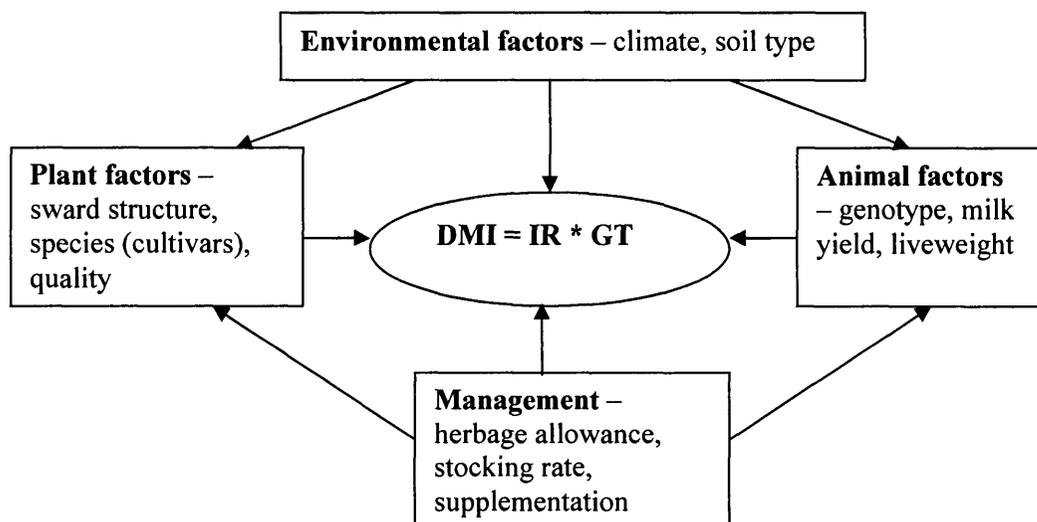


# CHAPTER 1

## GENERAL INTRODUCTION

The central feature of grazing systems, whether intensive or not, is the pasture-animal interface and herbage DMI is the major determinant of production (Forbes 1995; Ungar 1996; Dillon 2006). Better management and utilisation of the available resources should result in a better understanding and predictability of herbage DMI under grazing conditions. Forbes (1995) views daily DMI as the summation of individual discrete meals. Under grazing conditions there are alternate periods of eating and resting (fasting).

The utilisation of pastures by the grazing animal remains a complex biological process that is not well understood. Many factors interact to affect DMI and include environmental, plant, animal and management factors (Figure 1).



**Figure 1. Factors influencing herbage DMI and also the behaviour by grazing dairy cows.**

Allden and Whittaker (1970) described herbage DMI as the product of intake rate (IR) and time spent grazing (GT). Since then much of the continuing research on grazing behaviour has shifted to the utilisation of temperate pastures (Hodgson 1982; Mayne and

Wright 1988; Hodgson *et al.* 1994). Accurate estimates of herbage DMI are considered one of the most important tools for improving grazing management and production (Dillon 2006). An accurate estimation of daily herbage DMI can be achieved using the relationship between IR and GT (Gibb *et al.* 1998) because IR is known to be the product of bite rate (bites/min) and bite mass (g DM/bite) and GT is the product of meal duration and number of meals (Rook 2000). Sward height (SH), herbage allowance, tiller density, tensile strength, and fibre content are among the most important factors of plant origin (Penning *et al.* 1991; Gibb *et al.* 1997). Among the most important factors of animal origin are productive capacity, physiological status, lactation stage and liveweight, all of which determine nutritional demand (Gibb *et al.* 1999). Ambient temperature, relative humidity, and rainfall are important environmental factors (Champion *et al.* 1994).

Therefore, understanding the complexities of the pasture-animal interface requires an understanding of how the factors shown in Figure 1 interact. There has been substantial progress in the understanding of IR and GT over recent decades (see recent reviews of Illius and Hodgson 1996; Parsons and Chapman 1998; Rook 2000; Gibb 2006). The importance of grazing behaviour within the pasture-animal interface in determining the allocation of pasture and supplements for milk production is yet to be fully understood. While the elements of grazing behaviour and ingestion operate in all grazing environments, the pasture-animal interface will differ between temperate and tropical pasture and among animal species (Hodgson *et al.* 1994; Cosgrove 1997; Ungar 1996). Thus, deficiencies occur in quantitative data to estimate short-term IR for some situations.

As the complexity of a system increases the value of quantitative analysis of the system also increases. Although the conceptual relationships outlined in Figure 1 have been established, the quantitative relationships are less certain. Simulation models have been developed, which integrate the components of ingestive behaviour in estimating

daily herbage DMI, but they have not proved useful for predictive purposes (Rook and Yarrow 2001). Therefore, the research reported in this thesis focuses on the quantitative analysis of behaviour of grazing dairy cows to improve (1) the knowledge base for the pasture-animal interface and (2) the prediction of daily herbage DMI. This is achieved by quantifying (1) the effects of SH and grazing duration (GD) on behaviour of dairy cows grazing sub-tropical pastures; (2) the effects of SH and GD on the sward profile of sub-tropical pastures; (3) the temporal patterns of behaviour of grazing dairy cows; and (4) the time-dependent transition probabilities of behaviour in grazing dairy cows.

## CHAPTER 2

### LITERATURE REVIEW

#### 2.1. Introduction

Pasture based dairy systems result in lower feeding costs because grazed herbage is the cheapest source of nutrients (Kellaway and Porta 1993). Efficient pasture based grazing systems are characterised by high milk output/unit area, while confinement systems are characterised by high output/cow (Clark and Kanneganti 1998).

In grazed systems, low herbage dry matter intake (DMI) has been identified as a major factor limiting milk production (Leaver 1985; Kolver and Muller 1998) and Leaver (1985) suggested that high producing dairy cows fed pasture-only diets could reach a total DMI of 3.25% of body weight (BW) and herbage DMI of grazing dairy cows. With no quantity and quality restrictions it has been estimated that herbage DMI can reach 3.5% BW (Mayne and Wright 1988).

Herbage DMI is the product of grazing time (GT) and intake rate (IR) (Allden and Whittaker 1970) and IR the product of bite mass and bite rate. Bite mass is the product of bite volume and density of the herbage in the grazed horizon (Mayne and Wright 1988). Given the diversity of variables associated with the behaviour of the animal, grazing behaviour is important because of its immediate effect on the animal's productivity and also because of the consequences for future grazing opportunities, herbage composition and productivity.

There are a number of factors that affect animal grazing behaviour, including pre-grazing herbage mass (amount of pasture/unit area) and herbage allowance (amount of pasture offered/cow) (Poppi *et al.* 1987; Hodgson and Brookes 1999). Animal factors also

affect grazing behaviour, and include physiological state (lactation, pregnancy etc), liveweight, liveweight change and age. Consequently, all these factors are inexplicably linked to herbage DMI and interact in positive and negative ways.

