Nominal treatment effects

χ n=24, ϕ n=48

Probability values for the effects of sward height and patch area are given in sequential order of fitting and derived from analysis using Model 1.

5.7.1.2 Bite number, residence time and herbage removed

As a result of T1 and T2 being combined there was an imbalance in the factorialised experiment so the means are presented as 3 treatments and for main effects only. The initial analysis was conducted using a model of nominal sward height and nominal patch area (Model 1). Sward height fitted as a continuous variable after nominal treatment effects as a measure of within treatment variation was not significant for either bite number per patch (P=0.6489) or residence time per patch (P=0.7076).

$$\text{Treatment Model} = \text{Sward height}\ \ \text{Patch area} \qquad (1)$$

Using Model 1, there were strong negative effects of nominal sward height on bite number with mean bites of 30.9 recorded on short immature swards and 3.8 bites recorded on tall mature swards (Table 5.31 and Table 5.32). Within treatment sward height groups there was little evidence of a relationship between sward height and bite number, making it difficult to ascertain whether treatment differences were a result of the two chosen levels of sward height or due to the effect of contrasting vegetation structures. The dominant effect of treatment sward height appeared to override the effects of patch area between the tall mature sward choices and explained the lack of a significant effect of patch area on bite number. A separate analysis for the tall mature swards showed a significant effect of patch area on bites removed per patch (Table 5.31and Table 5.32).

Table 5.32 Extract from the analysis of variance output for bite number per patch in the first grazing session using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Main analysis					
Sward height†	1	17658.38	17658.38	221.84	0.0001
Patch area†	1	180.19	180.19	2.26	0.1417
Treatments 3 and 4					
Patch area†	1	180.19	180.19	10.62	0.0076

†Nominal treatment effects

When bite number was expressed as bites per unit area the effect of patch area was only marginally significant, indicating that the number of bites removed was in proportion to the size of the patch being grazed (Table 5.31). There was a very close relationship between bite number and patch residence time ($r= 0.99$) and further results are explained for bite number only.

It was not possible to relate the estimates of herbage mass removed from the patches with either capacitance probe readings taken from the centre section ($r= 0.00$ and $r= 0.04$ for short immature and tall mature swards respectively) or mean pregraze sward height from the grazed patches ($r= 0.05$ and $r= 0.00$ for short immature and tall mature swards respectively).

5.7.1.3 Bite rate

Rate of biting was analysed using Model 1 and the results of the analysis of variance showed strong negative effects of sward height, with faster bite rates recorded on short immature swards than on the tall mature swards. There was no effect of patch area on biting rate for the main analysis, or in a separate analysis of T3 and T4 (Table 5.33 and Table 5.34).

Table 5.33 Extract from the analysis of variance output for bite rate in the first grazing session using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Main analysis					
Sward height†	1	7544.22	7544.22	138.30	0.0001
Patch area†	1	207.54	207.54	3.80	0.0605
Treatments 3 and 4					
Patch area†	1	247.10	247.10	2.82	0.1318

†Nominal treatment effects

Table 5.34 Mean values for bite rate, bite depth and bite depth/sward height for the 3 treatments in the first grazing session in Experiment 3.

Analysis	Treatment	Patch area (m^2)	Sward height (cm)	Bite rate (bites min^{-1})	Bite depth (cm)	Bite depth / Sward height (%)
	1&2	0.80	13.4	69.2	4.7	34.8
	3	0.80	22.5	50.6	1.9	8.4
	4	0.45	21.2	45.5	1.4	6.3
Main analysis	sed			1.52^{δ}–3.15^{η}	0.28^{δ}– 0.72^{κ}	1.69^{δ}– 4.37^{κ}
	P value : Linear effect of sward height			-	0.0001	0.0001
	P value : Nominal sward height			0.0001	0.0001	0.0001
	P value : Nominal patch area			0.0605	0.6643	0.7892
Treatment 3 & 4	sed			3.04^{ε}– 4.00^{η}	1.00^{η}–1.26^{κ}	4.30^{η}–5.40^{κ}
	P value : Nominal patch area			0.1318	0.2951	0.3121

κ n=7, η n=11, ε n=19, δ n=47
Probability values for the effects of sward height and patch area are given in sequential order of fitting and derived from analysis using Model 1 and Model 2.

5.7.1.4 Bite depth

There was a strong negative effect of sward height on bite depth using Model 1 (Table 5.34 and Table 5.35). The mean change in sward height, postgrazing, was 4.7 cm for short immature swards and 1.7 cm for tall mature swards. The fitting of sward height as a continuous variable after nominal treatment effects showed there was greater variation in the relationship between sward height and bite depth on a within treatment basis (P=0.0002) than seen for bite number and bite rate. Subsequently Model 2, with the addition of a linear sward height regression effect fitted before nominal treatment effects, was used to analyse bite depth.

$$\text{Model} = \text{Sward height}^{\dagger}\ \ \text{Sward height}\ \ \text{Patch area} \qquad (2)$$

†Linear effect of sward height

The analysis of variance for this model (Model 2) supported the relationship between sward height and bite depth but additionally it showed a pattern of deviation from linearity (Table 5.36). As the experiment only involved comparison across two sward heights it was not possible to apply a quadratic term to the model. Nonetheless, the spread of the data and its aggregation into two groups suggested that the structural differences, a reflection of the manipulation procedures, probably contributed to the behavioural response exhibited. There was no significant effect of patch area on bite depth in either the main analysis or the separate analysis of T3 and T4 only (Table 5.36). On the short immature swards bite depth was approximately 35 % of sward height and for the tall mature sward the corresponding value was 7 %. The effect of patch area on bite depth as a proportion of height between T3 and T4 in a separate analysis did not attain significance (Table 5.34).

Table 5.35 Extract from the analysis of variance output for bite depth in the first grazing session using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Main analysis					
Sward height†	1	120.61	120.61	45.93	0.0001
Patch area†	1	0.78	0.78	0.30	0.5917
Treatments 3 and 4					
Patch area†	1	8.10	8.10	1.45	0.2951

†Nominal treatment effects

Table 5.36 Extract from the analysis of variance output for bite depth in the first grazing session using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Main analysis					
Linear effect of sward height	1	87.66	87.66	47.72	0.0001
Sward height[†]	1	67.91	67.91	36.97	0.0001
Patch area[†]	1	0.35	0.35	0.19	0.6643
Treatments 3 and 4					
Patch area[†]	1	8.1	8.1	1.45	0.2951

†Nominal treatment effects

5.7.1.5 Adjacent patch effects

There was no evidence that bites on the current patch were influenced by the sward height of the preceding patch nor that of the forthcoming patch in sequence. The results for the effect of succeeding patch sward height on bite number on the current patch are given in Table 5.37.

Table 5.37 Extract from the analysis of variance output for the influence of the sward height of the succeeding patch in sequence on bites removed per patch in the first grazing session using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Sward height[†]	1	18680.83	18680.83	192.30	0.0001
Patch area[†]	1	171.30	171.30	1.76	0.1978
[‡]Next patch sward height	1	35.57	35.57	0.58	0.5513

†Nominal treatment effects
‡Next = Succeeding patch

Table 5.38 Mean values for patch area, sward height, bite number, residence time and bite rate for the 3 treatments in the second grazing session in Experiment 3.

Analysis	Treatment	Patch area	Sward height	Bite number		Residence time (sec)		Bite rate (bites min^{-1})
		(m^2)	(cm)	patch	m^{-2}	patch	m^{-2}	
	1 & 2	0.80	8.8	18.6	23.3	15.8	19.8	71.8
	3	0.80	21.6	3.4	4.3	5.1	6.4	46.9
	4	0.45	20.8	1.0	2.3	2.7	5.9	40.3
Main analysis	sed		0.27^{ϕ}–0.38^{χ}	1.25^{ϕ}–1.77^{χ}	1.63^{ϕ}–5.32^{χ}	1.06^{ϕ}–1.49^{χ}	1.46^{ϕ}–2.06^{χ}	1.53^{λ}–3.02^{ν}
	P value : Sward height†		0.0001	0.0001	0.0001	0.0001	0.0001	0.0001
	P value : Patch area†		0.0351	0.1879	0.3979	0.1088	0.8048	0.0005
Treatment 3 & 4	sed		0.45^{χ}	0.84^{χ}	1.37^{χ}	0.89^{χ}	1.58^{χ}	2.26^{ι}–2.77^{ν}
	P value : Patch area†		0.0902	0.0160	0.1762	0.0183	0.7523	0.0084

†Nominal treatment effects

ν n=10, ι n=15, χ n=24, λ n=39, ϕ n=48

Probability values for the effects of sward height and patch area are given in sequential order of fitting and derived from analysis using Model 1.

5.7.2 Second grazing session

5.7.2.1 Treatment contrasts

There was a substantial contrast in sward height for the second grazing session, with means for [T1 and T2] of 8.8 cm, T3 21.6 cm and T4 20.8 cm (Table 5.38). No comparative estimates of herbage mass were available.

5.7.2.2 Bite number and residence time

The number of bites and residence time were analysed as for the first grazing session, using a model of nominal sward height and nominal patch area (Model 1) (Table 5.38 and Table 5.39). Both number of bites and residence time significantly declined with increasing sward height. There was no significant effect of patch area on either variable. However, again the dominant effect of sward height possibly limited the comparison between T3 and T4. A separate analysis showed significant effects of patch area on bites removed and residence time per patch for T3 and T4 (Table 5.39), though when the values were adjusted to per unit area, there was no effect of patch area (Table 5.38).

Table 5.39 Extract from the analysis of variance output for bite number per patch in the second grazing session using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Main analysis					
Sward height†	1	6468.17	6468.17	172.53	0.0001
Patch area†	1	67.69	67.69	1.81	0.1879
Treatments 3 and 4					
Patch area†	1	67.69	67.69	8.09	0.0160

†Nominal treatment effects

5.7.2.3 Bite rate

Using Model 1, the rate of biting declined with increasing sward height. There was a strong significant effect of patch area, which reflected the contrast between the two sward height groups. When the effect of patch area on T3 and T4 was analysed in a separate analysis patch area effects remained significant (Table 5.40 and Table 5.38).

Table 5.40 Extract from the analysis of variance output for bite rate in the second grazing session using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Main analysis					
Sward height†	1	8391.70	8391.70	184.22	0.0001
Patch area†	1	708.20	708.20	15.55	0.0005
Treatments 3 and 4					
Patch area†	1	570.88	570.88	14.87	0.0084

†Nominal treatment effects

Experiment 4 Separation of the effects of structural parameters, sward height and maturity, on foraging decisions

5.8 PATCH TREATMENTS and MANIPULATION

Experimental treatments were established over the period November to December 1996. Sets of 9 combinations derived from a matrix of 3 sward heights and 3 depths of regrowth, incorporating 5 mature stubble heights (Table 5.41), were arranged in 2 replicate blocks within each sequence. The allocation of treatments for adjacent patch effects was balanced for main effects only and approximate balance was achieved. Grazed patches were of approximate dimensions 0.70 x 0.87 m.

Table 5.41 Treatment structure for Experiment 4

	Regrowth depth (cm)		
Sward height (cm)	0	4	8
14	Treatment 1	Treatment 2	Treatment 3
18	Treatment 4	Treatment 5	Treatment 6
22	Treatment 7	Treatment 8	Treatment 9

A modification was made in this experiment to extend the number of sequences. In this case 4 of the 5 strips were halved horizontally to provide 8 sequences, with a 1.3 m division between one sequence and the next, and four cows grazed six of the 8 sequences (due to poor weather conditions the 2 remaining sequences were discarded) over 3 mornings. The increased sequence replication over earlier experiments made it possible to estimate the between-cow variation. Treatments were structured so that depth of regrowth increments followed multiples of the increments in sward height to provide balance in terms of absolute treatment differences. This involved a reduction in the range of sward heights but offered a greater number of comparison points between sward height (row means) as well as regrowth depth (column means) (Table 5.42).

Table 5.42 Pairing combinations for comparison across levels of sward height, stubble height and regrowth depth.

	Regrowth depth (cm)		
Sward height (cm)	0	4	8
14	14[‡]	10	6
18	18	14	10
22	22	18	14

‡Stubble height (cm)

Patch contrasts were created by weekly trimming for 4 weeks to 5 nominal stubble heights (6, 10, 14, 18, 22 cm) using a S.E.P. (1500 Special) mower with an adjustable sickle bar cutter levelled on skids. No sward compaction occurred due to the adjustment of the wheel width to 0.85 m. Variations in the depth of regrowth were achieved by synchronising 2, 1, 0 week periods of growth prior to grazing for the 8, 4 and 0 cm depths of regrowth respectively. The flush of growth that occurred in the 2 weeks prior to the commencement of the grazing runs created regrowth depths in excess of 0, 4 and 8 cm. In an attempt to bring the 3 sets of patch structures back to 3 approximate sward heights (maintaining the designed structure), the 0 cm regrowth treatments were trimmed back to their respective stubble heights three days prior to the grazing observations. For the 4 and 8 cm regrowth swards, half of the extra regrowth depth, estimated at 2-3 cm was trimmed off on the day prior to observations being undertaken.

5.9 SUMMARISED SWARD MEASUREMENTS

Table 5.43 Summarised sward measurements for Experiment 4

Measurement	Particulars
Sward height	15 readings pre and postgraze.
Herbage mass	Direct (herbage cuts) and indirect (capacitance probe) estimates of herbage pre and post graze. Stratified sampling technique used for pregraze mass.
Botanical composition	Stratified sampling technique.
Nutritive value	Three of the 6 sequences were bulked for each treatment stratum and across blocks within sequences and analysed for quality parameters using NIRS.
Strength properties	Force to fracture measured using an Instron testing machine.

For further details on measurement of sward height refer to section 3.3.1 and nutritive value 3.3.4 under "General sward measurements". For details on measurement of herbage mass refer to section 5.9.1, botanical composition refer to section 5.9.2 and strength properties refer to section 5.9.3 below.

5.9.1 Herbage mass

For each grazed patch, 6 random Corrected Meter Readings (CMR) using a Design Electronics Pasture Meter (Crosbie *et al.*, 1987) were taken prior to and after completion of the grazing observations. Using an electric shearing handpiece, all remaining herbage present was then removed to approximately 6 cm for all treatments except Treatment 3 where cuts were taken to 2 cm as a means of providing an equivalent estimate of the accumulation of mass in the lower 4 cm stratum within the sward profile. From the centre section three random CMR were taken and estimates of herbage mass assessed using a stratified sampling technique. A sward stick was used to gauge cutting heights, with a cut made when the height of the transparent tongue corresponded to the specified height (Figure 5.6). The upper stratum of regrowth swards was defined as the point where regrowth material joined older stubble material based on nominal sward height values and the lower stratum comprised the stubble material cut 6 cm above ground level. For the non-regrowth swards, estimates were made at 4 cm increments down the sward until 6 cm above ground level, primarily for comparative purposes with the regrowth swards (Figure 5.6). Samples retrieved provided estimates of mass within stratum or accumulated whole sward mass.

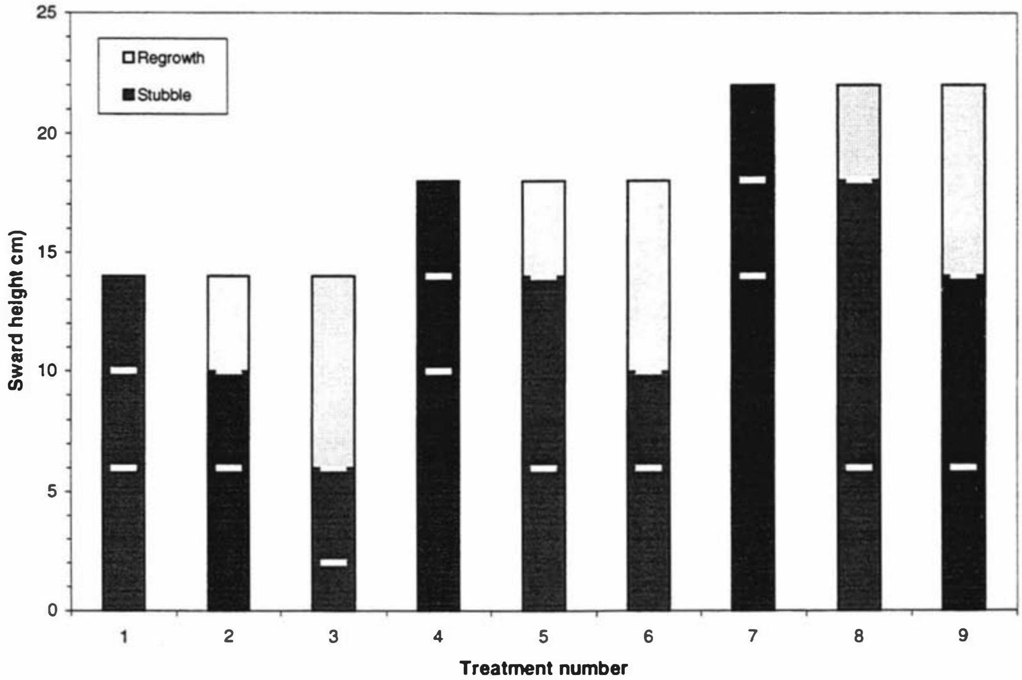

Figure 5.6 Stratified sampling of pregraze herbage mass from the centre section (white lines represent measurement height).

5.9.2 Botanical composition

Samples gathered in the field for each pair of patches were cut approximately 6 cm above ground level for all treatments except for T3 which was cut at 2 cm. In the laboratory, each sample of the regrowth treatments (T2, T3, T5, T6, T8 and T9) was cut into strata, using hand shears, at the interface between the regrowth and the stubble (based on nominal sward height values). There was no stratified cutting of the non-regrowth treatments. Samples were bulked according to the depth of regrowth and stubble height so that the regrowth strata of Treatments 2, 5 and 8 representing 4 cm were bulked together to form sub-group 1 and likewise the regrowth strata of Treatments 3, 6 and 9 representing 8 cm formed sub-group 2. Sub-group 3 consisted of the lower stratum (stubble) of Treatment 3 representing 4 cm above the 2 cm cutting height, sub-group 4 the lower strata of Treatments 2 and 6 representing 4 cm above the

6 cm cutting height, and sub-group 5 whole stubble and lower strata of Treatments 1, 5 and 9 respectively representing 8 cm above the 6 cm cutting height. The whole stubble of Treatment 4 and 7 and lower stratum of Treatment 8 were bulked together representing 12 and 16 cm respectively above the 6 cm cutting height and formed sub-group 6. The 6 sub-groups were then sub-sampled and dissected into the components, ryegrass leaf and pseudostem, ryegrass reproductive stem, other species, weed and dead material.

5.9.3 Force to fracture

The measurements described below do not take into account specimen cross-sectional area and so the procedures measure force to fracture as opposed to tensile strength (see Wright and Illius, 1995).

The force to fracture was measured using a universal testing machine (bench-top Model 4502 Instron Limited, High Wycombe, Buckinghamshire, UK) fitted with a 1kN load cell and connected via a GP-IB IEEE 488 interface to a computer. Force-displacement curves were plotted for each stratum sample test and the force to fracture (Newton) calculated from the maximum height of the curve. The top and bottom pneumatic clamps consisted of square jaws, approximately 50 mm x 50 mm and 40 mm x 40 mm respectively. The bottom clamp had one jaw surfaced with rubber and the other surfaced with a solid square cross bar (40 mm x 5 mm), displaced 10 mm from the top of the clamp plate, simulating the incisor grip. The top jaw clamp was surfaced both sides with fine emery paper (Aluminium Oxide 80J) as a means of minimising fracture at the clamp (Plate 5.1(a)).

Three test samples, each containing 3 tillers, including any attached reproductive material present, and standardised for sward height, were selected from an additional hand size sample from the centre section for each patch per sequence. Each test sample was held with the sheath end positioned in the top clamp (Plate 5.1(b)) and tension properties were measured by longitudinal pull. The top clamp moved away from the bottom clamp at a pre-set speed of 1000 mm/min.

Fracture site was controlled by the bottom clamp position. The 4 cm stratum sections were assessed by test samples held in the bottom clamp 3 cm down the lamina and in the top clamp 7 cm from the tip of the lamina. For 8 cm sections the corresponding clamping positions were 7 cm and 11 cm. An upper and lower stratum was assessed for the no-regrowth swards (T1, T4 and T7) with clamp positions of 3 cm and 7 cm, and 7 cm and 11 cm respectively (Table 5.44 and Figure 5.7). Any test samples that fractured in the vicinity of the top clamp were discarded.

Table 5.44 Clamp positions for estimates of force to fracture (Newtons), as determined using the Instron testing instrument. Measurements given are from the tip of the lamina.

	Upper stratum		Lower stratum	
	Top clamp†	Bottom clamp‡	Top clamp†	Bottom clamp‡
Regrowth				
Trt's 2, 5, 8	7 cm	3 cm		
Trt's 3, 6, 9	11 cm	7 cm		
No Regrowth				
Trt's 1, 4, 7	7 cm	3 cm	11 cm	7 cm

†surfaced with emery paper, ‡rubber surface and simulated incisor

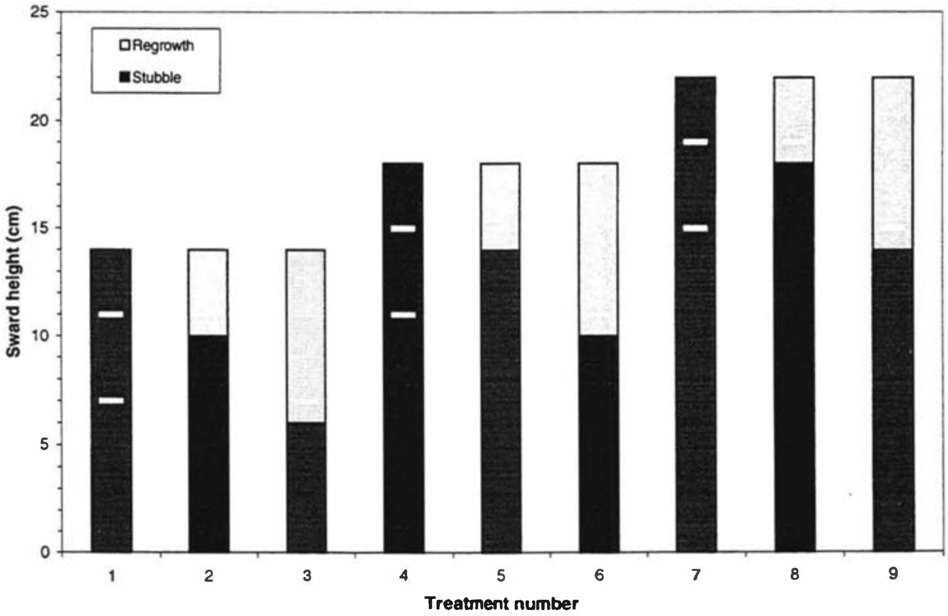

Figure 5.7 Division of strata for estimates of force to fracture for Experiment 4 (white lines represent the position of the bottom clamp)

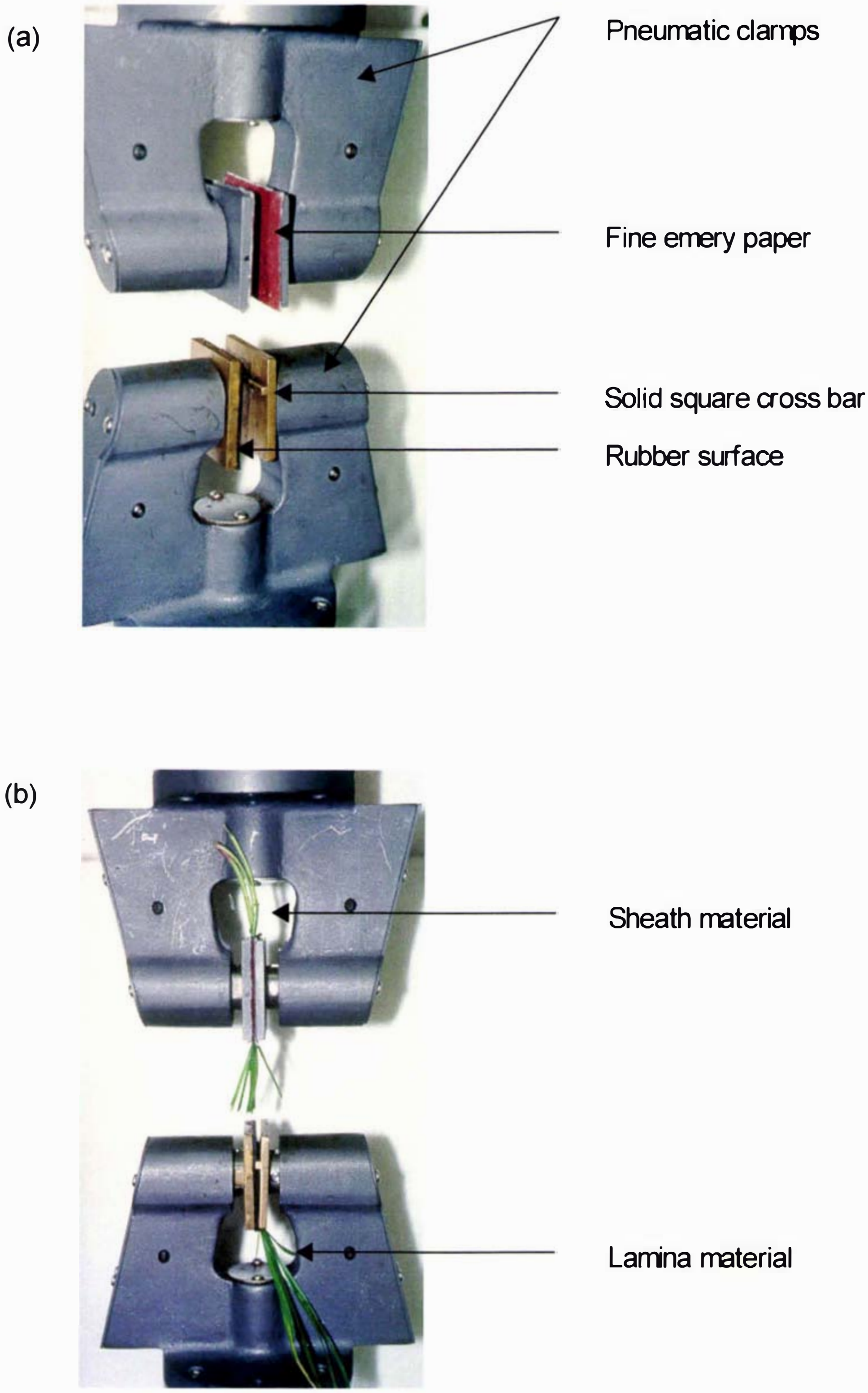

Plate 5.1 Instron testing instrument used to assess force to fracture (a) pneumatic clamp set-up (b) tiller test sample

5.10 RESULTS

5.10.1 Treatment contrasts

Treatment contrasts in the depth of fresh regrowth and sward height were successfully created through manipulation of stubble height and regrowth intervals. The mean sward heights and regrowth depths are presented in Table 5.45 with the means for the three regrowth depths being 1.7 cm, 6.4 cm and 9.6 cm and for the three sward heights 16.1 cm, 19.5 cm and 22.1 cm respectively. Whole sward estimates of dry mass increased with increasing sward height and declined marginally with regrowth depth. There was also a significant interaction between regrowth depth and sward height, though there was no evidence for consistency of patterns. Dry mass in the upper stratum declined with increasing sward height. The regrowths 1.7 and 6.4 cm had similar quantities of mass (84 and 82 g DM m^{-2}), possibly a reflection of the greater value for T1, whereas the deeper regrowth (9.6 cm) had considerably greater mass (136 g DM m^{-2}), which reflected the regrowth depth.

There was no significant difference in the percentage of ryegrass leaf, ryegrass stem, other species, weed and dead material between the 6.4 cm and 9.6 cm regrowths (Table 5.46). The proportion of ryegrass leaf was greater for the stubble of T2, T3 and T6 (groups 3 and 4) compared to the corresponding values for T1, T4, T5, T7, T8 and T9 (groups 5 and 6) (Table 5.47). Variation in ryegrass stem also followed similar patterns to leaf content with significantly lower values recorded for groups 3 and 4 than groups 5 and 6, and group 6 recording the highest proportion of stem.

Estimates of force to fracture of herbage in strata 1 (Table 5.48) differed significantly across the main effects of regrowth depth, reflecting the difference between regrowth (6.4 cm and 9.6 cm) and predominately stubble plus regrowth (1.7 cm), but the effect of sward height was negligible. The significant interaction reflected the inconsistent patterns across and between regrowth depths. The force required to sever herbage was substantially greater for the lower stratum than the upper stratum (Table 5.49) largely reflecting the presence of reproductive stem in the stubble fraction (see Table 5.47). The recorded values were not significantly different between T1, T4 and T7.

Table 5.45 Mean values for stubble height, regrowth depth, sward height, whole sward pregraze mass and upper stratum pregraze mass (stratum height given in parenthesis) for the 9 treatments in Experiment 4.

Treatment	Stubble height (cm)	Regrowth depth (cm)	Sward height (cm)	Pregraze mass (whole sward) (g DM m^{-2})	Pregraze mass (upper stratum) (g DM m^{-2})
1	13.3	3.1	16.4	322	106 (6.4 cm)
2	9.0	7.6	16.6	320	95 (6.6 cm)
3	6.2	9.2	15.4	281	163 (9.4 cm)
4	17.2	2.0	19.2	379	77 (5.2 cm)
5	13.3	6.6	19.9	363	86 (5.9 cm)
6	9.0	10.5	19.5	361	132 (9.5 cm)
7	22.0	0.0	22.0	408	70 (4.0 cm)
8	17.2	4.9	22.1	407	66 (4.1 cm)
9	13.3	9.0	22.3	417	114 (8.3 cm)
sed		0.35	0.35	11.9	14.43
P value : Regrowth depth†		0.0001	0.0498	0.0535	0.0001
P value : Sward height†		0.0001	0.0001	0.0001	0.0001
P value : Regrowth depth x Sward height†		0.0001	0.0204	0.0150	0.7548

†Nominal treatment effects

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.46 Mean values for botanical composition (% DM) for the regrowth stratum of T2, T5, T8 and T3, T6, T9 in Experiment 4.

Group	Treatment	Regrowth (cm)	Ryegrass Leaf	Ryegrass Stem	Other	Weed	Dead
1	2, 5, 8	6.4	78.7	8.5	1.3	7.4	4.1
2	3, 6, 9	9.6	83.7	9.7	0.8	3.4	2.3
sed			4.95	2.33	0.44	3.15	1.06
P value : Group			0.3562	0.6245	0.3078	0.2586	0.1619

Table 5.47 Mean values for botanical composition (% DM) for the stubble stratum for the 9 treatments in Experiment 4.

Group	Treatment	Stubble (cm)	Ryegrass Leaf	Ryegrass Stem	Other	Weed	Dead
3	3	6.2	70.4	12.8	0.2	0.1	16.5
4	2, 6	9.0	72.5	9.5	2.6	1.4	14.1
5	1, 5, 9	13.3	59.2	20.5	3.0	4.3	13.2
6	4, 7, 8	17.2 & 22.4	53.6	28.2	3.8	1.3	13.2
sed			6.65	5.51	1.02	2.42	2.63
P value : Group			0.0365	0.0179	0.0178	0.3985	0.5499

Table 5.48 Mean values for the force (Newtons) required to sever herbage samples at the interface between regrowth depth and stubble height, based on nominal regrowth depth and stubble height values, for the 6 regrowth treatments (T2, T3, T5, T6, T8 and T9) in Experiment 4. Comparative values from the stubble strata for T1, T4 and T7 are provided. All values determined using an Instron testing instrument.

Treatment	Regrowth (cm)	Sward height (cm)	Force to fracture (N)
1	3.1	16.4	18.1
2	7.6	16.6	8.5
3	9.2	15.4	8.9
4	2.0	19.2	14.6
5	6.6	19.9	11.3
6	10.5	19.5	9.8
7	0.0	22.0	10.5
8	4.9	22.1	11.9
9	9.0	22.3	13.1
sed			2.64
P value : Regrowth depth†			0.0148
P value : Sward height†			0.9888
P value : Regrowth depth x Sward height†			0.0163

†Nominal treatment effects

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.49 Mean values for the force (Newtons) required to sever herbage samples for the stubble stratum, based on nominal stubble height values, for T1, T4 and T7 in Experiment 4. All values determined using an Instron testing instrument.

Treatment	Regrowth (cm)	Sward height (cm)	Force to fracture (N)
1	3.1	16.4	29.8
4	2.0	19.2	34.8
7	0.0	22.0	33.1
sed			5.37
P value : Sward height†			0.6478

†Nominal treatment effects

The nutritive value of the upper stratum (Table 5.50) was relatively constant across treatments, with no significant differences for either of the main treatment effects for the parameters crude protein, acid detergent fibre, neutral detergent fibre, organic matter digestibility and metabolisable energy. Effect of regrowth depth attained significance for lipid and neutral detergent fibre content, and variation in sward height led to differences in lipid, carbohydrate and ash content. However these effects were small, contributing less than 20 % of the total sum of squares, and were not consistent across treatments. For the middle stratum (Table 5.51) regrowth depth led to differences in organic matter digestibility and the interaction between sward height and regrowth depth was significant for protein, lipid and acid detergent fibre but, overall, these effects were small relative to the partitioning of the sum of squares to sequence effects. For the lower stratum (Table 5.52) sward height influenced ash content. In general, the data from Table 5.50 to Table 5.52 suggest declining values for protein, lipid, carbohydrate, ash, organic matter digestibility and metabolisable energy and greater values for acid detergent fibre and neutral detergent fibre with increasing depth within the sward.

5.10.2 Bite number and residence time

Number of bites per patch ranged from 7.0 to 37.3, and residence time per patch from 6.9 to 35.5 sec (Table 5.53). A model of nominal regrowth depth and nominal sward height was used to analyse behavioural data.

$$\text{Model} = \text{Regrowth depth}|\text{Sward height} \qquad (1)$$

Cattle removed a greater number of bites and had longer patch residence times on swards which offered the greatest depth of regrowth (Table 5.53 and Table 5.54). Both bite number and patch residence time were negatively associated with sward height. Since the model was balanced, treatment effects were not influenced by the order of placement in the model. Further data will be presented with regrowth depth as the primary effect in the model given its dominance, except that where equal numbers of observations were not available, height will be also be considered as the primary effect. Bite number and patch residence time were closely correlated (r=0.99) and so further results will be reported for bite number only.

Table 5.50 Mean values for the content (% DM) of crude protein (CP), lipid, acid detergent fibre (ADF), neutral detergent fibre (NDF), carbohydrates-soluble sugars and starch (CHO), ash, organic matter digestibility (OMD), and metabolisable energy (ME) (MJ ME/kg DM), for the upper stratum for the 9 treatments in Experiment 4. Values determined by Near Infrared Reflectance Spectroscopy (NIRS).

Treatment	Regrowth (cm)	Sward height (cm)	CP	Lipid	ADF	NDF	CHO	Ash	OMD	ME
1	3.1	16.4	26.2	4.1	23.4	44.7	7.3	10.5	75.0	11.2
2	7.6	16.6	26.3	4.2	22.3	42.5	8.9	10.4	77.4	11.5
3	9.2	15.4	24.2	4.1	24.2	46.5	8.3	10.4	74.3	11.1
4	2.0	19.2	24.7	3.8	24.5	46.7	7.4	10.1	71.7	10.7
5	6.6	19.9	26.4	4.1	23.2	44.8	7.6	10.2	73.9	11.0
6	10.5	19.5	25.6	4.3	23.8	46.7	7.5	10.5	74.6	11.1
7	0.0	22.0	24.1	3.8	23.5	43.5	9.3	10.0	75.0	11.2
8	4.9	22.1	25.4	4.0	23.9	44.9	8.0	10.2	74.7	11.1
9	9.0	22.3	23.7	4.0	24.2	45.8	8.5	10.1	74.7	11.1
sed			1.14	0.09	0.80	1.32	0.64	0.20	3.69	0.29
P value : Regrowth depth†			0.0917	0.0007	0.1447	0.0271	0.8572	0.6346	0.4448	0.4443
P value : Sward height†			0.1463	0.0046	0.3824	0.1128	0.0284	0.0427	0.1743	0.1739
P value : Regrowth depth x Sward height†			0.5092	0.0256	0.3835	0.2476	0.0744	0.4005	0.4834	0.4866

†Nominal treatment effects

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.51 Mean values for the content (% DM) of crude protein (CP), lipid, acid detergent fibre (ADF), neutral detergent fibre (NDF), carbohydrates-soluble sugars and starch (CHO), ash, organic matter digestibility (OMD), and metabolisable energy (ME) (MJ ME/kg DM), for the middle stratum for the 9 treatments in Experiment 4. Values determined by Near Infrared Reflectance Spectroscopy (NIRS).

Treatment	Regrowth (cm)	Sward height (cm)	CP	Lipid	ADF	NDF	CHO	Ash	OMD	ME
1	3.1	16.4	15.3	3.1	32.0	56.5	6.9	9.2	70.3	10.5
2	7.6	16.6	19.9	3.8	27.4	50.9	7.7	10.3	73.8	11.0
3	9.2	15.4	16.5	3.4	29.4	52.5	8.6	9.7	73.4	10.9
4	2.0	19.2	17.5	3.1	30.6	55.5	6.8	9.7	65.8	9.8
5	6.6	19.9	17.1	3.3	30.9	56.1	6.8	9.7	69.0	10.3
6	10.5	19.5	19.2	3.6	28.2	52.4	7.4	10.1	72.8	10.8
7	0.0	22.0	18.9	3.4	28.3	52.2	8.1	9.8	70.5	10.5
8	4.9	22.1	15.8	3.2	30.6	55.6	7.4	9.3	70.8	10.5
9	9.0	22.3	16.3	3.4	29.2	53.2	8.0	9.5	73.7	11.0
sed			1.48	0.18	1.49	2.28	0.60	0.36	2.70	0.40
P value : Regrowth depth†			0.8972	0.0710	0.3177	0.2930	0.0709	0.6270	0.0380	0.4873
P value : Sward height†			0.5540	0.6963	0.8094	0.5635	0.0613	0.3490	0.1184	0.7614
P value : Regrowth depth x Sward height†			0.0145	0.0162	0.0370	0.1070	0.3110	0.0683	0.6753	0.0791

†Nominal treatment effects

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 1.

Table 5.52 Mean values for the content (% DM) of crude protein (CP), lipid, acid detergent fibre (ADF), neutral detergent fibre (NDF), carbohydrates-soluble sugars and starch (CHO), ash, organic matter digestibility (OMD), and metabolisable energy (ME) (MJ ME/kg DM), for the lower stratum for T4 and T7 in Experiment 4. Values determined by Near Infrared Reflectance Spectroscopy (NIRS).

Treatment	Regrowth (cm)	Sward height (cm)	CP	Lipid	ADF	NDF	CHO	Ash	OMD	ME
4	2.0	19.2	15.3	3.2	31.8	56.2	7.9	9.2	70.8	10.6
7	0.0	22.0	11.9	2.9	32.7	57.2	8.0	8.6	70.0	10.4
sed			1.47	0.09	1.01	1.26	0.17	0.08	2.59	0.39
P value : Sward height†			0.1509	0.0677	0.4427	0.5193	0.7912	0.0215	0.7873	0.7851

†Nominal treatment effects

Table 5.53 Mean values for bite number, residence time and herbage removed for the 9 treatments in Experiment 4.

Treatment	Regrowth (cm)	Sward height (cm)	Bite number	Residence time (sec)	Herbage removed (g DM m^{-2})
1	3.1	16.4	8.4	7.9	84.3
2	7.6	16.6	28.5	25.9	162.6
3	9.2	15.4	37.3	35.5	198.2
4	2.0	19.2	7.0	6.9	97.2
5	6.6	19.9	17.1	15.3	131.2
6	10.5	19.5	35.3	34.2	175.6
7	0.0	22.0	7.8	8.2	97.5
8	4.9	22.1	11.2	10.2	112.4
9	9.0	22.3	26.6	25.3	158.6
sed			2.76	2.63	11.94
P value : Regrowth depth†			0.0001	0.0001	0.0001
P value : Sward height†			0.0001	0.0001	0.0017
P value : Regrowth depth x Sward height†			0.0005	0.0003	0.0035

†Nominal treatment effects

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 1

Table 5.54 Extract from the analysis of variance output for bite number using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Cow	3	2548.06	849.35	5.44	0.0989
Sequence x Cow	3	468.36	156.12	3.68	0.0147
Regrowth depth†	2	23151.59	1630.23	127.05	0.0001
Sward height†	2	3260.45	11575.80	17.89	0.0001
Regrowth depth x Sward height†	4	2021.99	505.50	5.55	0.0005

†Nominal treatment effects

The correlation between bite number and force to fracture (regrowth stratum) was highly significant (r= -0.38, P=0.0001). Covariance analysis indicated a significant strength by regrowth depth interaction effect on bite number (F=6.13, P=0.0034) but the magnitude of this effect was small compared to the dominant effect of regrowth depth (F=138.03, P=0.0001). This result largely occurred as a consequence of the fit for 9.6 cm regrowth depth (r^2=0.37) compared to regrowth depths 1.7 and 6.4 cm (r^2=0.02 and r^2=0.04 respectively). Greater variability in force to fracture recorded for swards of little regrowth (1.7 cm regrowth depth) was also influential in forming a negative relationship between bite number and force to fracture.

There was no indication of relationships between bite number and any of the parameters of nutritive value, either in correlation analysis or covariance analysis.

5.10.3 Herbage removed

The calculation of herbage removed per patch, obtained from direct estimates of herbage, pregraze from the centre zone and postgraze from the grazed patches, yielded poor predictions. Non-linear regression analysis establishing relationships between capacitance probe readings and postgraze direct cuts were analysed and a series of equations fitted. Separate or combined pre and post graze quadratic or modified exponential functions did not improve the predictions over the standard linear relationship. Separate linear equations for pregraze (eqn 1) and postgraze (eqn 2) mass were subsequently used to predict pregraze and postgraze mass on the grazed patches.

$$\text{Pregraze mass (g DM m}^{-2}\text{)} = -180.03(\pm 62.71) + 1.76(\pm 0.19)\text{ (Probe CMR) } r^2 = 0.36 \qquad \text{eqn (1)}$$

$$\text{Postgraze mass (g DM m}^{-2}\text{)} = -218.38(\pm 21.38) + 1.69(\pm 0.08)\text{ (Probe CMR) } r^2 = 0.65 \qquad \text{eqn (2)}$$

Herbage removed (g DM m^{-2}) was then calculated as the difference between the predictions of pregraze and postgraze mass. These estimates are presented in Table 5.53. Treatment effects on herbage removed in relation to regrowth depth and sward height were very similar to those for bite number. Figure 5.8 illustrates the interaction between the effect of regrowth depth and sward height for both bite number and herbage removed per patch, and shows the strong and positive correlation (r = 0.75, P=0.0001) between the two dependent parameters. There were strong negative relationships between sward height and bite number or herbage removed in the deeper regrowths (6.4 and 9.6 cm) but there was little indication of similar patterns over the shallow regrowth swards (1.7 cm).

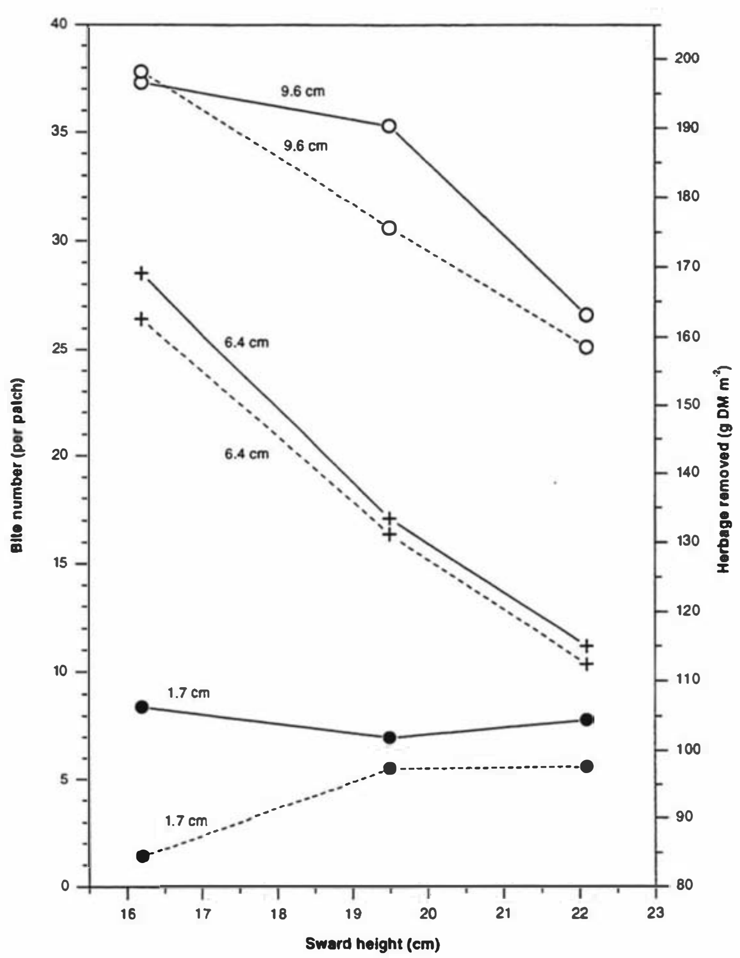

Figure 5.8 Relationship between sward height and bite number (——) or herbage removed (g DM m^{-2}) (------) for 1.7 (●), 6.4 (+) and 9.6 (O) cm regrowth depths respectively.

5.10.4 Between cow variation

The variation between cows in the number of bites per patch was assessed using sequence x cow as an error term. The results of the test for cow effects are presented in Table 5.54. The mean number of bites removed per patch and per cow approached significance only at 0.1 probability. Nevertheless, with only 3 df, there was some evidence for intra-species variation and this supports the range in values recorded between cows (range 14.4 to 27.8). However, the main interest was in between-cow contrasts in allocation of bites across treatments. None of the cow by treatment interactions, either between or within patches, approached significance (Table 5.55), suggesting that though variability existed between cows in the number of bites removed, their preferential behaviour was similar.

Table 5.55 Extract from the analysis of cow by treatment interaction, between patches using mean square error as the error term, and within patches using treatment(sequence x block) as the error term.

Source	DF	SS	MS	F Value	Pr > F
Between patches					
Regrowth depth† x Cow	6	456.85	76.14	1.58	0.1666
Sward height† x Cow	6	360.88	60.15	1.24	0.2940
Regrowth depth† x Sward height† x Cow	12	726.12	60.51	1.25	0.2660
Within patches					
Regrowth depth† x Cow	6	456.85	76.14	0.95	0.4650
Sward height† x Cow	6	360.88	60.15	0.75	0.6117
Regrowth depth† x Sward height† x Cow	12	726.12	60.51	0.75	0.6954

†Nominal treatment effects

5.10.5 Bite mass

Bite mass was calculated by dividing the estimated herbage removed per patch (see section 5.10.3) by the number of prehended bites per patch. Values were calculated for patches where greater than 4 bites were removed. Using Model 1 sward height had a strong positive association with bite mass whereas the effect of regrowth depth on bite mass was strongly negative (Table 5.56 and Table 5.57). The effect of the interaction between sward height and regrowth depth was marginally significant. Further analysis

Table 5.56 Mean values for bite mass and bite rate for the 9 treatments in Experiment 4. Values are calculated from patches where 4 or more bites were removed.

Treatment	Regrowth (cm)	Sward height (cm)	Bite mass (g DM bite^{-1})	Bite rate (bites min^{-1})
1	3.1	16.4	6.90	61.1
2	7.6	16.6	4.31	65.8
3	9.2	15.4	4.43	62.6
4	2.0	19.2	9.63	56.8
5	6.6	19.9	5.95	67.3
6	10.5	19.5	3.64	60.6
7	0.0	22.0	11.19	54.0
8	4.9	22.1	8.58	62.9
9	9.0	22.3	4.60	62.9
sed	0.35	0.35	1.141^{θ}-1.368^{ϖ}	2.90^{χ}-3.18^{ψ}
P value : Regrowth depth†			0.0001	0.0001
P value : Sward height†			0.0002	0.2243
P value: Regrowth depth x Sward height†			0.0613	0.3436

†Nominal treatment effects

ϖ n=16, ψ n=20, θ n=23, χ n=24

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 1.

and models fitting linear effects of regrowth depth and sward height and nominal treatment parameters did not change the conclusion drawn from Model 1.

Table 5.57 Extract from the analysis of variance output for bite mass using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Regrowth depth†	2	747.47	373.73	24.98	0.0001
Sward height†	2	285.26	142.63	9.53	0.0002
Regrowth depth x Sward height†	4	140.32	35.08	2.34	0.0613
Reverse fit					
Sward height†	2	261.00	130.50	8.72	0.0004
Regrowth depth†	2	771.73	385.87	25.79	0.0001

†Nominal treatment effects

The correlation between bite mass and bite number was negative (r= -0.65) and, though highly significant (P=0.0001), plotted data showed the need for caution in the interpretation of this data, primarily given that indexes are swayed by the tendency for extreme values and errors accumulated on patches with few bites. The value for T8 possibly inflates the mean bite mass on the medium depth swards (Table 5.56). The assumption of constant variability was broken and in further analysis bites were weighted (SAS weight procedure) as a means of compensating for the spread of data, so that greater value was given to patches with a greater number of bites removed from them and vice versa. The log of bite number was also used in the analysis of variance with log values translated back to absolute values permitting the lines of curvature to be plotted for associations between bite number and bite mass for each of the three levels of regrowth depth (Figure 5.9) and three levels of sward height (Figure 5.10) in addition to a pooled relationship. Figure 5.9 and Figure 5.10 are plotted with the omission of the highest 10 values (5 %) recorded above 30 g DM bite^{-1}. Both figures demonstrate the decline in bite mass with increasing bites removed across levels of regrowth depth and sward height. For the three regrowth categories (Figure 5.9) the bite mass values reflected the contrast in the number of bites removed (Table 5.58). The variation in the slope of the three lines attained significance, with the slope decreasing from the shallow regrowth depth to the deeper regrowth depth. The effects for sward height did not attain significance (Table 5.58).

The pattern of variability reinforces the caution required in making inferences with bites removed in circumstances where fewer than 10 or 15 bites per patch are taken. An analysis omitting the first 9 bites (log bites) showed that the curvilinear relationship between bite mass and bite number for the three regrowth depths in fact reflected the high variability associated with estimates of bite mass where fewer than 10 bites were removed (P=0.4433). The significance of the sward height effect remained unchanged (P=0.8375). Even taking into consideration the fact that the bite mass values were exceedingly high, across the two deeper regrowth depths the quantity of herbage removed by cows was largely proportional to the residence time per patch, and in this experiment bite number since grazing bites and patch residence time were strongly correlated.

Table 5.58 Extract from the analysis of variance for the interactions between bite mass and log bite number.

Source	DF	SS	MS	F Value	Pr > F
Log Bites	1	2525.31	2525.31	200.70	0.0001
Regrowth depth †	2	143.15	71.58	5.69	0.0052
Log Bites x Regrowth depth†	2	132.19	66.09	5.25	0.0076
Sward height†	2	2.39	1.19	0.09	0.9096
Log Bites x Sward height†	2	59.67	29.84	2.37	0.1010
Regrowth depth† x Sward height†	4	73.56	18.39	1.46	0.2235
Log Bites x Regrowth depth† x Sward height†	4	85.11	21.28	1.69	0.1622

†Nominal treatment effects

There were no significant differences between animals in the mean bite mass (P=0.7130) although one cow recorded a lower value (5.72 g DM bite^{-1}) compared to the remaining 3 cows (6.63, 6.17 and 6.70 g DM bite^{-1}).

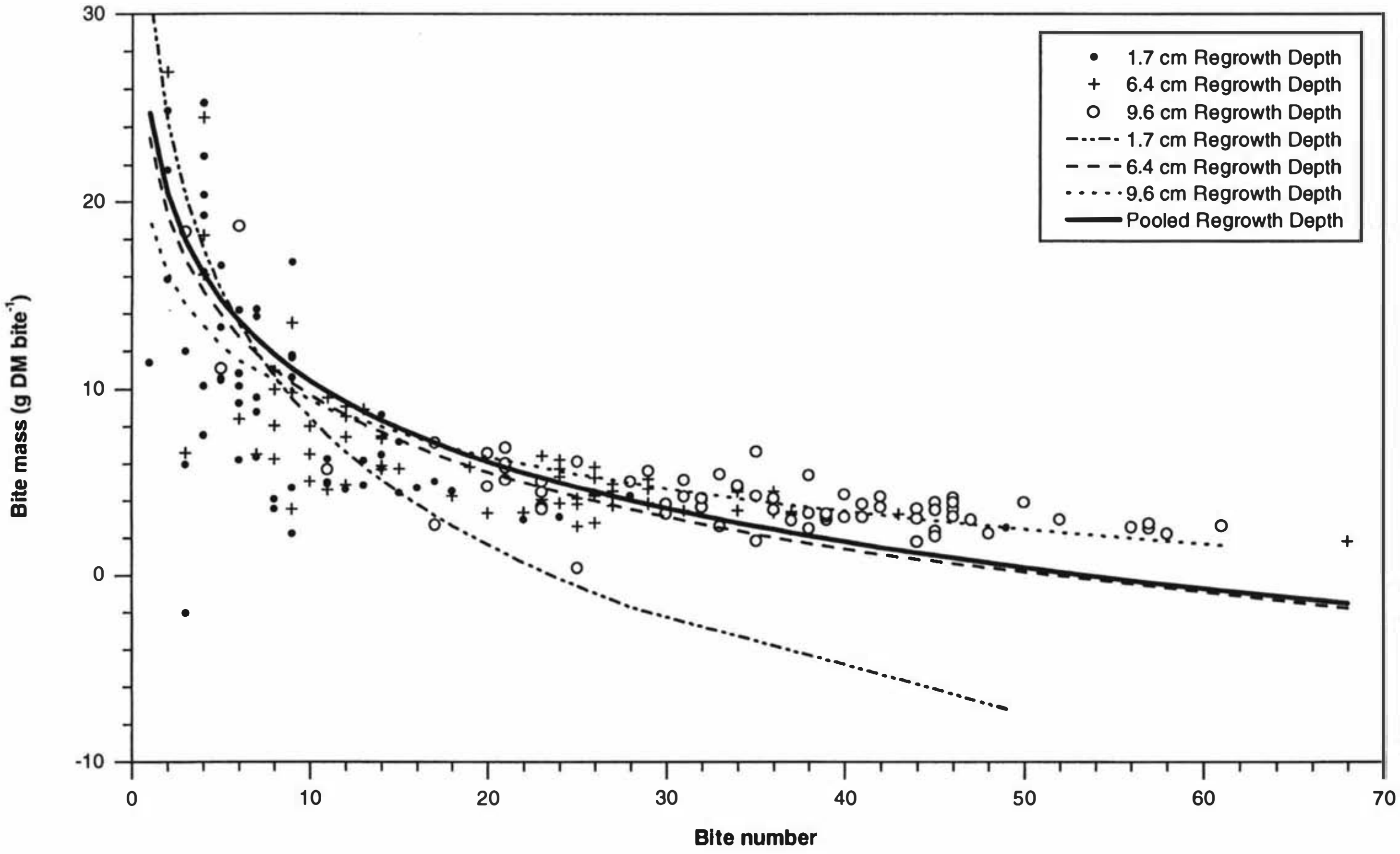

Figure 5.9 Relationship between bite mass and bite number for the three regrowth depths. Pooled relationship Bite mass=24.76 (±0.71) -14.33 (±0.57)Log Bite number, 1.7 cm regrowth depth Bite mass=31.11 (±2.09) -22.67 (±2.36)Log Bite number, 6.4 cm regrowth depth Bite mass=23.47 (±1.41) -13.77 (±1.13)Log Bite number, 9.6 cm regrowth depth Bite mass=19.16 (±1.15) -9.82 (±0.78)Log Bite number.

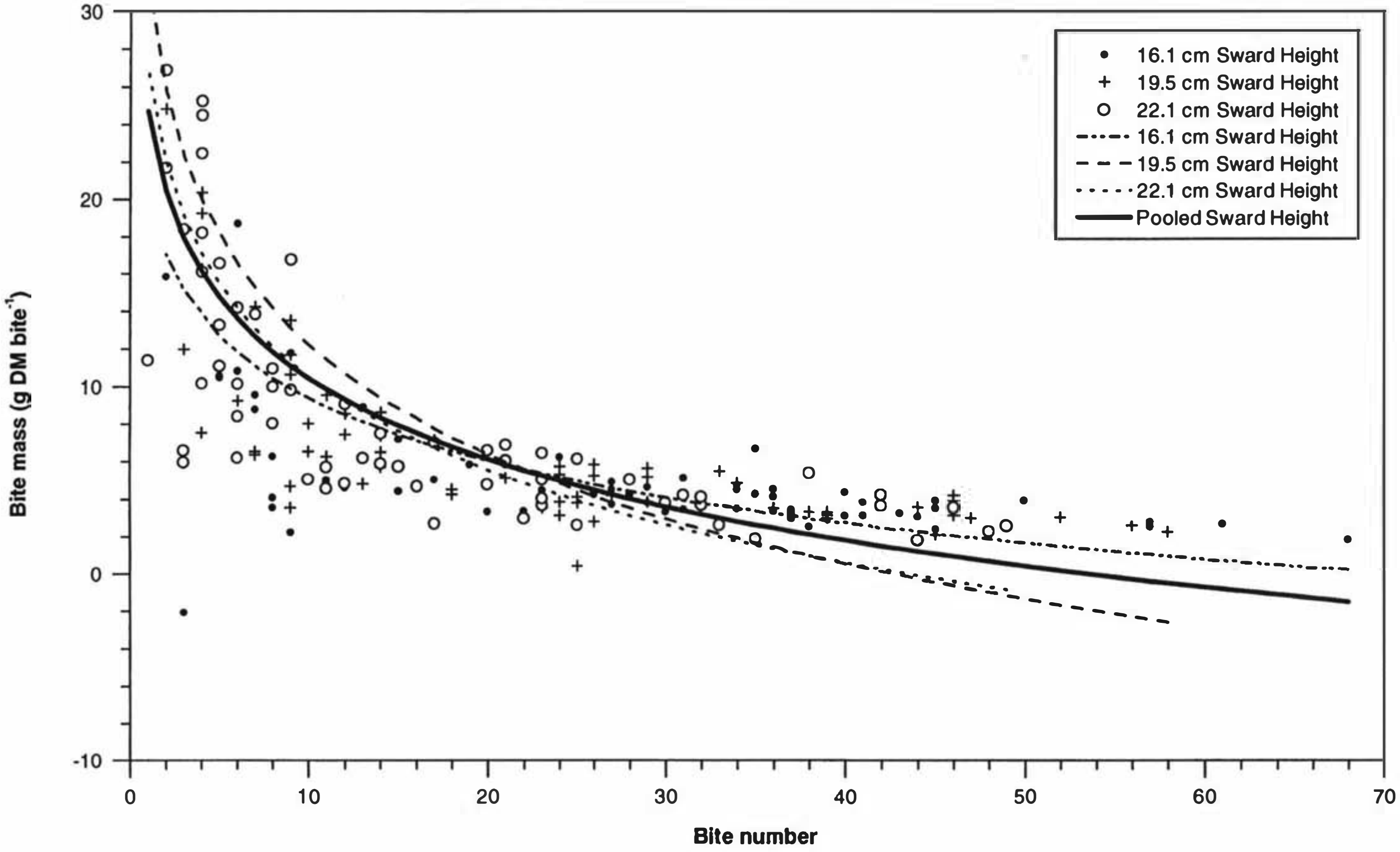

Figure 5.10 Relationship between bite mass and bite number for the three sward heights. Pooled relationship Bite mass=24.76 (±0.71) -14.33 (± 0.57)Log Bite number, 16.1 cm sward height Bite mass=20.41 (±1.42) -11.04 (±1.06)Log Bite number, 19.5 cm sward height Bite mass=31.63 (±2.03) - 19.41 (± 1.62)Log Bite number, 22.1 cm height Bite mass=27.02 (±1.48) -16.50 (±1.32)Log Bite number.

5.10.6 Bite rate

Rate of biting was strongly related to regrowth depth, and largely reflected the contrast between regrowth depths 1.7 cm and 6.4 cm. The effect of sward height on bite rate did not attain significance (Table 5.56 and Table 5.59). There was no significant within treatment variation (P=0.6741) measured by fitting a linear regression effect of regrowth depth (or sward height).

Table 5.59 Extract from the analysis of variance output for bite rate using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Regrowth depth†	2	2146.26	1073.13	10.64	0.0001
Sward height†	2	306.79	153.40	1.52	0.2243
Regrowth depth x Sward height†	4	459.57	114.89	1.14	0.3436
Reverse fit					
Sward height†	2	276.33	133.16	1.37	0.2596
Regrowth depth†	2	2176.72	1088.36	10.79	0.0001

†Nominal treatment effects

5.10.7 Bite depth

Within each of the 3 sward heights, animals increased the depth of penetration with increasing regrowth depth (Table 5.60), with mean bite depth of 4.2 cm, 6.4 cm and 7.6 cm across regrowth depths of 1.7, 6.4 and 9.6 cm respectively. Sward height had little influence on bite depth (Table 5.61). However, fitting a continuous linear regression term for regrowth depth (or sward height) after nominal treatment parameters showed a significant within treatment variation effect (P=0.0001). Fitting a linear effect of regrowth depth prior to the nominal treatment terms (Model 2) supported the result shown in Table 5.61 that bite depth was strongly related to the depth of regrowth (Table 5.62).

Model = Regrowth depth† Regrowth depth|Sward height (2)

†Linear effect of regrowth depth

Table 5.60 Mean values for bite depth and bite depth/sward height for the 9 treatments in Experiment 4. Values are calculated from patches where 4 or more bites were removed.

Treatment	Regrowth (cm)	Sward height (cm)	Bite depth (cm)	Bite depth / Sward height (%)
1	3.1	16.4	3.8	23.3
2	7.6	16.6	6.9	41.3
3	9.2	15.4	7.1	45.6
4	2.0	19.2	4.0	20.7
5	6.6	19.9	6.6	33.2
6	10.5	19.5	8.2	42.6
7	0.0	22.0	4.8	21.4
8	4.9	22.1	5.8	26.1
9	9.0	22.3	7.6	34.1
sed			$0.27^{\theta} – 0.33^{\varpi}$	$1.34^{\theta} – 1.60^{\varpi}$
P value : Linear effect of regrowth depth			0.0001	0.0001
P value : Linear effect of sward height			0.0001	0.0001
P value : Linear regrowth depth x linear sward height			0.0001	0.0001
P value : Nominal regrowth depth			0.2088	0.3752
P value : Nominal sward height			0.9200	0.9562
P value: Nominal regrowth depth x sward height			0.0125	0.0065

ϖ n=16, θ n=23

Probability values for the effects of regrowth depth and sward height are given in sequential order of fitting and derived from analysis using Model 3.

The addition of the linear regrowth term in Model 2 also led to an increase in the sum of squares for the nominal sward height term, which attained significance (Table 5.62). This reflected the fact that there was variation in the depth of regrowth across levels of sward height for each of the 3 regrowth depths. Nonetheless, this effect was small relative to the dominant effect of regrowth depth on bite depth.

Table 5.61 Extract from the analysis of variance output for bite depth using Model 1.

Source	DF	SS	MS	F Value	Pr > F
Regrowth depth†	2	355.98	117.99	106.97	0.0001
Sward height†	2	5.70	2.85	1.71	0.1865
Regrowth depth x Sward height†	4	28.05	7.01	4.21	0.0037
Reverse fit					
Sward height†	2	7.92	3.96	2.38	0.0988
Regrowth depth†	2	353.76	176.88	106.31	0.0001

†Nominal treatment effects

Table 5.62 Extract from the analysis of variance output for bite depth using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of regrowth depth	1	414.36	414.36	477.80	0.0001
Nominal regrowth depth†	2	2.57	1.28	1.48	0.2335
Nominal sward height†	2	27.64	13.82	15.94	0.0001
Nominal regrowth depth x sward height†	4	32.22	8.05	9.29	0.0001

A revised model (Model 3) which fitted linear regression effects of regrowth depth and sward height before nominal treatment parameters was used for further analysis of bite depth patterns. The results from the analysis of variance for this model (Model 3) are shown in Table 5.63.

Model = Regrowth depth†|Sward height† Regrowth depth|Sward height (3)

†Linear effect of regrowth depth and sward height

The main result from this output was that the linear terms between them explained the large majority of the variation in bite depth which suggests that there was little variation left over that could be attributed to the effects of preparation procedure on patch characteristics.

Table 5.63 Extract from the analysis of variance output for bite depth using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of regrowth depth	1	414.36	414.36	477.96	0.0001
Linear effect of sward height	1	32.61	32.61	37.62	0.0001
Linear regrowth depth x linear sward height	1	17.05	17.05	19.67	0.0001
Nominal regrowth depth	2	2.76	1.38	1.60	0.2088
Nominal sward height	2	0.14	0.07	0.08	0.9200
Nominal regrowth depth x sward height	3	9.98	3.33	3.84	0.0125

For T2, T5 and T8 grazed height approximated the interface between regrowth and stubble material. By comparison for T3, T6 and T9 grazed height was off-set from the interface (Figure 5.11). Animals penetrated deeper into the stubble strata with increasing sward height for T1, T4 and T7. However, there was no evidence that animals removed a constant proportion of sward height (Table 5.64 and Table 5.60). Values as a function of sward height corresponded to 37.8, 33.3 and 27.8 % for 16.1, 19.5 and 22.1 cm sward heights respectively, and the proportion of sward height removed increased with increasing regrowth depth. This effect is clearly illustrated in Figure 5.11 by the staggered effect of grazed height within a height level. The significant interaction in Table 5.60 reflected the fact that as a consequence of the variation in regrowth depth within a regrowth level, bite depth as a proportion of sward height declined with increasing sward height for the two deeper regrowths. There was, however, no declining trend of the proportion removed as a function of sward height across the 1.7 cm, regrowth depth.

Table 5.64 Extract from the analysis of variance output for bite depth/sward height using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of regrowth depth	1	12706.83	12706.83	619.61	0.0001
Linear effect of sward height	1	116.89	1161.89	56.66	0.0001
Linear regrowth depth x linear sward height	1	1180.05	1180.05	57.54	0.0001
Nominal regrowth depth	2	40.68	20.34	0.99	0.3752
Nominal sward height	2	1.84	0.92	0.04	0.9562
Nominal regrowth depth x sward height	3	269.65	89.88	4.38	0.0065

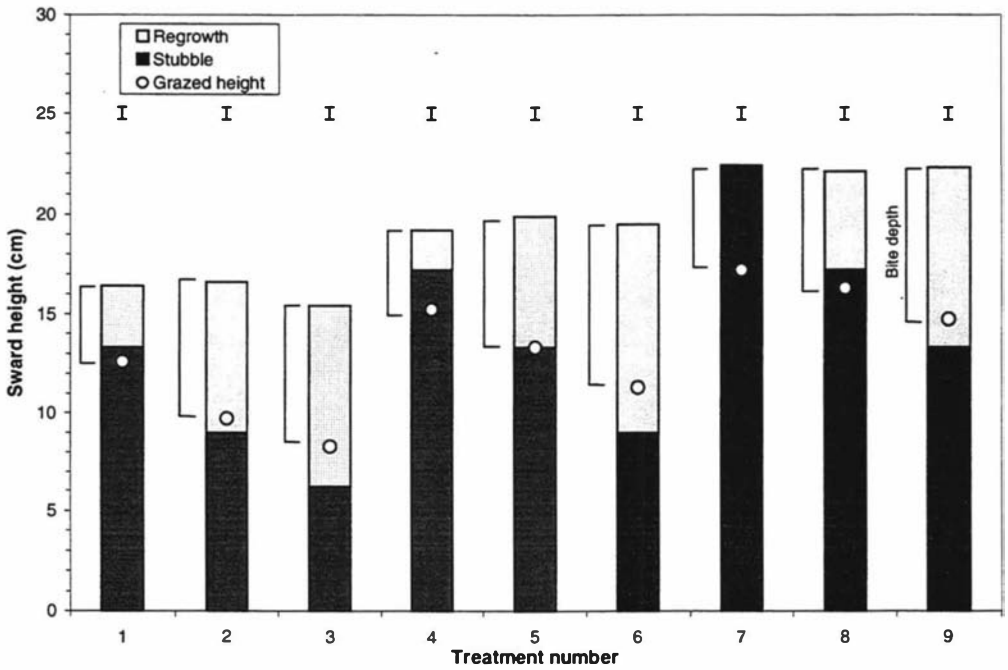

Figure 5.11 Grazed height relative to the interface between stubble height and regrowth depth (vertical bars represent sem).

Using bite number as a covariate on bite depth showed the residual effect of bite number to be highly significant, indicating an influencing factor independent of treatment effects. Further analysis involved the log transformation of bite number, with log values translated back to absolute values allowing for the lines of curvature to be plotted for associations between bite number and bite depth for each of the three levels of regrowth depth (Figure 5.12) and three levels of sward height (Figure 5.13) in addition to a pooled relationship. The pooled relationship within levels of regrowth depth shows a strong association between regrowth depth and bite number, implying an initial "adjustment" phase of increasing bite depth with increasing bite number over the first 10-20 bites on a patch, followed by an "adjusted" phase where bite depth showed little further change over a substantial range of bite number (20-65 bites). Curves for the three regrowth depth treatments (Figure 5.12) were separate, reinforcing the suggestion that for each regrowth depth, bite depth was a reflection of the number of bites removed. The curves were also parallel, determined by the lack of a significant Log Bites x Regrowth depth interaction (Table 5.65). Curves for the three sward height treatments (Figure 5.13) essentially overlapped, supporting a much smaller effect of bite number on bite depth. The slope of the curve for 19.5 cm was greater (4.54 ± 0.58) than that of 16.1 cm (3.76 ± 0.51) or 22.1 cm (3.64 ± 0.63) but this difference did not attain significance (Log Bites x Sward height, $P>0.05$) (Table 5.65). Reversing the fit of Log Bites x Regrowth depth and Log Bites x Sward height had no effect on the interpretation of significance.

Table 5.65 Extract from the analysis of variance for the interactions between bite depth and log bite number.

Source	DF	SS	MS	F Value	Pr > F
Log Bites	1	336.51	336.51	362.06	0.0001
Regrowth depth †	2	75.96	37.98	40.87	0.0001
Log Bites x Regrowth depth†	2	0.29	0.14	0.16	0.8563
Sward height†	2	11.77	5.88	6.33	0.0033
Log Bites x Sward height†	2	0.61	0.31	0.33	0.7197
Regrowth depth† x Sward height†	4	9.75	2.44	2.62	0.0441
Log Bites x Regrowth depth† x Sward height†	4	10.71	2.68	2.88	0.0305

†Nominal treatment effects

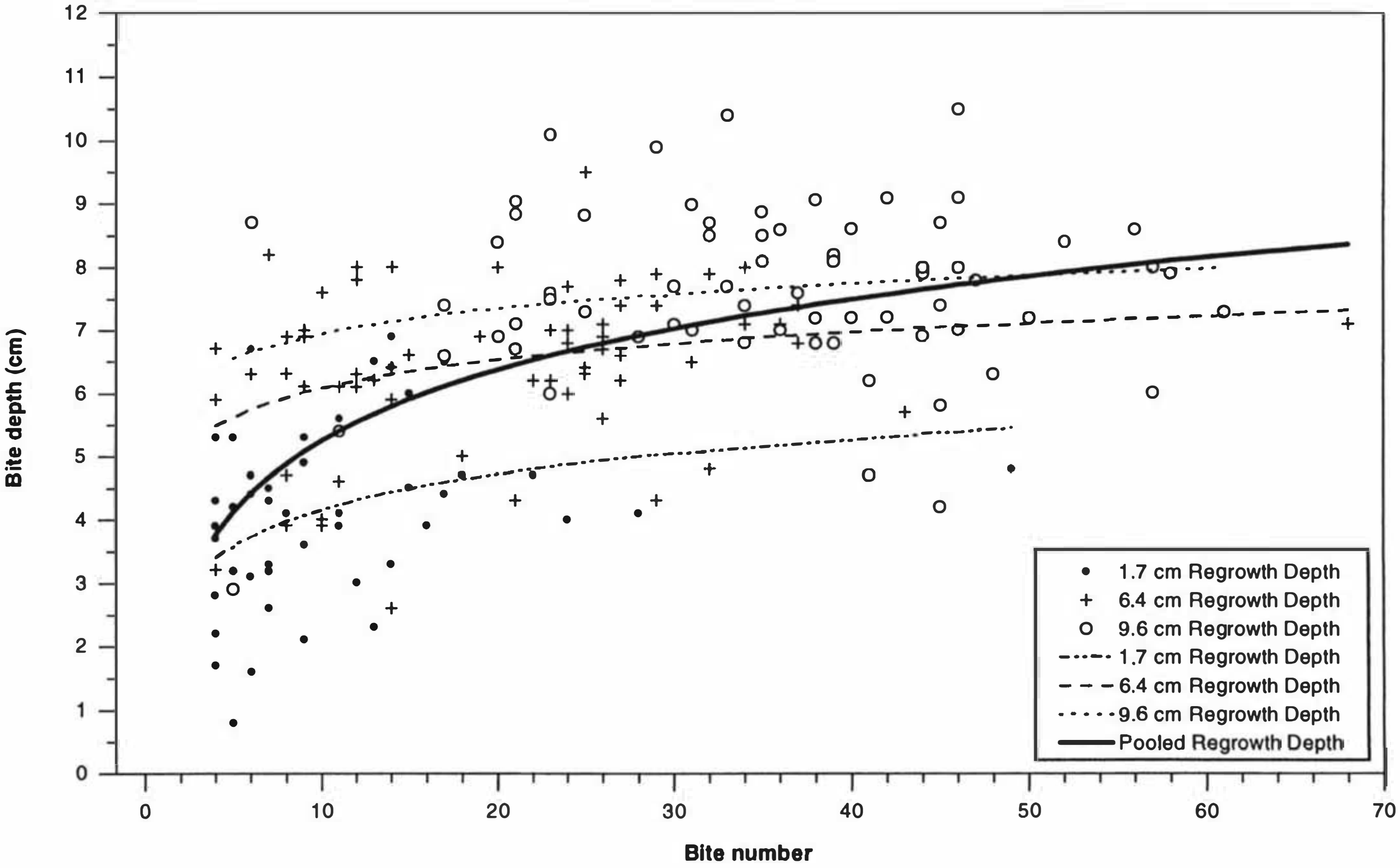

Figure 5.12 Relationship between bite depth and bite number for the three regrowth depths. Pooled relationship Bite depth=1.50 (±0.41) + 3.74 (±0.32)Log Bite number, 1.7 cm regrowth depth Bite depth=2.26 (±0.71) + 1.89 (±0.72)Log Bite number, 6.4 cm regrowth depth Bite depth=4.58 (±0.67) + 1.49 (±0.53)Log Bite number, 9.6 cm regrowth depth Bite depth=5.63 (±1.16) + 1.32 (± 0.76)Log Bite number.