Many short-term studies have identified the important ingestive behavioural components of herbage DMI and the influential interacting components of the sward canopy. This considerable knowledge and understanding about how animals graze has been included in recent comprehensive reviews addressing animal grazing behaviour including Mayne and Wright (1988), Ungar (1996), Rook (2000), Vallentine (2001), Chilibroste *et al.* (2005) and Gibb (2006) and therefore will not be repeated here.

The grazing animal is confronted with a feed source that can be heterogeneous in both the vertical and horizontal distribution and may contain many different species. In such situations the animal must make behavioural choices within the constraints imposed by the sward and by its own anatomy. These choices will not only affect the animal's nutritional status, but will also feed back on the productive capacity of the sward via the resulting pattern of defoliation.

*Thus, an understanding of the fundamental processes of foraging and grazing behaviour is a prerequisite for the design of efficient grazing management systems. An important reason for quantifying the behaviour of grazing dairy cows is to devise methods of supporting increased nutritional requirements of high yielding grazing dairy cows. Quantifying how grazing behaviour interacts with sward, animal and environmental factors will help in determining deviations from normal that may signal constraints to optimal herbage DMI and hence, enable management changes to reduce stress and improve performance.*

The following overview of the behaviour of grazing dairy cows as influenced by sward, animal and environmental factors are to provide a baseline for information and

description of behaviour to date. The close links between grazing behaviour and herbage DMI make it difficult to review one without the other and consequently quantitative measurements of pasture and animal factors are reported. The aim of this review is to determine how quantification of the behaviour of grazing dairy cows can improve the decisions made in terms of pasture utilisation, rotation length, supplementary feeding and stocking density.

## **2.2 Theory of foraging behaviour**

Grazing ruminants face many challenges while foraging (Provenza and Balph 1990) including the need to match their nutritional needs with the nutrients available. Nutritional needs change as a consequence of age, physiological state, and environmental conditions, while the availability of nutrients varies with plant species, climate and other factors and along with toxins in plants will also vary in space and time.

Analytical approaches are complementary to synthetic approaches with the understanding that patch choice may be motivated by sensory stimuli, by post-ingestive feedback resulting from previous choices, and by dietary experience. The complementarity of approach is illustrated by the fact that short-term dietary experiences cannot be excluded from Optimal Foraging Theory (OFT), even though OFT stresses the importance of natural selection in determining behaviour. The basic premise of the main synthetic approach is OFT which suggests that animals forage optimally as a result of natural selection, since optimal foraging enables the animal to maximise its reproductive output or 'fitness' (Krebs and McCleery 1984). Fitness maximisation has often been translated into efficiency of foraging, and for practical reasons, has often been equated with short-term DM IR.

Therefore, optimisation-based predictions have been developed to include the animals' dietary experiences. The difficulty in dissociating the different approaches is well illustrated by the question posed by Illius *et al.* (1999): "do animals eat a plant species faster because they prefer it (sensory stimulus) or do they prefer it because they can eat it faster (optimisation of behaviour)?"

### **2.2.1 The patch**

Illius and Hodgson (1996) define a patch as a spatial aggregation of bites over which instantaneous IR remains relatively constant and thus a patch can be as large as a paddock. Instantaneous intake rate on the patch is determined by bite mass and the functional relationship relating bite mass to the time required in handling it. Time/bite can be split into prehension and mastication times. The animal is considered to be subject to two constraints: (1) the time required toprehend a bite, which is independent of bite mass; and (2) the time required chewing the harvested material, which is proportional to bite mass (Newman *et al.* 1994; Prache 1997) and varies with plant species (Newman *et al.* 1994). On vegetative swards, SH and bulk density are the main determinants of bite mass and instantaneous IR (Black and Kenny 1984; Burlison *et al.* 1991). On mature swards, bite mass is also affected by the presence of stems and dead material. Green leaf mass (GLM)/unit area has been shown to be the best predictor of bite mass and instantaneous IR across different phenological stages of the sward (Penning *et al.* 1989; Prache *et al.* 1998). Not all the factors involved are taken into account by SH or GLM, because they are either one- (SH) or two-dimensional (GLM) descriptors, while bites are taken in three dimensions (Ungar 1996).

The effect of scale of patchiness may have marked effects on the animals' foraging decisions, although it has not received much research attention. Two types of patchiness may involve searching costs: (1) small-scale, with constraints due to selection

of preferred from less preferred food items, and (2) larger scale with constraints due to moving and locating alternative patches. Larger scale heterogeneity may impose constraints on the visual perception of alternative patches and spatial memory. In an operant conditioning test, sheep walked with the same frequency to resources that had the same edible biomass relative to the distance to the patch (Dumont *et al.* 1998).

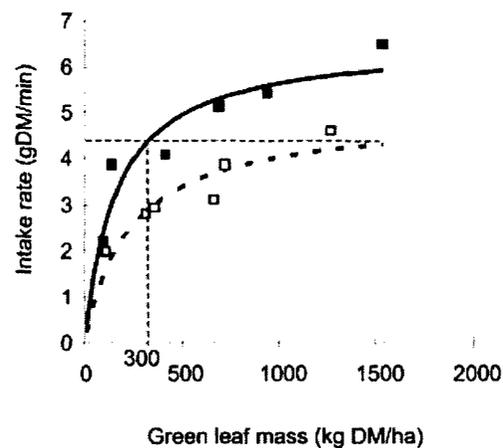
The animal is motivated to move because of forage depletion in the patch and the expectation of intake opportunities in other patches. It has to make a trade-off between continuing to graze the current patch where it is experiencing diminishing marginal rewards, and moving to another patch, thereby incurring a time cost. If the animal seeks to maximise IR, the Marginal Value Theorem (MVT, Charnov 1976) predicts that the animal will leave the patch when IR within the patch equals the average IR for the whole environment. Demment and Laca (1993) and Laca *et al.* (1993) have globally validated MVT, but Bazely (1988) observed a longer residence time than predicted by the MVT.

### **2.2.2 Diet preference**

Two situations may be distinguished when considering sward characteristics: (1) those where the animal can graze the preferred patch without having to search for it, and (2) those where preferences are modified by a cost of searching. Animals generally prefer patches where they can eat rapidly, when the cost of searching is negligible (Black and Kenney 1984). However, preference is not absolute and IR is often less than predicted from optimisation theory. For example, Newman *et al.* (1994) found that on adjacent monocultures of grass and clover, the proportion of clover in the diet of sheep is about 70%, even though sheep generally eat clover faster than grass. Therefore, “Why would animals express partial preference and choose mixed diets?” In the short-term, the necessity for the animal to consume the different patches to evaluate their profitability, difficulty or lack of interest of the animal in discriminating, and discrimination errors,

have been proposed as explanations (Illius *et al.* 1999). Diurnal pattern in preferences, search for a balance of nutrients, avoiding an excess of protein, and digestive constraints as explanations of partial preferences and mixed diets on a daily scale basis have been proposed (Newman *et al.* 1995).