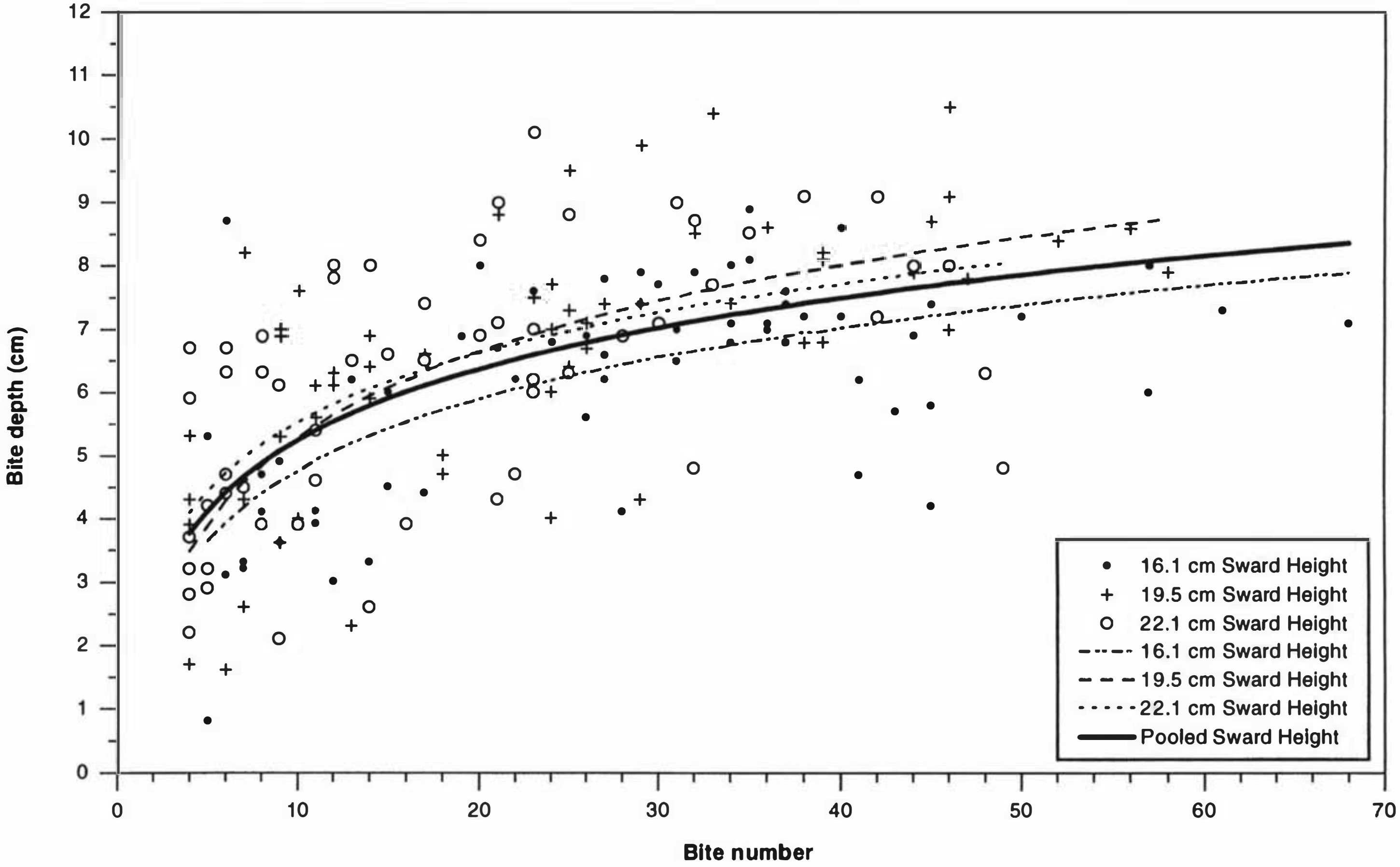

Figure 5.13 Relationship between bite depth and bite number for the three sward heights. Pooled relationship Bite depth=1.50 (±0.41) + 3.74 (±0.32)Log Bite number, 16.1 cm sward height Bite depth=1.00 (±0.71) + 3.76 (±0.51)Log Bite number, 19.5 cm sward height Bite depth=0.75 (±0.75) + 4.54 (±0.58)Log Bite number, 22.1 cm sward height Bite depth=1.89 (±0.76) + 3.64 (±0.63)Log Bite number.

5.10.8 Adjacent patch effects

There was no significant effect of the preceding patch sward height or regrowth depth on the number of bites removed from the current patch (Table 5.66). However there was a strong interaction (P=0.0194) between these two parameters. Further investigation showed this interaction to be associated with T7. Examination of the design showed that although each main effect level was preceded by approximately equal numbers of levels of main effects, 6 of the 12 patches which were allocated T7 on the preceding patch received the highest sward height treatment. Consequently it would appear the significant interaction is a chance effect. Neither sward height nor regrowth depth (or an interaction) of the succeeding patch in sequence influenced the number of bites removed from the current patch.

Table 5.66 Extract from the analysis of variance table for the influence of the regrowth depth and sward height of the adjacent patch in sequence on bites removed from the current patch in Experiment 4.

Source	DF	SS	MS	F Value	Pr > F
Regrowth depth†	2	23151.59	11575.80	132.71	0.0001
Sward height†	2	3260.45	1630.23	18.69	0.0001
Regrowth depth† x Sward height†	4	2021.99	505.50	5.80	0.0004
Prev* Regrowth depth†	2	42.31	21.16	0.24	0.7853
Prev* Sward height†	2	176.50	88.25	1.01	0.3687
Nxt# Regrowth depth†	2	191.02	95.51	1.10	0.3400
Nxt# Sward height†	2	6.20	3.10	0.04	0.9651
Prev* Regrowth depth† x Prev* Sward height†	4	1095.81	273.96	3.14	0.0194
Nxt# Regrowth depth† x Nxt# Sward height†	4	226.11	56.53	0.65	0.6301

†Nominal treatment effects
*Prev = Preceding patch, #Next = succeeding patch

However, herbage mass removed on the current patch was influenced by the sward height of the preceding patch (Table 5.67). Mass removed from the current patch was greatest if the preceding patch had been short (means 146.7, 129.8 and 128.2 g DM per patch for 16.1, 19.5 and 22.1 cm swards respectively). The interaction between sward height and regrowth depth was also marginally significant (P=0.0640) and the same argument as for bite number can be adopted here. There were no significant effects of the sward height or the depth of regrowth of the succeeding patch in sequence on the quantity of herbage removed from the current patch.

Table 5.67 Extract from the analysis of variance table for the influence of the regrowth depth and sward height of the adjacent patch in sequence on herbage removed from the current patch in Experiment 4.

Source	DF	SS	MS	F Value	Pr > F
Regrowth depth†	2	256931.88	128465.94	82.56	0.0001
Sward height†	2	23515.04	11757.52	7.56	0.0011
Regrowth depth† x Sward height†	4	29030.08	7257.52	4.66	0.0021
Prev* Regrowth depth†	2	2870.15	1435.07	0.92	0.4023
Prev* Sward height†	2	16111.48	8055.74	5.18	0.0079
Nxt# Regrowth depth†	2	498.33	249.16	0.16	0.8523
Nxt# Sward height†	2	70.40	35.20	0.02	0.9776
Prev* Regrowth depth† x Prev* Sward height†	4	14504.35	3626.09	2.33	0.0640
Nxt# Regrowth depth† x Nxt# Sward height†	4	4518.25	1129.56	0.73	0.5771

†Nominal treatment effects
*Prev = Preceding patch, #Nxt = succeeding patch

5.11 DISCUSSION

The primary objective of the three experiments presented in this chapter was to assess whether preference was influenced by the structural characteristics of plants. Across the three experiments, patches of vegetation were organised to present cattle with contrasts in whole sward maturity as well as swards with defined strata of leaf and stem. Black and Kenney (1984) have argued that animals preferentially select the forage offering the greatest potential rate of intake and this is in line with the rate maximisation concept (Marginal Value Theorem) (Charnov, 1976). However, the accumulating evidence across species implies that foraging behaviour on two component grass-clover (Parsons *et al.*, 1994a; Cosgrove *et al.*, 1995; Penning *et al.*, 1997) and grass-heather (Clarke *et al.*, 1995; Hester *et al.*, 1996) mosaics does not necessarily support this concept, though there may be a stronger case for its importance when animals are grazing a monospecific sward. In this context, and given the substantial number of studies defining the control of rate of intake, the secondary objective of the studies was to monitor the manner in which preference behaviour on any individual patch, for example depth of penetration, may have been modified by the possible constraints imposed by plant structural effects, such as the ratio of leaf:stem and the regrowth depth:stubble height interface. Although the two objectives essentially reinforce each other, they will first be discussed separately.

There are two main areas of difficulty in interpreting data of the kind presented in this chapter relative to existing published material. The first is that preferential behaviour has been monitored by a number of different means. Many of the recent studies investigating structural effects have attempted to match behaviour to an index of nutritive value such as digestible protein, and under these circumstances few, if any, of the other indices of nutritive value are given. Further, additional descriptive information on canopy structure is often not presented, making interpretation across studies extremely difficult. The second issue that arises is the added complexity of the fact that structural and maturity effects are naturally confounded in field based experiments. Where behaviour may be matched to an index of nutritive value, which usually favours the shorter and less mature sward over the tall mature sward (eg. Illius *et al.*, 1987), it has not always been clear whether the relationship between the behavioural pattern and sward maturity would hold if the short immature sward is associated with a reduced intake rate. These issues need to be borne in mind throughout the discussion that follows.

5.11.1 Sward structure and morphology effects on preferential grazing behaviour

In Experiment 2, cattle exercised choice for the taller swards, increasing the number of bites removed with increasing sward height. This preferential selection of taller swards is in agreement with the unpublished data of Clark *et al.* discussed by Illius and Gordon (1990), Illius *et al.* (1992) and Dumont *et al.* (1995a and 1995b) and is predicted by the morphophysiology and size model of Illius and Gordon (1987). The curvilinear (quadratic) response pattern between bite number and sward height takes the form of the typical functional response curve (Spalinger *et al.*, 1988; Demment and Laca, 1994). The curve depicted in Figure 5.3 shows that above approximately 14 cm further increases in sward height gave rise to only marginal increases in the number of bites removed. A declining rate of biting with increasing sward height is almost invariably associated with increasing bite mass (Hodgson and Jamieson, 1981; Phillips and Leaver, 1986; Langvatn and Hanley, 1993; Wallis de Vries and Daleboudt, 1994; Dumont *et al.*, 1995b; Wilmshurst *et al.*, 1995). Although there were no estimates of bite mass in this particular experiment, there was a declining rate of biting with increasing sward height and this suggests, indirectly, that the marginal response in the number of bites removed was a reflection of the size of each bite harvested.

In the literature it is widely established that bite mass is the main determinant of intake rate, where the other component in the equation is the rate of biting (Hodgson, 1985). Penning *et al.* (1994) have argued that bite mass is more sensitive to variations in green leaf mass than sward height on rotationally grazed pastures. If preference is strongly related to patterns of potential rate of intake then it should follow that preferential behaviour will be directly correlated with bite mass and any lower order variables that influence this bite dimension. In Experiment 2 there was an increase in ryegrass leaf content with increasing sward height and similar relationships (green material with sward height) has been observed in another study (Dumont *et al.*, 1995b). This clearly demonstrates one of many of the confounding effects between sward height and other patch characteristics. As a consequence of this, in Experiment 2 the relationship between bite number and sward height was only marginally stronger than that of bite number and leaf mass. It was not possible to establish whether cows were responding to sward height and leaf mass independently or additively, and further studies are required to define the separate effects of leaf mass and sward height on preferential grazing behaviour. The sward contrasts presented to animals in Experiment 3 were aimed at separating out this confounding effect.

Additionally, in Experiment 2 there was a strong reluctance by cattle to prehend bites and spend time grazing the short, 8.3 cm swards. Similar observations with cattle on 7 cm cocksfoot swards were reported by Dumont *et al.* (1995a). The similarity between these results is supportive of the argument that cattle are constrained by the shape of their harvesting apparatus. With short tillers generally considered stiffer, the "sweeping effect" of the tongue is less effective at capturing and grasping tillers, and tillers spring back from the mouth escaping severance (Laca *et al.*, 1993a). The shortness of tillers themselves add further difficulties in prehension. However, the time spent grazing on short swards can be related to the contrast between the choices offered and the duration of the recording period, and this is reflected in the fact that the magnitude of the values presented for the short swards was greater in Experiment 2 compared to those in the study by Dumont *et al.* (1995a).

In Experiment 3, the addition of a strong maturity contrast (leaf:stem ratio 2.51 for short immature swards and 0.72 for tall mature swards) saw a reversal of the preference pattern established in Experiment 2. Cattle under these circumstances preferentially grazed the short immature sward (13.4 cm) over the tall mature sward (21.9 cm) at both similar (T1&T2 vs T4) and different (T1&T2 vs T3) quantities of whole sward herbage mass per patch. There are a number of other published studies supporting the concept that animals, when faced with the choice between a short immature sward and a tall mature sward, preferentially select the short immature choice. Illius *et al.* (1987) reported that cattle grazing a predominantly ryegrass sward preferentially grazed short (8-9.5 cm) patches over tall (15-16.5 cm) patches, where the tall patches could be considered more mature given their lower organic matter digestibility. However, according to digestive physiology theory, feeding by cattle on forage lower in nutritive value may be offset by the more efficient digestion of stemmy material as their digestive tract has evolved to allow extended retention of the cell wall fraction of forages, a component which increases with plant maturation (Minson, 1982). More recently greater contrasts in sward maturity have been targeted. Red deer were offered a series of timothy swards at different stages of maturation, achieved through differential sowing dates (Langvatn and Hanley, 1993). Mature swards were characterised by greater herbage mass but were of lower nutritional quality as measured by the concentration of digestible protein and dry matter digestibility. In the later trials when there was a strong contrast between swards in the stage of maturity, utilisation of the immature swards was higher than that of the more mature swards. Wallis de Vries and Daleboudt (1994) categorised patches within both a browntop/fescue and a perennial ryegrass grassland as short and immature (<7 cm, no flowering stems), tall and immature (>7 cm, no flowering stems) and mature (variable height, 3 or more flowering stems). Steers responded to the contrast in maturity and nutritive value between the short/tall immature swards and the mature swards with a greater proportion of their bites removed from the immature swards. Wilmshurst *et al.* (1995) offered wapiti free choice of a mixed-species sward, with patches manipulated for synchronised periods of regrowth. Wapiti preferentially selected the swards with 4 weeks regrowth, the forage being less mature than that on the 10 week swards. Using strips of cocksfoot, Dumont *et al.* (1995a and1995b) found that cattle concentrated their time on the vegetative (18 cm) sward when it was paired with a reproductive sward (no comparative value for sward height was given but the assumption would be that the height of the reproductive sward was greater than 18 cm). What is clear from these five studies, as was the case with Experiment 3, is that sward height and sward maturation effects are essentially confounded. There appears to have been little attempt at separating out the independent effects of sward height and maturity on preferential behaviour, and this must raise concerns over the interpretation of existing studies, since it remains obscure as to what the magnitude of the effect of sward maturation would be when short immature swards are associated with a lower rate of intake. This in turn raises questions over whether larger bodied animals select for nutrient intake rather than the rate of dry matter intake. These effects need to be determined in future studies.

Unfortunately in Experiment 3 the accidental grazing by calves of the experimental site negated the opportunity to manipulate patch area to obtain the contrast in green leaf mass per patch. Nonetheless, leaf mass (consideration of ryegrass leaf only) was greater on T3 (84.5 g DM patch^{-1}) than T1&T2 (63.4 g DM patch^{-1}). That this did not encourage cows to graze the tall swards with an apparent greater mass of ryegrass leaf suggests that some other more dominant factor or a series of interacting factors may override potential bite mass. Cattle are commonly referred to as exhibiting a more passive grazing style since they generally exhibit less discrimination between sward components under intensive pastoral systems than sheep (Grant *et al.*, 1985; Nicol and Collins, 1990), although on a tropical forage where the canopy structure presents a sparse mass of tall flowering stems cattle can adjust their degree of selectivity by pushing aside the flowering stem to graze selectively on leaf at the base of the sward (Ruyle *et al.*, 1987). This contrasts with the active grazing style by sheep who have the capability to select between leaf and stem when finely interspersed (L'Huillier *et al.*, 1984), and are also more willing than cattle to penetrate deeper into the sward canopy to preferentially select green leaf rather than grazing indiscriminately within in the surface strata when a large proportion of reproductive stem material is distributed within the surface strata (L'Huillier *et al.*, 1986). No supporting data was collected on the distribution of leaf within the sward canopy but the preference for short immature swards does indicate that it is not the total amount of green leaf mass that is important but rather that the intermingling of leaf and stem components into a fine scale mixture may create negative effects on patch appraisal and assessment (Demment and Laca, 1993).

An additional objective of Experiment 3 was to assess whether, after some depletion of the initially preferred sward, animals would switch to the initially less preferred sward. The observations from the second grazing session showed quite clearly that while mean sward height (grazed and ungrazed material) on the short patches declined from 13.4 cm initially to 8.8 cm after the first grazing session, a level which would be expected to restrict bite depth, and bite mass (Dumont *et al.*, 1995b), given the constraints imposed by the harvesting apparatus, animals did not switch their preference from grazing the short sward to the taller mature sward. This result contrasts with the behaviour in Experiment 2 where animals showed little interest in a short vegetative sward only 8.3 cm high, and also in Experiment 1 (Chapter 4) with vegetative swards of 8.9 cm in height. Under different experimental conditions to that used in the experiments reported in this chapter, both cattle (Dumont *et al.*, 1995a and 1995b) and wapiti (Wilmshurst *et al.*, 1995) have been observed to exhibit behaviour where sward height overrides any effect of maturity. In the study by Dumont *et al.* (1995b) cattle preferentially grazed the reproductive sward when the sward height of the vegetative sward was 11 or 7 cm. The main finding from the study by Wilmshurst *et al.* (1995) was that wapiti preferred the patches with intermediate levels of herbage mass (4 weeks growth, sward height unspecified) and this coincided with the highest rate of energy gain as predicted by their model. However, wapiti spent approximately 20 % of their time grazing patches of 8 and 10 weeks growth, on herbage characterised by greater concentrations of acid and neutral detergent fibre, but very little time (<2 %) on short swards (2 weeks growth). These authors went on to explain that the observation that animals spent lesser amounts of time in patches with more herbage mass kept in line with the predictions by the energy gain model, but the net energy gain curve they constructed in Figure 5 of their paper suggests the net energy intake would have been greater on the patches with 2 weeks growth than those with 8 or 10 weeks growth. The near avoidance of the short patches with 2 weeks growth suggests that the short sward height over-rode any maturity effect or matching of net energy intake.

Although sheep are nutrient concentrators and their body size relative to metabolic requirements is high compared to cattle (Gordon and Illius, 1988; Hodgson *et al.*, 1994), Prache *et al.* (1997) found that within a sward comprising vegetative and reproductive tillers, sheep initially grazed vegetative tillers preferentially, but consumption of reproductive tillers (partial switch) increased substantially as the height of the vegetative tillers declined below 8-9 cm irrespective of the relative proportion of vegetative tillers available in the sward. The absence of any reversal in preference by cattle to the tall mature swards in Experiment 3 was perhaps a surprising result. One factor which may have contributed to the decision to continue grazing from the short swards in Experiment 3 but not in Experiment 2 was the contrast in whole sward leaf bulk density, a sward characteristic identifiable with tropical forages (Stobbs, 1973). Though the non-destructive nature of the experimental design made it difficult to estimate mean conditions in the second session of grazing, leaf bulk density on the short patches in Experiment 2 prior to the first grazing session was substantially greater (0.73 mg leaf DM cm^{-3}) than that on the short (8.3 cm) sward in Experiment 2 prior to grazing (0.31 mg leaf DM cm^{-3}). The potential influence of leaf bulk density on preferential behaviour cannot be established from this experiment alone. In the literature the influence of bulk density for temperate forages has largely been ignored on the premise that sward height is considered the dominant factor influencing bite mass (Hodgson, 1985). Recently, WallisDeVries *et al.* (1998) have added that even in the presence of a flowering canopy, bulk density may not have an impact on the bite mass of cattle. Whether these principles extend to leaf bulk density is less clear. In perhaps a more isolated argument, Burlison *et al.* (1991), working with sheep, suggested that on very short swards bulk density may assume greater importance than height. Combined with a faster rate of biting permitted through animals biting and chewing simultaneously, activities which are not mutually exclusive on vegetative swards, and so processing herbage faster than the rate at which they could ingest it (Laca *et al.*, 1993a), the preference for short swards with a high leaf bulk density may be the strategy adopted to maximise intake rate, at least in the short term.

The mean length of time taken to traverse the sequence of 24 patches was 6.4 minutes (range 4.8 to 10.6 minutes), and it could be argued that the length of the grazing observation period may not have been sufficient time to observe animals switching their preference over to the tall mature sward. Both Bailey (1995) and Duncan *et al.* (1994) reported consistency in preference patterns with time for cattle and sheep respectively, but patch choices in these studies did not offer strong contrasts in sward maturity. In contrast, Dumont *et al.* (1995b) have shown that preference can change over time, and in their study a switching pattern, from the initially preferred 11 or 18 cm vegetative sward to the paired alternative reproductive sward, became evident after 10 minutes of grazing. However, preference is likely to be scale dependent and change according to the rate of depletion. The small patch size (0.76 m^2) relative to the strips (432 m^2 per 3 heifers) used by Dumont *et al.* (1995b) only serves to emphasise the reluctance of animals to switch to the tall mature sward in Experiment 3. Further, the leaf:stem ratio of the reproductive sward in Experiment 3 was substantially lower than the reproductive sward in the study by Dumont *et al.* (1995b) (0.75 vs 1.78), and this contrast may partially assist in the explanation of the contrasting patterns and the absence of a switching pattern. Again, this demonstrates that the relative magnitude in contrast between choices in the environment is an equally important concept in preferential behaviour. The fact that the second grazing session was conducted on the following day, which meant animals had to re-acquaint themselves with information on the range of choices, may also have contributed towards the non-switching pattern. However, though the time taken to traverse the sequence on the following day was even shorter (3.9 minutes, range 1.2 to 6.6 minutes), animals were still reluctant to remove a greater number of bites from the tall mature swards, which does suggest that animals were willing to expend more energy, through searching, in the expectation that they would encounter patches offering greater patch profitability than the perceived reward from the mature patches.

Given the importance of the potential trade-off between forage quality and quantity to the foraging animal, and also the implications over temporal scales of the spatial variation in the environment, more attention needs to be given to how contrasts in sward height and canopy structure influence foraging decisions. It is not known whether one can define, with confidence, what level of maturity contrast between patches of vegetation may be required to over-ride potential benefits from sward height effects. Researchers in France (see Dumont *et al.*, 1995a and 1995b; Prache, 1997; Prache *et al.*, 1998) have focussed recent foraging behaviour studies on whole sward contrasts between vegetative and reproductive swards but there remains very little evidence for how the strata of leaf and stem interact to influence grazing decisions (but see Flores *et al.*, 1993). The goal of Experiment 4 was to address these concerns.

Swards in Experiment 4 were established to study the association and trade-off between the effects of plant maturity and sward height. Contrasts in maturity were achieved at each of the three sward heights through the manipulation of the regrowth and stubble strata. Cattle preferentially grazed those patches with the greatest depth of regrowth whether preference was defined according to the number of bites removed or herbage removed. This result is in contrast with Experiment 3 where the short immature and tall mature swards offered similar depths of regrowth perched on different stubble heights, but the depth of regrowth had little impact on preference. In Experiment 4, fewer bites were removed when the grazed stratum constituted both leaf and stem. This pattern, in association with the results from Experiment 3, strengthen the argument that cattle avoid long residence times on those patches where both leaf and stem are encompassed within the same bite; therefore cattle perceive reproductive stem in the grazed stratum as a major negative determinant of patch profitability, certainly on the initial encounter with patches of this type.

The negative relationship between the number of bites removed and sward height *per se* that was evident for the two deeper regrowth depths was an unexpected finding but reinforces the importance of the effect of canopy structure on preferential behaviour. There was some indication that preferential behaviour was not constrained to just the depth of regrowth but also to herbage mass within that stratum for the deeper regrowth swards. For example the depth of regrowth was similar across T3, T6 and T9 with the taller stubble contributing to the variation in sward height. Herbage mass and leaf mass was greatest in the upper stratum for T3, followed by T6 and then T9. Bite number declined over this sequence. For the medium regrowth depths (T2, T5 and T8) there was not the same consistency in the depth of regrowth and bite number declined with increasing sward height. Values for herbage mass in the upper stratum were similar for T4 and T7, with only a small difference in the depth of the stratum. Bites removed were similar across these two treatments. However, there was inconsistency between the data sets of the amount of herbage removed, when grazing was confined within the regrowth depth (T2, T3, T6 and T9), to the estimate of herbage mass within this strata (comparison of Table 5.45 and Table 5.53), which would suggest animals penetrated the interface. In further discussion, emphasis is given to the penetration patterns determined from the measurements of sward height pre and post graze since this data set is much tighter than that of the herbage mass estimates.

5.11.2 Can lower-order variables assist with the explanation of preferential foraging behaviour?

The set of three experiments reported in this chapter demonstrate the marked influence that structural effects have on preferential foraging behaviour. Cattle showed a consistent pattern for selection of short immature swards once stronger contrasts in plant maturity were introduced in Experiments 3 and 4. These observations, alongside those from two component plant species mixes, raises further questions on whether cattle are "rate maintainers" (Hodgson *et al.*, 1994), applied in the sense that there is an incentive for cattle to select tall swards even if these swards are associated with concomitant declines in nutritive value. More recently (see Illius and Hodgson, 1996) greater emphasis has been placed on the drive to understand the causal mechanism/s underlying foraging behaviour and the cues which are used as determinants of patch behaviour. Of particular interest, in this thesis, was whether cattle modify some behavioural component in response to any decline in rate of intake caused by the selection of shorter patches. Unfortunately the inability to derive accurate estimates of herbage mass in Experiment 4 made direct reference to rate of intake difficult.

There is also need for caution with the comparison of results where regrowth depth has been the measure rather than lamina length. The experiments reported in this thesis measured regrowth depth and though it is considered here as a close approximation to lamina length, regrowth depth may underestimate true lamina length.

5.11.2.1 Is bite penetration regulated by the separate effects of leaf, pseudostem and stem strata?

In Experiments 2 and 4, measurements of bite depth were made from patches where three or four (Experiments 2 and 4 respectively) or more bites had been removed. This benchmark was set because where fewer than four bites were removed it was difficult to ascertain the grazed areas. In this way there was no concern over the bite depth assessment incorporating estimates of material left ungrazed. Patches were never fully depleted in either the vertical or horizontal plane, so bite depth was considered a function of a single bite as opposed to a series of successive bites taken within the vertical plane. For Experiment 3, postgraze height constituted the mean patch sward height for the second session of grazing. This had two major implications, (a) it underestimated bite depth on the first day of grazing and (b) it violated the concept that the influence of sward characteristics on animal behaviour can only be assessed from within the grazed areas of the sward canopy (see Ungar, 1996).

The following material in this section discusses the influence of the presence of leaf, pseudostem and stem fractions and the potential effect of the density and strength of these components on the variations in bite depth and the height at which grazing settled. It also addresses a recent argument that these structural features may influence the applied bite forces, with bite penetration reflecting the relationship between reward and costs. However, in all three experiments, this argument could not be substantiated. Each experiment is discussed in turn, which leads to a degree of overlap in the arguments across experiments. Where arguments are first mentioned, effort has been made to discuss these in greater depth and carry the principles through to remaining experiments where applicable.

In Experiment 2, bite depth was linearly related to sward height (Mursan *et al.*, 1989; Burlison *et al.*, 1991; Mitchell *et al.*, 1991; Laca *et al.*, 1992a; Flores *et al.*, 1993; Bakker *et al.*, 1998). Although the comparison between swards with equal stubble heights (T2, T3 and T4; T5, T6 and T7; T8 and T9) revealed that bite depth was always greatest on the swards with the deepest regrowth, breaking sward height down into the components of regrowth and stubble did not lead to any further improvement in the prediction of bite depth. The consistent penetration by cattle into the stubble, which was of vegetative leaf and pseudostem, suggested that bite penetration was not constrained by the regrowth:stubble interface. Subsequently, there was no evidence of a relationship between bite depth and the depth of the leafy layer, assumed in Experiment 2 as the depth of regrowth, whether linear, or curvilinear as found by Curll and Wilkins (1982)(see Ungar, 1996). Neither was there any indication to suggest that lamina length may play a greater role at taller sward heights as found by Bakker *et al.* (1998) with sheep and guanacos. However, there was evidence that some characteristic of the stubble stratum was limiting further penetration down the stubble profile, particularly for the taller swards. Results from early studies with sheep (Barthram and Grant, 1984) postulated that animals may constrain their bite depth to avoid penetration into a stratum of pseudostem, and therefore bite depth would effectively be determined by the depth of the leafy stratum (Curll and Wilkins, 1982; Hodgson, 1985). However, more recent studies provide no consensus of view about the influence of pseudostem, lamina length, regrowth depth and sward height on bite depth. Edwards *et al.* (1993), Arias *et al.* (1990) and Illius *et al.* (1995) have inferred similar conclusions to that of the earlier studies. However, Flores *et al.* (1993) fed cattle hand constructed swards made from tillers of dallisgrass and varied the pseudostem:sward height ratio to either 0.00, 0.38, 0.50 or 0.70 across two sward heights of 8 and 16 cm. Cattle readily penetrated into the young pseudostem irrespective of the pseudostem:sward height ratio within the canopy. Similar observations have been found by Mitchell (1995) with sheep and goats grazing seedling swards constituting young leaf and pseudostem. The swards used by Flores *et al.* (1993) lacked an inverse relationship between sward height and herbage mass, distribution, which may have influenced results, although Ungar *et al.* (1991) found that a lower stratum of high bulk density did not influence bite depth. This later result may reflect the fact that the study only investigated the influence of bulk density for swards less than 10 cm in height. However, the swards used by Mitchell (1995) exhibited changes in bulk density with increasing canopy depth, suggesting that bulk density is a possible, but unlikely, factor operating to influence penetration. Complicating the issue is the finding by Mitchell (1995) that avoidance of pseudostem reflected the age of pseudostem development as much as its vertical placement in the canopy. This result then suggests that the force required to fracture pseudostem, which increases with plant age and is three times that of the force required to fracture leaf in tensile mode (Wright and Illius, 1995), could influence bite depth relationships. Additionally, Gong *et al.* (1996b) reported that sheep penetrated into a stratum of pseudostem on short swards but on taller swards grazed height approximated the top of the pseudostem strata.

Parsons *et al.* (1994a) commented that pseudostem height is usually 0.6 sward height. This is substantiated by Mursan *et al.* (1989) who recorded pseudostem height as a fraction of sward height as 0.52 and 0.58 for ryegrass swards 5 and 10 tall respectively, and to a lesser extent Edwards *et al.* (1995) with ratios of 0.40 to 0.50 for ryegrass swards over the range 4 to 14 cm. Adopting a conservative approach and accepting the top of the pseudostem as 0.60 of stubble height, pseudostem height could be estimated for the sward in Experiment 2 (Table 5.68).

Table 5.68 The proximity of grazed height to estimated pseudostem height in Experiment 2.

Treatments	T1	T2-T4	T5-T7	T8-T9
Pseudostem height estimate	2.4	4.8	7.2	9.6
Measured grazed height	4.6	6.4	8.3	10.4
Difference	2.2	1.6	1.1	0.8

There is clearly some limitation to this approach, which requires caution, but nonetheless the difference values for T5-T7 and T8-T9 were within the range that Illius *et al.* (1995) interpreted from their results as evidence for the avoidance of pseudostem material. The greater differences for the short swards most likely reflected the greater constraints imposed by the harvesting apparatus of cattle as opposed to goats in the study by Illius *et al.* (1995). Even so, without quantification of the height of pseudostem in the sward it is pure speculation as to whether grazed height (sward height – bite depth) reflected the position of the pseudostem in the stubble stratum. Measurement of pseudostem height in vegetative swards was undertaken for Experiment 5 (Chapter 6) and further discussion on the potential role of pseudostem constraints will be confined to Experiment 5.

In Experiment 2, grazed height settled at a similar position across each level of stubble height for T3 to T9 (Figure 5.4), and also closely approximated the position from which the estimates of strength were made for T5 to T9 (Table 5.5 and Figure 5.1). The variation in strength across these five treatments at the level of grazed height was in the order of 10 Newtons and not significant. The matching pattern of herbage strength and bite depth could be interpreted as implying a maximum force that animals were willing to apply (Hodgson, 1985), particularly since sward height did not constrain bite depth on the taller treatments, although Laca *et al.* (1993a) did not find supporting evidence for a maximum bite force. The estimates given in Table 5.5 represent the force required to sever 3 tillers and do not provide an indication of the applied force per bite. Consequently, there was little basis for defining the biting effort required per unit area or directly relating the data to that by Illius *et al.* (1995).

Illius *et al.* (1995) demonstrated that grazed height is more determined by the forces animals apply, which is influenced by the canopy structure rather than the structural strength of individual canopy components, for example leaf population density is more important than the strength of individual leaves. Woodward (1998), modelling the data of Mitchell *et al.* (1993), also predicted that the energy used to sever a bite increased substantially with increasing density at any given level of sward height. The botanical dissection data in Experiment 2 showed an increase in leaf content with increasing sward height, indicating that the number of leaves per unit area increased with increasing sward height. This was further substantiated by the strong significant increase in leaf bulk density with increasing sward height (0.35, 0.49, 0.58 ± 0.017 for the three sward height groups respectively, P=0.0001), and suggests that the severance of a bite with increasing sward height might have incurred a greater cost. No estimates of bite area were collected but it is unlikely there would have been substantial reductions in bite area since relatively large increases in bulk density are required for a small change in bite area (Mitchell, 1995; Woodward, 1998), and the strength of herbage was relatively consistent across treatments. However, Experiment 2 was not a study of the resistance to defoliation and so there was insufficient data to verify whether the marginal energy intake rate was similar across treatments and whether the trend for grazed height to be elevated with increasing sward height reflected an efficient balance between cost and reward as proposed by Illius *et al.* (1995).

Bite depth generally approached 45-50 % of sward height in Experiment 2. The concept of an upper limit on the depth of penetration, which is regulated by the harvesting apparatus, has been put forward as an alternative explanation (Laca *et al.*, 1992a; Demment and Laca, 1993). Cattle grazing swards of dallisgrass which were vertically homogeneous (Laca *et al.*, 1992a) removed approximately 50 % of sward height if the sward was 100 % lamina indicating no impediment from a pseudostem stratum across a range of bulk densities. In support of a maximum bite depth concept Edwards *et al.* (1995) reported that a similar proportion of height was removed from clover swards as from grass swards, though the canopy structure of clover does not present a lower stratum of pseudostem. There was only a slight discrepancy between actual and predicted/potential bite depth based on the 50 % of sward height concept (Table 5.69).

These results indicate that animals may have been more constrained by a maximum depth of penetration as opposed to any pseudostem or characteristic of the stubble stratum limiting penetration (Flores *et al.*, 1993). Even so, the concept of animals grazing to a constant 50 % of sward height has not always been substantiated, particularly on mini-swards or hand-constructed swards (see Illius *et al.*, 1992; Illius *et al.*, 1995; Mitchell, 1995; Gordon *et al.*, 1996).

Table 5.69 Comparison between measured and predicted bite depth calculated on the maximum bite depth concept for Treatments 1 to 9 in Experiment 2.

Treatment	T1	T2	T3	T4	T5	T6	T7	T8	T9
Measured bite depth	3.7	5.1	6.6	5.7	6.6	10.6	8.2	8.3	10.4
Predicted bite depth†	4.2	5.3	6.7	6.3	7.2	9.7	8.3	9.1	10.6

† Predicted as 50% of measured sward height

In Experiment 3 bite depth was underestimated, as postgraze height included grazed and ungrazed areas. This makes it difficult to comment on regulation of bite depth. Even so, Treatments [1 and 2] were similar in sward composition with Treatment 3 of Experiment 2. Comparison of these treatments revealed bite depth was reduced on Treatments [1 and 2] in Experiment 3 compared to Treatment 3 in Experiment 2 (4.7 vs 6.6 cm). An estimate of 6.4 cm was obtained for Treatments [1 and 2] in Experiment 3 when grazed height was calculated using the bottom 50 % of the postgraze recordings. While calculation of grazed height in this manner over-estimates bite depth, the important point made is that the general pattern of grazing depth exercised by animals on Treatments [1 and 2] in Experiment 3 is comparable with the comparative values for Treatment 3 in Experiment 2. Nonetheless, it is possible that this is an isolated coincidence.

The strength of the upper stratum (top third) in Experiment 3 was substantially greater for tall mature swards and this reflected the presence of reproductive flowering stem within this stratum. The upper stratum (top third) measurement for the tall mature swards (96.5 N), however, was similar to the lower stratum (middle third) measurement for the short immature sward (89.2 N) indicating consistency between sward types around the stubble:regrowth interface. Bite number was strongly correlated with residence time per patch leading to the assumption that leaf was not being selectively grazed. Whilst the shear strength required to fracture three tillers may have been similar, the increased ratio of stem to leaf for the tall mature swards over the short immature swards (1.39 vs 0.40 respectively) and the greater bulk density would have predictably increased the force required to sever herbage encompassed in each bite for the tall mature swards.

For Experiment 4, it was not considered possible, within the constraints operating, to formulate a balanced design which maximised the number of comparison points of stubble height and regrowth depth across sward heights, in addition to targeting the interface to rest at above or below 50 % for the two deeper regrowth depths respectively. The consequence of choosing the balanced design was that the stubble:sward height ratio increased with increasing sward height. It did, however, still allow for study of the influence that the stubble height:regrowth depth interface, when greater than 50 % of sward height, may have on bite penetration.

The greater vertical heterogeneity in Experiment 4 swards led to the relationship between sward height and bite depth, as found in Experiment 2, breaking down. This result indicated that cattle were not responding to sward height directly but simply as an indicator of differences in regrowth depth. The depth of regrowth was therefore only a partial determinant of bite depth. These results contrast with the results presented by Flores *et al.* (1993), where bite depth of steers on reproductive swards was considered to be regulated by the depth of lamina material. This appears to be the only other study of the kind that has differentiated between the effects of lamina length and sward height on penetration within the canopy of swards with mature stem in the lower stratum. The results from this study indicated that bite depth only approximated less than 50 % of sward height when the reproductive stem in the canopy occupied more than 50 % of sward height. In Experiment 4, bite depth expressed as a fraction of sward height declined linearly with an increasing stubble height:sward height ratio (r^2=0.95), and is in agreement with the general principle put forward by Flores *et al.* (1993). However, on a treatment basis, cattle responded to the stratum of stem in a different manner to the cattle in Flores' study. In Experiment 4, the stubble height:sward height ratio was slightly above 0.50 for T2 (0.54) and T9 (0.60), which according to Flores *et al.* (1993) should have constrained bite depth. However, under the conditions in Experiment 4, this explanation appears weak since the ratios for T3 and T6 were 0.40 and 0.46 respectively, but animals failed to exploit the full depth of the regrowth strata of these two treatments. In contrast, when the stubble height:sward height ratio increased above 0.50, for 1.7 cm and 6.4 cm regrowth depths, animals progressively increased their penetration into the stubble stratum with increasing sward height but processing cues led to an early patch departure.

These patterns lead to the conclusion that stubble height is an important determinant of bite depth but it may only be a partial determinant, not an absolute determinant as previously thought (Flores *et al.*, 1993).The extent to which the stubble stratum determines the depth of a bite may be influenced by the age and composition of the stubble stratum. The use of a control treatment has been stressed (Flores *et al.*, 1993) and one was not included in the treatments in Experiment 4, primarily since the objective was not to directly assess bite depth behaviour in response to the different ratios of stubble height to regrowth depth. But even so, T3 was the basis of comparison and could be considered as a control in respect of the interaction between bite depth and the stubble:regrowth interface.

The concept of a potential bite depth appears to fit this data set for T3 and T6 of the deeper regrowth treatments, as the discrepancy between potential bite depth and actual bite depth was small for T3 (0.6 cm) and T6 (1.5 cm), and may simply reflect the difference between incisor height, the slippage of gathered tillers and measured bite depth (Ungar *et al.*, 1991; Laca *et al.*, 1993a). It follows that if animals are influenced by the presence of an old stratum of pseudostem or dead material, for one reason or another, then one would expect that a stratum of reproductive stem and dead matter would initiate a more extreme response from animals. Laca *et al.* (1992a) found that lucerne stem in the lower canopy did not appear to have any negative effect on penetration by cattle, though there may be differences between legumes and grasses which are yet to be recognised. Even so, the implication of the scaling of power with muscle mass (Illius *et al.*, 1995) is that large bodied animals have the potential to exert greater forces, thereby penetrating deeper into the canopy, and may not be as sensitive to constraints imposed by a stratum constituting reproductive stem. On the premise that body mass may be a major determinant of bite depth, one might have expected the steers in the study by Flores *et al.* (1993) to have been less sensitive to a stratum of stem than the cows in Experiment 4 on the basis of the difference in mean liveweight (750 kg vs 504 kg). However, Gordon *et al.* (1996) have argued that, in the interaction between canopy structure and the harvesting apparatus, both mouth size and shape are more important than body mass in explaining variation in bite mass. Given the generalised relationship between bite depth and bite mass (though this was not found in Experiment 4), the assumption can be made that their argument equally applies to bite depth. Additionally, these authors also found evidence suggesting that the effects of body mass on bite depth may be potentially more important at taller sward heights. This is consistent with the observation that the willingness to overcome the constraint of the lower stratum increased with increasing sward height. It is conceivable that, for cattle, the range in sward heights (8 and 16 cm) offered by Flores *et al.* (1993) may have been too restrictive to cause any measurable change in penetration pattern with increasing height. The consumption of reproductive material may constitute a greater cost to the animal in terms of the force required to sever a bite as well as in the processing of that bite, but on tall swards the reward may justify that cost. Therefore the act of grazing on a bite by bite basis may represent a balancing act of the costs and rewards for each bite (Hughes *et al.*, 1991; Illius *et al.*, 1995).

Illius *et al.* (1995) suggested that animals are more willing to overcome the resistance to defoliation after a 2-3 hour period of food deprivation, but these comments are not supported by observations that steers did not increase penetration into the reproductive stem stratum after undergoing a 19 hour fast (Flores *et al.,* 1993). A more recent study (Patterson *et al.*, 1998) confirms this view as these authors reported no significant changes in the bite depth of dairy cattle after fasts of 1 hour or 13 hours. Likewise, differential levels of hunger did not give rise to variations in bite penetration of steers grazing hand constructed swards of dallisgrass in the studies by Griggs *et al.* (1991). Furthermore, the shapes of the relationships between bite depth and bite number found in Experiment 4 would suggest that the boundary of the grazed stratum may not have been established in the study by Flores *et al.* (1993), in which steers only removed one set of 10 bites per sward board. However, it may not be correct to suggest that animals overcome or discriminate against reproductive material as a barrier to grazing at the bite level when bite depth is measured from a mean population of bites and a mean stem height from a population of tillers as noted by Flores *et al.* (1993). On patches with a degree of depletion, the overlapping bite effect would minimise any errors in estimation of bite depth arising from the wide curvature of individual bites. As postgraze measurements were taken from the grazed areas this meant that for patches where fewer bites were removed, there was probably greater precision since there were effectively more readings for every bite removed. Even considering these limitations it does not appear that such a discrepancy could explain the marked contrast in behaviour between the two studies. It is conceivable that the variation in the structure of the lower stratum for Experiment 4 and the study by Flores *et al.* (1993) reflected the contrasting response pattern. The hand constructed swards used by Flores *et al.* (1993) were built so that the lower stratum constituted only reproductive stem, and therefore contrasts with swards which animals would encounter grazing *in situ.* By contrast the stubble stratum of swards in Experiment 4 constituted leaf and stem, with leaf contributing over 50% of the dry matter. This structural feature, the mix of leaf and stem in the lower stratum, is proposed as a likely explanation for the determination of whether reproductive stem is an absolute or partial determinant of bite depth. However, species differences (dallisgrass vs ryegrass) cannot be ruled out as another possible determining factor.

There was no clear explanation as to why the recorded estimates of tensile strength for Experiment 4 increased with sward height within the two deeper regrowth depths, whereas the opposite occurred for the shallow regrowth treatments (Table 5.48). These patterns at best may be explained by the variation in mean tiller size between samples of randomly selected tillers. The poor correlation between bite number and herbage strength probably reflected in part the fact that the position of the upper stratum measurements did not correspond to the grazed stratum, as regrowth depth was greater than planned for, and grazing was not always confined to the regrowth stratum.

On the mature swards (shallow regrowth depth) in Experiment 4 penetration into the sward increased despite a general trend of increasing herbage strength down the sward profile. With increasing penetration there may have been reductions in bite area reflecting the number of sweeping tongue movements declining in response to increasing herbage strength (Laca *et al.*, 1993a). As with the tall mature sward in Experiment 3, the slower rates of biting are primarily a reflection of the greater time and physical effort to detach material with increasingly more stem encompassed within the bite. Bouts of exclusive chewing movements were never observed. Consequently it was unlikely that animals were consciously aware of the greater energy requirement for comminution of stem. Continued grazing of the mature swards, however, might have led to a small further increase in bite penetration but a lower overall bite energy concentration, and the marginal costs may not have justified this. The consistency in the number of bites removed from these three treatments suggests clearly that animals can perceive patch value very quickly.

To summarise this section on bite depth regulation, the results from Experiment 2, where swards were in a vegetative phase of growth, agreed with the literature in suggesting that sward height is the main determinant of bite depth. Animals did penetrate into the stubble stratum but the absence of direct estimates of pseudostem made it difficult to comment on the role of pseudostem as a determinant of further increases in penetration depth. The concept of a maximum bite depth matched the data set with minimal discrepancy but as yet there is no rationale for this concept. Animals penetrated to a similar depth for treatments with equal stubble heights. Leaf density may be an important determinant of the applied bite force, controlling the depth of penetration according to a cost-reward concept. Experiment 4 introduced greater contrasts in the composition of leaf and stem strata as well as the vertical position of each strata within the canopy. The findings showed that bite depth was strongly influenced by the depth of regrowth, but this effect was partial and not absolute since animals increased penetration into the stubble stratum with increasing sward height. Nonetheless, a stratum of stem above the height of potential bite depth does appear to influence preferential behaviour. Increasing penetration into the stubble led to increases in bite mass and would be predicted to increase intake rate, given the smaller variation in rate of biting, but animals did not respond by increasing the residence time or number of bites removed on these treatments. This indicates that animals may have recognised the lower nutritive value of the stubble fraction through the need for a greater bite force and handling time per bite, and the necessity for greater proportioning of energy costs associated with chewing subsequent bites (Illius *et al.*, 1995). The contrast in the characteristics of the regrowth and stubble strata on the degree of discrimination is covered in the integrating discussion (Chapter 7).

These results clearly have major implications with a view to modelling and the ability to predict (a) the location of a bite, (b) the depth of a bite and (c) the composition of herbage within a bite within strata. It is most common for variation in canopy structure across swards of different phenological stage to be defined only in terms of whole sward estimates. The importance of defining canopy structure and the effect on preferential grazing cannot be emphasised too much.

5.11.2.2 Relationship between bite depth and bite number

Investigation of the relationship between bite depth and bite number within grazed patches was confined to Experiment 4, primarily because there were well defined strata of regrowth and stubble, but also because of the substantial number of observations resulting from the increased sequence replication. Using linear regression analysis, bite depth increased with increasing bite number across the 3 sward heights, but the fitting of log curves provided an improved fit to the data values implying that the relationship was not linear. The minor variation between curves for the three sward heights reinforced the importance of the depth of the regrowth stratum on bite depth. For the pooled relationship between bite depth and bite number for the three regrowth depths (Figure 5.12) there was only a small increase in bite depth with increasing bite number over the range from 20 to 60 bites. The shape of the three individual curves over the first 40 bites suggests that in an environment where animals are continually encountering a diverse range of choices the strategy on depth of penetration begins a new cycle at every patch. Initially animals appraised swards with caution, grazing shallow and progressively increasing the penetration into the sward canopy. After a patch dwell time of approximately 20 seconds (based on 60 bites per minute) animals, having removed around 20 bites, had established the potential bite depth for the sward in question and the depth of a bite then became largely independent of bite number. At some point not shown in this study, penetration into a lower stratum must occur (Laca *et al.*, 1994). There is no set point for the penetration into a lower stratum since it will be scale dependent. In the study by Laca *et al.* (1994) penetration into a lower stratum on tall swards (20 cm) occurred after approximately 40 bites had been prehended, whereas in Experiment 4 there was no indication of a substantial increase in bite depth between 40 and 60 bites on the deepest regrowth treatments, and this largely reflected the larger patch area offered (0.76 m^2 vs 0.46 m^2). The similarity in the shapes of the individual curves for the three regrowth depths 1.7 cm, 6.4 cm and 9.6 cm indicated consistent patterns of behaviour within treatments, though the relationship was more relaxed in the deeper regrowths suggesting that the adjustment phase will vary according to canopy structure.

Re-plotting Figure 5.11 to identify data for individual cows showed that there was no suggestion that differences in liveweight (487-522±9.3 kg) explained the adjustment phase of the curve (see Illius *et al.*, 1995). Further, the plot was supported by the lack of any relationship between mean bites per patch and mean bite depth across cows. There were too few observations to be able to define more accurately whether the adjustment phase was association or causation. Nonetheless, the spacing between curves clearly demonstrated the influence the depth of the regrowth stratum exerts on the mechanism animals use during grazing. The asymptotic-like relationship after 20 bites supports other studies where grazing has been described as stratum orientated (Ungar and Noy Meir, 1988; Laca *et al.*, 1994; WallisDeVries *et al.*, 1998), and therefore it is essential that the strata within the sward canopy are defined (see Ungar *et al.*, 1992).

While it could be argued that the grazing pattern shown in Figure 5.12 is of the form that would be expected of a wise grazer, there has been little material to demonstrate patterns in bite penetration over sets of bites within a patch, and even the study by Laca *et al.* (1994) only reported the number of bites removed from the second stratum for each set of bites. Initially the illustration of an adjustment phase may appear to be an issue of minor importance, but it does have implication to the scaling-up of decisions and behaviour from small scale studies of a few bites to larger spatial scales, now widely described as a major issue of concern (Stuth, 1991; Demment and Laca, 1993).

The curves demonstrate that up to as many as 15 to 20 bites on a patch may be interpreted as "sampling" bites, bites that animals use for assessing patch value and for reinforcement to depart from or remain grazing on the patch. The practical implication is that studies which record bite depth over less than 15 to 20 bites are possibly presenting the depth of "sampling" bites as opposed to "maximum willingness to penetrate" and the results of such studies should be treated with caution (eg. Laca *et al.*, 1992a (6 bites); Flores *et al.*, 1993 (10 bites)). Laca *et al.* (1994) did argue that results from short term studies on hand-constructed swards have been consistent with results from field studies where animals removed both a greater number of bites and moved freely between sward patches. Even so, the data for Experiment 4 does suggest that, had the steers in the study by Flores *et al.* (1993) had the opportunity to remove more than 10 bites, penetration may not have been constrained to the depth of the leaf stratum. There may also be important differences between behavioural responses on uniform swards (where the bite provides an adequate picture of the whole sward) compared to very patchy swards. These issues warrant further investigation.

5.11.2.3 Relationship between bite mass, regrowth depth and patch depletion

Of the three studies reported in this chapter, estimates of bite mass were made only for Experiment 4. Intra-species variation, analysed as the cow x treatment interaction, was not significant, consistent with the findings by Laca *et al.* (1992a) and WallisDeVries *et al.* (1998). The following section addresses the within–grazed stratum relationship between bite mass and the number of grazing bites, focussing on the data given in Table 5.53, Table 5.56 and depicted in Figure 5.9.

The values recorded for bite mass below 20 bites in Figure 5.9 and Figure 5.10 are exceedingly high (even deemed impossible) and reflect the difficulties associated with estimating herbage removed using indirect estimates and also from patches where little herbage has been removed (see also comments by Illius *et al.*, 1999). Nonetheless, placing the focus on the patterns within and across sward heights and regrowth depths, there was evidence for the importance of canopy structure on bite mass. Bite mass increased with increasing sward height, consistent with other reports for cattle (Mursan *et al.*, 1989; Arias *et al.*, 1990; Laca *et al.*, 1992a; Laca *et al.*, 1994; Dumont *et al.*, 1995b; WallisDeVries *et al.*, 1998) and sheep (Burlison *et al.*, 1991). Figure 5.9 demonstrated a consistent decline in bite mass with increasing number of bites removed, although the magnitude of the decline is much greater for the current study than that found in other studies (Laca *et al.*, 1994; Distel *et al.*, 1995; WallisDeVries *et al.*, 1998). However, the decline could not be significantly related to bite number which is not in agreement with recent evidence (Laca *et al.*, 1994; Distel *et al.*, 1995; WallisDeVries *et al.*, 1998).

An indirect and approximate estimate of bite area can be made using the minimum and maximum bulk density values of the upper stratum from Table 5.45, based on measurements given in Figure 5.6, the actual sward height values given in Table 5.45, and from the contour diagrams constructed by Ungar (1996) from the data by Laca *et al.* (1992a). A mean patch area of 0.76 m^2 theoretically offered a maximum of between 54 and 63 non-overlapping bites. The very few observations (3 %) of bite number in excess of 54 bites per patch suggested that patch area did not constrain the placement of bites to the extent that with patch depletion an increasing number of bites would have been prehended from a lower stratum. This is substantiated by the relatively stable relationship between bite depth and bite number across regrowth depths after the initial adjustment period (<20 bites) is accounted for. Bite mass is the product of bite depth, bite area and the bulk density of the material encompassed within the bite (Hodgson, 1986). On swards for which animals exhibit strong preference, the fore feet are stationary, and cattle position bites close to an earlier bite. This behaviour necessitates a degree of bites overlapping within a stratum (WallisDeVries *et al.*, 1998). Since the variation in bulk density was small, and not sufficient to compensate, the decline in bite mass was most probably a reflection of the increasing bite overlap with increasing bite number which reduced the effective area per bite.

The steeper decline in bite mass over the first 20 bites (adjustment phase) compared with the second 40 bites for each of the three regrowth depths (Figure 5.9) is more difficult to explain, particularly when bite depth was increasing with bite number over the same range. On the initial encounter with a patch, cattle were cautious grazers with bite penetration being shallow. Animals may have adjusted bite area, but it has long been considered that the influence of bite area on bite mass is of relatively minor importance where there is little variation in the density of the sward canopy across sward types. Without direct estimates of bite area it is difficult to make any further comment on this effect. There would, however, have been a strong contributing influence from the bias introduced from the estimates of herbage removed from patches over this range leading to erroneously high estimates of bite mass. A large proportion of the shallow regrowth swards were within this range. Supporting this was the more consistent estimate on patches with greater than 10 to 15 prehended bites. Nonetheless, Laca *et al.* (1994) using more controlled procedures and where bite mass was estimated from the weight of the extrusa recovered after a set number of bites, commented that over the range of 10 to 60 bites, bite depth increased from 11.8 to 14.6 cm for the tall sparse sward in their study. The estimates of bite mass presented in Table 2 of their paper showed that, over the first 10 to 30 bites, bite mass was relatively insensitive to increasing bite number, though there was indication of a slight declining trend in bite mass. Few bites were recorded being removed from the lower strata over the same range of bite number. The generalised pattern appeared to follow a similar pattern to that in Experiment 4; an increasing depth of penetration into the sward with little, if any declining effect on bite mass over the first 10 to 30 bites removed. The relative magnitude of the steepness of the declining effect measured in Experiment 4 was probably simply a reflection of the variability associated with the precision of the bite mass estimates where fewer than 10 bites were removed. The general similarity between the two results does suggest the pattern observed in Experiment 4 is in fact a real effect, being a very typical response to animals initiating grazing on a patch.

Unlike Prache (1997), who reported results from a study with ewes grazing vegetative or reproductive swards, Experiment 4 advanced the investigation of the potential influence of sward canopy structure since cattle had (a) the opportunity to choose between sward types at one grazing and (b) there was greater definition of heterogeneity in the vertical plane. The generalised relationship between bite mass and sward height held true for the data in Experiment 4. Whereas Prache (1997) found that with continual defoliation of swards, at any given level of sward height, bite mass was always greater for the vegetative sward, the results from Experiment 4 showed the reverse; bite mass was greatest on the more mature sward. This may reflect the stage of development of the reproductive sward since stem is heavier than leaf when considering the mass of each bite taken. Prache's results conform with an earlier paper (Prache and Petit, 1995) that bite mass is sensitive to green leaf mass across swards of varying maturity. Other things being equal, vegetative swards constitute greater concentrations of green leaf. As there was not always uniformity in regrowth depth across treatments within sward structures, the data presented for Experiment 4 is a classical example within one experiment of the influence the depth of the regrowth stratum exerts on bite mass. Within each of the three structures (1.7 cm regrowth depth, 6.4 cm regrowth depth and 9.6 cm regrowth depth) bite mass increased with increasing sward height only when the depth of the regrowth stratum was smaller than the depth of penetration, as was the case for 1.7 and 6.4 cm regrowth depths. Additionally, for the 6.4 cm regrowth depth this effect is exaggerated further because of the fewer bites removed from the taller sward across the three treatments within this structure. The results from Experiment 4 confirm the comments made by WallisDeVries *et al.* (1998), that bite mass estimates are subject to both the initial sward conditions and the degree of depletion, and the results of Experiment 4 extend the definition of initial sward conditions beyond sward height and bulk density to include the composition and spatial arrangement of herbage within the canopy.

Across treatments, bite mass (three fold difference) had a greater effect on intake rate than did the rate of biting (one fold difference). However, the poor correlation between preference and bite mass suggests that, under short-term studies where animals are faced with patches with added complexity in the canopy structure in the vertical plane, then cattle may not always forage in accordance with the rate maximisation concept as has been suggested by Distel *et al.* (1995), where cattle grazed swards vertically homogeneous, and otherwise only varying in sward height and bulk density.

Though it is acknowledged that direct comparison of the absolute values of bite mass with other studies is virtually impossible, the consistency of the observed responses does provide confidence in the inferences drawn. To summarise, the results from Experiment 4 echo the growing number of studies which infer that sward height is not necessarily a reliable predictor of bite mass (Penning *et al.*, 1994; Prache and Petit, 1995; Prache, 1997). However, neither do the results support the concept of whole sward green leaf mass as a predictor of bite mass as these authors have postulated. Instead another dimension, the depth of regrowth and stubble height and their subsequent effect on the interaction between bite depth and bite mass, adds to the complexity of modelling patch preference.

5.11.2.3 Do animals maintain, increase or decrease rate of biting in face of structural constraints on grazing behaviour?

Rate of biting is a function of the time allocated to manipulative movements for gathering and prehending herbage, chewing and manipulation of herbage collected into a bolus and swallowing, relative to the time specifically committed to biting activity. Black and Kenney (1984) suggested that the rate of biting was strongly influenced by the ease of prehension, and therefore is a direct response to the morphology and structure of the sward canopy (Hodgson, 1986). In the experiments presented in this chapter, caution is needed in interpreting effects on rate of biting since animals were continuously moving from patch to patch, and rate of biting on any one patch may also, in part, reflect the quantity of herbage in the mouth, having been ingested from the preceding patch. However, as noted in the previous chapter these effects would have been minimised by the 1-2 second break between patches and the ability of cattle to bite and chew simultaneously (Laca *et al.*, 1992b). The bite rates presented in Table 5.7, Table 5.34 and Table 5.56, in absolute terms, generally fit into the upper limit of the range suggested by Hodgson (1982), and are similar to those recorded for cattle grazing ryegrass swards by Demment *et al.* (1993) (56 to 65 bites min^{-1}) and for cattle grazing cocksfoot swards under field conditions (64 to 71 bites min^{-1}) (Dumont *et al.*, 1995b) but slower than the values recorded by Laca *et al.* (1994) (76 and 84 bites min^{-1}) with cattle grazing hand constructed swards of leaf lamina.

The results of Experiment 2 were consistent with the literature in showing a declining rate of biting on tall swards, which has been correlated with increasing bite mass (Black and Kenney, 1984; Illius *et al.*, 1987; Spalinger *et al.*, 1988; Laca *et al.*, 1992a; O'Reagain *et al.*, 1993; Langvatn and Hanley, 1993; Wallis de Vries and Daleboudt, 1994; Wilmshurst *et al.*, 1995; Gordon *et al.*, 1996; Prache, 1997). The data from Experiment 3 also showed significant negative effects of sward height on rate of biting, largely attributable to the contrasting maturities ie. short immature vs tall mature swards, with short immature swards promoting faster rates of prehension. Similar reductions in biting rate of sheep across swards in the vegetative and reproductive phase of development were observed by Gong *et al.* (1996a). Prache (1997) found with ewes that there was little difference in time per bite between a reproductive and vegetative sward at the beginning of grazing when both sward types offered a large number of easily accessed leaves. In Experiment 3, while leaf mass was greater on T3, the tall mature sward, it appears that cattle, as has been suggested by Demment and Laca (1993) may not have had the motivation to be selective in the choice of plant components, which probably reflects the shape and size of the harvesting apparatus. The ingestion of stem increases handling time per bite (Ruyle *et al.*, 1987; Prache, 1997), and is a reflection of the time associated with chewing (increase in mastication) and preparation of the material for swallowing, which is in itself a direct reflection of the increased fibre content of plant material (Spalinger *et al.*, 1986). Animals on tall mature swards in Experiment 3 also appeared to place bites randomly across the patch, indicating that they were searching, by means of sampling, probably for green forage amongst the stem material. This behaviour also would have given rise to a decline in the number of bites prehended per minute.

The established relationship between rate of biting and sward height was not evident from the data in Experiment 4 (Table 5.56) as bite rate remained largely constant with increasing sward height. Rather, rate of biting reflected the contrasting structures across the 3 sward heights. The initial contrast was between the slower rate of biting (mean 57 bites min^{-1}) on the shallow 1.7 cm regrowth swards and the faster rate of biting (mean 65 bites min^{-1} and mean 62 bites min^{-1}) on the 6.4 cm and 9.6 cm regrowth depth swards respectively; the contrast between the two deeper regrowths was only marginally significant (P=0.0351). The slower rates of biting on the 1.7 cm regrowth depth swards (T1, T4 and T7) probably reflected the greater handling time associated with bites of larger mass (Table 5.56), matching the penetration into the stubble stratum. There would also have been the requirement for the adjustment of the ratio of manipulative to ingestive jaw movements (Laca *et al.*, 1993a) to counteract the proportion of stubble material encompassed within the bite. The decline in rate of biting with declining regrowth depth for these three treatments supports this interpretation. There were no consistent relationships between rate of biting and green leaf mass or the density of leaf in the grazed stratum. Instead it appears there may have been a compensatory relationship with depth of penetration into the sward canopy, of similar nature to the general relationship of increasing bite rate in face of restrictions on bite mass (Hodgson, 1985). Rate of biting was faster on those swards where grazing appeared to be constrained by the regrowth:stubble interface (ie. T2 vs T3; T5 vs T6). A similar comparative observation was not recorded for T8 and T9 which recorded identical rates of biting, and this reflects the fact that there was greater penetration past the interface in T8 compared with T2 and T5. However, the data on bite mass does not provide supporting evidence for this argument, although the absolute values are confounded with patch depletion. Alternatively it is reasonable to consider that the maintenance of a high bite rate on the shorter treatments (T2 and T5) may indicate that animals attempted to regulate bite depth and manipulate bite rate as a mechanism to increase intake rate. While chewing during rumination forms the greater contribution to particle comminution, the act of chewing during initial ingestion is still an important component in the process of the breakdown of digesta particles to the critical size (see Pérez-Barbería and Gordon, 1998). Ingestion of material from the stubble stratum would have increased the size of ingested particles and led to an increase in the energy costs to masticate these particles (Illius *et al.*, 1995). The potential increase in bite mass from short swards may not have offset the lower bite rate, which brings to attention the concept of rewards and costs. Combined with the data from Experiment 3, where maturity contrasts prevailed, the marked preference for shorter swards with a leafy regrowth depth does indicate that the selective behaviour observed appears to support the view that animals may maximise intake rate through the trade-off between bite mass and bite rate (Laca *et al.*, 1992a) or maximise nutritional gain (Senft *et al.*, 1987). These relationships require greater clarification, particularly the question of whether animals foraging in line with the former suggestion maintain this behaviour over the course of a days grazing (see Dumont *et al.*, 1995a).

5.11.3 Nutritive value

The following material briefly covers the relationships between preference and the key nutritional parameters, crude protein and water soluble carbohydrate concentration (Van Soest, 1982), and organic matter digestibility. In general, the fine scale of observation incurs the consequence that the data presented is not appropriate to reinforce any argument that animals may select for nutritional gain rather than for dry matter intake.

The data from Experiment 3 showed that cattle preferentially grazed the patches which contained a higher concentration of crude protein. Similar observations have been reported from a number of other field-based studies (Bazely, 1990; Jaramillo and Detling, 1992; Langvatn and Hanley, 1993; Duncan *et al.*, 1994; Bailey, 1995). Emerging evidence from laboratory-based studies suggests that ruminants exhibit associative behaviour, and can regulate the dietary intake of protein (Kyriazakis and Oldham, 1993), and this can occur in the absence of an increase in DM intake (Görgülü *et al.*, 1996). However, for the experiments presented in this thesis, it is unlikely that there would have been an immediate feedback response given that Provenza (1995) reported that an hour of time elapses before a negative feedback response to tannin content is registered by the animal. The possibility that animals form strong preferences for foods relative to the changes in the ratio of volatile fatty acids (VFA), produced in the rumen by microbial fermentation, has been raised by Provenza and Balph (1990). However, there is still a response lag of around 15 minutes which rules out VFA's as a mechanism animals use for foraging at the scale of a bite.

In Experiment 2, had the concentration of protein ranked high in the selection criteria it could have been expected that there would have been a trade-off between sward height and crude protein concentration for the short treatments (T1-T3). This was clearly not the case. Further in Experiment 2, the number of prehended bites increased with increasing sward height although there was no significant increase in crude protein content across T4-T9. Likewise there was no consistent relationship between bites prehended and the crude protein concentration within the regrowth stratum for the two deeper regrowth depths in Experiment 4. These findings support the conclusions drawn by Ganskopp *et al.* (1996) and Harvey *et al.* (1996) (see Rutter *et al.*, 1997) that crude protein is a weak selection cue and that patch selection does not appear to reflect the need for animals to maintain a carbon/nitrogen balance. However, over longer temporal scales this effect requires greater clarification.

The structure of the tall mature sward in Experiment 3 was considered typical of the herbage cattle encounter during the summer months in New Zealand. The recorded concentrations of crude protein using *in vitro* standards were extremely low for T3 and T4 and to a lesser extent for T1 and T2 (Table 5.30) given that the minimum crude protein requirement for lactation and growth is 15 % (Norton, 1982). On this basis the tall mature sward was closer in matching the nutritive value of a good tropical forage than a temperate forage (Norton, 1982). The high estimates of dead material within the botanical dissections, relative to Experiments 2 and 4, may have contributed to the low crude protein estimates. The similarity in whole sward estimates of organic matter digestibility was also surprising given the variation in the leaf:stem ratio between sward types. Furthermore, using *in vitro* standards, the estimates of organic matter digestibility were only marginally greater than 60 %, which for an immature temperate forage is particularly low (Ulyatt, 1981). However, the contrast in preference was marked and had animals been able to innately sense variations in crude protein concentration one might have expected animals to have spent greater time on the tall mature swards, particularly in the second grazing session when the height of the immature swards would have constrained bite mass. Rather the data suggests that crude protein ranked low in the criteria for selection and that cattle relied on cues other than nutritional gain alone (Longhurst *et al.*, 1979). Additionally, in another experiment running concurrently with Experiment 3, and not reported in this thesis, the same animals were observed to willingly walk the length of 25 patches, in search of other more desirable patches, with little attempt at grazing, if some characteristic of the sward acted as a deterrent to grazing.

In Experiment 3 crude protein concentration was strongly confounded with other features of the canopy structure (Norton, 1982; Henry *et al.*, 1996). However, water soluble carbohydrate did not follow a similar pattern with changes in plant maturity (Hogan *et al.*, 1969), rather there was an inverse relationship between crude protein and water soluble carbohydrate concentration (Table 5.30). An inverse relationship was also reported by Bazely (1990). Dove and colleagues (Dove, 1998) suggest that the animals' preference for swards and plant parts is related to the water soluble carbohydrate concentration. A study by Ciavarella *et al.* (1998) achieved variations in water soluble carbohydrate concentration without any significant effects on the nitrogen concentration, *in vitro* digestibility and neutral detergent fibre content of the herbage. In Experiment 3 preference did not appear to be adverse to a lower concentration of water soluble carbohydrate. Shading the sward for 40 hours, the procedure used by Ciavarella *et al.* (1998), may adjust sward brightness, subtle enough for detection by sheep but not by the human eye. Likewise leaf may be brighter than stem, and so brightness may be the cue used for selection (Bazely, 1990) aside from touch sensations. It certainly would help to explain why sheep do not necessarily select the most digestible leaf within the leaf stratum (Clark, 1993). On the first day of exposure, sheep in the study by Bazely (1990) preferentially grazed tall swards with a lower soluble carbohydrate concentration and higher nitrogen concentration over shorter, lighter green background swards with a lower nitrogen and higher water soluble concentration. Even though sward height was confounded with water soluble carbohydrate concentration, sward height was obviously a stronger cue than water soluble carbohydrate. This is supportive of the data in Experiments 2 to 4, confirming that morphological characteristics, particularly the arrangement and structure of plant fractions which affect the ability to harvest, manipulate material for swallowing, rumination time and subsequent passage rates

(Vincent, 1983; Spalinger *et al.*, 1986), may be potentially more important than forage quality characteristics. Dove (1996) comments that simple sugars, which are correlated with water soluble carbohydrate concentration, may be used as the selection cue. However, a similar argument as that for the scale of response for protein also applies to water soluble carbohydrate concentration. Detailed explanations of canopy structure in addition to nutritive value have long been stressed (Laredo and Minson, 1973; and Hogan *et al.*, 1987) but the focus has remained on nutritive value with the subsequent dismissal of the importance of handling time (Ungar and Noy-Meir, 1988). Recently Woodward (1998) has renewed the call for more detailed information on canopy structure.

5.11.4 Adjacent patch effects

Illius and Gordon (1990) commented that animals may have poor information uptake and retention on the premise that they are repeatedly observed to sample patches even for just a few bites. There was no evidence from the three experiments reported in this chapter (sections 5.4.5, 5.7.1.5 and 5.10.8) that the number of bites removed from the current patch was influenced by the characteristics of the succeeding patch in sequence (Experiments 2, 3 and 4). Further, while treatments were not balanced for a measure of preceding patch effects in Experiment 2, in Experiments 3 and 4 there was no evidence that the characteristics of the preceding patch in sequence influenced the number of bites removed from the current patch. However, in Experiment 4, the analysis did indicate a significant preceding patch effect of sward height on the quantity of herbage removed. This effect appeared to be the consequence of the greater quantity of herbage removed when the sward height of the preceding patch was 16.1 cm than when it was 19.5 or 22.1 cm, but it was an effect that was very much less than the influence of the current patch characteristics on current patch behaviour (regrowth depth F=82.56; preceding patch sward height F=5.18).

These results suggest that cattle either have difficulty in retrieving stored information to aid subsequent decision making or they put more emphasis on current patch evaluation. These comments are also supported by the pattern of bite depth penetration beginning a new cycle at each patch (Figure 5.12). Retrieval of information is considered a separate process from the uptake and retention or storage of information (Packard *et al.*, 1990). Whether information from previous experience of patch conditions or how animals perceived the value of the succeeding patches in sequence was being processed and retained is much harder to substantiate. A more rigorous test for adjacent patch effects was incorporated into the objectives for Experiment 5, and so further discussion on these effects will be dealt with in Chapter 6.

5.11.5 Sampling behaviour

As there was no strong evidence that animals retrieved stored information gained from one patch to make informed choices at the next patch, it is clear that animals relied on the need to sample patches to determine patch reward, possibly relying on handling cues as a mechanism. It is hardly a matter of debate in the literature that animals sample, even within a designated monospecific forage source (Illius *et al.*, 1987; Langvatn and Hanley, 1993; Wallis de Vries and Daleboudt, 1994; Wilmshurst *et al.*, 1995; Dumont *et al.*, 1995a and 1995b), removing bites or spending time in patches that are deemed less than optimal according to the concept of rate maximisation. The observation that animals repeatedly spent time on tall mature patches (T3 and T4 in Experiment 3; T1, T4 and T7 in Experiment 4) despite the fact that they consistently spent more time grazing short, immature herbage supports the argument that there is an incentive for animals to seek tall swards, predicted by the incisor breadth model (Illius and Gordon, 1987). The continual process of removing a few bites from the tall patches may indicate the potential value of patch height as a cue, but the cue does not always correlate with patch value (Illius and Gordon, 1993). In Experiment 3, the sequence of treatments did not alter for the second session of grazing. If animals had formed an association that tall swards were the non-preferred patch type (poor patches) in the first grazing session and had retained a strong spatial memory of the location of food patches (Edwards *et al.*, 1996; Laca, 1998), in the second session they should have ignored the tall mature swards. That animals did not completely ignore the tall patches suggests that when grazing in a competitive environment animals may place little value on spatial memory retention. However, it is difficult to separate out the individual effects of poor association from poor spatial memory.

Kendrick (1990) has argued that sheep have the ability to recognise visually, at the next encounter, a preferred patch. Given that there were no clear patterns of animals rejecting tall mature swards after the first encounter (T3 and T4 in Experiment 3; T1, T4 and T7 in Experiment 4), this suggests that cattle may have difficulty in forming immediate associations between patch cues and patch rewards. This does not however negate the possibility that cattle are capable of forming associations, rather it may suggest that the length of exposure to the sward types was not sufficient to learn the association. Schaeffer and Sikes (1971) showed that whilst dairy calves adapt to a novel learning environment, they do vary in the rate of learning. In another study Kovalčik and Kovalčik (1986) showed that the learning ability of heifers was substantially greater than for mature cows but, six weeks following the initial learning tests, mature cows exhibited a more stable memory, thus implying a greater ability to retrieve information from the learning tests. Edwards *et al.* (1997), considered that a feature of their study was the ability of sheep to form an association quickly and reliably (few discrimination errors made after six trial runs), but the response was not immediate as at the first exposure sheep made choices that were not significantly different to those if they had foraged at random. In the three experiments reported here, animals had only one exposure (two for Experiment 3) with replication of patch choices, implying that repeated exposure is an essential premise for animals to form associations, and replication of patch types within an exposure will not suffice. Furthermore, Edwards *et al.* (1997) presented sheep with more recognisable and distinguishable cues, ryegrass and white clover from which leaf shape may have been the mechanism for recognition since animals are generally thought to be able to discriminate between shapes (Baldwin, 1979 and 1981). There is less convincing evidence that cattle exhibit high levels of acuity (Entsu *et al.*, 1992). Where the changes in the appearance of food resources are much more subtle, as with the local variation in sward height, there remains uncertainty as to whether (a) cattle fail to discriminate between small variations in height or (b) they respond visually to the small variation which is sufficient for immediate learning or activation of associations, which reinforces the argument that patches are worth the effort to exploit.