Preference is sensitive to the relative vertical availability in different plant species within the sward. Animals may trade off quality for quantity and switch to the less preferred item, when greater benefit is to be obtained (Harvey and Orr 1996). If it is assumed that animals seek to maximise IR, the switch to the less preferred patch may be predicted from potential IR on each patch. For example, sheep rotationally grazing swards containing reproductive patches in a vegetative background, should consume the vegetative patches as long as their GLM will allow a higher IR than the reproductive ones (Figure 2). Hence, if animals seek to maximise IR they should switch to reproductive patches when the GLM on vegetative patches becomes lower than 300 kg DM/ha (about 9cm SH; Dumont *et al.* 1995).



**Figure 2. Prediction of diet choices based on dry matter intake rate maximisation: an example on swards containing reproductive patches (dotted curve) in a background of vegetative patches (solid curve) (after Prache *et al.* 1998).**

Intake rate may be limited by searching constraints and such constraints may induce the animal to consume easier-to-reach food patches that may be less preferred

(Clarke *et al.* 1995) and to develop search strategies. For example, it may walk faster (Roguet *et al.* 1998), increase daily GT (Prache *et al.* 1998), or learn about the location of food and use its spatial memory together with visual cues (Dumont and Petit 1998; Edwards *et al.* 1997). The cost of searching is difficult to assess but indirect indicators such as the animal's degree of selectivity expressed as the difference between diet and sward composition, intake/distance walked and proportion of potential bites encountered removed may be used (Prache *et al.* 1998; Roguet *et al.* 1998).

Decision variables describe the type of decisions animals can make to affect their intake and hence, performance. Quality of items accepted in the diet, grazing time, bite weight, time spent at each patch type and others are typical decision variables. In the case of the dairy cow, intake is largely dictated by how much milk it is producing, with high producing cows having a higher intake than lower producing cows at the same stage of lactation. Heavier cows will also eat more than lighter cows. These factors will dictate the likely decisions taken by the cow on what to eat and how much of it. Grazing management systems that incorporate an understanding of the cow's grazing behaviour will ensure high pasture utilisation and hence, herbage DMI. This will also lead to higher per ha as opposed to per cow production.

## 2.3 Measuring herbage DMI and grazing behaviour

One of the main hindrances to improving production per cow has been the inability to accurately estimate and hence, predict herbage DMI. Allden and Whittaker (1970) summarised daily herbage DMI as:

$$DMI = IR \times GT$$

*Equation 1*

where DMI is herbage DMI (kg/d); IR is intake rate (kg/min); GT is time spent grazing (min).

Equation 1 has been extended further (Mayne and Wright 1988) such that IR is the product of bite mass and bite rate, while GT is the product of meal duration and number of meals. Improvement in the understanding of the pasture-animal interface has been dependent on the development of methodologies for measuring the components of grazing behaviour as described by Equation 1. Since its introduction, the simple model proposed by Allden and Whittaker (1970) has formed the basis for much of the research of the pasture-animal interface.

Recording GT is a labour intensive task and is usually limited by daylight and may disturb the animals, resulting in abnormal behaviour. These limitations have resulted in the development of automatic methods for recording grazing behaviour and some systems record the position and acceleration of the animal's head, while others record jaw movements (Rook 2000). Direct recording of bite weight or diet selection requires the use of oesophageally fistulated animals which is expensive and may compromise behaviours and accuracy of records. Therefore, bite weight is often calculated as the product of the number of bites and the total DMI over a given period. In short-term experiments, turves or artificially constructed swards can be weighed before and after grazing to obtain a direct measurement of DMI (Laca *et al.* 1992). However, a major concern with the use of this method is that it does not represent normal foraging opportunities. Herbage DMI has often been estimated by cutting herbage before and after grazing. However, this method is subject to bias because of plant growth and senescence and selective grazing by the animal. However, within grazing systems that are over short periods of one or two days this may not be the case. Herbage DMI can also be estimated over a period of days using indigestible markers. There have been many types of markers used but more recently the

attention has focussed on the use of natural alkanes in plant cuticular waxes (Dove and Mayes 1996). These have also been proposed as a means of indirectly estimating diet composition and hence, preference. Herbage DMI can be estimated over a period of 1h by weighing the animal before and after grazing. This method requires the collection of faeces and urine excreted during this period, and also an estimate of insensible weight loss because of evaporation from the respiratory tract and other gaseous losses (Penning and Hooper 1985). Lippke (2002) and Gordon (1995) review these techniques for estimating herbage DMI in more detail.

The above methods have enabled the grazing behaviour calculations developed by Alden and Whittaker (1970) to be used in more practical applications. First, they broadly define the physical constraints to herbage DMI and can be used to show that some supplementation with high energy concentrates is required in high producing herds (> 27 kg milk/d) on pastures even if 'ideal' herbage could be offered throughout the grazing session. Second, they emphasize the importance of grazing management systems that consistently provide high quality pastures to the lactating dairy cow so that she is able to take large bites of leafy herbage. This requires the intervals between grazing to be adjusted so that the pasture is at the optimum in terms of quality at any point in time and it may be necessary to either make hay or silage or introduce extra supplements to the daily ration to achieve the quality of ration required (Fulkerson and Trevaskis 1997).

The major components of Equation 1 are IR and GT and these factors will now be examined in greater detail.

## 2.4 Factors affecting intake rate

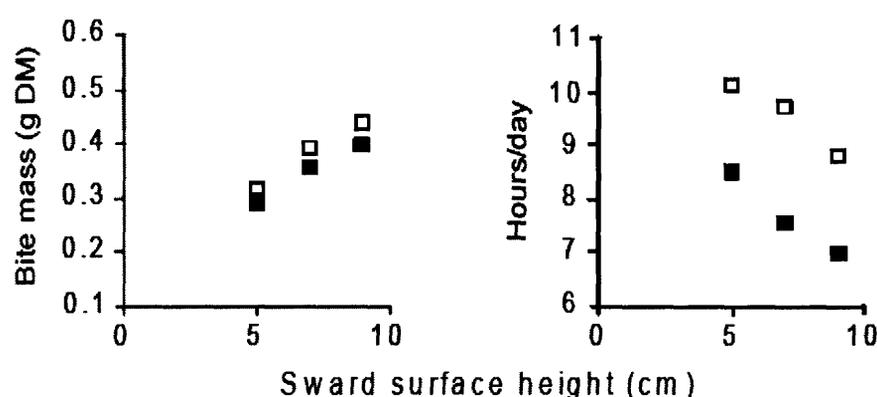
Intake rate is defined as the amount eaten per unit of time and is usually expressed as g DM/min. It is the product of bite mass and bite rate. Bite mass is the product of bulk density and bite volume of the horizon being grazed. Bite volume is the product of bite area and bite depth.

Bite area is constrained by the size of the animal's mouth and Illius and Gordon (1987) found that the breadth of the incisor arcade was proportional to body mass to the power 0.36 ( $M^{0.36}$ ) ie larger animals have a larger bite volume. However, they also predicted that when SH was non-limiting, bite mass could be scaled with  $M^{0.75}$ , but it scaled with  $M^{0.36}$  on very short swards when animal's had the same incisor breadth. Thus the critical SH at which this occurs is shorter for smaller animals. Gut capacity can constrain the digestion of herbage as it increases faster than metabolic rate and body size does. Thus, large animals have a relatively long retention time of food in their gut, allowing them to digest fibre more fully and to subsist on low quality diets. Small animals, by contrast, are forced to be more selective to obtain a higher quality diet (Demment and van Soest 1985).