In Experiment 3 there were greater contrasts in visual cues, a reflection of there only being two levels of height. According to Stephens and Krebs (1986), sampling is correlated with the contrasts in choices, but this argument does not appear to hold true for the observations in Experiment 3. Further, this rule uses the premise that animals are capable of retrieving stored information for subsequent decision making over short and long temporal scales, but there is no conclusive evidence for this in Experiments 2 to 4 reported here. Though 38% (18 of 48) of patches allocated T3 or T4 in Experiment 3 were not grazed, a closer examination revealed that the majority of these patches (15 of 18) were assigned to T4. As the sward of T4 was considered to be of similar height and structure to that of T3, the rejection of these patches may have reflected their position within the foraging path. To avoid increasing the distance between patches, patches assigned to T4, as a consequence of patch size reduction, only extended across half the width of a standard patch. Animals walked down the length of each sequence with a foraging path approximately in the middle of the patches. To initiate grazing on patches assigned T4, they were required to forage in a position with their head turned aside (see postures defined by Jiang and Hudson, 1993), which would have equated to a deviation from 0^0 (moving directly forward) to approximately 45^0 or 315^0, dependent on which side of the sequence animals grazed. This would have represented a substantial adjustment for the animal in terms of body balance. Also, as a direct consequence of the positioning of the fore legs the effective feeding station area, the semi-circular area in front of, and to each side of the animal, would have been reduced. This apparent reluctance to sample T4 suggests that animals are adverse to make deviations from their foraging path and such patterns of behaviour should be clearly separated from any evidence for the acquisition and retrieval of information.

Contrary to these arguments for the lack of evidence for association, animals in Experiment 2 missed 67 % (8 of 12) of those patches assigned T1 (sward height 8.3 cm) which suggests that some form of recognition was at play. Two cows failed to sample T1 entirely and one cow removed only one bite at the first patch and ignored subsequent patches of T1. The fourth cow removed 7 bites at the first encounter but only 1 bite at both the subsequent encounters. The first encounter of T1 was at the 8th and 7th patch for sequence 1 and 2 respectively. Consequently the general pattern across cows suggests that, since animals had some prior knowledge of patch conditions they were likely to encounter, having grazed 7-8 patches within the sequence, they recognised very short swards. It is, however, difficult to rationalise how animals would have sensed the potential difficulties in severance of short herbage, particularly when there is little evidence for short-term information recall from previous grazing experiences, and the accumulating evidence also points towards the necessity for definition of patch value through the accumulation of information from the removal of a few bites. The ability of animals to recognise very short patch heights (c. 8 cm) when they appear to have limited ability to differentiate between heights of taller swards appears at odds with a visual perception role. One possible mechanism may be the extension of the head and neck. Where there is a steady stream of continuous patches animals are engaged in searching for food with head down (for changes to this pattern see Chapter 6). Jiang and Hudson (1993) have reported that various foraging positions influence the effective area of feeding stations, and the neck angle may influence patch departure. Whilst there appears to be no existing evidence it is feasible to postulate that the animals' willingness to manipulate the neck angle may influence the preference for patches low in the height spectrum, and therefore initiation of grazing. On this premise there may be an optimum range for the neck angle and patches where the neck angle falls outside of this range are subsequently ignored on further encounters.

However, in contrast to this concept is the finding that animals in the second grazing session of Experiment 3 maintained their preference for the short immature swards even in light of swards only being 8.8 cm tall prior to the second grazing session. This result suggests that one possible strategy might be for animals to adjust their neck angle as a means to graze herbage from the shorter swards only in circumstances where the characteristics of the few other offered choices are considered of low reward value. This could reflect a rational decision to avoid travelling for long distances without food ie. minimising the travel costs per bite or the necessity to switch and graze patches incurring greater handling costs per bite. Although the circumstances are different, Bazely (1990) found that sheep in her studies stayed on ryegrass patches longer than expected according to foraging theory, possibly reflecting the risk of not finding another preferred patch quickly, when the contrasts in choices were either good or poor patches. Of the limited data available, the pattern of evidence suggests that animals adjust their behaviour according to the choices offered, and this may include grazing patches under 8-9 cm, patches which in an environment with greater choice would be rejected. Subsequently any strategy may involve staying longer than the rule of rate maximisation (but see Kyriazakis, 1997), but any disadvantages are offset by the minimisation of travel costs per bite. The extension of the neck angle may be one possible mechanism animals employ to graze shorter swards, either directly related to sward height or used as a "rule of thumb" in that outside the optimum range bite penetration may lead to the ingestion of soil particles. Since animals normally reject very short patches there must be an associated cost, possibly the reduced awareness of competitors and environmental surroundings when the neck angle declines. However, as the animal must consume food for metabolic requirements, foraging for immediate needs may outweigh the principles for longer term food intake. These issues require greater clarification.

Patterns of sampling behaviour in these three experiments may have been influenced by the regular spacing of patches. The consequences of selectivity and sampling may assume more or less importance when food patches are randomly distributed within the environment and less is known about encounter rate with vegetation types (Thornley *et al.*, 1994; Clarke *et al.*, 1995). Chapter 6 incorporates a greater variation in inter-patch distance, and further discussion will be dealt with in that chapter.

5.12 CONCLUSION

In conclusion, the three studies reported in this chapter have attempted to tie together, under similar experimental conditions and the same set of animals, the influence of sward structural and morphological contrasts on preferential grazing behaviour. Little attention was given to defining relatively small differences between treatments, with greater emphasis being placed on the patterns across treatments. Experiment 4 appears to be one of the first field studies that has attempted to separate out the influence of regrowth depth and stubble height, and thus the relative importance of sward height and maturity on foraging decisions. The studies reinforce the view that foraging decisions are highly sensitive to the vertical distribution of plant components. Under vegetative sward conditions (Experiment 2) decisions appear to reflect the variations in sward height. The addition of sward maturity adds to the complexity of the decisions animals face and the results of Experiment 3 suggested animals may trade-off maturity for leaf within the grazed stratum. This was confirmed with the data presented for Experiment 4. For larger bodied animals, such as cattle, leaf mass may not necessarily be a sufficiently reliable measure for the prediction of foraging behaviour because, when offered a similar whole-sward leaf allowance, cattle exercised a choice for patches where reproductive stem encompassed within a bite was minimised (Experiment 3).

The variation in the patterns and relative importance of the regrowth and stubble strata on the depth of bite penetration raises the need for awareness of the contrast between the two strata in addition to defining their height. The implication of the bite depth data presented in Experiment 4 is that if the proportions of regrowth:stubble height were altered then changes in bite depth patterns would follow. Stubble height was only a partial regulator of bite penetration but strongly influenced patch residence time. Bite depth as a proportion of initial sward height varied across the studies, clearly raising questions about the validity of generalising relationships between bite depth and sward height. Despite the number of studies over the last decade that have made reference to the influence of pseudostem constraints on bite penetration and the manner in which bite depth and bite mass may be interrelated with the reward relative to the cost of procuring a bite (eg. Hughes *et al.*, 1991; Illius *et al.*, 1995), there still remains no conclusive evidence as to why grazing is observed to settle at the height it does. There is a clear need to resolve this question.

In all the experiments reported in this thesis, patch encounter rate of each sward type within each experiment was constant. In environments exhibiting considerable heterogeneity, short immature patches may be preferentially grazed but if longer-term behaviour follows the prediction that cattle benefit in terms of daily intake rate by grazing tall mature swards (Illius and Gordon, 1987), then the encounter rate with tall mature patches would need to be high. In intensive production systems this is unlikely to occur, although the opposite may hold true for extensive ecosystems. The limited evidence for adjacent patch effects suggests that the behaviour on the current patch is independent of other patches in sequences, and raises concern over the assumptions of optimality models where animals are assumed to calculate the rate of previous and expected gain. The implication of these responses will be discussed further in Chapter 6.

SIX

SPATIAL DISTRIBUTION

Experiment 5 An evaluation of the influence of inter-patch distance in relation to sward height and patch area on the foraging behaviour of dairy cattle

6.1 INTRODUCTION

The influence of the characteristics of individual patches on discriminatory behaviour was considered in Chapters 4 and 5. The distribution of rich and poor patches in the environment is also expected to influence the degree of depletion and residence time on any patch (Demment and Laca, 1993). The classical foraging model predicts that animals will accept or reject food types (zero-one rule) but current evidence suggests that ruminants spend much of their time as generalist herbivores, grazing amongst rich and poor patches (for example see grass-clover comparisons by Illius *et al.*, 1992; Parsons *et al.*, 1994a). The premise that animals should depart from a patch when the net gain from staying drops to the expected gain from travelling to, and beginning at, a new patch forms the structure of many linear models. However, there are mixed reports on optimal patch departure in addition to rate maximisation as a currency for patch selection in ruminants (Bazely, 1988; Laca *et al.*, 1993b; Distel *et al.*, 1995).

There was little evidence from Experiments 1 to 4 that the characteristics of either the preceding or succeeding patches influenced behaviour on the current patch, raising some concern about extrapolation of the theory of optimality to grazing ruminants. Evidence in the literature suggests that animals are capable of carrying images or mental maps of their perceived environments (Bailey *et al.*, 1989; Hosoi *et al.*, 1995) which suggests that in the experiments to date, animals may have quickly assessed the image of a sequence of patches in close succession and adjusted their behaviour accordingly. The focus of this final experiment was on the spatial distribution of patches, with the key objective being to rigorously assess the capabilities of animals for computing sets of patch choices. Inter-patch distance was varied in addition to contrasts in patch area and the conventional variable patch height. The contrasts in patch height offered variations in potential rate of intake and the contrast in patch area provided the opportunity to maintain intake rate for different durations.

6.2 PATCH TREATMENTS and MANIPULATION

Sets of 8 combinations of 2 patch areas (manipulation of patch length), 2 patch distances and 2 sward heights in a 2 x 2 x 2 factorial design were set up over November to December 1997 (Table 6.1). Due to restriction on strip length each set of 8 treatment combinations was replicated over one complete block (patches 2 to 9) with an additional half block (patches 10 to 13), which over 4 sequences provided a further 2 blocks, confounding the three factor interaction. A patch at either end of each sequence made it possible to test behaviour for adjacent patch effects. In this experiment, current patch distance refers to the distance the animal has to walk from the current patch to reach the next patch in sequence (Figure 6.1). For adjacent patch effects, preceding patch distance then refers to the distance the animal had walked between the last and the current patch (Figure 6.1), and succeeding patch distance refers to the distance in front of the next patch in sequence (Figure 6.1). Randomisation was restricted as in Experiment 4 to balance the effect of adjacent patch effects over the levels of the main effect and then approximately over levels of the two factor interactions.

Table 6.1 Treatment structure for Experiment 5

	Inter-patch distance			
	0.45 m		5.00 m	
	Patch area		Patch area	
Sward height	Small	Large	Small	Large
Short	Treatment 2	Treatment 1	Treatment 6	Treatment 5
Tall	Treatment 4	Treatment 3	Treatment 8	Treatment 7

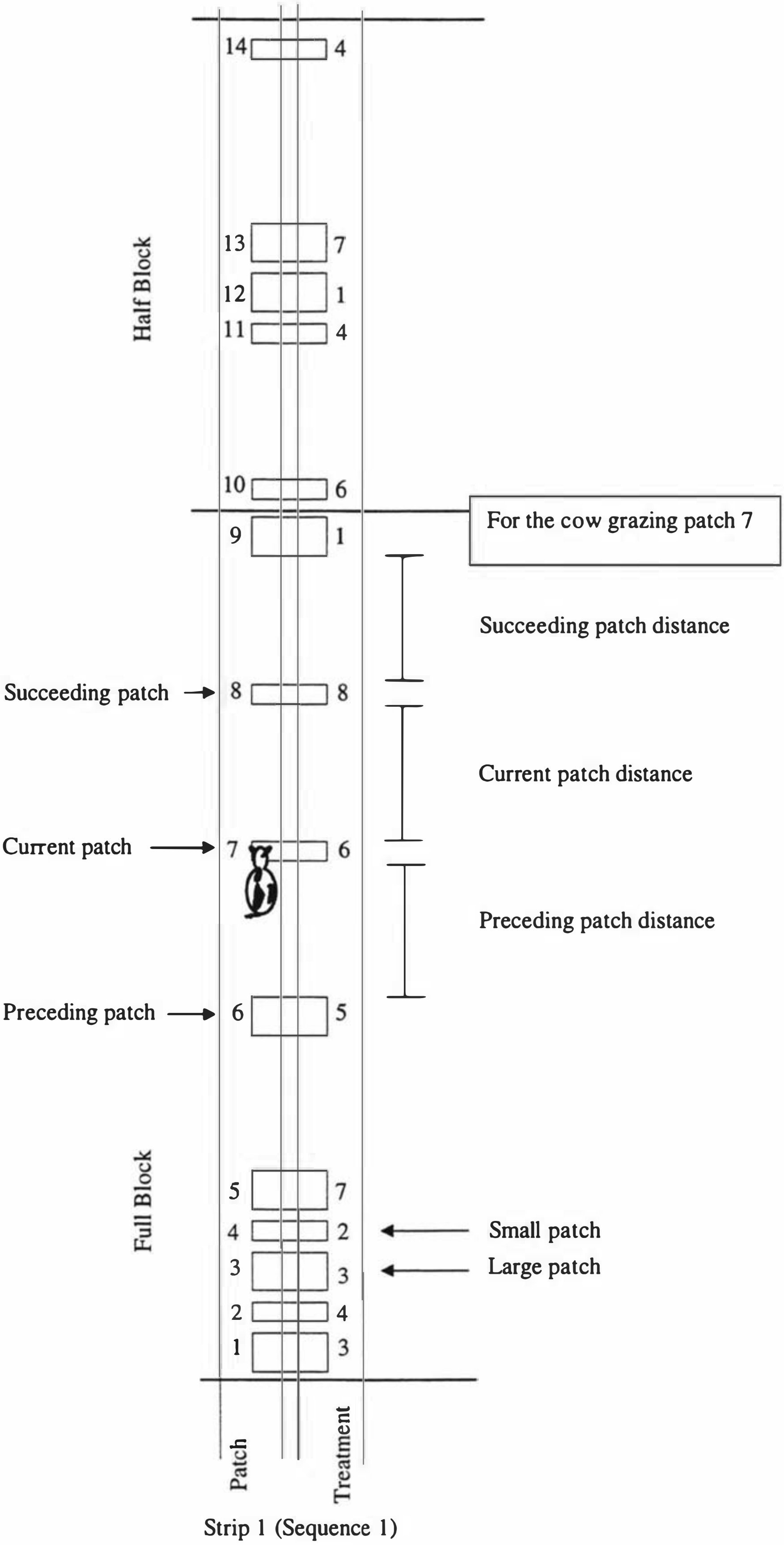

Figure 6.1 Illustration of sequence structure for strip 1 in Experiment 5. Patch distance effects are illustrated for the grazing of patch 7.

Patch area contrasts were created by adopting the standard size, referred to here as a 'small' patch, used in Experiment 4 (0.70 x 0.875 m) and increasing the length dimension by a factor of 2, providing a 'large' patch with dimensions 1.40 x 0.875 m. Patch distance contrasts were achieved by increasing the distance between patches for half of the treatments from 0.45 m to 5.0 m. Contrasts in sward height were achieved by synchronised regrowth intervals, 5 weeks for the tall sward and 3 weeks for the short sward after mowing to a common residual height of 5 cm.

Given the time required for collection of estimates of herbage mass pre and post graze, the experiment was split in half and 4 cows each grazed 2 sequences in a balanced design, over 2 days, a week apart.

6.3 SUMMARISED SWARD MEASUREMENTS

Table 6.2 Summarised sward measurements for Experiment 5

Measurement	Particulars
Sward height	15 or 30 readings pre and post graze for small and large patches respectively.
Pseudostem height	7 or 14 readings for small and large patches respectively from the centre section.
Herbage mass	Direct (herbage cuts) and indirect (capacitance probe) estimates of herbage pre and post graze.
Botanical composition	Samples were bulked according to sward height combination within each block and half block for each of the 4 sequences. Each sub-sample was dissected into the components, ryegrass leaf, ryegrass pseudostem, other species leaf, other species pseudostem, weed and dead material.
Nutritive value (whole sward)	Samples were bulked according to sward height, short or tall, within each block for each sequence and nutritional parameters assessed using NIRS.

For further details on measurement of sward and pseudostem height refer to section 3.3.1 and botanical composition refer to section 3.3.3 under "General sward measurements". For details on measurement of herbage mass refer to section 6.3.1 below.

6.3.1 Herbage mass

For each grazed small and large patch 10 or 20 Corrected Meter Readings (CMR) using a GrassMaster Pasture Meter (Tru-Test Limited, 1997) were taken respectively prior to and upon completion of the grazing observations. From the centre section 5 or 10 CMR were taken for small and large patches respectively. All remaining herbage post graze on the grazed patches and that within the centre section was removed using an electric shearing handpiece to 5 cm.

6.4 RESULTS

6.4.1 Treatment contrasts

Sward contrasts were established by controlling the distance between patches, control of patch length to create different patch areas, and by manipulation of sward height with different regrowth intervals. The mean values for these parameters are presented in Table 6.3 with the means for the distance between patches being 0.45 m and 4.80 m, patch area 0.73 m^2 and 1.26 m^2 and sward height 17.3 cm and 22.3 cm.

The experiment was designed on a model of nominal sward height, nominal patch area and nominal current patch distance (Model 1). However, largely as a result of the split grazing sessions, there was within treatment variation in sward height. Fitting sward height as a continuous variable before the nominal treatment effects allowed for a clearer definition of treatment effects on the sward characteristics of individual patches (Model 2). Within the 4 sub-set pairs of treatments [T1&T2], [T3&T4], [T5&T6] and [T7&T8] sward height was consistency shorter on small patches than large patches. The addition of the linear regression effect to the model acted additionally as a conventional covariate. In this sense, the probability values presented for patch area effects have been adjusted for the variation in sward height between patch areas. Where mean values for significant patch area effects are presented throughout this experiment the mean values have been adjusted, otherwise the unadjusted means for other variables are presented.

$$\text{Model} = \text{Sward height}|\text{Patch area}|\text{Current patch distance} \qquad (1)$$

Model = Sward height† Sward height|Patch area|Current patch distance (2)

†Linear effect of sward height

There was a strong linear relationship between sward height and pseudostem height. The difference between the means for pseudostem height (9.6 vs 13.0±0.29 cm) for the two nominal groupings of sward height was also significant (Table 6.3). Pseudostem as a percentage of sward height was significantly different for short and tall swards (P=0.0176) but in absolute terms the difference was small (55.4 vs 58.8 ± 1.5% for short and tall swards respectively). The dominant effect on the pregraze herbage mass present per unit area and bulk density was sward height (Table 6.3).

There were no significant differences in botanical composition between the two sward height treatment categories (Table 6.4). For both sward height categories, leaf (ryegrass and other grass) comprised approximately 50 % of total DM and pseudostem 40 % of total DM. The relative contribution of other grasses, predominantly *Poa annua* leaf and pseudostem, to total DM was high (55 % for 17.3 cm swards and 47 % for 22.3 cm swards).

Short swards contained significantly higher levels of crude protein, lipids and carbohydrates and lower values of acid detergent fibre and neutral detergent fibre. These short swards also recorded greater organic matter digestibility and metabolisable energy content than the taller swards (Table 6.5).

Table 6.3 Mean values for patch distance, patch area, sward height, pseudostem height, pregraze mass and bulk density for the 8 treatments in Experiment 5.

Treatment	Patch distance (m)	Patch area (m^2)	Sward height (cm)	Pseudostem height (cm)	Pregraze mass† (g DM)		Bulk density‡ (mg DM cm^{-3})
					patch	m^{-2}	
1	0.45	1.22	18.3	10.6	262.0	216.2	1.20
2	0.45	0.72	16.6	9.1	134.8	187.8	1.16
3	0.45	1.22	22.7	13.9	331.4	270.8	1.24
4	0.45	0.64	21.3	12.6	169.5	258.0	1.23
5	4.80	1.31	17.8	9.2	263.0	199.5	1.14
6	4.80	0.77	16.5	9.8	160.6	205.2	1.23
7	4.80	1.28	23.3	13.7	372.4	288.0	1.21
8	4.80	0.76	21.9	11.6	194.5	250.3	1.145
sed			1.52	0.81	21.69	17.25	0.084
P value : Linear effect of sward height			n/a	0.0001	0.0001	0.0001	0.0140
P value : Nominal sward height			0.0001	0.0138	0.6582	0.0084	0.0042
P value : Nominal patch area			0.0579	0.1401	0.0001	0.2454	0.2321
P value : Nominal current patch distance			0.8299	0.1104	0.1091	0.8596	0.8110

Probability values for the effects of sward height, patch area and patch distance are given in sequential order of fitting.

† Direct estimates from the centre section, adjusted for patch and unit area.

‡ Calculated using the direct estimate of pregraze mass

Table 6.4 Mean values for botanical composition (% DM) for the 2 sward height groups in Experiment 5.

Sward height (cm)	Treatment	Ryegrass Leaf	Ryegrass Pseudostem	Other Grass Leaf	Other Grass Pseudostem	Dead
17.3	1, 2, 5, 6	21.8	13.3	28.5	26.7	9.7
22.3	3, 4, 7, 8	26.2	17.5	24.8	22.5	9.0
sed		3.57	2.82	2.42	3.52	1.39
P value : Sward height		0.2526	0.1776	0.1702	0.2646	0.6479

Table 6.5 Mean values for the content (% DM) of crude protein (CP), lipid, acid detergent fibre (ADF), neutral detergent fibre (NDF), carbohydrates-soluble sugars and starch (CHO), ash, organic matter digestibility (OMD), and metabolisable energy (ME) (MJ ME/kg DM), as determined by Near Infrared Reflectance Spectroscopy (NIRS) for the 2 sward height groups in Experiment 5.

Sward height (cm)	Treatment	CP	Lipid	ADF	NDF	CHO	Ash	OMD	ME
17.3	1, 2, 5, 6	21.3	3.8	23.4	43.8	10.3	10.6	81.2	12.1
22.3	3, 4, 7, 8	17.9	3.5	26.2	47.6	9.6	10.5	78.8	11.8
sed		0.53	0.04	0.09	0.40	0.26	0.15	0.64	0.10
P value : Sward Height		0.0001	0.0001	0.0001	0.0001	0.0097	0.5890	0.0020	0.0023

6.4.2 Bite number, residence time and herbage removed

Fitting sward height as a continuous variable after the nominal treatment effects showed that the extent of the within treatment variation was significant for the 3 behavioural parameters, bite number per patch (P=0.0473) and per unit area (P=0.0172), residence time per patch (P=0.0195) and per unit area (P=0.0080), and herbage removed per patch (P=0.0003) and per unit area (P=0.0001). Subsequently, a linear sward height regression effect was fitted in the model before nominal treatment effects (Model 2).

6.4.2.1 Bite number and residence time

Number of bites per patch ranged from 22.4 to 58.2 (Table 6.6). After adjustment for patch area effects, the range was 33.3 to 44.7 (Table 6.6). The initial analysis of variance output for bite number per patch using Model 2 revealed a significant effect of nominal sward height but no significant linear relationship between sward height and bite number (Table 6.7). Data is presented in pictorial form (eg. Figure 6.2) to assist with the interpretation of the probability values. An interaction term, a linear regression effect of sward height x nominal sward height was also added to the model (Model 3) to assess whether parallel lines were an appropriate fit for the two sward height groups (Table 6.8).

Model = Sward height†|Sward height Sward height|Patch area|Curent patch distance (3)

†Linear effect of sward height

Table 6.6 Mean values for bite number, residence time and herbage removed for the 8 treatments in Experiment 5.

Treatment	Patch distance (m)	Patch area (m^2)	Sward height (cm)	Bite number		Residence time (sec)	
				patch	m^{-2}	patch	m^{-2}
1	0.45	1.22	18.3	49.6	40.7	46.7	38.3
2	0.45	0.72	16.6	24.4	34.0	22.2	30.8
3	0.45	1.22	22.7	40.4	33.3	38.7	31.8
4	0.45	0.64	21.3	22.4	35.2	20.8	32.8
5	4.80	1.31	17.8	58.2	44.2	54.6	41.5
6	4.80	0.77	16.5	34.2	44.7	31.4	41.2
7	4.80	1.28	23.3	51.9	40.9	50.8	40.0
8	4.80	0.76	21.9	31.8	42.0	31.0	41.0
sed				4.96	4.93	4.84	4.90
P value : Linear effect of sward height				0.0543	0.3404	0.0110	0.0993
P value : Nominal sward height				0.0001	0.0103	0.0001	0.0149
P value : Linear sward height x Nominal sward height				0.1718	0.3901	0.2294	0.4585
P value : Nominal patch area				0.0001	0.6215	0.0001	0.7329
P value : Nominal current patch distance				0.0004	0.0066	0.0003	0.0048

Probability values for the effects of sward height, patch area and patch distance are given in sequential order of fitting and derived from analysis using Model 3.

Table 6.7 Extract from the analysis of variance output for bite number per patch using Model 2.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	587.33	587.33	3.87	0.0575
Nominal sward height	1	3344.37	3344.37	22.06	0.0001
Nominal patch area	1	8890.17	8890.17	58.64	0.0001
Nominal current patch distance	1	2216.18	2216.18	14.62	0.0006

The results from the analysis of variance table using Model 3 (Table 6.8) showed that patch area had the greatest influence on the number of prehended bites. When bite number was adjusted for differences in patch area (Table 6.9), the strong significance shown in Table 6.8 was no longer evident. This indicated that the number of bites prehended was in direct proportion to the area of the patch. Further, on a patch basis, there was marginal evidence for a linear regression relationship between sward height and bite number (Table 6.8) but after adjustment for patch area effects this effect was no longer significant at 0.1 probability (Table 6.9). This discrepancy for the influence of sward height on bite number per patch and per unit area appears to largely reflect the confounding effect between sward height and patch area.

Table 6.8 Extract from the analysis of variance output for bite number per patch using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	587.33	587.33	3.98	0.0543
Nominal sward height	1	3344.37	3344.37	22.67	0.0001
Linear sward height x Nominal sward height	1	287.87	287.87	1.95	0.1718
Nominal patch area	1	8753.80	8753.80	59.33	0.0001
Nominal current patch distance	1	2314.18	2314.18	15.69	0.0004

The analysis of variance tables for bite number, expressed on a patch basis and on a per unit area basis (Table 6.8 and Table 6.9) showed a significant nominal sward height effect, indicating an effect of sward height treatment on bite number. These effects are plotted in Figure 6.2 where the solid line represents the linear sward height effect fitted first and the dotted lines represent the linear sward height effects. Figure 6.2 illustrates that for any nominal treatment level, fewer bites were removed from the taller swards, suggesting an additional treatment effect unrelated to sward height. The separate lines representing the two sward height groups were essentially parallel, showing that there was no interaction between linear and nominal sward height effects, and this is substantiated in Table 6.8 and Table 6.9.

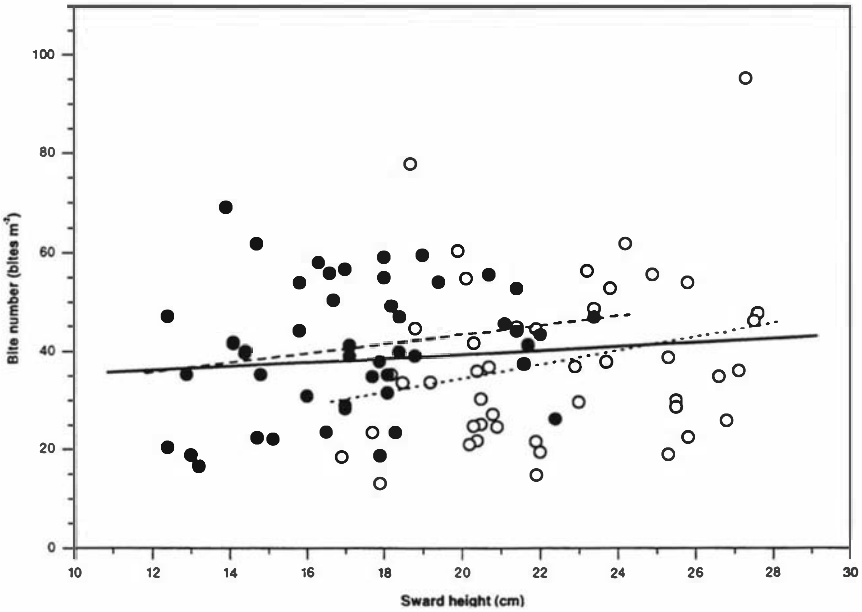

Figure 6.2 Relationship between sward height and bite number per unit area for short (•) and tall (O) treatments. Linear relationships are fitted for short (——) treatments, tall (……) treatments and a pooled (——) relationship.

Table 6.9 Extract from the analysis of variance output for bite number per unit area using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	136.20	136.20	0.94	0.3404
Nominal sward height	1	1078.26	1078.26	7.41	0.0103
Linear sward height x Nominal sward height	1	110.40	110.40	0.76	0.3901
Nominal patch area	1	36.15	36.15	0.25	0.6215
Nominal current patch distance	1	1222.55	1222.55	8.40	0.0066

Current patch distance influenced the number of prehended bites, with animals responding to a larger patch distance of 4.80 m by prehending c. 20 % more bites irrespective of the height of the patch. The influence of patch distance was the strongest effect on bite number after adjustment for patch area effects (Table 6.9).

The analysis of variance output for residence time followed similar patterns to bite number and this is reinforced by the strong correlation between these two parameters (r=0.98).

6.4.2.2 Herbage removed

Caution was exercised over the direct estimates of the mass of herbage removed per patch in light of conclusions from Experiment 1 and 4. In this experiment a series of calibration equations was developed using direct DM cuts, capacitance probe readings and sward height measurements to predict pregraze and postgraze mass. Linear regressions for separate pregraze and postgraze functions were fitted and four methods for estimating the mass of herbage removed were assessed.

Defining the parameters used in the equations:

SHCentre	measured sward height of the centre section using a sward stick; mean of 7 or 14 sward height readings for small and large patches respectively
SHGrazed	measured sward height of the grazed patches using a sward stick; mean of 15 or 30 sward height readings for small and large patches respectively
CMRCentre	corrected meter reading (CMR) from the capacitance probe of the centre section; mean of 5 or 10 readings by 2 sets for small and large patches respectively
CMRGrazedPre	corrected meter reading (CMR) from the capacitance probe of the grazed patches before the grazing session; mean of 10 or 20 readings by 2 sets for small and large patches respectively
CMRGrazedPost	corrected meter reading (CMR) from the capacitance probe of the grazed patches upon completion of the grazing session; mean of 10 or 20 readings by 2 sets for small and large patches respectively

DirectDMCentre	direct estimate of pregraze herbage mass of the centre section, adjusted for per unit area (ie. g DM m^{-2})
DirectDMGrazed	direct estimate of postgraze herbage of the grazed patches, adjusted for per unit area (ie. g DM m^{-2})

Details on the four methods for calculation of estimates of the mass of herbage removed per unit area are given below and the treatment means are presented in Table 6.10.

In method 1:

The mass of herbage removed was calculated for each grazed patch using the estimates of the direct herbage mass of the centre section and grazed patches (ie. DirectDMCentre – DirectDMGrazed)

In method 2:

A regression of the herbage mass per unit area of the centre section (DirectDMCentre) on the corrected meter reading of the centre section (CMRCentre) and then substituting the CMR with the corrected meter reading of the grazed patch pregraze (CMRGrazedPre) gave equation 1.

$$\text{Pregraze mass (g DM m}^{-2}\text{)} = -113.53\ (\pm 71.674) + 0.05\ (\pm 0.010)\ (\text{CMRGrazedPre}) \quad r^2 = 0.34 \qquad (1)$$

A regression of the herbage mass per unit area of the grazed patch postgraze (DirectDMGrazed) on the corrected meter reading of the grazed patch postgraze (CMRGrazedPost) and then substituting back the CMR of the grazed patch postgraze gave equation 2.

$$\text{Postgraze mass (g DM m}^{-2}\text{)} = -142.23\ (\pm 21.538) + 0.06\ (\pm 0.004)\ (\text{CMRGrazedPost}) \quad r^2 = 0.67 \qquad (2)$$

The mass of herbage removed was then calculated for each grazed patch using the estimates from equation 1 and 2.

In method 3:

A regression of the herbage mass per unit area of the centre section (DirectDMCentre) on the sward height measurement of the centre section (SHCentre) and then substituting SH with the sward height of the grazed patch pregraze (SHGrazed) gave equation 3.

$$\text{Pregraze mass (g DM m}^{-2}\text{)} = 21.69\ (\pm 24.525) + 10.66\ (\pm 1.210)\ \text{(SHGrazed)} \quad r^2 = 0.63 \tag{3}$$

The mass of herbage removed was then calculated for each grazed patch using the estimates from equation 3 and the direct estimates of postgraze mass (ie. equation 3 – DirectDMGrazed).

In method 4

The mass of herbage removed was calculated for each grazed patch using the estimates from equations 2 and 3.

The method with the lowest mean square error was expected to predict the least biased estimates. On this basis the direct estimates obtained with method 1 would have been the least biased (SS, 6993, 29530, 6996 and 8569 for methods 1 to 4 respectively, df= 38). However, since probability values are determined using the treatment(sequence x block) as an error term, this error term was used as the basis for improvement testing. The values for treatment(sequence x block) are given in the bottom row of Table 6.10, and demonstrate the improvement from method 1 to method 4. The improvement between method 3 and 4 was not significant. In further calculations the least bias was introduced for estimates of bite mass when using estimates of the mass removed from method 3.

Table 6.10 Mean values for the mass of herbage removed for the 8 treatments in Experiment 5 using the four methods described in section 6.4.2.2. The sum of squares estimate used as the error term for calculating probability values is given as a comparative assessment of methods.

Treatment	Patch distance (m)	Patch area (m^2)	Sward height (cm)	Herbage removed (g DM m^{-2})			
				Method 1	Method 2	Method 3	Method 4
1	0.45	1.22	18.3	49.5	44.7	50.6	43.6
2	0.45	0.72	16.6	24.3	39.4	34.6	27.4
3	0.45	1.22	22.7	39.6	46.2	32.8	36.0
4	0.45	0.64	21.3	40.8	48.5	31.2	29.1
5	4.80	1.31	17.8	40.2	37.7	52.2	41.7
6	4.80	0.77	16.5	57.5	48.1	50.2	48.8
7	4.80	1.28	23.3	59.6	41.1	41.9	50.4
8	4.80	0.76	21.9	24.1	60.5	28.7	45.4
sed				16.16	11.49	8.05	7.75
P value : Linear effect of sward height				0.8570	0.0004	0.2050	0.0001
P value : Nominal sward height				0.6205	0.0277	0.0001	0.0001
P value : Linear sward height x Nominal sward height				0.6756	0.7223	0.1539	0.4095
P value : Nominal patch area				0.2230	0.0132	0.6412	0.3573
P value : Nominal current patch distance				0.4199	0.8164	0.1509	0.0040
Sum of Squares for Trt(Sequence x Block) df =33				51685	26137	12827	11880

Probability values for the effects of sward height, patch area and patch distance are given in sequential order of fitting and derived from analysis using Model 3.

Further discussion on the mass of herbage removed, bite mass and intake rate relate to estimates obtained from the calculations using method 3. Animals removed between 20.3 and 69.1 g DM per patch, and after adjustment for unit area, the adjusted range was 28.7 to 52.2 g DM m^{-2}. Similar to grazing bites, there was a small significant linear regression at 0.1 probability between sward height and the mass of herbage removed on a patch basis but this effect was not present after adjustment per unit area (Table 6.11 and Table 6.12). The mass of herbage removed was proportional to patch area (Table 6.12). There was a small effect of current patch distance on the mass of herbage removed per patch but this effect did not attain significance after adjustment for patch area effects (Table 6.11 and Table 6.12). Residual sward height had the strongest effect on the mass of herbage removed (Table 6.11 and Table 6.12), indicating that there were different relationships between individual patches, and between means for the two sward height treatments. As with grazing bites, less herbage was removed from the taller swards at any nominal treatment level, again suggestive of a treatment effect additional to height. The correlation between the mass of herbage removed and bite number was weaker (r = 0.37) than that of bite number and residence time (r = 0.98) because residence time was measured more reliably than the mass of herbage removed.

Table 6.11 Extract from the analysis of variance output for herbage removed per patch using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	1475.42	1475.42	3.26	0.0800
Nominal sward height	1	19904.04	19904.04	44.01	0.0001
Linear sward height x Nominal sward height	1	1413.96	1413.96	3.13	0.0863
Nominal patch area	1	11471.35	11471.35	25.36	0.0001
Nominal current patch distance	1	2299.66	2299.66	5.08	0.0309

Table 6.12 Extract from the analysis of variance output for herbage removed per unit area using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	649.79	649.79	1.67	0.2050
Nominal sward height	1	13630.83	13630.83	35.07	0.0001
Linear sward height x Nominal sward height	1	828.05	828.05	2.13	0.1539
Nominal patch area	1	85.98	85.98	0.22	0.6412
Nominal current patch distance	1	840.71	840.71	2.16	0.1509

6.4.3 Bite Mass

Bite mass was calculated using the indirect estimates of herbage removed, calculated using method 3. With method 3 there were still a number of negative estimates of bite mass, although the relative bias introduced from these estimates was lower than that for the estimates of bite mass recorded in Experiment 4. At least four bites were prehended from every patch, therefore all patches were included in the assessment of bite mass. There was significant within treatment variation when a linear sward height regression effect was fitted after the nominal treatment terms (P=0.0001), and so Model 3 was used to analyse bite mass. The output from the analysis of variance using Model 3 showed that there was no evidence of a significant linear relationship between sward height and bite mass (Table 6.13). However, across the two sward height treatments the mean bite mass was greater for the short sward height treatment (1.18 vs 0.90 ± 0.082 g DM bite^{-1}) (Table 6.14 and Figure 6.3). Patch area or current patch distance did not influence the amount harvested per bite (Table 6.13).

Fitting bite number per patch as a covariate after treatment effects in Model 3 indicated that the number of bites removed had no strong significant effect on the measured bite mass (P=0.0889).

Table 6.13 Extract from the analysis of variance output for bite mass using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	0.46	0.46	1.39	0.2466
Nominal sward height	1	6.89	6.89	20.91	0.0001
Linear sward height x Nominal sward height	1	0.03	0.03	0.09	0.7672
Nominal patch area	1	0.00	0.00	0.00	0.9953
Nominal current patch distance	1	0.00	0.00	0.00	0.9744

Table 6.14 Mean values for bite mass, bite rate and intake rate for the 8 treatments in Experiment 5.

Treatment	Patch distance (m)	Patch area (m^2)	Sward height (cm)	Bite mass (g DM $bite^{-1}$)	Bite rate (bites min^{-1})	Intake rate (g DM min^{-1})
1	0.45	1.22	18.3	1.22	64.2	77.7
2	0.45	0.72	16.6	1.11	66.9	72.6
3	0.45	1.22	22.7	0.93	62.6	57.1
4	0.45	0.64	21.3	0.89	65.3	59.3
5	4.80	1.31	17.8	1.26	64.2	81.4
6	4.80	0.77	16.5	1.14	65.6	74.9
7	4.80	1.28	23.3	1.04	62.1	63.4
8	4.80	0.76	21.9	0.74	62.3	45.6
sed				0.23	1.59	14.73
P value : Linear effect of sward height				0.2466	0.0002	0.4711
P value : Nominal sward height				0.0001	0.6629	0.0001
P value : Linear sward height x Nominal sward height				0.7672	0.9995	0.7471
P value : Nominal patch area				0.9953	0.2053	0.8253
P value : Nominal current patch distance				0.9744	0.1757	0.8923

Probability values for the effects of sward height, patch area and patch distance are given in sequential order of fitting and derived from analysis using Model 3.

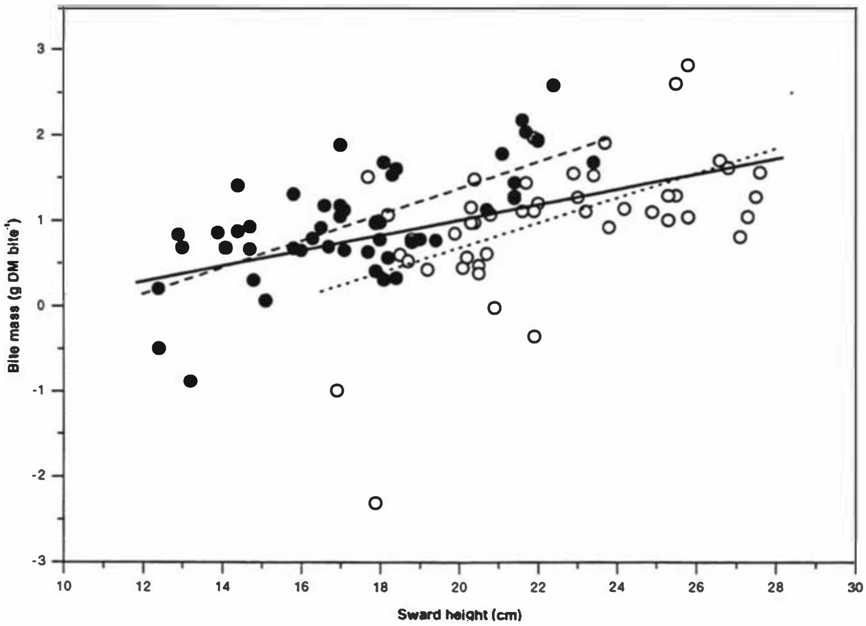

Figure 6.3 Relationship between sward height and bite mass for short (•) and tall (O) treatments. Linear relationships are fitted for short (-----) treatments, tall (......) treatments and a pooled (——) relationship.

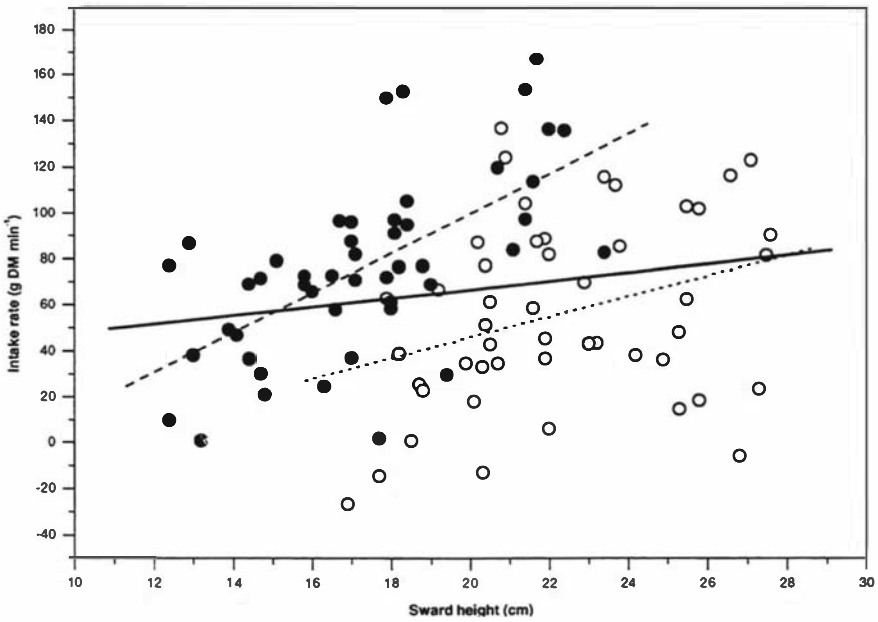

Figure 6.4 Relationship between sward height and intake rate for short (•) and tall (O) treatments. Linear relationships are fitted for short (-----) treatments, tall (......) treatments and a pooled (——) relationship.

6.4.4 Bite rate

Model 3 was used to analyse rate of biting in light of the strong within treatment variation in sward height. The analysis of variance output showed that there was a strong linear relationship between the number of prehending bites per minute and sward height (Table 6.15). There was no evidence for significant differences between sward height groups (65.2 vs 63.1 ± 0.56 bites min^{-1} for short and tall swards respectively). Neither patch area effects nor patch distance effects attained significance (Table 6.15).

Table 6.15 Extract from the analysis of variance output for bite rate using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	276.68	276.68	18.18	0.0002
Nominal sward height	1	2.94	2.94	0.19	0.6629
Linear sward height x Nominal sward height	1	0.00	0.00	0.00	0.9995
Nominal patch area	1	25.41	25.41	1.67	0.2053
Nominal current patch distance	1	29.15	29.15	1.91	0.1757

6.4.5 Intake rate

Rate of intake was calculated indirectly using the estimates of bite mass and bite rate. The effects of treatment parameters on the rate of intake were similar to those for bite mass (Table 6.16 and Figure 6.4), and this was reinforced by the strong correlation between bite mass and rate of intake (r= 0.98). The contrast in mean rate of intake across the two sward height treatments (76.7 vs 56.3 ± 5.21 g DM min^{-1}) attained significance (Table 6.16), an effect which largely reflected the fact that bite mass was greater on the short sward height treatment and, although not significant, that mean bite rate was also slightly greater on the short sward height treatment (section 6.4.4). The effects of patch distance and patch area did not attain significance (Table 6.16).

Table 6.16 Extract from the analysis of variance output for intake rate using Model 3.

Source	DF	SS	MS	FValue	Pr>F
Linear effect of sward height	1	691.84	691.84	0.53	0.4711
Nominal sward height	1	27748.67	27748.67	21.32	0.0001
Linear sward height x Nominal sward height	1	137.61	137.61	0.11	0.7471
Nominal patch area	1	64.45	64.45	0.05	0.8253
Nominal current patch distance	1	24.24	24.24	0.02	0.8923

6.4.6 Bite depth

Using Model 3 the analysis of variance output showed that the depth of grazing was positively and linearly related to sward height (Table 6.17 and Figure 6.5). There were small significant effects of nominal sward height, reflecting the fact that bite penetration was greater for the short sward at any nominal treatment level (Table 6.18 and Figure 6.5). There was also a small effect of patch area on bite depth, with the data suggesting a slightly deeper bite (9.1 vs 8.6 ± 0.15 cm) on small patches after adjustment for the confounding effect between sward height and patch area.

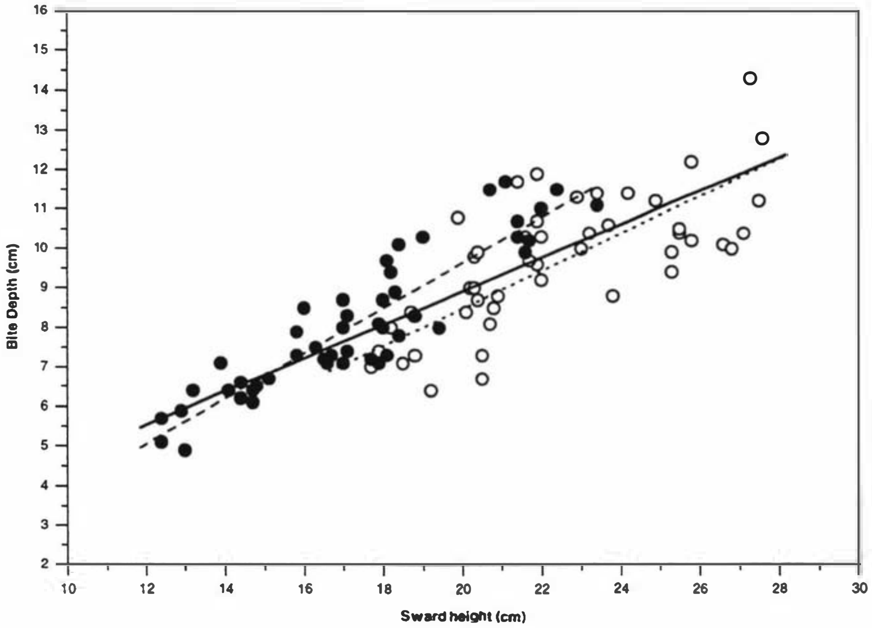

Figure 6.5 Relationship between sward height and bite depth for short (•) and tall (O) treatments. Linear relationships are fitted for short (----) treatments, tall (......) treatments and a pooled (——) relationship.

Table 6.17 Mean values for bite depth and bite depth/sward height for the 8 treatments in Experiment 5.

Treatment	Patch distance (m)	Patch area (m^2)	Sward height (cm)	Bite depth (cm)	Bite depth / Sward height (%)
1	0.45	1.22	18.3	8.3	44.7
2	0.45	0.72	16.6	8.0	48.0
3	0.45	1.22	22.7	9.6	41.6
4	0.45	0.64	21.3	8.9	41.8
5	4.80	1.31	17.8	8.1	45.1
6	4.80	0.77	16.5	8.1	48.4
7	4.80	1.28	23.3	10.0	43.1
8	4.80	0.76	21.9	9.9	45.0
sed				0.43	2.18
P value : Linear effect of sward height				0.0001	0.2060
P value : Nominal sward height				0.0020	0.0014
P value : Linear sward height x Nominal sward height				0.4317	0.6548
P value : Nominal patch area				0.0275	0.0156
P value : Nominal current patch distance				0.2244	0.2002

Probability values for the effects of sward height, patch area and patch distance are given in sequential order of fitting and derived from analysis using Model 3.

Table 6.18 Extract from the analysis of variance output for bite depth using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	190.81	190.81	174.05	0.0001
Nominal sward height	1	12.37	12.37	11.29	0.0020
Linear sward height x Nominal sward height	1	0.69	0.69	0.63	0.4317
Nominal patch area	1	5.83	5.83	5.32	0.0275
Nominal current patch distance	1	1.68	1.68	1.53	0.2244

The height at which grazing settled was strongly related to the height of the pseudostem (P=0.0001) (r= 0.75). Examining treatment averages in Figure 6.6 it is clear animals grazed to the interface between lamina and pseudostem for T1, T2, T3, T4, T5, T7 and T8. As a test for the relative importance of pseudostem height on bite depth, pseudostem height as a linear regression variable was fitted after the linear and nominal sward height terms (Model 4).

Model = Sward height†|Sward height Pseudostem height† Sward height|Patch area|Current patch distance (4)

†Linear effect of sward height and pseudostem height

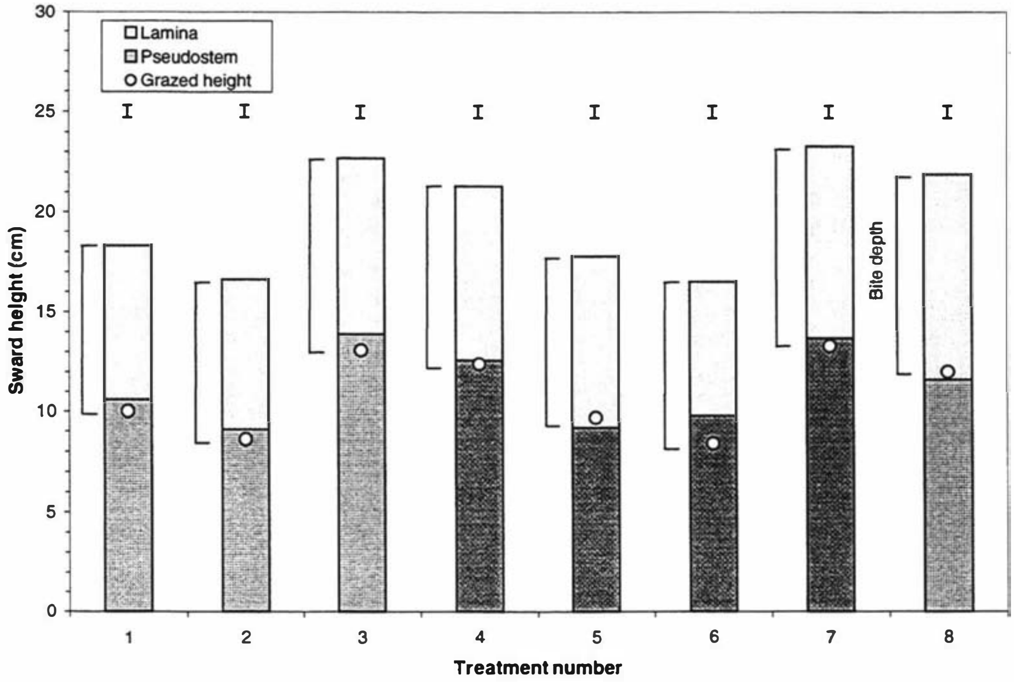

Figure 6.6 Depth of penetration relative to pregraze height and pseudostem height (vertical bars represent sem).

The analysis of variance output using Model 4 (Table 6.19) showed a small significant linear relationship between bite depth and pseudostem height in addition to the strong linear relationship between bite depth and sward height. However, much of the pseudostem height effect would have been absorbed by the linear sward height effect because the two variables were not independent of each other. Reversing the order of fit so that the linear effect of pseudostem height was followed by the linear sward height effect showed a stronger significant influence of both pseudostem height and sward height on bite depth, although sward height remained the more dominant effect of the two. The sum of squares were approximately halved for the nominal sward height term but still attained significance (Table 6.19).

Table 6.19 Extract from the analysis of variance output for bite depth using Model 4.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	190.81	190.81	203.46	0.0001
Nominal effect of sward height	1	12.37	12.37	13.19	0.0010
Linear sward height x Nominal sward height	1	0.69	0.69	0.74	0.3958
Linear effect of pseudostem height	1	7.71	7.71	8.22	0.0073
Nominal patch area	1	3.62	3.62	3.87	0.0580
Nominal current patch distance	1	0.58	0.58	0.62	0.4362
Reverse fit					
Linear effect of pseudostem height	1	76.00	76.00	81.04	0.0001
Linear effect of sward height	1	129.61	129.61	138.21	0.0001
Nominal effect of sward height	1	5.67	5.67	6.05	0.0195
Linear sward height x Nominal sward height	1	0.30	0.30	0.32	0.5755

The analysis of variance output for bite depth expressed as a percentage of sward height showed that across the two sward height treatments depth of penetration was proportional to sward height, equivalent to approximately 45 % between 12 and 28 cm (Table 6.20 and Figure 6.7). The significant nominal sward height effect, which reflects the comparison between means, showed bite depth relative to sward height to be greater on short swards (47 % vs 43% ± 0.77 %). However, there was no indication of any consistent change with sward height, substantiated by the interaction not being significant (Table 6.20). There was a strong trend for the proportion of sward height removed to be greater on small patches (Table 6.17) and this was reflected in the significant patch area effect in Table 6.20.

Table 6.20 Extract from the analysis of variance output for bite depth/sward height using Model 3.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	47.61	47.61	1.66	0.2060
Nominal sward height	1	349.77	349.77	12.23	0.0014
Linear sward height x Nominal sward height	1	5.69	5.69	0.20	0.6584
Nominal patch area	1	186.18	186.18	6.51	0.0156
Nominal current patch distance	1	48.87	48.87	1.71	0.2002

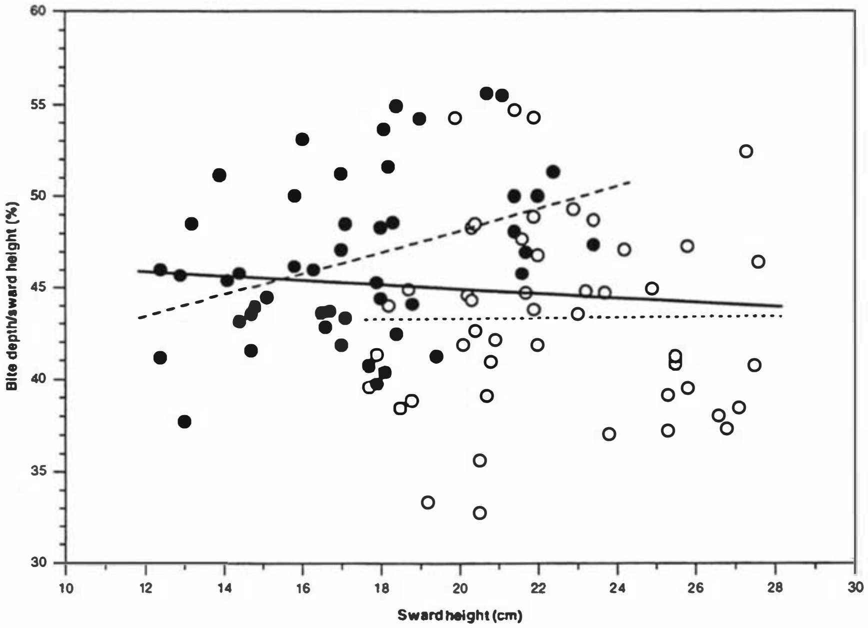

Figure 6.7 Relationship between sward height and bite depth/sward height for short (•) and tall (O) treatments. Linear relationships are fitted for short (----) treatments, tall (......) treatments and a pooled (——) relationship.

6.4.7 Adjacent patch effects

Analysis of both the preceding and succeeding patch effects on the number of bites removed from the current patch showed that the treatment characteristics of sward height, area and distance of the adjacent patches had little influence on behaviour on the current patch (Table 6.21 and Table 6.22).

Table 6.21 Extract from the analysis of variance table for the influence of the sward height, patch area and patch distance of the preceding patch in sequence on bites removed per unit area from the current patch in Experiment 5.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	215.06	215.06	1.21	0.2797
Nominal sward height	1	1401.76	1401.76	7.90	0.0086
Linear sward height x sward height	1	284.62	284.62	1.60	0.2151
Nominal patch area	1	124.74	124.74	0.70	0.4085
Nominal current patch distance[1]	1	1239.33	1239.33	6.98	0.0130
Prev[†] Sward height (SH)	1	6.91	6.91	0.04	0.8449
Prev[†] patch area (PA)	1	436.62	436.62	2.46	0.1273
Prev[†] patch distance (PD)[2]	1	75.25	75.25	0.42	0.5199
Prev[†] SH x Prev[†] PA	1	12.60	12.60	0.07	0.7918
Prev[†] SH x Prev[†] PD	1	37.05	37.05	0.21	0.6510
Prev[†] PA x Prev[†] PD	1	106.45	106.45	0.60	0.4447
Prev[†] SH x Prev[†] PA x Prev[†] PD	1	21.75	21.75	0.12	0.7287

[†] Prev =Preceding patch

[1, 2] see Figure 6.1

Probability values are given in sequential order of fitting.

Table 6.22 Extract from the analysis of variance table for the influence of the sward height, patch area and patch distance of the succeeding patch in sequence on bites removed per unit area from the current patch in Experiment 5.

Source	DF	SS	MS	F Value	Pr > F
Linear effect of sward height	1	59.56	59.56	0.38	0.5404
Nominal sward height	1	838.46	838.46	5.40	0.0271
Linear sward height x sward height	1	22.91	22.91	0.15	0.7036
Nominal patch area	1	37.13	37.13	0.24	0.6284
Nominal current patch distance[1]	1	1023.42	1023.42	6.59	0.0155
Next sward height (SH)	1	89.53	89.53	0.58	0.4536
Next patch area (PA)	1	87.55	87.55	0.56	0.4586
Next patch distance (PD)[2]	1	13.39	13.39	0.09	0.7710
Next SH x Next PA	1	174.13	174.13	1.12	0.2981
Next SH x Next PD	1	31.74	31.74	0.20	0.6544
Next PA x Next PD	1	327.70	327.70	2.11	0.1567
†Next SH x Next PA x Next PD	1	38.31	38.31	0.25	0.6230

†Next = Succeeding patch
[1, 2] see Figure 6.1
Probability values are given in sequential order of fitting.

6.5 DISCUSSION

Experiments 1 to 4 focussed on an understanding of the patterns of activity that develop when cattle are offered choices of different patch combinations. This final experiment provided a more rigorous test of the manner in which animals assessed opportunities given variations in patch area and patch dispersion. In this context observations revealed more about selective behaviour than preference, since preference was modified by opportunity.

The following discussion is structured with the early sections covering the descriptive material of herbage mass, bite mass and bite depth, followed by sections discussing the effect of sward height, patch area and inter-patch distance on selective behaviour. Discussion then focuses on the effects of adjacent patch effects on foraging decisions and covers areas of speculation. The data presented in this chapter pertaining directly to foraging theory is not conclusive, neither supporting or discrediting the limited data that is available on foraging theory in ruminants.

The reader is advised to refer again to Figure 6.1 for clarification of the terms used in discussing patch sequence effects.

6.5.1 Herbage mass

The consistency in the patterns of the mass of herbage removed, though the variability was exceptionally high, across and within regrowth depths in Experiment 4 provided confidence in the double sampling procedure, and it was used again in the current study. Capacitance probe readings are subject to a magnitude of error, as are direct estimates of herbage mass, and substantial depletion is required for readings to consistently detect a sizeable difference reliably. Increasing the number of corrected meter readings from 6 (Experiment 4) to 15, and this latter figure to 30 for the larger patches, appeared an efficient and logical means to counteract variability associated with fluctuating readings. However, it incurred an expense of resource time that could have been given to the collection of other measurements (eg. tensile strength estimates). Calibration of pregraze mass on sward height pregraze (equation 3) led to a significant improvement over the calibration of pregraze mass on the capacitance probe reading (equation 1) which perhaps underlines the variation which is introduced with capacitance probe readings. Predictions of postgraze mass (equation 2) were derived from the values used to develop the equation, and use of the same readings for the estimates has its drawbacks.

While the estimates demonstrate that with further experimentation and refinement of the sampling procedures it should be possible to develop calibration methods that will enable predictions of herbage mass and bite mass at the patch level, the level of precision required for between-treatment comparisons, and the implications on the prediction of intake rate, leave some cause for concern. Additionally, calibration procedures lose their value when sward contrasts in the vertical plane are introduced. The difficulty associated with estimating directly the mass of herbage removed (ie. the difference method) is hardly a new problem in grazing studies. However, few studies have attempted to formalise a way to counteract it, which adds weight to the argument that there is an urgent need to extend the scale of study and to address these difficulties. An example of this is the recent work by Ungar *et al.* (1997) who conducted an evaluation of the methods to estimate bite mass under field conditions. These authors also found that even with the selection and trimming of patches of alfalfa for uniformity, direct estimates of the mass of herbage removed derived from the difference method using quadrats adjacent to the grazed patch, and the residual herbage mass on the grazed patch, yielded biased and unreliable predictions. These authors showed that the use of calibration methods (herbage mass only) proved important in the estimation of the mass of herbage removed. An alternative method that is generally unexplored but potentially useful, largely because of its non-destructive properties, would be the use of spectral reflectance (King *et al.*, 1986; Nagy and Zilinyi, 1993) but the level of precision at small scales would also require clarification. In general, further development work in the estimation of herbage mass will greatly assist in over turning the negative image of conducting small scale experiments in the field, as well as minimising the requirement for fistulated animals, which is increasingly being seen as an animal welfare concern. As emphasised throughout this thesis, and also by Ungar *et al.* (1997), values obtained through any calibration method should still be treated with caution and efforts should be directed towards defining and quantifying changes within the vertical profile of swards.

6.5.2 Bite mass

Comparison of absolute values of bite mass between studies has its limitations due to contrasts in bulk density and sward height across individual studies. Nonetheless, bite mass is more sensitive to variations in sward height than in bulk density (Laca *et al.*, 1992a). Comparison taking into account experimental details is valid as long as these constraints are borne in mind. Table 6.23 tabulates the results of a series of selected studies over the last decade that have assessed the bite mass of cattle under short-term conditions at swards heights within proximity of the mean heights of each of the two sward height treatments in the current study. It was encouraging that even though there remains concern over the reliability of using indirect estimates of bite mass in assessing relationships across and within treatments in this study, the estimates were within a range that can be expected under the short-term nature of the study.

Table 6.23 A summary of the bite mass estimates of cattle from a selection of short term studies.

Study	Patch area	Expt. details	Sward height (cm)	Bite mass (g DM $bite^{-1}$)
Current study	adjusted	- Perennial ryegrass		
	to 1.0 m^2	- 40.9 bites	17.3	1.18
		- 37.8 bites	22.3	0.90
Casey *et al.* (1997)	0.36 m^2	- Perennial ryegrass		
		- 25 bites	*	0.66 – 1.27
Flores *et al.* (1993)	0.40 m^2	- Dallisgrass HCS		
		- 19 hour fast		
		- 10 bites	16	1.30
Laca *et al.* (1992a)	0.20 –	- Dallisgrass HCS		
	0.50 m^2	- 6 bites	15	c. 0.8 – 1.8
			18	c. 1.2 – 2.2
			30	c. 2.0 – 3.8
Laca *et al.* (1994)	0.36 m^2	- Wheat HCS		
		- 30 bites	20	1.2
Patterson *et al.* (1998)	200 m^2	- Perennial ryegrass		
		- 1 or 3 hour fast	c. 16	c. 1.1
WallisDeVries *et al.* (1998)	0.14 m^2	- *Setaria lutescens*		
		- 15 bites	16.4†	c. 1.2
		- 25 bites		c. 0.8
		- 15 bites	20.3 ‡	c. 1.5
		- 25 bites		c. 1.0

* Sward height not specified
† SM sward type
‡ ST sward type

6.5.3 Bite depth

Grazed height closely approximated the interface between regrowth depth and pseudostem height, which suggested that animals were constrained by the height of pseudostem. However, the results of the analysis (Table 6.21) showed that bite penetration was still influenced by a further attribute of sward or animal origin. Figure 6.6 clearly presents the basis for an argument that bite penetration was constrained by the interface between the stubble and regrowth. One possible sward attribute that would have given a consistent effect across treatment would have been the change in bulk density between the stubble and regrowth strata. Although Ungar *et al.* (1991) considered the influence of bulk density effects on bite penetration to be insignificant for swards shorter than 10 cm, these effects need re-examining in light of the cost-reward concept proposed by Illius *et al.* (1995).

Bite penetration was greater on small than on large patches after adjustment for the difference in sward height across patch areas. This pattern subsequently led to a significant effect of patch area on the proportion of sward height removed in a bite. There is no clear explanation for this effect. A greater bite depth is suggestive of a smaller bite area, which was the case although the indirect estimates of bite area were not significantly different between patch areas. In order to achieve the similar bite mass between patch areas the differences in bite volume must have been compensated by differences in bulk density. This was not supported by the similarity in bulk density estimates across patch areas using the direct estimates of pregraze herbage mass to calculate bulk density. There was, however, a significant patch area effect on bulk density (P=0.0408) if bulk density was calculated using the pregraze estimates derived from equation 2 (1.24 vs 1.18 for small and large patches respectively). Nonetheless, while Laca *et al.* (1992a) found that cattle grazing lucerne swards exhibited a compensatory effect between sward characteristics and bite dimensions, the contrasts in bite volume and bulk density in their study were substantially greater than in the current study. Additionally the significance of the patch area effect in the current study was very small (<3 %) relative to the total sum of squares partitioned amongst the treatment effects.

Demment and Laca (1993) discussed the bite depth relationships and commented that published evidence showed that, even in the absence of sward profile constraints, cattle remove approximately 50 % of sward height, for sward heights between 4 and 30 cm. However, there has been inconsistency in the sward fraction removed between studies spanning spatial and temporal scales, with the general trend for the fraction to be greater for laboratory-based studies using sward boards, seedling trays or sown trays (eg. Mitchell *et al.* 1991; Laca *et al.*, 1992a; Illius *et al.*, 1995; Gordon *et al.*, 1996) than for those obtained in field conditions (eg. Wade *et al.*, 1989; Orr *et al.*, 1997). That the finding of this study supports the 45-50 % rule found in the original study by Laca *et al.* (1992a) using natural swards *in situ* is very encouraging. The matching pattern of grazed height with pseudostem height in this study could then be considered coincidental since the proportion removed across treatment approximated a constant 45 %. However, while there was indication of a similar association between bite depth and sward height across a series of patches, the finding that the proportion of sward height removed with a bite was greater on the short sward treatment (Figure 6.7) raises questions about the constant proportionality argument, and how the association between bite depth and sward height may be dependent upon the structural variation.

6.5.4 Animals preferentially grazed and achieved larger bites and greater rates of intake from the patches assigned to the short sward height. Why did this occur?

In contrast to the results presented for Experiments 1 and 2 where swards were in a vegetative phase of growth, and the data of Laca *et al.* (1993b), there was no significant linear relationship between patch grazing bites (or residence time) and sward height across the two height treatments, though there was a relationship within each of the sward height treatments. This behaviour clearly suggested that there was variation in one or more additional sward property attributes arising from the preparation procedures. This was further substantiated by the greater number of bites removed per unit area on the short treatments over the tall treatments. The overlap between nominal sward height treatments probably reflects the fact that the two grazing sessions were carried out a week apart. However, it was not clear what preparation procedure would have influenced within-treatment behaviour when residual sward height effects had generally been small for Experiments 1 to 4.

The effect may reflect the timing of nitrogen applications, which varied between experimental sessions due to weather conditions, though the consequences for sward state are not easy to define. Visual observation indicated that the shorter swards were darker, particularly in the second grazing session. While sward brightness may have been used as a cue (Bazely, 1988 and 1990), brightness alone would not have accounted for the greater rate of intake on these swards since brightness is essentially a property of the visual appearance as opposed to a sward structure or morphological characteristic. Although the overlap in sward height was not intended it did allow for study of the effect of sward characteristics on behaviour at a common height. The following section discusses the variation in intake rate and then works through the lower order components of rate of intake for explanation. However, any explanation for the contrast is to an extent hypothetical.

Rate of intake was always greater at any sward height on the patches assigned the short treatment (Figure 6.4). As residence time at any height was also greater on the short sward height treatment these observations do not provide support for the hypothesis that cattle monitor rate of intake as a determinant of patch residence time. Further investigation is required to quantify these observations. The regression lines for the two sward height treatments showed that the bite mass at any level of sward height between 18 and 23 cm was greater on the short swards (Figure 6.3), which primarily reflected the fact that bite penetration was greater at any height within this range since there was little variation in bite rate over the corresponding range. The role of pseudostem as an inhibitor of bite penetration in Experiments 2, 3 and 4 was considered in Chapter 5, but estimates of pseudostem height were not made in those experiments. In Experiment 5 (the current study), for the short sward group pseudostem height was a constant proportion of sward height across the range in height from c. 12 cm to 24 cm (Figure 6.8). However, for the tall sward treatment the corresponding linear fit was variable over the range c. 17 to 28 cm, the fraction declining between 17 and 24 cm (Figure 6.8). This contrast implies that on the short swards animals could have extended penetration before being constrained by pseudostem tissue that would have increased the applied force required for severance (Wright and Illius, 1995; Illius *et al.* 1995).

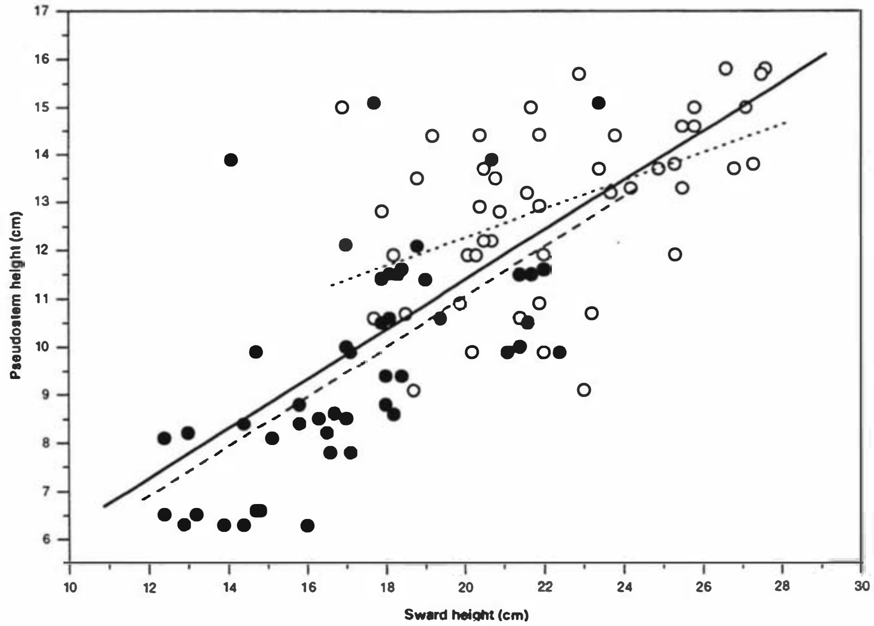

Figure 6.8 Relationship between sward height and pseudostem height for short (•) and tall (O) treatments. Linear relationships are fitted for short (—–) treatments, tall (......) treatments and a pooled (——) relationship.

Direct comparisons between the results of this study and that of Flores *et al.* (1993), at a common sward height and pseudostem to sward height ratio (Table 6.24), showed general agreement. There was no convincing evidence that the pseudostem to sward height ratio was responsible for the greater bite penetration on the short swards as the difference in bite depth was small (0.8 cm) and non significant (using the sed 0.43 from Table 6.17) when the ratio contrast was 0.55 on the short sward treatment and 0.66 on the tall sward treatment at a sward height of 17 cm.

Table 6.24 Comparison between bite depth at two pseudostem:sward height ratios, at a common sward height, in Experiment 5 with the data of Flores *et al.* (1993).

	Sward height (cm)	Pseudostem height (cm)	Pseudostem: Sward height ratio	Bite depth (cm)
Expt. 5 (short sward)	17	9.4	0.55	7.9
Expt. 5 (tall sward)	17	11.3	0.66	7.1
Sward D†	16	8.0	0.50	9.5
Sward C†	16	11.0	0.69	9.8

† Flores *et al.* (1993)

Furthermore, at taller sward heights (22 cm) the bite depth contrast was greater (1.4 cm) with a smaller contrast in the pseudostem to height ratio (0.54 and 0.58 for short and tall treatment respectively). Possible reasons for the greater values in bite depth in the study by Flores *et al.* (1993) are not discussed here. The analysis of variance output (Table 6.19) indicated that pseudostem height acted as a partial barrier to bite penetration on a patch basis, but it was not the explanation for the observed difference in bite penetration between the two sward height treatments.