Cangiano *et al.* (2002) found that the effect of liveweight on bite dimensions was not significant when cows grazed forages of wheat, oats, forage sorghum, millet, and lucerne. They concluded that bite area and bite weight were determined principally by sward structure (eg height and bulk density) rather than by mouth dimensions. According to their results, when forage intake or ingestive behaviour are to be explained, sward measurements should describe successive horizons equal to 50% of SH to reflect the bite depth measured in cattle. Also, these results indicated that lighter animals could get a nutritional advantage since they may achieve a relatively higher bite weight/ kg liveweight.

Bite rate for dairy cows is in the range 55-65/minute and Chacon and Stobbs (1976) have suggested that the maximum number of bites/d a Jersey cow can take was 36,000. Therefore, a cow grazing at 60 bites/min for 510 minutes would take 30,600 bites during grazing. Pasture bite sizes vary from 0.2 to 0.6 g DM/bite and probably average 0.3 g DM/bite over a grazing season. It seems that variation in bite size is the most important factor determining how much pasture a cow can eat/d and is the variable most influenced by sward characteristics (Mayne and Wright 1988).

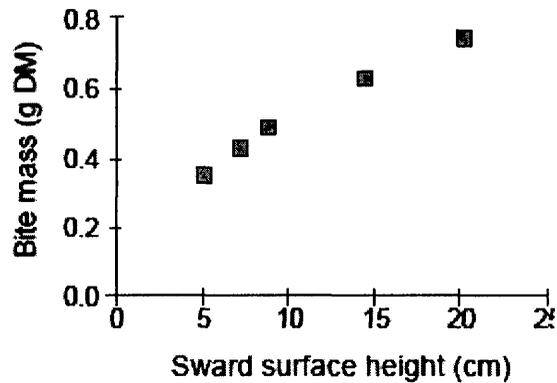
Gibb *et al.* (1999) found that in dairy cows the grazing behaviour variables are affected by factors such as the physiological state of the animal, eg lactating v. non-lactating, and genetic potential for milk production is also known to be a factor affecting IR (Christie *et al.* 2000). While it appears that increased nutritional demand can cause dairy cows to increase bite mass and IR consistently, the major response by the animal is to increase its time spent grazing in 24h (Figure 3). The practical implications of the fundamental constraint of sward state on bite mass and its consequences for herbage DMI demonstrate a focus for improving intake/animal. However, just offering taller swards may not to be the simple solution.



**Figure 3.** Effect of physiological state (lactating □, non-lactating ■) on the response to sward surface height in bite mass and total grazing time (h/d) by dairy cows (after Gibb *et al.* 1999).

There is a close relationship between IR of sheep and herbage availability (Allden and Whittaker 1970) and when herbage availability is greater than 3000 kg DM/ha, IR and GT were relatively constant. However, as herbage availability decreased from 3000 to 500 kg DM/ha, there was a fourfold reduction in IR and a twofold increase in GT. This result has been used to show that as IR decreases the animal increases its GT to compensate. Allden and Whittaker (1970) also found that bite size increased linearly with changing tiller length. The number of bites/min, however, showed a steady decline after an initial increase. Chacon and Stobbs (1976) found that neither GT nor bite rate fully compensated for the declining bite weight.

Sward height has been identified as the major determinant of bite mass on temperate swards and the effect is primarily on bite depth rather than bite area (Mayne and Wright 1988). Wade *et al.* (1989) found that dairy cows consistently removed 34% of the height of marked tillers. This was irrespective of tiller height and whether or not the tillers had been grazed previously. Illius *et al.* (1995) calculated that most of the energetic cost of grazing was from chewing rather than biting and that whatever the bite depth, energy gain exceeded energy cost. Therefore, energy use in biting alone cannot explain why animals remove only the surface layer of the sward. This is confirmed by Barthram (1980) and Barthram and Grant (1984) who found that for swards continuously grazed by sheep, depth of grazing was independent of SH above 6cm, but inhibited by the presence of pseudo-stem horizon below this SH. The relationship between bite mass and SH is shown in Figure 4.



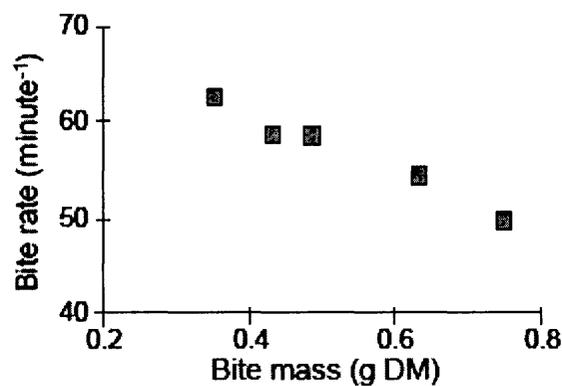
**Figure 4.** Effect of sward surface height on bite mass of lactating dairy cows (after Gibb 2006).

Sward height cannot be used indiscriminately to compare swards of different structure (Rook 2000). Theoretical models (eg Ungar and Noy-Meir 1988) and experimental studies have shown that the regression of bite mass on SH differs for swards of different structures. Prache and Petit (1995) found that the relationship differed between reproductive and vegetative swards and Penning *et al.* (1994) found that the relationship differed between continuously or rotationally grazed swards. However, the relationship with green leaf mass was similar in the different treatments reported in these experiments and closer than that of SH. These differences in relationships with SH are mainly because of the leaf: stem ratio (Stobbs 1973a, b).

An important determinant of bite mass is the bulk density of the grazed horizon. Gong *et al.* (1996) found that as a result of the vertical distribution of bulk density, bite mass was greater for legumes than for grasses despite a shallower bite depth. Bulk density was greatest close to the ground for grasses but near the top of the sward for legumes. The time required searching for each bite and the time to process each bite are major constraints on bite rate. Herbivores grazing dense homogeneous swards can be assumed to require minimal searching time as because not only is the next bite readily available, but it can be searched for while the current bite is being processed (Spalinger and Hobbs 1992)

and Gross *et al.* (1993b) confirmed that processing time is limiting if the time to process a bite is longer than that required to find the next bite.

However, when bite mass decreases there is an increase in bite rate (Figure 5), which results not only from an increase in the rate of movement of the jaws, but also from an increase in the proportion of total grazing jaw movements which are represented by bites.



**Figure 5. Effect of bite mass on bite rate of lactating dairy cows (after Gibb 2006).**

The increase in bite rate in response to reduced bite mass does not fully compensate for the effect of shorter SH and therefore, IR is reduced on shorter swards (Figure 6). The response by the animal to the reduction in short term IR is to increase GT over 24h. Because of the competing demands of ruminating and idling activity, this is usually insufficient to fully compensate for the reduced short term IR and thus herbage DMI is less on shorter swards (Gibb *et al.* 1996; Figure 7). There is scope for the future plant breeding and use of more rapidly comminuted cultivars to reduce the time necessary for ruminating and idling. These might prove beneficial in allowing GT to increase.

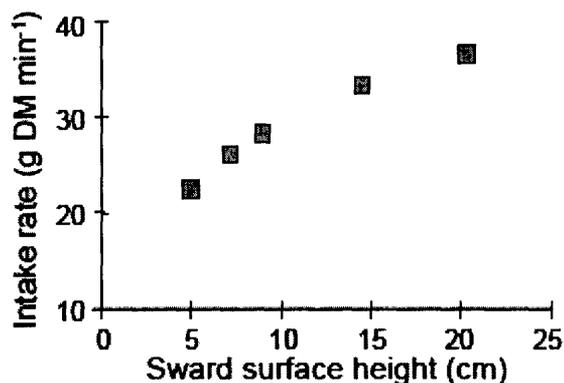


Figure 6. Effect of sward surface height on short-term intake rate by lactating dairy cows (after Gibb 2006).

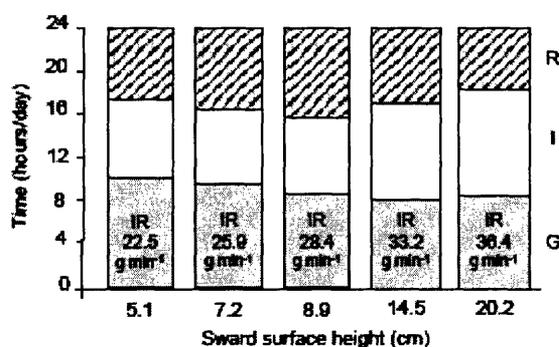


Figure 7. Effect of sward surface height on time spent grazing (G), idling (I) and ruminating (R) by lactating dairy cows (after Gibb 2006).

The structural strength of accessible pasture components has been suggested to influence the determination of bite dimensions and bite mass, and that the upper limit to the force ruminants are prepared to exert to sever a bite may be important (Tharmaraj *et al.* 2003; Hughes *et al.* 1991). Illius *et al.* (1995) demonstrated that the number of tillers constrained bite mass and was determined by the force required to sever a mouthful. Ease of prehension is related to biting rate, herbage shear force and bite mass, as smaller mouthfuls often lead to an increase in biting rate. It is difficult to isolate the individual effects of sward characteristics, such as height, mass, leaf area and nutritive characteristics on ingestive behaviour, since these factors are linked, and experiments that

have attempted to vary SH have generally varied herbage mass as well. These interrelationships between characteristics of swards lead to confounding when trying to isolate the importance of a particular characteristic.

Tharmaraj *et al.* (2003) tested the hypothesis that SH and herbage allowance affected herbage DMI and diet selection through their effects on the pattern of defoliation which is influenced by the resistance to prehension bites. They found that the volume of herbage defoliated and herbage DMI increased with SH and herbage availability. Corresponding to an increase in herbage availability from 35 to 70 kg DM/cow.d, there was a proportional increase in the total defoliation area and herbage DMI by 0.24 and 0.55 in the short sward compared with 0.16 and 0.32 in the tall sward, respectively. The results of this experiment suggest that a consistent spatial pattern of reduction of the canopy exists during defoliation by cows and that the volume of sward canopy defoliated is the major variable affecting IR.

Both animal and sward factors affect herbage DMI through their effects on IR. Practical application of the principles and results outlined above has led to pasture management guidelines based on SH (Nicol 1987; Fulkerson and Donaghy 2001). *However, there is a need to further quantify factors affecting IR when dairy cows graze pastures differing in SH in terms of grazing behaviour. Such quantification will help to improve the prediction of herbage DMI and hence, production through a better understanding of the effects sward factors has on grazing behaviour.*

## 2.5 Factors affecting grazing time and temporal patterns of behaviour

The grazing dairy cow divides its day into three main activities: grazing, ruminating and idling. When considered with other criteria, these activities and also deviation from the normal may signal constraining factors and suggest management changes. Ruminants commonly spend between 7-12h/d grazing, including time spent searching for as well as consuming forage (Arnold and Dudzinski 1978). Cattle spend more time grazing and less time resting as stocking rate increases, when SH is short, as nutritive value of a pasture declines and on heterogenous swards. Given one or more of these constraints cattle that normally graze 8h/d may increase GT to up to 12h/d (Campbell 1969).

Grazing time is influenced by sward structure, daylight hours, the level of milk production, cow genotype and rumen fill. It becomes a serious limitation to herbage DMI particularly when the SH falls below a critical height (~4-5cm for cattle) because prehension is hampered as intake/bite decreases and bite rate increases (Rook *et al.* 1994; Baker *et al.* 1981). Increasing the level of supplemental starch and protein decreases GT (Krysl and Hess 1993), although total DMI may actually increase. In their study, cattle receiving no supplement grazed approximately 1.5h/d more than protein supplemented cattle, resulting in forage intakes of 12.3 and 31.0g OM/kg BW for supplemented and unsupplemented cattle, respectively. Pulido and Leaver (2001) found that as concentrate level increased, GT decreased in cows grazing pasture continuously or when IR was higher.

Time spent grazing can be an important compensatory mechanism to counteract the effect of variation in bite mass and IR. An upper limit to GT is set by the need for the cow to undertake other activities such as ruminating. However, cows in negative energy

balance have been shown to graze for up to 12h/d when sward state is limiting IR (Rook *et al.* 1994). The inability of high producing cows grazing pasture to harvest enough herbage during the time available is an important factor limiting their milk production. This is especially true if the DM content of herbage is low, such as for fresh wet spring growth which may contain only 12-16% DM. For example, a cow with a herbage DMI requirement of 15kg DM/d has to eat ~100 kg of wet pasture if the DM content is 15%. Therefore, the demands that are placed on the dairy cow to eat this quantity of herbage can be more fully appreciated if they are expressed in terms of grazing behaviour. Also, the type of grazing management system used will influence whether the cow can consume this amount of herbage required.

Physiological state of the animal can affect GT. Penning *et al.* (1995) found that lactating and dry ewes grazed for 582 and 478 min/d, respectively. Gibb *et al.* (1999) recorded lactating and dry dairy cows grazing for 583 and 451 min/d, respectively, on 7cm sward surface height grass swards. Such increases in GT may reduce ruminative efficiency by reducing rumination time/unit of herbage DMI (Gibb *et al.* 1999). Both GT and bite rate act as compensatory factors to avoid reductions in herbage DMI when bite mass decreases, however this compensatory mechanism is only partial. For example, the upper limit of GT to compensate for a reduction in bite mass is determined for the time required for other activities such as ruminating (Rook 2000). Under poor pasture conditions (eg very short pasture), all three variables decline (Hodgson and Brookes, 1999). High genetic merit cows (32 kg/d of milk) had significantly higher GT and biting rate than low genetic merit cows (24.8 kg/d) supplemented with concentrate (Bao *et al.* 1992). Grazing time of cows fed a ryegrass pasture was measured visually for a period of 7 h between morning and evening. The high genetic merit cows grazed longer (218 vs.