Bulk density declined with increasing sward height. As pregraze mass was linearly related to sward height, at a common sward height any variation in bulk density reflects the variation in tiller density. Illius *et al.* (1995) demonstrated that greater forces are required to defoliate to a given level for swards with a higher tiller population. This implies that on the short swards the applied bite force may have been less, encouraging animals to increase the depth of penetration on the short swards. However, the contrast in bulk density in absolute terms was small even at a sward height of c. 22 cm (0.25 mg DM cm^{-3}), and other studies have concluded that the effects of bulk density on bite mass are small (WallisDeVries *et al.* 1998). Illius *et al.* (1995) postulated that the force an animal is willing to apply is governed more by the canopy structure rather than by the strength of individual herbage components. However, for Experiment 5 the greater concentration of neutral detergent fibre, possibly arising from an increase in the mean cell wall thickness (Spalinger *et al.*, 1986) on the tall sward treatment may have increased tensile strength (Wright and Illius, 1995). Therefore the lower penetration depth on the taller sward height group may reflect the marginal reward-cost concept proposed by Illius *et al.* (1995) but these effects require further clarification. Estimates of bite area calculated from the indirect estimate of bite mass, were substantially lower on the tall sward treatments at any given sward height (123.7 vs 78.5 ± 13.8 for short and tall treatments respectively). This may have reflected the lower efficiency of tiller gathering, as the number of tongue sweeps declines with increasing herbage strength (Laca *et al.*, 1993a). Unfortunately no estimates of strength or applied bite force were collected to verify these points.

Short, frequently grazed patches (shorter regrowth interval) commonly have a shorter average leaf length than tall patches (Jaramillo and Detling, 1992) which can be correlated with a lower leaf shear strength because of a lower cross sectional area (Inoue *et al.*, 1994). While this may be expected to influence the effort required for particle comminution rather than impede the harvesting process, the positive influence on bite formation and so processing for swallowing should not be under-estimated even though there was no evidence for a faster prehension biting rate on short swards. Duncan *et al.* (1994) also found that preferential grazing of nitrogen fertilised heather swards which might have been expected to have a lower breaking strength was not correlated with prehension biting rate, and the data in Experiment 4 also showed that there was only a marginally significant effect on rate of biting, irrespective of penetration depth into reproductive stem for the two deeper regrowth swards.

Summarising this section, herbage strength appears the most likely reason for the preference for patches assigned to the short sward height treatment over the tall sward height treatment at a given sward height. However, it cannot be ruled out that animals were selecting for nutritional gain (Senft *et al.*, 1987; Langvatn and Hanley, 1993; Dove, 1998), although currently it is not clear over what temporal scale such responses occur.

6.5.5 What effects do sward height, patch area and patch distance have on selective behaviour?

Animals were not sensitive to variations in sward height between sward height treatments or patch area when any of the indices of grazing bites, residence time or mass of herbage removed were expressed per unit area. Patch residence time (and grazing bites) strongly reflected inter-patch travel distance, which is in agreement with predictions from patch models of the optimal foraging domain (Stephens and Krebs, 1986), and the data of Bazely (1988) and Laca *et al.* (1993b) with sheep and cattle respectively. It is also in agreement with other species, bluejays (Kamil *et al.*, 1993) and pigeons (Davison and McCarthy, 1994; McCarthy *et al.*, 1994), although, in a recent indoor study, Dumont *et al.* (1998) reported that the proportion of test time eating good hay declined with the increasing distance sheep had to walk. While the analysis of variance output did not indicate a corresponding effect of inter-patch distance on the mass of herbage removed, this index did nonetheless respond to patch distance (37.3 vs 43.3 ± 2.85 g DM m^{-2} for 0.45m and 4.80m respectively), but the effect did not attain significance due to the wide variation in estimates (se 2.85 vs 1.74 for the mass of herbage removed and bites per unit area respectively).

Cattle in this study exhibited a clear ability to perceive the current patch distance up to at least a distance of 4.8 m. Laca *et al.* (1993b) reported cattle could modify patch residence time with increasing inter-patch distance to at least a distance of 8.4 m (the greatest distance they examined). Visually, it was clear that animals recognised the discontinuity in patch distribution and monitored the distance they had to walk. This control was displayed by the fact that when the inter-patch distance was short the head remained down in a searching position. By contrast, where there was a large inter-patch travel distance, upon departure from the current patch animals automatically lifted their head and neck, and within the last half a metre of approach to the next patch the head and neck were dropped back into the searching position. The mechanism for this search behaviour is unclear though it may relate to the variation in brightness between patch and inter-patch distances.

Data from Experiments 1 to 4 suggested that patch behaviour incorporates a component of sampling, as a mechanism for reinforcement of patch value. It therefore follows that sampling should be influenced by the area of the patch encountered (Illius *et al.*, 1987). This was clearly the case, with 77 % more bites removed from large than small patches. The 77 % increase in grazing bites corresponded with an increase in patch area of 72 %, showing a matching pattern of prehended bites with patch area. The proportional relationship between grazing bites and patch area was consistent at both patch distances (patch area x patch distance interaction, P=0.5870). There are few studies in the literature that have assessed behaviour to varying patch area (size) effects. Ginnett and Demment (1995) fed giraffes hand constructed patches of *Acacia melanoxylon* (R. Br.) at two patch sizes (21 shoots and 42 shoots) and found no significant effects of patch size on cropping variables. Using mixed grass-clover swards, Armstrong *et al.* (1993) did not find any change to the relationship between clover intake and clover in the sward at different patch areas. By contrast Griggs *et al.* (1991) found that steers grazing hand constructed swards of dallisgrass showed greater selectivity for large tall patches (15 cm, 400 cm^2 vs 15 cm, 100 cm^2), and Clarke *et al.* (1995) investigating the behaviour of sheep for grass and heather found that the total residence time on grass was lower when the same area and mass of one large grass plot was divided into 12 small plots. While the conclusions on the influence of patch area (size) differ across the studies, they do indicate that sheep, cattle and giraffes perceive patchiness, an element that Focardi *et al.* (1996) viewed as an inappropriate assumption in foraging models.

6.5.6 Can a common patch departure rule be defined?

Assessing whether animals use a common departure rule was not a primary objective at the initiation of this experiment and unfortunately the variability in the intake rate data set severely limits the conclusions that can be drawn. The larger patches offered animals the opportunity to remain grazing for a longer duration, with or without due consideration of patch depression effects: After adjustment of bites per unit area, the evidence that animals adjusted bite number and patch residence time, departing from patches after a constant number of prehended bites irrespective of sward height and patch distance, suggests that animals may follow some common departure rule. Recently, Roguet *et al.* (1998a) found that ewes, when visiting feeding stations of the same height for the first time, nearly always left the stations after a similar dwell time, with dwell time increasing with increases in sward height. An implicit assumption of optimality theory is that animals attempt to meet some common currency and attention has been given to tests of intake rate maximisation (Laca *et al.*, 1993b). In this experiment the absence of patch area effects on intake rate indicates the possibility that cattle were monitoring patch depletion through patch intake rate as well as the spatial dispersion of the nearest ungrazed patch in sequence. While estimates of intake rate are suspect given the degree of variability, these points were supported by the constant mass of herbage remaining post grazing (direct estimate) between the two patch areas (188.7 vs 196.4 ± 2.84 g DM m^{-2}, P=0.6415). However, not supporting these patterns was the constant rate of intake with increasing inter-patch distance. A matching pattern of selection with organic matter intake rate was found by Distel *et al.* (1995), and recently, using an indoor methodology, Dumont *et al.* (1998) reported that preference for good hay across two distances the sheep had to walk was related to the energy gain. Wilmshurst *et al.* (1995) also considered that deer selected patches that optimised the rate of energy gain. In the current study both organic matter intake rate and energy intake may have influenced patch residence time but these effects cannot be verified in light of the concern over the reliability of intake rate estimates.

The data of Laca *et al.* (1994), Distel *et al.* (1995) and WallisDeVries *et al.* (1998) demonstrated that patch depression effects occur even when grazing is confined to a single stratum, and consequently average patch intake rate can be anticipated to decline with patch depletion. These effects should be greater with increasing inter-patch distance, as has been demonstrated by Laca *et al.* (1993b). However, in the current experiment bite mass was unaffected by increasing patch dwell time as there was no strong evidence for depression in bite mass within the grazed stratum with increasing number of grazing bites, up to 80 bites. Furthermore, estimates of postgraze herbage mass were constant across inter-patch distance effects. However, there was no evidence that cattle grazed to a residual herbage mass threshold, across sward heights, as a possible 'rule of thumb' as suggested by Focardi *et al.* (1996) since the level of herbage remaining postgraze varied with sward height treatment, although this result may have been confounded with the variation between sward height treatments. The observation that animals were not experiencing patch depression effects raises the unanswered questions: (a) what mechanism animals used to monitor the number of grazing bites and patch residence time to exercise a proportional relationship between patch area and (b) if the rate of forage acquisition was not declining with time why did animals depart from patches before forage intake rate began to decline with increasing inter-patch distance? Ginnett *et al.* (1999) have argued that, under a scenario where animals do not experience patch depression, the optimal strategy would be for the animal to remain until all forage is depleted, but the observations in the current experiment do not fit this hypothesis. Furthermore, these authors went on suggest that the results of Focardi *et al.* (1996) showed the deer actually solved a simple marginal value theorem problem. However, animals may have satisfied only one criterion of the marginal value theorem, in which a key concept is that animals demonstrate that they can calculate the expected rate of gain. For animals to exhibit such behaviour one would expect them to adjust behaviour on a patch relative to the awareness of the characteristics of neighbouring patches within the perceptive field. The depth of this perceptive field is largely un-investigated but the previous four studies, and this study, have demonstrated that patch behaviour is primarily determined by the costs incurred in travel to the next patch and the sward characteristics of the current patch which, combined with a time factor, govern patch depression irrespective of the opportunity presented in ungrazed neighbouring patches.

It was unfortunate that, given the variability associated with the estimates of intake rate, the assessment of whether animals departed from patches in accordance with the balance between intake rate and inter-patch distance could not be undertaken. Nonetheless, evidence to substantiate an answer to this question would have required the collection of the mass of herbage removed after sequential sets of bites (eg. Ginnett *et al.*, 1999), which was not practical in the context of the experiment reported here.

There are conflicting reports on whether animals forage in a manner where they monitor the average rate of intake within the environment. Laca *et al.* (1993b), working with cattle, found a good agreement between the observed and predicted residence times, while the opposite held true for Distel *et al.* (1995). However, these authors found a good agreement between predicted and observed rates of organic matter intake. Bazely (1988) on the other hand found strong evidence of 'overstaying' when compared with the predictions of patch residence time. Similar observations of a longer dwell time than predicted by maximisation theory has been reported with bluejays and pigeons (Kamil *et al.*, 1993; Davison and McCarthy, 1994; McCarthy *et al.*, 1994). Jiang and Hudson (1993) discussed how the cropping rate of wapiti within a feeding station, compared to the average cropping rate, influenced departure rules. However, it appears that these authors took no account of travel time between patches, thus assuming marginal costs. The presence of competition is likely to modify behaviour (Mitchell, 1990), and Forbes (1995) considered competition as a possible explanation for the observed responses in the study by Bazely (1988). By contrast cattle in the studies of Laca *et al.* (1993b) and Distel *et al.* (1995) grazed as individuals. The current study was unable to clarify any of these issues.

6.5.7 Is patch behaviour determined by the characteristics of adjacent patches in sequence?

Illius and Gordon (1990) commented that a sophisticated animal would use information gained before, during and after ingestion to adapt its foraging tactics. There is little understanding of the level of information animals possess and yet this is an essential premise of optimal foraging theory. It is probable that the lack of evidence to define such capabilities is a direct reflection of (a) the difficulty of quantifying how an animal perceives the environment, since it is a feature that is not directly measurable, and (b) the small number of studies which incorporate experimental designs that objectively test the animals' capability for gathering information and their ability to use that information to make informed choices at a following patch or grazing session. Additionally, progress via repeatedly offering a range of environments and monitoring animal responses has a high resource cost associated with it. In a number of experiments (Bailey *et al.*, 1989; Edwards *et al.*, 1996; Laca, 1998; Dumont and Petit, 1998) evidence for knowledge retention has been presented, and the mechanism is referred to as a backward chaining search strategy (Packard *et al.*, 1990). By contrast to the evidence for spatial memory, which may be of limited use in intensive production systems, there have been fewer tests of whether herbivore behavioural patterns differ within and between patches.

The design used in the experiments reported in this thesis offered two powerful advantages: (a) it provided the opportunity to investigate the role of patch carry-over effects which had previously been identified (Illius *et al.*, 1992) and (b) treatments were balanced so that each treatment followed every other treatment with equal frequency, thus avoiding circumstances where patch selection could be a function of the frequency with which each patch was encountered (Illius *et al.*, 1987).

In the current study, while the current patch distance (ie. distance from current to succeeding patch, refer to Figure 6.1) influenced the dwell time and number of grazing bites on the current patch, interpretation of the analysis of variance output presented in Tables 6.21 and 6.22 showed that decisions on the current patch were not influenced by the succeeding patch distance (ie. distance from succeeding to succeeding about one patch, refer to Figure 6.1) in sequence regardless of whether the distance was 0.45 m or 4.80 m. Likewise, any information gained from the preceding patches (refer to Figure 6.1) did not appear to reflect the decisions on the current patch. As pointed out in the earlier discussions, this contrasts with the work of both Illius *et al.* (1992) and Distel *et al.* (1995), who reported that patch selectivity was not exclusively a function of the patch being grazed. In both of these studies animals were offered paired swards, whereas in the studies presented in this thesis, animals were given a greater array of options to choose from. The observed lack of response to contrasts in terms of distance between adjacent patches may be related to the trade-off between the perceptive field and foraging efficiency, and thus the balance in time spent eating relative to the time involved in deciding what to eat (Packard *et al.*, 1990). Alternatively, the observed lack of response to conditions on the adjacent patches may indicate the diversity of the ecosystem within which animals' forage. A dairy cow in an intensively stocked system where the competition for food is high, can ill afford to base decisions about the current patch in the expectation that the next desired patch within her perceptual view will be available upon exiting the current patch at the optimal time. Additionally, feeding behaviour on a short-term basis does not match short-term fluctuations in the animal's internal state (Kyriazakis, 1997). Nonetheless, as noted by Kyriazakis (1997), if short-term behaviour is erratic, how is it that animals can exercise control over behaviour covering a wider temporal scale?

These results, combined with the corresponding data in Experiments 1 to 4, raise questions over the assumptions that characterise the linear based optimal foraging patch use models. These concerns have been discussed by Packard *et al.* (1990). However, the finding that patch decisions are independent of the position of other patches within a foraging path is promising in light of the recent trend towards describing behaviour using a hierarchical approach (Senft *et al.*, 1987; Demment and Laca, 1993). Decisions at the patch level are essentially the same as those at the bite level. As the selection of patches appears to be independent of the factors governing patch depletion and the location of a bite, integration of these patch mechanisms with those parameters that characterise behavioural strategies across greater spatio-temporal scales should be possible.

6.5.8 Is the current interpretation of sampling correct?

Encounter rate is a critical concept of optimal foraging models and is artificially linked with the animal's perception and capability to monitor average patch conditions since the theory crudely assumes animals have perfect knowledge of the choices in the environment. This is rarely the case (Packard *et al*., 1990). As Mitchell (1989) has pointed out, it is the information possessed by the animal which determines the behavioural response, yet we have very little understanding of the perceptual capabilities and the implementation of information gained within the decision making hierarchy.

As with the earlier experiments (Chapters 4 and 5), sampling was an integral component of the decision making process. According to Mitchell (1989), a forager may possess two types of information, being either a *myopic* forager who knows, at most, the location and quality of one resource item at a time, or a *periscopic* forager who knows the location and expected quality of more than one resource item at a time. A periscopic forager expresses partial preferences but a myopic forager does not. A myopic forager will update its memory net of patch values to the effect that after the first encounter of a rich item, the number of poor patches selected declines (Mitchell, 1989). The experiments presented in Chapters 4 and 5 have shown that animals did not consistently display behaviour that would suggest that they possess information defined as a myopic forager, as the behaviour of ignoring poor patches after encountering patches where the marginal return was higher was not observed. A similar result was obtained in the current experiment.

For a periscopic forager, patch selection incorporates a travel time cost in addition to a handling cost for any resource. Mitchell (1989) demonstrated with hummingbirds that the probability of a poor patch being selected was related to its value relative to the rich patches and also to the spatial arrangement of patches. Poor patches, (in the context of this thesis, patch value is related to potential rate of intake as a currency), are thus more likely to be selected if the contrast in patch value is small and if the poor patch is surrounded by rich patches. The results of the preferential behaviour for grass and heather from the study of Clarke *et al*. (1995) support this theory. Sheep were observed to select heather, the poorer patch type, if the heather patch was spatially located en route to a rich grass patch. In a linear design, as used in this thesis, the marginal cost to the animal of sampling a poor patch was relatively low since the animals were only moving in one direction of travel and the rich patches were to be visited anyway. This could be viewed as a limiting feature of the experimental design. However, Spalinger *et al.* (1988) found that when plant density was high, deer foraged in a straight trajectory, selecting bites within a path width approximately 0.6-0.8 m wide. Patch width in the current study was 0.875 m. Distel *et al.* (1995) showed that steers foraged in a linear path even though they had the opportunity to deviate from a linear path where patches were arranged in a mosaic without any constraints on movement. In more extensive ecosystems animals tend to forage following topographic contours to the effect that there is little evidence of zigzagging (Senft *et al.*, 1987), and Ward and Saltz (1994) observed that foraging efficiency was greater when gazelles moved between patches in a direct path. The decision to remain at a patch will therefore be a direct function of the characteristics of the patch and the inter-patch travel time. In this sense, sampling does reinforce patch value. However, this behaviour should not be confused with mis-identification, but rather considered on the basis of the marginal cost, and therefore could be viewed as an efficient strategy that minimises the change from poor to rich patches within the environment.

6.6 CONCLUSION

The scale of spatial heterogeneity within a forager's environment is a direct consequence of how the forager places bites in space and then responds to that resultant heterogeneity. This study examined the effect of sward height, patch area and inter-patch distance on foraging decisions.

Behaviour was not related to sward height across the two sward height treatments, and this effect was attributed to the possibility that the tensile strength of herbage may have been lower for the shorter sward height treatment. However, within each height treatment, behaviour followed the established relationships for control of intake rate. The current study was unable to provide any further evidence on the issues surrounding the importance of pseudostem height as a regulator of bite penetration. However, the direct measurements of pseudostem height in this study did suggest that the pseudostem:regrowth interface was a strong partial regulator of the penetration of a bite, reinforcing the comments made in Chapter 5 that further research is required to clarify this issue.

After adjustment for patch area, the decision to remain foraging on a patch was strongly related to the inter-patch travel distance between patches. However, there was no evidence that cattle departed from patches in accordance with the theory of maximisation of dry matter intake rate. Larger patches provided animals with approximately 3-4 feeding stations within the patch, creating a more continuous arrangement of feeding stations as opposed to a discrete feeding station/patch. Consequently, heterogeneity within a patch would have been expected to be larger and animals were observed to respond to this at the scale of a bite. Animals adjusted the number of grazing bites and residence time to the area of the patch, suggesting that they were monitoring the rate of depletion. Even so, their departure from patches when there was no evidence for patch depression effects, and the finding that the postgraze residual mass was similar across inter-patch distances, do not conform with the predictions of optimality. The limited precision of the estimates of intake rate is acknowledged as the weak link with much of this interpretation, but nonetheless the data reinforces the view that there is much research to be done to understand the rationale for foraging decisions before researchers will be able to define a range of optimal strategies for a set of constraints within any ecosystem.

Furthermore, the finding that increasing inter-patch distance did not encourage animals to utilise information gained from foraging on the preceding or the expectation of the value of the succeeding patch in sequence provides support for the earlier finding that behaviour about the current patch was independent of other patches in sequence.

SEVEN

INTEGRATING DISSCUSSION and CONCLUSION

7.1 INTRODUCTION

The key objective of this thesis was to describe the preferential grazing behaviour of dairy cattle when offered a diverse range of choices *in situ* and, in doing so, to increase understanding of the rationale behind the decision making process. Implicit in this is an understanding of the trade-off between alternative criteria for selection. Foraging behaviour occurs over multiple scales (Senft *et al.*, 1987), and Gordon and Lascano (1993) organised the decision making process into a series of short term tactical and longer term strategic decisions. The work in this thesis focussed on short term decisions at the patch level and the interactions between the structural properties of the vegetation (sward height, bulk density and the distribution of herbage mass in the vertical dimension), all variables that integrate to control bite dimensions (Mitchell *et al.*, 1991; Ungar *et al.*, 1991; Laca *et al.*, 1992a; Flores *et al.*, 1993; Laca *et al.*, 1993a). Additionally, patch selective behaviour is thought not only to be controlled by the characteristics of individual patches but also by the location of the patch to neighbouring patches with different characteristics, carry-over effects of foraging style from patch to patch, and patch encounter rate (Illius *et al.*, 1987; Illius *et al.*, 1992; Demment *et al.*, 1993). The experiments described in this thesis addressed these issues by examining the role of within and between patch behaviour. The focus was on improving fundamental understanding of biological systems as opposed to collection of data contributing directly to the efficiency and profitability of agricultural systems.

The hypotheses stated at the end of the review of literature (Chapter 2) were investigated using a linear sequence of patches, modified from the procedures described by Laca *et al.* (1993b). Treatment combinations were structured to provide replication of combinations, within each sequence, and to provide a balance over a series of 4 (Experiments 1, 2, 3 and 5) or 6 sequences (Experiment 4). Balance across sequences allowed for the monitoring of within and between patch behaviour, as the animal progressed down a sequence.

The focus of this final chapter is (a) to provide an evaluation of the procedures used to assess preferential behaviour, (b) to draw conclusions about the role of sward structural cues on the selective behaviour of dairy cattle and (c) to relate the observations of selective behaviour to the principles of foraging theory. The aim is to summarise and integrate the detailed discussions of experimental results in Chapters 4 to 6.

7.2 EVALUATION OF EXPERIMENTAL PROCEDURES

7.2.1 Methodologies

7.2.1.1 Linear patch sequence

A linear sequence of patches *in situ* in the field (Laca *et al.*, 1993b) was a key feature of the experimental procedure described and used in the experiments throughout this thesis. Patches were created and manipulated within strips of a perennial ryegrass monoculture. Ryegrass was chosen since it is the most widespread pasture specie found on farms in New Zealand, largely due to its flexibility in response to variations in management (Harris and Chu, 1985). It was a deliberate decision to omit white clover in order to avoid confounding variation in patch structure with simultaneous variations in botanical (species) composition.

The linear sequence of patches enabled the monitoring of preferential behaviour to a sequence of choices similar to that randomly encountered by animals grazing within a foraging path in the field. This provided the opportunity to offer a wider range of complexity of choice than the common 'two choice' contrast used in laboratory-based procedures. Relative to the laboratory-based approach, the field-based procedures allowed for indication of whether cattle were willing to walk past a patch (no bites prehended) to acquire the opportunity to graze at another patch in sequence, behaviour which cannot be observed when animals are confined to metabolism crates. Additionally, there was an extension of the scale of decision making from a bite (Laca *et al.*, 1992a) and small patch (feeding station) (~0.36 m^2 Distel *et al.*, 1995) to a larger patch (~0.80 m^2).

The experiments reported in Chapters 4 to 6 placed emphasis on sward structure, combinations of treatments and sequencing compared with the study by Laca *et al.* (1993b) where only one treatment (10/10, 15/5 or 12.5/7.5 cm sward heights) and one inter-patch distance was replicated in a linear arrangement. Recently, Roguet *et al.* (1998a) have described methodology (modular 'head-crush') used to study the feeding station behaviour of ewes. In the reported study by these authors, ewes were only exposed to one treatment combination at a single exposure (eg. 8 feeding stations all 7 cm sward height), similar to the study by Laca *et al.* (1993b). This effectively constrains the number of treatments (height and height x inter-patch distance) and/or replication that could be incorporated at any one time and renders the apparatus less effective than the design described in this thesis for assessing trade-off decisions.

Using a linear sequence, as in the experiments reported in this thesis, cattle were prohibited from turning backwards. Other studies in the literature have noted that herbivores do not display a marked turning behaviour, rather following a linear path of foraging (see Spalinger *et al.*, 1988; Focardi *et al.*, 1996). For example, Distel *et al.* (1995) offered animals a mosaic of 16 patches arranged in a four by four column-row design and commented that cattle grazed in a straight trajectory and only turned when they reached the end of a column.

7.2.1.2 Strength properties

Leaf and stem strength was assessed using two different procedures; a Warner Bratzler shear apparatus and an Instron testing instrument. Henry *et al.* (1996) and Wright and Vincent (1996) have discussed the various forms of equipment for measuring and expressing tissue strength, and concerns arising over the difficulty of making objective comparisons across studies. Estimates of strength properties of herbage involve considerable human and time resource input. Where estimates of strength provide supplementary data to a central objective, as was the case in this thesis, detailed estimates of leaf width and thickness to relate strength to leaf cross sectional area were not warranted in view of the extra resources required. Therefore, estimates given in Table 5.5, Table 5.29, Table 5.48 and Table 5.49 provided a relative measure of shear or tensile strength for comparison across treatments within each of the experiments. Also, tiller or strata measurements could not be converted to estimates of biting effort because it was not feasible to attempt measurements of tiller population density, the number of leaves per tiller or bite area during the course of the three experiments subject to these constraints (Illius *et al.*, 1995).

The Warner Bratzler shear apparatus (Experiments 2 and 3) had the advantage that samples could be processed relatively quickly, and this enabled a larger number of samples to be gathered at any one time in the field. Samples could not be stored in a chiller even for a short period of time (30 minutes) without the leaf blades beginning to exhibit visible signs of wilting. However, similar constraints to those described by Easton (1989) were encountered; a number of samples deformed prior to rupture and the fracture site was frayed. The large majority of the upper strata recordings, particularly for Experiment 2, were less than 6.75 kg (c. 67 N) which fell within the first quarter of the salter spring scale. Easton (1989) noted that recordings from the second quarter were the most accurate. The reliability of the absolute values therefore is questionable but even so, as a general measure across treatments they were still sufficiently sensitive to detect the contrast in plant material at the fracture site for the upper stratum recordings and the progressive increase in strength down the sward profile in Experiment 2.

Concern over the reliability of estimates using the Warner Bratzler apparatus in Experiments 2 and 3 (see also Wright and Vincent, 1996) led to the use of the Instron testing instrument in Experiment 4. Force displacement curves were plotted for each recording, and curves where material deformed prior to rupture was easily recognised and subsequently discarded. A common concern addressed in recent studies measuring the forces in tension has been the avoidance of stress concentration at the clamp or plate site leading to fracture at this point (Wright and Illius, 1995; Henry *et al.*, 1996). The pair of jaw clamps on the top pneumatic clamp and one of the jaw clamps on the bottom pneumatic clamp in Experiment 4 were surfaced with emery paper and rubber, respectively (Plate 5.1(a)). This was successful in eliminating slippage, although the jaw clamps did require periodic cleaning to maintain the friction between the jaw clamp and plant material (see Westfall *et al.*, 1992). There was no indication to suggest that the pair of jaw clamps surfaced with emery paper caused excessive damage to the leaves at the clamping point as noted by Evans (1967). The solid cross bar on the jaw clamp of the bottom pneumatic clamp (Plate 5.1(a)) was used to simulate incisor impact on gathered herbage, although Vincent (1983) has commented that the biting action of large bodied animals, like cattle, does not function as a concentrator of stress, and so does not make herbage easier to break.

The absolute values for the upper (regrowth) stratum were much higher than recorded by Wright and Illius (1995) and Henry *et al.* (1996) and this largely reflected the greater number of leaves per sample as opposed to a single leaf test. However, given that in most samples a minimum of three leaves were clamped at the site of fracture, the absolute force per leaf would have been smaller than the general range of values recorded by Wright and Illius (1995) and Henry *et al.* (1996). This probably reflected the degree of stress concentration at the point of contact with the simulated incisor. Nonetheless, this effect would have been constant across all samples with respect to data interpretation.

There was substantial variation between samples which appeared to reflect the variation in tiller size and also possibly the number of leaves per tiller, both factors that were not standardised. Nonetheless, as discussed for Experiments 2 and 3, the measurement procedure was consistent across treatments between strata, within treatments. The estimates of strength in Experiment 4 indicated that there was likely to be clear penalties to the animal, in terms of biting effort as well as time per bite, with increasing penetration into a stratum comprising reproductive stem.

7.2.1.3 Spatial distribution of herbage

The stratified sampling procedure described for Experiment 4 will be a critical procedure in future experiments if one is to accurately predict the location and composition of a bite. The use of a garden vacuum leaf blower was an efficient means for the collection of the mass within strata. It is, however, a very laborious and resource consuming procedure, even for small (0.40 m^2) patches (centre section). Given the importance of these measurements and the fact that the data is pooled, detailed measurements from a representative number of patches would probably suffice. An alternative procedure that provides a comprehensive inventory on the spatial structure of swards is the inclined point quadrat (Grant, 1993), but it too has a high resource demand. Further, the data obtained using this apparatus does not offer the potential to calculate the relative proportions of structural components between the grazed and ungrazed strata, which have been identified in this thesis as a potentially important consideration in understanding foraging decisions.

7.2.1.4 Nutritive value

The most widely used biochemical parameters for measuring the nutritive value of herbage are crude protein (Nitrogen x 6.25 %), fibre (ADF, NDF) and carbohydrate content (CHO) (Van Soest, 1982). Within each of the data sets of nutritive value for the three experiments presented in Chapter 5 (Table 5.6, Table 5.30, Table 5.50, Table 5.51 and Table 5.52) contrasts in leaf and stem proportions were not consistent with measures of nutritive value. This was clearly illustrated in the contrast between Experiments 2 and [3 and 4]. In Experiment 2, where there was only a planned contrast in sward height, and all other preparation procedures were constant across treatments, there were significant differences in nutritive value between treatments. In Experiment 3 and 4 however, with much stronger contrasts in whole sward leaf (Experiment 3) and leaf within strata (Experiment 4) proportions, there was a remarkable consistency in whole sward and within strata nutritive value between treatments.

There were contrasts between estimates of nutrient concentration derived from duplicated NIRS and conventional chemistry procedures in Experiment 3. The particularly low values recorded for OMD using *in vitro* standards was a concern. However, the relative patterns of nutritive value between treatments in terms of whole sward or between strata contrasts was a more important measure than the absolute values themselves. All samples used for nutritive value analysis were those previously dried (80^0C for 24 hours) for estimates of pregraze herbage mass for each pair of patches. Drying temperatures in the range 65-80^0C have been recommended by Schmidt *et al.* (1970). NIRS calibration equations are developed from samples dried at 60^0C but there is considerable variation across studies in the drying temperature used and the duration of the drying period. For example Cosgrove *et al.* (1998), reporting on the degree of spatial and vertical variability of herbage mass within a single paddock, dried samples at 40^0C for 40 hours before grinding and analysing samples using NIRS facilities as used for the experiments in this thesis.

A more important contributing factor towards the insensitivity of estimates of nutritive value across treatments within experiments may have been the number of samples analysed. Cosgrove *et al.* (1998) defined the minimum number of samples required for predicting nutritive value from dairy pastures as given in Table 7.1. The number of samples analysed per treatment effect (sward height for Experiments 2, 3 and 5, and regrowth depth and sward height for Experiment 4 – Table 5.6, Table 5.30, Table

5.50-Table 5.52 and Table 6.5) are shown in Table 7.2. Using the guidelines from Table 7.1 for treatment effects there was a sufficient number of samples for the accurate prediction of protein and fibre but only sufficient samples for reliable predictions of *in vitro* digestibility and metabolisable energy from the upper stratum for Experiments 3 and 5. Reliable estimates of nutritive value from samples gathered in the field will be essential if the effort to separate out the trade-offs between structural and nutritive value properties in future studies is to be successful.

Table 7.1 The minimum number of samples required for accurate estimation of nutritive value within a dairy pasture as defined by Cosgrove *et al.* (1998).

Nutritive value parameter	Minimum No. of samples†	Accuracy level
Crude protein (%), Neutral Detergent Fibre (NDF) (%), Acid Detergent Fibre (ADF) (%)	6 (all 4 strata)	± 50 g/kg
in vitro digestibility (%)	12 (3 upper strata) 19 (bottom stratum)	± 25 g/kg
Metabolisable Energy (ME) (MJ/kg DM)	12 (3 upper strata) 48 (bottom stratum)	± 0.5 MJ/kg ME

† stratum was defined as $^1/_4$ of canopy height

Table 7.2 A summary of the number of samples, for each treatment effect, used to determine the significance of nutritive value within each experiment for Experiments 2 to 5.

Expt.	No. samples per treatment	No. samples Per treatment effect
2	1 sample/sward height group/block	6/sward height group (1/block x 3 blocks x 2 sequences)
3	1 sample/trt/block	12/swrad height group (1/trt/block x 6 blocks x 2 trts/sward height group)
4	1 sample/trt/sequence	9/regrowth depth level (1/trt/sequence x 3 sequences x 3 trts/regrowth depth) 9/sward height level (1/trt/sequence x 3 sequences x 3 trts/sward height)
5	1 sample/pair of trt [T1&T2], [T3&T4], [T5&T6], [T7&T8]	12/sward height trt (1/pair x 6 blocks x 2 pairs/sward height trt)

7.2.2 Patch characteristics

7.2.2.1 Manipulation of sward characteristics

Sward height was measured from leaves in their natural position, defined by Rhodes and Collins (1993) as surface height. Contrasts in overall sward height and in stubble and regrowth height were established successfully, but the use of a continuous sward height variable (linear sward height regression) in the statistical model across all experiments indicated strong within treatment variation in sward height. Rhodes and Collins (1993) reported a mean coefficient of variation (c.v.) of around 34 % from 50 random measurements across a grazed sheep and cattle paddock ranging in mean height from 2 to 6 cm. In general, the control over pregraze sward height and measures of postgraze height was particularly good as supported by the low coefficient of variation values, range 3.0 to 19.5 and 6.6 to 39.0 for pregraze and postgraze respectively.

Preparation procedures were less effective in creating controlled variations in herbage bulk density. The relatively few studies that have attempted to manipulate tiller and herbage bulk density under field conditions (see section 4.5.1) demonstrate the difficulty of the task. There is emerging evidence on the influence of tiller density (see Illius *et al.*, 1995) and changes in stratum bulk density on bite depth patterns (see Wade *et al.*, 1989), suggesting that the roles of tiller and bulk density should not be overlooked. There is therefore a need to develop preparation procedures that will enable the influence of contrasting and independent effects of density to be incorporated into field-based studies.

Manipulation of patch area was an effective method of controlling the mass of green leaf. However, in further studies patches should be centred in the raceway so that animals do not need to adjust their orientation to maintain balance while grazing. Although the behavioural responses did not suggest that patch location within the width of the raceway influenced behaviour, with a different set of treatments (eg. weaker maturity contrast) this effect could have assumed greater importance.

In vegetative swards, the association between leaf percentage and sward height (Experiment 1 and Experiment 2, excluding T1) indicates the necessity to control variations in leaf and sward height independently in selective behaviour studies if the objective is to identify the cues animals respond to. The adoption of staggered stubble heights and differential regrowth periods was effective in creating treatment contrasts across studies, particularly for contrasts in whole sward or between-strata leaf:stem ratios. Trimming prior to the grazing sessions (Experiments 2 and 4) was also a useful procedure for decreasing heterogeneity in surface sward height.

In Experiments 3 and 5 which incorporated patch area contrasts the smaller patch area was always associated with a slightly shorter sward height (c. 10 % shorter). These two experiments used an adjusted rotary lawn mower for patch preparation. In Experiment 5, the treatment means for stubble height, pseudostem height and sward height suggested that the mower was cutting at a lower height on smaller patches. The sickle bar cutter on the S.E.P. mower used for Experiment 4 was more efficient at cutting evenly across the patch, and particularly so because the cutter bar extended the full width of the patch.

7.2.3 Monitoring preferential behaviour

The relative value of grazing bites and residence time as indices of preference was discussed in Section 4.5.4 of Chapter 4, and so the key points will only be summarised here. Over short temporal scales the consistency across the five studies in the pattern of grazing bites and residence time (Table 7.3) indicates that either index is as good as the other. Similar conclusions have been drawn by Illius *et al.* (1999) in a recent study investigating intake rate maximisation in goats. Residence time offers advantages as an index since it is easier to measure without the need to be in close proximity to the foraging animal, which is relevant for field studies. Additionally, grazing bites may introduce a bias as a consequence of the inverse relationship between bite mass and bite rate (see section 4.5.4). On the other hand, Illius *et al.* (1999) argue that the prehending of a bite represents a clear decision by the animal and one that can easily be observed, whereas measures of residence time are more difficult to make, presumably because of the need for electronic recording equipment. If estimates of bite mass are to be obtained through dividing the total estimate of the mass of herbage removed by the number of bites taken, either from the collection of herbage from a fistula or a combination of direct cuts and calibration procedures, then the corresponding number of bites is a necessity.

Table 7.3 Comparison of correlations between grazing bites and residence time, and grazing bites and herbage removed, for Experiments 1 to 5.

Expt.	Correlation between grazing bites and residence time	Correlation between grazing bites and herbage removed
1	r = 0.99	r = 0.09
2	r = 0.99	n/a
3	r = 0.99	n/a
4	r = 0.99	r = 0.73
5	r = 0.98	r = 0.37

n/a no estimates presented for Experiments 2 and 3.

Given that most electronic recording devices can now be programmed to input data for specified operations, the collection of both grazing bites and residence time is recommended. Categorising bites as prehension or manipulative bites will become important, particularly with choices offering maturity contrasts. However, visual observations alone make it difficult to monitor bite types. Collection of prehension, manipulative and chewing jaw movements from video records requires a clear focus on the subject's jaw at all times. An alternative automatic procedure that offers potential is the acoustic monitoring device (Laca *et al.*, 1992b). However, visual observations as a back-up would still be recommended.