204 min) and at a higher biting rate (63.5 vs. 60.8 bites/min) than the low genetic cows. This would have an effect on pasture utilisation and supplementation strategies.

Animals do not always use GT to compensate for low IR, even though it may appear to be the case. For example, Hendricksen and Minson (1980) found that cattle grazing a tropical forage legume reduced GT when they were forced to eat stem material, even though IR was lower and their rumens were not distended. Rook *et al.* (1994) found that cows offered a supplement and grazing a very short sward decreased GT compared to cows offered the same supplement on a taller sward, despite the lower herbage IR on the shorter sward. These results were obtained using a continuous grazing system. Jamieson and Hodgson (1979) found that in short-term rotational systems animals graze for less time at low herbage availability in anticipation of a new allowance later.

Although animals may increase total GT in an attempt to compensate for constraints on IR, an underlying pattern of grazing activity is discernable. Gibb *et al.* (1997) describes typically three major periods of grazing activity for temperate climates. The actual timing of the meals will be modified depending upon such events as removal for milking, photoperiod and temperature. This basic temporal pattern can be modified under daily paddock allocation management, depending on the time of introduction to a fresh pasture area (Orr *et al.* 2001). Soca *et al.* (1999) found that cows given access to pasture for only 6h/d commencing at 1200h had a longer initial grazing meal compared to those cows given access to pasture for 8h/d commencing at 0600h (120 v. 82 min). These cows were also more likely to be found grazing during the first 4h after introduction (0.81 v. 0.54). However, ruminating and resting time were less.

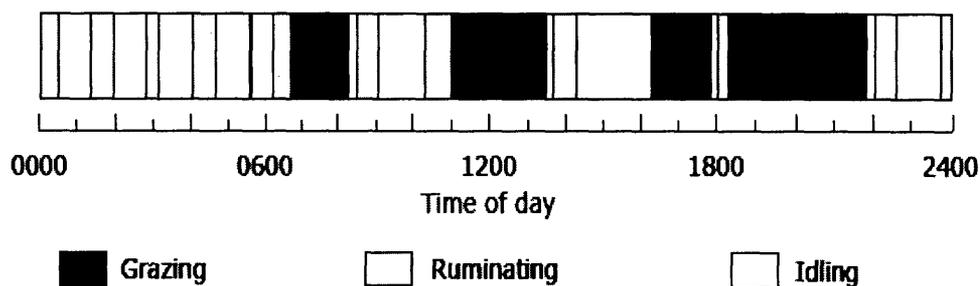
Meal duration can be influenced by the capacity of the rumen, the requirement for rumination to breakdown ingested material and the rate of passage of digesta from the rumen. The nutritive characteristics of different plant species are important and further

studies of the kinetics of digestion at grazing are needed to explore the importance of these characteristics on GT. Chilbroste *et al.* (1999a) attempted to gain insight into the main mechanisms controlling DMI, IR and GT during the first session after morning milking by investigating the effects of the length of the grazing session, the combination of starvation and rumen fill before grazing and the characteristics of the sward available to grazing cows. They found that increasing the length of a grazing session increased DMI, the proportion of time spent actively eating and the DM rumen pool size after grazing. Williams *et al.* (2005) found that at the same herbage DMI, perennial ryegrass resulted in higher rumen fill than Persian clover. Cows grazing perennial ryegrass at high herbage allowance spent less time eating and more time ruminating than those grazing the clover. However, there were no differences in average DM in the rumen for cows grazing Persian clover, with herbage DMI between 5.5 and 20.4 kg DM/d. Although rumen DM varied throughout the day as meals were consumed, little time was spent ruminating and it appeared the primary effect of increasing herbage DMI was increased passage from the rumen on this herbage type.

The amount of available daylight may constrain GT and many studies have shown that around 80% of grazing occurs during daylight hours, but the proportion of grazing at night increases as day length decreases (Rook *et al.* 1994). Social facilitation and competition between animals can also constrain GT. Rook and Huckle (1995) found that animals grazing in groups are more synchronised than would be expected by chance. The start of meals is also more synchronised than the end, suggesting the start of meals is subject to social facilitation, while the end is under physiological control. Curll and Davidson (1983) found that previous experience affected the ability of sheep to alter both their GT and IR in cross-over experiments between high and low stocking rate treatments.

Major grazing bouts for lactating dairy cows have been observed in the morning, with a longer bout in the afternoon (Rook *et al.* 1994; Gibb *et al.* 1997). Forbes *et al.* (1987) found that in lactating dairy cows, the critical inter-meal interval was between 5 and 7 min, with little variation between cows or within seasons or physiological states of the cows. The basic temporal pattern of grazing in dairy cows, under continuous stocking management was demonstrated by Gibb *et al.* (1997). The increase in afternoon grazing activity has been interpreted as an optimum foraging strategy to harvest pasture of higher digestibility with higher concentrations of water soluble carbohydrates (WSC) and DM (Gibb *et al.* 1998). It is also known that cattle adapt feeding behaviour in anticipation of future events, and energy requirements, and therefore can be hyperphagic under certain conditions (Baile and McLaughlin 1987), primarily associated with their higher risk of predation during darkness.

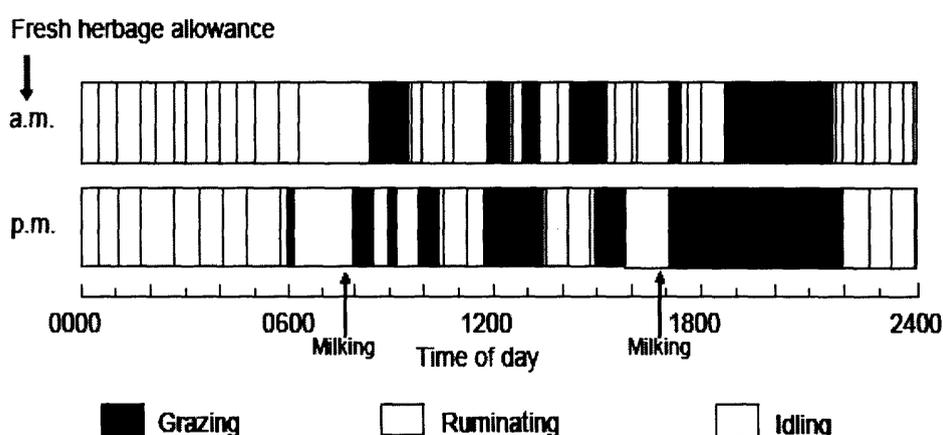
Continuous grazing can provide conditions in which sward state varies little over the course of a day so that, with the exception of removal for milking, there is a minimally perturbed temporal pattern of grazing, ruminating and idling activity. Figure 8 illustrates such a pattern for a cow during a dark-phase period of the moon. During the hours of darkness the cow performs alternating periods of idling and ruminating. However, on return to pasture at 0630h, following morning milking, the animal undertakes a relatively short grazing meal of approximately 90 minutes duration, followed by alternating periods of idling and ruminating. In the late morning (c. 1100h) the cow undertakes a second grazing meal, of slightly longer duration (approximately 150 minutes) followed during the early part of the afternoon by further periods of idling and ruminating. On returning to the paddock at 1600h following afternoon milking, the vast majority of the remaining time until dusk is occupied in grazing.