Estimates of the mass of herbage removed were not essential for an assessment of preferential behaviour, particularly in view of the consistency of preference as monitored by bite number and residence time. However, such estimates would provide the opportunity for indirect estimates of bite mass and approximate estimates of bite area, so long as they are accurate. Such additional measurements offer scope for further understanding of how sward characteristics modify grazing decisions, for example the patch depletion curves depicted in Figure 5.9 and Figure 5.10. Herbage removed as an index showed a weaker correlation with grazing bites in Experiment 5 relative to Experiment 4 (Table 7.3), even though the accuracy of predictions was greater for the estimates recorded in Experiment 5 (Mean square Treatment(Sequence x Block) and Root Mean square error = 1711.52 and 48.0 for Experiment 4 and 388.69 and 13.57 for Experiment 5 respectively). There was no clear explanation for this discrepancy. On the evidence for Experiment 5 alone caution would need to be exercised in relying solely on either the mass of herbage removed or grazing bites as an index, particularly where there is variation in the spatial aggregation of patches. Difficulties encountered and scope for increasing the precision of measures of the mass of herbage removed have been discussed in section 6.5.1.

7.2.4 Bite rate

As patch residence time did not exceed 2 minutes, and only on very rare occasions were animals observed to lift their head and perform exclusive chewing movements, the values presented for rate of biting throughout the thesis represent the near maximal bite rate (Laca *et al.*, 1992b). Variations in bite rate are primarily a response to sward conditions (Hodgson, 1986), and so caution should be exercised in placing emphasis on bite rate responses, particularly in the absence of detailed information on sward canopy structure, especially the proportions of leaf:stem and regrowth:stubble.

7.2.5 Animal state

Since Hodgson (1982) commented that it did not appear that state-dependent effects influenced preference, Newman *et al.* (1994), Edwards *et al.* (1994) and Villalba and Provenza (1999) have all shown that 24 hour, 18 or 24 hour and 15 hour fasts, respectively, influenced food selection and preferences. Additionally, preference was considered to be more strongly influenced by physiological state than food structure (ground or whole alfalfa and barley) in the study reported by Villalba and Provenza (1999). However, the magnitude of the hunger drive has not been shown to influence the choice behaviour of heifers (2, 16 or 24 hr fasts) offered choices between strips of vegetative and reproductive swards of contrasting structure (Dumont *et al.*, 1995b). It is also of note that a minimum period of 2-3 hours removal from grazing is the norm for lactating dairy cows under New Zealand's intensive management regime. According to Newman *et al.* (1994) and Edwards *et al.* (1994) fasting decreases the level of selectivity displayed by the animal, but the data from Experiments 3 and 4 where there were strong contrasts in plant phenology between patches showed that animals exhibited a very marked preference. In light of this behaviour it is considered unlikely that the 2-3 hour period of food deprivation in all five experiments had any strong influence on grazing choice. Whatever the influence fasting may have had on bite mass, (a) the effect was consistent between experiments and across sward contrasts within each experiment, and (b) for Experiments 4 and 5 greater importance was attached to patterns between sward contrasts rather than to absolute values since there was an element of bias in the estimates arising from the difficulties encountered with estimates of the mass of herbage removed, particularly with Experiment 4.

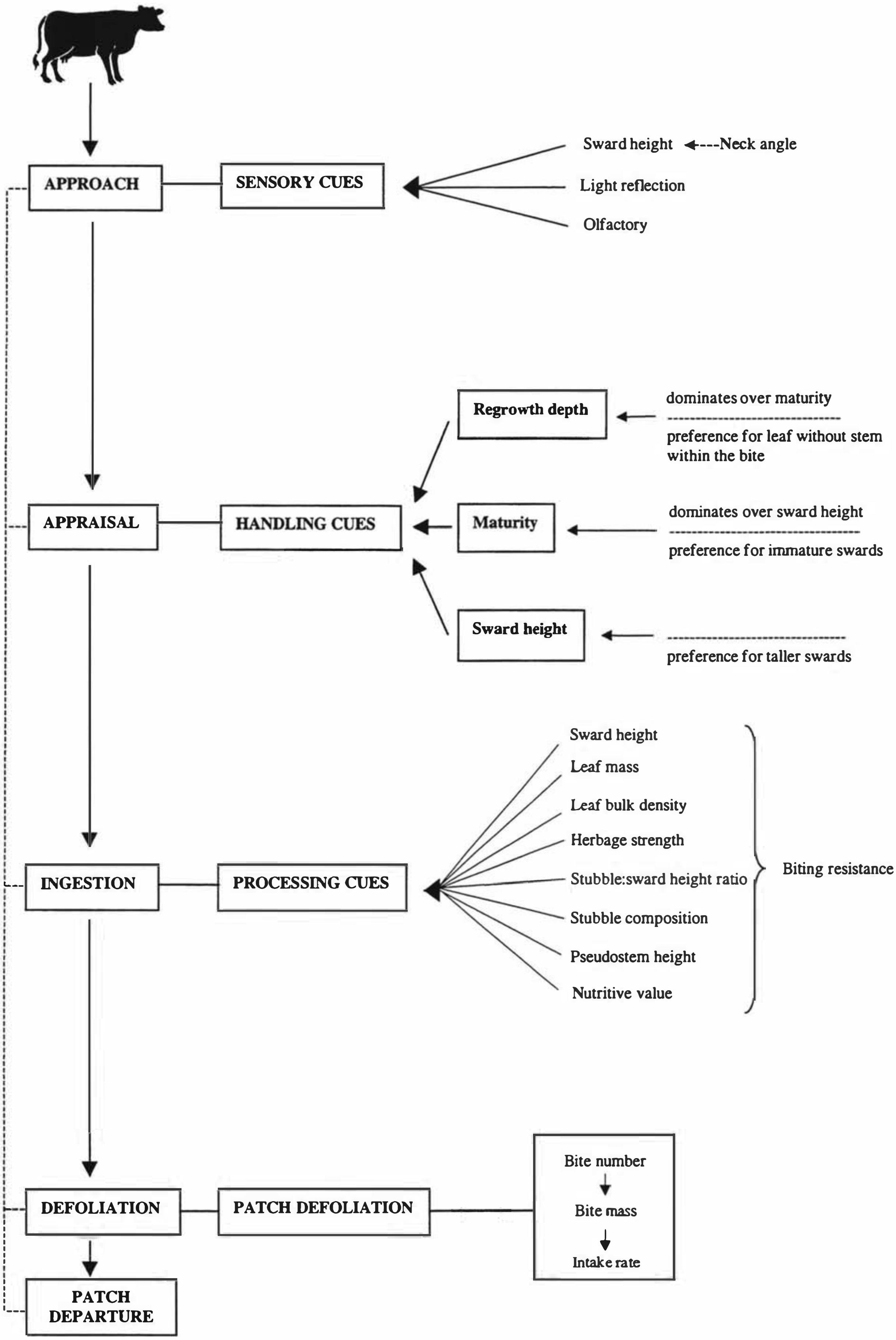

Figure 7.1 The patch grazing cycle.

7.3 CUES and CHOICES

In the introduction to this thesis there was reference to the fact that cattle, even when foraging under intensive grazing conditions, are faced with the continual need to balance decisions about where and how long to graze, using the stream of information which is relayed to them through feedback mechanisms. The objective of this section is to summarise the key processes and cues that led to the observed responses discussed in Chapters 4 to 6.

The patch grazing cycle can conveniently be categorised as four key pathways of information termed Approach, Appraisal, Ingestion and Defoliation (Figure 7.1). Section 7.3.1 covers the Approach and Appraisal phases of foraging which primarily involve the key cues controlling preference and selective behaviour. Section 7.3.2 covers the phases of Ingestion and Defoliation which are more concerned with how the processing cues influence forage removal and patch departure decisions.

7.3.1 Approach and Appraisal

The limited evidence that behaviour (ie. the number of grazing bites) at a specific patch was dependent on other patches in sequence (Tables 4.17, 5.24, 5.37, 5.66, 6.21 and 6.22) suggests that cattle do not use long range perception of potential patch characteristics to guide patch decision making; rather, patches are assessed upon approach on a patch by patch basis. In traversing a series of patches cattle are able to sense and respond to variations in sward height. Observations from the studies reported in this thesis suggest that the visual cue is the dominant mechanism used in this initial appraisal of patch profitability. However, it is likely that the need to manipulate the neck angle also has an influence on approach decisions. The cows exhibited sensitivity to sward height with a threshold of 12-13 cm evident (based on mean sward height values and data points in Figure 4.1 and Figure 5.3). The findings of Dumont *et al.* (1995a and 1995b), although confounded with maturity contrasts, showed general agreement on the sensitivity to sward height. It can be concluded from these two papers that when heifers were given a choice between an 11 cm vegetative sward and a tall (sward height unspecified) reproductive sward, they were largely indifferent to the time spent grazing either choice (see Figure 1 Dumont *et al.*, 1995b and Figure 2 Dumont *et al.*, 1995a).

In Experiment 2 there was indication that cattle were able to form associations between approach cues and patch rewards after encountering a sequence of 7-8 patches. This supports the growing evidence that animals are capable of forming associations between cues and food rewards (eg. Edwards *et al.* 1997), even within a monoculture. Nonetheless, with greater contrasts in heterogeneity, visual cues may not reflect variations in patch profitability (Illius and Gordon, 1990) and sampling becomes an integral component of the appraisal phase. Such patterns of behaviour were demonstrated in Experiments 3 and 4. In the former experiment, the limited sampling of the tall mature (T4) sward (10 to 13 % of foraging time) demonstrated the point that animals recognised the potential value of a patch from the visual cue of sward height, but that sward height as an approach cue was conditioned by the following appraisal and ingestion phases of foraging. Reliance on a visual cue for patch selection was therefore not absolute.

When offered a stronger maturity contrast, cattle preferentially grazed the short immature swards on the first grazing session in Experiment 3, and retained this clear preference on the second grazing session even though the mean patch sward height for the immature swards had declined to 8.8 cm, below the sward height threshold defined in Experiments 1 and 2 with swards in a vegetative phase of growth. These results are in contrast to the patterns of preferential behaviour described by Dumont *et al.* (1995b). It can be predicted from the data presented by these authors that heifers would have spent a greater proportion of their time grazing the tall reproductive sward when the alternative vegetative sward declined to 8-9 cm. A dominant approach cue operating under the circumstances described in Experiment 3 might have been an olfactory response to prior grazing, with the mechanism being a response to the smell of saliva on vegetation. Clarke *et al.* (1995) have offered a similar explanation (olfactory response to prior grazing) as one possible cue that sheep and deer may have used to select patches which had been preferentially grazed in the previous period. Nonetheless the evidence from Experiment 3 reinforced the earlier observations of Illius *et al.* (1987), who observed that cattle avoided 15-16.5 cm (ungrazed and 56.2% OMD) swards and preferred the 8-9.5 cm (grazed and 69.7% OMD) swards, suggesting a balance in the trade-off between sward maturity and height, with an adjustment to the visual cue threshold determined, in part, by the contrast in patch heterogeneity and the structural features of the canopy, and therefore the constraints imposed on handling the mature swards and the need to minimise the costs incurred per bite.

The contrasts in time spent exploiting short immature patches, across studies, reflect the contrasts in sward structure between alternatives, across studies. This was clearly apparent between the studies of Dumont *et al.* (1995a and 1995b), both covering a temporal scale of 30 minutes, particularly for the short vegetative (7 cm). Clarifying this, in one of the paired studies (Dumont *et al.*, 1995a) the 7 cm vegetative sward was higher in nitrogen and the green:dead ratio was more favourable (0.70 vs 0.40), and these characteristics probably assisted with the greater exploitation of the 7 cm sward in the later study (41% vs 20%) through their integrated effects on biting effort. Consequently, more accurate definition of the trade-off between maturity and sward height across studies, both in this thesis and with other published studies, is generally hampered by the absence of a complete inventory of detailed sward canopy data which would allow for better understanding of the degree of discrimination with contrasts in sward maturity.

To summarise, sward height (probably integrated with the need to manipulate the neck angle for grazing) was an important and dominant approach cue, determining the degree of exploitation and avoidance of patches. The point of sensitivity will be of flexible origin, dependent upon sward structural contrasts, and therefore a greater understanding of how structural variables influence decision making and the subsequent degree of discrimination should provide valuable insights into the ability to predict foraging strategies.

The two additional handling cues investigated in this thesis as potentially influencing the initial approach response to sward height were sward maturity and regrowth depth. When there was either no contrast in maturity between patch treatments (Experiment 1) or the contrast between the regrowth and stubble strata was not strong enough to generate a more selective response by cattle (Experiment 2) then sward height was the dominant handling cue influencing patch preference. These findings were supportive of an earlier study (Clark and co-workers, reported in Illius and Gordon, 1990), and probably reflect the complementary effects of processing cues on the mechanics of grazing (bite depth and bite mass). However, when stronger contrasts in patch maturity were offered in Experiment 3, cows showed a clear preference for the short immature sward (see Illius *et al.*, 1987; Wallis de Vries and Daleboudt, 1994), irrespective of a similar depth of regrowth, suggesting that sward maturity clearly ranked higher in the selection criteria than either sward height or regrowth depth. In Experiment 4, in addition to demonstration of the separate influences of sward height and maturity on preference, the important finding was that the preference for immature swards was best explained by the depth of regrowth. There is little, if any, other work which has attempted to separate out the influence of these handling cues on selective behaviour. The contrast in the response to the depth of regrowth between the results of Experiment 3 and 4 can be best explained by the characteristics of the grazed stratum, although this could not be fully clarified in the absence of stratified sampling of the swards types in Experiment 3. The observations from Experiment 4 reinforced the patterns observed in Experiment 3, suggesting that the depth of regrowth over-rides sward maturity as the dominant handling cue in circumstances where the regrowth stratum does not constitute reproductive (flowering) stem.

The three key handling cues identified in the studies reported in this thesis can therefore be broadly ranked as follows;

a) Regrowth depth

b) Sward maturity

c) Sward height

The relation between handling and approach cues then indicates that the initial importance of sward height may be modified by subsequent handing cues.

7.3.2 Ingestion and Defoliation

Section 7.3.1 was concerned with the factors influencing decisions on where to graze. Patch defoliation is discussed in this section in terms of the important processing cues that impact upon on the mechanics of grazing, the pattern of defoliation and the time spent foraging at the patch.

7.3.2.1 Leaf mass

The preceding sections have reconfirmed that the distribution of herbage mass in space is an important concept in predicting the selective behaviour of foraging animals (see Laca *et al.*, 1994). A number of recent studies (eg. Prache, 1997; Prache *et al.*, 1998) have concluded that green leaf mass is a stronger processing cue than sward height or total mass, being a better predictor of bite mass across swards of different phenological development. The results of Experiment 3 showed that the distribution of leaf assumed greater importance than whole sward green leaf mass in influencing preferential patch behaviour. It could not be ascertained, due to the absence of estimates of bite mass and so intake rate, whether the behavioural pattern would have held if the shorter and immature sward was associated with a reduced rate of intake. Demment *et al.* (1993) have reported that steers removed a greater number of bites from patches that provided the greater patch intake rate. On short swards, leaf bulk density may potentially be an important variable in attaining sustainable patch intake rates. In an early report Arnold and Dudzinski (1978) commented that sheep grazing swards with a similar leaf length obtained a greater daily intake on the sward type with the greater density of leaf. Leaf density and its role in conjunction with the cost-reward concept (Illius *et al.*, 1995) warrants further investigation. Nonetheless, the observations suggested that cattle are strongly deterred from foraging on patches where leaf and stem are comprehended within the same bite, even though the greater muscle mass of cattle, compared with sheep, would assist with the severance of herbage offering greater resistance. The difference between the findings in this study and that of Prache *et al.* (1998) probably reflect the contrasts between the quantity and distribution of leaf mass, though there may also be important inter-animal species effects which would reflect the variation in the configuration of the harvesting apparatus between sheep and cattle. Furthermore, Prache *et al.* (1998) additionally noted intra-animal species variation in the selectivity response for whole sward green leaf mass. Given the findings from Experiment 3 the effects of intra-animal species in addition to inter-animal species variability deserves further attention.

7.3.2.2 Nutritive value

The absence of strong preference-nutritive value relationships across treatments in Experiments 2 to 4 demonstrated the dominant importance of canopy structure over nutritive value in influencing patch choice and patch residence time. This lends support to the conclusions of Villalba and Provenza (1999) that, when nutritive value is similar, food structure is more important than nutritive value, and is also consistent with Spalinger *et al.* (1986) who had earlier suggested that when the available choices are of acceptable nutritional quality, patch selection should be determined by structural characteristics. Nevertheless, it is questionable whether under natural grasslands greater variation in nutritive value can be achieved without corresponding increases in structural contrasts. Furthermore, it will remain difficult to separate out the effects of nutritive value and structural strength on selective behaviour.

7.3.2.3 Bite penetration

A distinction is drawn in this thesis between stem and stubble height. Stubble height is defined as the height at which swards were repeatedly cut over a defined period of time. Stem height is defined either as the height of first contact with reproductive stem or seed head, or the height of the ligule of the youngest mature leaf on vegetative tillers (pseudostem height). Stem height was not measured, except in the case for pseudostem in Experiment 5, and stem could have been present both within the stubble and above it.

When the offered sward choices comprised vegetative leaf and pseudostem (Experiment 1 and 2) sward height was the cue impacting on the depth of penetration over and above any separate effects of regrowth depth or stubble cutting height (Tables 4.13, 5.21 and 5.22). The consistency in the level at which grazing settled in Experiment 2 suggested that pseudostem height or the costs of bite procurement may act as inhibitors to bite penetration, but these effects could not be verified without a direct measure of pseudostem height. There were strong indications that pseudostem height was a persuasive cue in determining depth of penetration in Experiment 5. This effect, however, was not absolute as the effect of sward height on bite penetration was stronger than pseudostem height (Table 6.19), and bite depth was not significantly influenced by the pseudostem:sward height ratio at a common sward height (Table 6.24). This clearly illustrates the difficulty of separating the effects of non independent variables in their natural state.

When the complexity of choice was increased by working with patches constituting herbage in a reproductive growth phase, the relative importance of the stubble stratum on patch choice was determined by the degree of maturity and resistance of stem material within that stratum. This was amply demonstrated in the comparison of the contrasting responses between Experiments 2 and 4 (Tables [5.21&5.22] and 5.63). There is little published evidence that provides indication of the relative contrast in biting resistance between the upper and lower strata of swards, but the observed animal response to the controlled variation in the stubble:regrowth interface in Experiment 4 showed strong support for the suggestion that the resistance to severance and the associated biting effort conditions the depth of penetration into the canopy. The magnitude of the contrast in tensile strength of the regrowth and stubble strata in Experiment 4 was greater than three while in Experiment 2 the magnitude of the contrast in shear strength only approximated two. These results suggest very clearly that when the magnitude of the regrowth:stubble interface contrast exceeds three, the selective responses indicate that animals are more conscious of their actions on positioning bites in space. This conclusion reinforces the likelihood of an interaction between stem maturity and the positioning of the interface which combine to act as a strong processing cue impacting on both within and between patch choice (see section 7.3.1). Further work in this area would help to clarify this conclusion.

The studies presented in this thesis have included supporting data on stubble height and regrowth depth, which has been lacking in a number of other field studies on selective behaviour. Nevertheless, there is no clear evidence to support or discredit the argument that pseudostem directly influences the depth of penetration, particularly in light of the coincidental matching of pseudostem height in sown swards with the proposed potential bite depth (bite depth approximates 50 % of sward height) concept (see Laca *et al.*, 1992a but see section 7.3.2.3.1). There is a clear indication from the studies presented in Chapters 4 to 6 that the lack of clear consensus on this issue in the literature probably reflects the variation in the age of stem development across studies (see Mitchell, 1995), and therefore the importance of the biting effort-reward function. It follows that if animals are assumed to forage to maximise the rate of dry matter intake (see Charnov, 1976; Illius *et al.*, 1999), they should attach importance to the costs associated with the procurement of a bite. The required biting effort for associated reward will then be an important source of information that animals are constantly monitoring (Illius *et al.*, 1995; but see Kyriazakis, 1997). If, however, animals forage to meet a nutritional gain, and nutritive value is strongly and inversely correlated with herbage strength, then the costs of procurement relative to the marginal reward gained with deeper penetration would probably be an unlikely basis for determining patch use.

In conclusion, despite the breadth of available data there still remains little basis for predicting the location and composition of a bite or whether animals forage to maximise intake rate. Further research into these issues will be fundamental. Sward structural effects (depth of regrowth, the age of stem development and the regrowth:stubble interface) and their integrated effects in determining the costs of bite procurement relative to bite reward deserve immediate attention.

7.3.2.3.1 The constant proportionality concept

In most studies in which bite depth has been measured, reference has been made to the consistency of bite depth as a proportion of sward height (the constant proportionality concept). Table 7.4 shows the range of variation in bite depth as a proportion of sward height for four of the experiments reported in this thesis using the significance of the linear regression relationship, independent of treatment effects (first entry of the analysis of variance), as an indication of the consistency of proportionality. Data from Experiment 3 is excluded as postgraze readings of sward height were taken randomly across grazed and ungrazed areas.

Table 7.4 Summary of the variation in bite depth/sward height for Experiments 1, 2, 4 and 5. Data from Tables 4.16, 5.23, 5.64 and 6.20.

Expt.	Sward height (cm)	Bite depth/ Sward height (%)	Constant proportionality	F value	Pr > F	sed
1	8.9 – 21.3	44.6 – 55.1	Yes	0.04	0.8369	1.99 – 2.94
2	8.3 – 21.2	44.4 – 55.0	No	12.58	0.0011	2.33 – 5.71
4	15.4 – 22.3	20.7 – 45.6	No	56.66	0.0001	1.34 – 1.60
5	16.6 – 23.3	41.6 – 48.4	Yes	1.66	0.2060	2.18

There was clearly substantial variation in proportionality across the sward types in the four studies (Table 7.4). The range in sward height and bite depth/sward height were almost identical for Experiments 1 and 2, but the analysis indicated that there was only evidence for a constant proportionality for Experiment 1. The more structured pattern of response in Experiment 1, compared to the greater random treatment variation independent of sward height in Experiment 2), suggests that the proportionality concept is coincidental as opposed to cattle exhibiting an objective decision about defoliation patterns to a constant depth of sward height. In Experiment 5, (Figure 6.7) bite depth was a constant proportion of sward height across sward treatments and the across-treatment evidence for constant proportionality was largely the reflection of cattle grazing close to the interface between pseudostem and regrowth. The strong variation in bite penetration patterns, a direct consequence of the vertical position of the stubble:regrowth interface in Experiment 4 (Table 5.60 and Figure 5.11) further demonstrated that the interface was a stronger cue than sward height. Consequently there is weak evidence from the data presented in this thesis to support the constant proportionality concept.

Comparing data across studies, there is a lack of clarification about the measurement of bite depth. In some studies (eg. Wade *et al.*, 1989; O'Reagain and Grau, 1995) bite depth was measured as the difference between the extended height of a tiller and the depth of defoliation of that tiller, in some as the difference between sward height and grazed height (refer to the terminology section) from a series of alternative sampling positions within or across alternative swards (eg. Edwards *et al.*, 1995) or from a series of replicated patches where there was variation about a common mean (Chapters 4 to 6), and in some using a styrofoam disk (eg. Arias *et al.*, 1990) while other studies do not define adequately how bite depth was measured (eg. Patterson *et* *al.*, 1998). These technique variations add to the confusion surrounding the prediction of bite depth (see also Ungar, 1996). This issue needs to be addressed, particularly given the importance of the interface as a processing cue influencing the depth of defoliation and the subsequent flow of information back to the animal on patch profitability.

The results presented in this thesis indicate the need for caution in the assumption of a constant proportionality concept in building predictive models of foraging strategies. More detailed canopy structure descriptions will need to be built into models to better describe the location and composition of a bite. There is also a strong argument for measurements of bite depth to be standardised across studies.

7.3.2.4 Patterns of behaviour with increasing number of bites removed

Investigation of the patch appraisal cycle showed that cattle are cautious grazers, as demonstrated by the pattern of increase in bite depth to reach an asymptote with increasing bite number on individual patches in Experiment 4 (Figure 5.12 and Figure 5.13). There is no other comparable evidence in the literature. This evidence has two important implications: (a) it further raises concerns over the scaling up of information on foraging behaviour from the feeding station (few bites) to the small patch (tens of bites) and (b) the fact that the initial bites are continually being conditioned by the information pathways arising from the handling and processing cues associated with those bites provides support for the suggestion that cattle appraise each patch as having its own intrinsic worth, and preceding patch behaviour has little impact on behaviour about the current patch (Table 5.66 and Table 6.21).

There was no evidence from Experiments 4 and 5 to indicate that any decline in within-stratum bite mass was a reflection of increasing bite number as found by Laca *et al.* (1994), Distel *et al.* (1995) and WallisDeVries *et al.* (1998) with cattle, even where there was greater precision in the estimates of bite mass in Experiment 5. This decline is usually interpreted in terms of increasing bite overlap with patch defoliation (see Laca *et al.*, 1994). Laca *et al.* (1994) demonstrated that for a 20 cm sward with a bulk density of 0.66 mg DM cm^{-3} the decline in bite mass was smaller for the first 30 bites than for subsequent sets of bites from 0.36 m^2 patches. This point of inflection translates to 83 bites per square metre. The absence of strong consistent declines in bite mass may, in part, reflect the fact that there were few patches where greater than 50 and 60 bites were removed in Experiment 4 and 5 respectively (Figure 5.9 and Figure 6.2). Furthermore, Hongo (1998) recently found that for sheep grazing orchardgrass and timothy swards for 1 minute, and removing approximately 40 bites, the percentage of bite overlap was 4-14 % ie. a maximum of 6 of the succeeding bites were within the zone of the previous bite. The lack of evidence for declining bite mass with increasing number of grazing bites per patch in Experiment 5 does not then necessarily contradict published material. However, the development of a method to estimate accurately the mass of herbage removed at the patch scale under field conditions will be an important prerequisite to further progress in this area. The observation that animals repeatedly departed from patches when the effects of bite overlap would have had minimal influence on the patch rate of intake, further suggests that the decision to depart from patches may not be related to the monitoring of a declining rate of intake as the number of potential bites diminishes.

Information on the relationships between bite mass and the number of grazing bites that characterise the grazing cycle at a patch are of relatively recent origin, but there has been no parallel evidence for the cycle of bite penetration, and neither relationship has previously been reported from field monitoring procedures in the absence of fistulated animals. The cues influencing the location and composition of bites appear to have a stronger influence on patch departure than any potential bite overlap and subsequent reduction in bite area and bite mass arising from the placement of bites in space. These inferences need further evaluation, but they do emphasise the importance of field based environments which allow animals to depart from patches in their own time.

7.4 FORAGING THEORY

There is a clear linkage of the material discussed in the preceding section covering cues and choices with the material in the following section relating to foraging theory. However, the issues have been discussed separately, primarily to reinforce the different scales and phases of decision making. This approach better provides an indication of whether foraging behaviour conforms with the assumptions defined by models, which predict the optimal strategy (particularly patch departure times) which ruminants should adopt using the flows and pathways of information integrated throughout the patch grazing cycle.

Foraging theory is built around two key concepts, these being (a) that at some point in the level of patch depletion the animal experiences diminishing marginal returns in the rate of forage intake and (b) that there is a travel time cost associated with movement from one patch to another (Charnov, 1967). Implicit in this is the assumption that animals forage to meet some common goal. Rate of dry matter intake has been offered as a currency (Laca *et al.*, 1993b; Illius *et al.*, 1999) but other studies have suggested that animals seek to maximise their rate of energy intake (Wilmshurst *et al.*, 1995; Dumont *et al.*, 1998) or the rate of digestible protein intake (Langvatn and Hanley, 1993). If behaviour over short temporal scales is to meet a common goal then one must assume that animals are able to integrate information gained from previous foraging experiences, both short term and long term, while monitoring the declining rewards from increasing defoliation on the current patch. This information, put together with the expectation of future patch rewards, must then form the basis for making decisions about the number of bites to remove and the duration of grazing about the current patch. However, many of these assumptions have yet to be directly tested. Critical tests of optimal foraging theory were not the primary objective at the outset of this thesis, with the consequence that there was no basis for analysing observed and predicted patterns since no gain functions were calculated. Nevertheless, the patch sequence was balanced in Experiments 1 to 5 to provide information on between and within patch behaviour effects and Experiment 5 tested the critical assumption of inter-patch distance effects.

The role of searching is now well recognised (see Shipley *et al.*, 1996; Roguet *et al.*, 1998b), but there is little knowledge of what importance animals place on previous foraging experiences, particularly information from immediate past encounters with patches and the use of their memory net during future patch encounters, and this continues to hinder modelling programmes. The experiments in this thesis sought to further the understanding of information acquisition and the potential role played by information gained in subsequent patch decision making. While cattle showed a remarkable level of control in monitoring patch area effects (ie. matching bites per unit area), collectively the current studies found contrasting results to two earlier published studies (Laca *et al.* 1993b; Distel *et al.*, 1995). The important distinctions were that (a) between and within patch behaviour was independent (Experiments 1 to 5), and (b) the rate of patch depletion was independent of current patch distance (ie. the distance between the current patch and the succeeding patch in sequence, refer to Figure 6.1; Chapter 6). Illius *et al.* (1992) suggested that animals carried over the grazing style from the last grazed patch. Although the data presented in this thesis does not lend support to these conclusions, given the control animals showed over the adjustment in bite penetration with increasing bite number it is possible that they may have adjusted bite penetration during the initial series of bites. Clarification of this could not be obtained because bite depth values were the mean of a series of measurements and determined over a series of patches. Nonetheless, the limited evidence for monitoring alternative patch conditions (see Tables 4.17, 5.24, 5.37, 5.66, 6.21 and 6.22) begs the question of the validity of extrapolation of optimality theory in its current form to ruminants. Stephens and Krebs (1986) have argued that such results should not imply that cattle do not forage optimally, and indeed this probably holds true as a host of behavioural responses can be incorporated into models of optimal foraging as specified constraints. However, the variable, if limited, data currently published does raise questions about the framework under which optimality is applied to grazing ruminants; ie. should researchers crudely assume that ruminants forage according to the same laws that apply for carnivores and then merely adapt the theory to fit the behaviour of ruminants by using alternative constraints, or should the theory itself be over-hauled?

The cost of information to the forager will vary according to the scale of patch aggregation. The issue of sampling has been raised throughout this thesis as it has been an integral component of the appraisal phase. The five studies presented here have shown that cattle do not fail to discriminate between alternatives when there are clear sensory cues, but under circumstances where the cues and rewards are intermingled (eg. tall mature sward), sampling is possibly the only means by which animals can condition the approach cues, and in this sense there is little value to be gained by the animal in placing emphasis on learning associations. Studies which have shown evidence for spatial memory retention (eg. Edwards *et al.*, 1996) have by and large found that animals require a period of repeated exposure to learn of the associations. As the number of possible associations between cues and rewards lie on a continuum and animals forage in competitive environments, there is then a need for caution over complete anthropomorphism with reference to studies which state that animals fail to discriminate between alternatives, without due consideration of the costs involved in failing to discriminate, and particularly across short temporal scales.

The finding that cattle adjusted the number of grazing bites and residence time per patch in response to variations in inter-patch distance (Table 6.6) clearly suggested that animals were constantly monitoring inter-patch distance using visual cues, and adjusting the departure rules according to the relayed messages. However, the observation that animals removed herbage at a constant rate irrespective of inter-patch distance (Table 6.10) did not conform with the theory of optimality and the results of an earlier study by Laca *et al.* (1993b), where steers were reported to adjust patch residence time in a manner which maximised the rate of intake. According to the limited data presented by Laca *et al.* (1993b) the finding obtained from Experiment 5 may reflect the contrast in heterogeneity, since these authors showed that when sward choices were all 10 cm, patch residence time increased with increasing inter-patch distance but there was no clear trend in the rate of intake with increasing inter-patch distance (see Figure 1 and 2 of Laca *et al.* 1993b). Of the few other authors which have commented on patch departure and optimality theory in ruminants (eg. Jiang and Hudson, 1993) questions about the statistical base on which the inferences were made are of concern.

Evidence from Experiment 5 indicated that animals may forage to a common residual herbage mass (Focardi *et al.*, 1996), but this was not substantiated with a greater range of patch contrasts in Experiment 4 (Table 5.45 and Table 5.53). The possibility that green leaf mass was used as a departure rule in Experiment 5, as suggested by Roguet *et al.* (1998b), could not be substantiated with data from any of the other experiments. However, this incomparability between data sets, reflects, in part, the inadequacies in estimating herbage mass in the earlier studies. It may also be that there are different gain functions for each sward height x inter-patch distance combination (Ginnett *et al.*, 1999), for cattle to be able to achieve a similar rate of intake with different patch residence times. These issues could not be clarified as rate of intake for incremental sets of bites was not collected (see Laca *et al*., 1994; Ginnett *et al*., 1999) and issues of this kind need addressing in future studies.

The concept of optimal foraging strategy provides a basis for developing ideas on herbivore foraging behaviour, but it is limited in the context of describing foraging activity at finer scales. As a consequence, a clearer understanding of the patterns of behaviour within a grazing cycle and the distinction of between and within patch behaviour as shown in the studies reported in this thesis, combined with the results of research on the nature of gain functions, will continue to be important for the development of a unified framework for predicting foraging responses.

7.5 CONCLUDING COMMENTS

The series of five experiments focussing on sward structural characteristics and selective foraging behaviour in dairy cows presented in this thesis has furthered the understanding of foraging behaviour, particularly the emphasis given to quantifying the trade-off decisions implicit within the patch grazing cycle. With reference to the three hypotheses stated in section 2.9 (Chapter 2); (a) sward maturity was a stronger handling cue than sward height, and the role of bulk density on trade-off decisions requires further evaluation; (b) the structural components, leaf:stem and regrowth:stubble and their spatial distribution strongly influenced the patch grazing cycle through their effect on patch defoliation; (c) animals evaluated each patch as having its own intrinsic value to the effect that there was limited evidence for any relationship for between and within patch behaviour. Needless to say the experiments have demonstrated that there is still much progress to be made in understanding many of the fundamental principles governing foraging behaviour before modelling programmes will be able to define optimal strategies for ruminants. Progress has been made in defining some of the principles involved, but the complexity of the questions at hand will provide direction for research well into the next century.

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AMENDMENTS

Page	Line	Comments
2	6	Replace *sequence* with *sequences*
3	18	Insert *can* following *this*
4	24	Omit *and indices*
9	20	Replace *selective* with *discriminatory*
11	11	Replace *specie* with *species*
12	22	Replace *has* with *have*
13	9, 13, 25	Replace *specie* with *species*
14	24	Omit *semi colon* following *1995*
18	8	Replace *on* with *in*
18	11	Omit *that* following *as*
21	9	Replace *raises* with *raise*
21	16	Replace *1993* with *1993a*
22	2	Omit *by man* following *anthropomorphism*
22	19	Replace *(1993)* with *(1993a)*
24	30	Replace *specie* with *species*
25	16	Replace *specie* with *species*
43	9	Replace *was* with *were*
43	18	Replace *and the sward with the* with *on the sward in the*
45	9	Replace *was* with *were*
45	15	Replace *is* with *are*
51	9	Replace *specie* with *species*
62	12	Replace *was* with *were*
67	5	Italicise *et al.* and insert *1993,* before *60-63%*
77	3	Replace *was* with *were*
79	6	Replace m^2 with m^{-2}
115	7	Replace *an electric shearing handpiece* with *the S.E.P (1500 Special) mower*
116, 118	Figure 5.6, 5.7	Insert into caption *Stubble height and regrowth depth are based on nominal treatment values*
120	20	Replace *strata 1* with *the upper stratum*
129	13	Insert *mass* following *herbage*
141	Figure 5.11	Insert into caption *Stubble height and regrowth depth are based on actual treatment values*
148	14	Replace *has* with *have*
150	28	Omit *in* following *within*
150	29	Replace *strata* with *stratum*
150	30	Replace *strata* with *stratum* and *was* with *were*
154	5	Replace *strengthen* with *strengthens*
154	24	Replace *strata* with *stratum*
157	22	Replace *strata* with *stratum*
158, 160	Table 5.68, 5.69	Insert units (cm)
159	13	Replace *was* with *were*
165	1	Replace *strata* with *stratum*
173	22	Replace *is* with *are*
175	20	Replace *adverse* with *averse*
179	12	Replace *1993* with *1993b*
180	6	Replace *(1993)* with *(1993b)*
187	18	Replace *consistency* with *consistently*
191	11	Replace *is* with *are*
210	12	Replace *is* with *are* and *or* with *nor*
211	8	Omit *sizeable* before *difference*
213	6	Replace *stubble and regrowth* with *lamina and pseudostem*
222	31	Replace *(1993)* with *(1993a)*
224	3	Replace *succeeding to succeeding about one* with *succeeding to succeeding but one*
224	16	Replace *animals'* with *animals*
229	12	Replace *specie* with *species*
232	14	Replace *was* with *were*
232	22	Replace *is* with *are*
233	15	Replace *was* with *were*
236	10	Insert *%* following *19.5* and *39.0*
244	6	Insert *sward* following *vegetative*
245	22	Replace *handing* with *handling*
247	12	Insert *height* following *stem*
250	8	Replace *depth* with *proportion*
255	23	Replace *1993* with *1993a*
255	30	Replace *incomparability* with *incompatibility*
258	2	Arnold and Hill 1972 - Replace *Phtochemical* with *Phytochemical*
274	18	Semiadi *et al.* 1995 - Replace *Agrictural* with *Agricultural*
275	24	Tribe and Gordon 1949 - Replace *vison* with *vision*