**Figure 8. Typical temporal pattern of grazing, ruminating and idling activity by a dairy cow under continuous variable stocking management (after Gibb 2006)**

Not only was the late afternoon and evening the time when the longest periods of almost uninterrupted grazing activity occurred, it was also the time of highest bite mass, bite rate and IR. Under such a regime it appeared that in excess of 60% of daily herbage DMI was occurring during the period between afternoon milking and dusk. Orr *et al.* (2001) examined the hypothesis that under daily grazing management allocation of fresh herbage following afternoon milking (PM) rather than following morning milking (AM) would allow greater herbage DMI before it had been fouled and trampled. Despite cows being offered their fresh pasture either after the morning milking or after the afternoon milking, meals during the earlier part of the day were short and fragmented. However, the major grazing meal of the day occurred after afternoon milking for both groups. This can probably be attributed to the higher herbage DM and WSC content of the herbage at this time. When their fresh allocation was after the afternoon milking, the PM cows had a higher GT than the AM cows at this time of day (Figure 9). The benefit accrued from offering the same grazing area, but following afternoon rather than morning milking, was an increase in milk yield of about 5% and an increase in fat and protein content of the milk of 4.7 and 0.4 g/kg, respectively. Similar results have been obtained by Trevaskis *et al.* (2004) where offering a fresh grazing area following afternoon milking resulted in an

increase in milk yield by 2.1 L/d (8%) compared to cows given a fresh grazing area following morning milking.



**Figure 9. Typical temporal patterns of grazing, ruminating and idling activity by dairy cows under daily paddock-stocking management provided with the same daily herbage allowance either following morning milking or following afternoon milking (after Gibb 2006).**

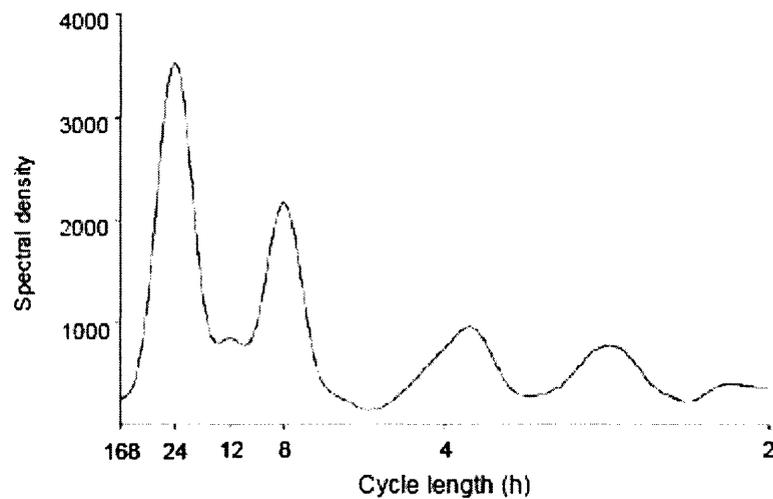
Quantification of the temporal patterns of grazing dairy cows has been limited to only a few management/research scenarios. Many research studies that have included grazing behaviour as part of their objectives have mainly presented the total time spent in the various behavioural activities. In many cases the statistical analysis of the behavioural data revealed no differences between treatments. However, even though two treatments may show no differences in their mean values, their transient behaviour may be significantly different. For example, animals within one treatment may respond slowly to deviations from their mean values, while animals on another treatment may respond rapidly. Hence, depending on the purpose of the treatment, one response may be more preferable than another and a simple comparison of the treatment means may well mask any cyclic differences.

Stroup *et al.* (1987) discussed experimental design issues associated with investigating feed intake of animals in feedlots and highlighted the inadequacies of the analysis of designs such as Latin squares, crossover etc using standard ANOVA procedures. The ANOVA procedure for row-column designs assumes that there is no row x column interaction. Using the traditional ANOVA procedure on data sets with substantial row x column interaction will produce biased estimates of treatment means and inflated estimates of experimental error. To overcome this problem, Stroup *et al.* (1987) suggested the use of finite Fourier transformations and spectral analysis to account for the cyclic variation in feed intake data for feedlot fed cattle.

Deswysen *et al.* (1993) using Fourier analysis noted differences in grazing cyclicality among heifers with different pedigrees for milk production and also found that individual heifers exhibited different complex rhythm components for both time spent eating and ruminating. Seman *et al.* (1997) found that spectral analysis was also valuable in describing grazing behaviour when they compared steers grazing either endophyte infected or endophyte free tall fescue pastures. Spectral analysis has also been used to relate dietary quality and herbage species to the behaviour of grazing steers (Seman *et al.* 1999) and to determine the differences in feeding and lying behaviour of steers in feedlots (Wilson *et al.* 2005).

Examination of grazing activity by spectral analysis from continuous recordings of sheep behaviour over several days showed that in addition to a peak of activity occurring at a cycle length of 24h, an additional peak occurs with a periodicity of 8h (Champion *et al.* 1994; Figure 10). Phillips (1992) has suggested that this 8h periodicity reflects attempts by the grazing animal to maintain optimum fibre status within the rumen. Similar cycles of grazing activity have been demonstrated in dairy cows, although the intensity of the 8h peaks are not equal and are influenced by management factors, such as milking

times, and natural phenomena, such as the weather and phases of the moon (Albright and Arave 1997).



**Figure 10. Smoothed periodogram of grazing behaviour by grazing sheep (after Champion *et al.* 1994).**

Time spent grazing and associated temporal grazing patterns are affected by both animal, environmental and sward factors. *The recent investigations on time of day grazing a fresh pasture have improved our knowledge of how to maximise herbage DMI and increase production. However, the effects of time of day on GT, including grazing pattern, has yet to be quantified. Quantifying the underlying cyclical responses to changes in pasture allocation using spectral analysis could possibly assist in the design of feed allocation systems for grazing dairy cows.*

## 2.6 Management factors that maximise herbage DMI

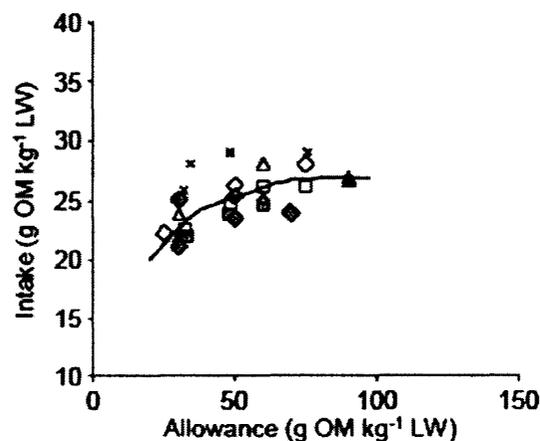
Numerous management options exist that are beneficial to the maximisation of herbage DMI and have the potential to enhance the efficiency of pasture based systems. In practice, management factors interact with the environmental, plant and animal factors discussed earlier. On rotationally grazed pastures, pasture allocation is commonly described in terms of daily herbage allowance, i.e. kg DM/cow.d. Daily herbage allowance is often estimated to ground level or at a cutting height of 4 or 5 cm, assuming that the material below the cutting height is unavailable for grazing. Other management factors include stocking rate, supplementation and feed allocation (Dillon 2006). Understanding the interactions between animal, sward and environmental factors that influence herbage DMI will help producers to make better management decisions and hence, improve profitability and sustainability. Therefore, since factors that influence herbage DMI also influence grazing behaviour, an improved understanding of grazing behaviour will also enhance management decisions that can maximise herbage DMI.

### 2.6.1 Herbage allowance

It is unclear what herbage allowance is required to maximise herbage DMI. Leaver (1985) proposed maximum herbage DMI at an herbage allowance between 45 to 55 g DM/kg of BW or 27 to 33 kg DM/cow.d for a 600-kg cow. Herbage DMI increased as herbage allowance increased, but at a declining rate with a plateau when herbage allowance was 10 to 12% of BW or 60 to 72 kg DM/cow.d for a 600-kg BW cow (Hodgson and Brookes 1999). Doyle *et al.* (1996) showed that herbage DMI continues to increase as herbage allowance increases up to 15 kg DM/100 kg of BW or 90 kg DM/cow.d for a 600kg BW dairy cow. Herbage DMI increased nonlinearly from 11.2 to

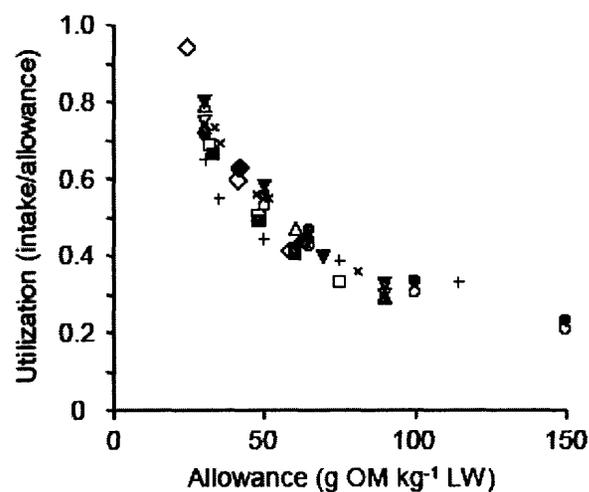
18.5 kg DM/cow.d as herbage allowance increased from 20 to 70 kg DM/cow.d, with a plateau at an herbage allowance of 55.2 kg DM/cow.d (Dalley *et al.* 1999).

A curvilinear relationship between daily herbage allowance and daily herbage DMI has been demonstrated in many experiments. Amongst those reported for dairy cows (Greenhalgh *et al.* 1966; 1967; Combellas and Hodgson 1979; Le Du *et al.* 1979; Peyraud *et al.* 1996), daily herbage OM allowance has ranged between about 25 and 90 g kg<sup>-1</sup> LW (Figure 11). Quantification of this relationship by fitting the data to the asymptotic equation  $y=a+br^x$  found that the optimum herbage allowance to maximise herbage DMI (26.3 g OM/kg LW) is reached at ~90 kg DM/cow.d, and herbage DMI increased 0.085 g OM/kg LW/g OM/kg LW of increase in herbage allowance up to 90 kg DM/cow.d (Figure 11). From such relationships it is evident that to achieve unrestricted daily intakes, daily herbage allowances equivalent to between 3 and 4 times maximum daily intake must be provided.



**Figure 11.** Effect of daily herbage OM allowance on daily herbage OM intake by dairy cows grazing perennial ryegrass swards (Greenhalgh *et al.* 1966 □ and 1967 ■; Le Du *et al.* 1979, expts 1 ◇ and 2 ◆; Combellas and Hodgson 1979, high △ and low ▲ herbage mass; Peyraud *et al.* 1996 × after Gibb 2006). — fitted line ( $y=a+br^x$ )

Gibb (2006) expressed these same data as utilisation (daily herbage DMI/daily herbage allowance) upon daily herbage allowance and clearly demonstrated the problem of poor sward utilisation when high daily herbage allowance is offered in order to maximise daily DMI/animal (Figure 12). However, if high utilisation of the pasture is required, then restrictive daily herbage allowance must be provided, which will result in reduced herbage DMI/animal.



**Figure 12. Effect of daily herbage OM allowance on utilisation (OM intake/OM allowance). Source data as in Figure 11. (after Gibb 2006).**

Bargo *et al.* (2003) summarised the relationship between herbage DMI and herbage allowance from seven studies (Peyraud *et al.* 1996; Dalley *et al.* 1999, 2001; Stockdale 2000b; Delaby *et al.* 2001; Wales *et al.* 2001; Bargo *et al.* 2002a). In those studies, cows ranged from 19 to 182 days in milk and produced from 23.0 to 45.8 kg/d of milk at the start of the experiment, grazed at an herbage allowance from 12.1 to 70 kg DM/cow.d, and consumed 6.7 to 20.5 kg DM/cow.d of pasture. Observations were weighted as described by St-Pierre (2001) to account for unequal replications and

variances of the means across studies. The regression analysis for herbage DMI resulted in a best-fit model that included terms for herbage allowance and its quadratic term viz:

$$DMI = 7.79 (\pm 1.49) + 0.26 (\pm 0.06) HA - 0.0012 (\pm 0.0007) HA^2 \quad \text{Equation 2}$$

$$R^2 = 0.95.$$

where DMI = herbage DMI; HA = herbage allowance

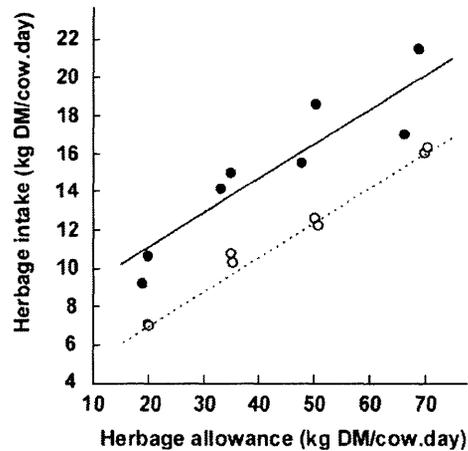
Based on Equation 2, the optimum herbage allowance to maximise herbage DMI (21.9 kg/d) is reached at 110 kg DM/cow.d, and herbage DMI increased 0.26 kg/kg of increase in herbage allowance up to 110 kg DM/cow.d.

However, the relationship between herbage DMI and herbage allowance is not always curvilinear. Wales *et al.* (1999) found that daily herbage DMI increased linearly from 7.1 to 16.2 kg DM/cow.d as herbage allowance increased from 20 to 70 kg DM/cow.d for dairy cows grazing irrigated perennial ryegrass-white clover swards at either a low herbage mass (3100 kg DM/ha) or a high herbage mass (4900 kg DM/ha) (Figure 13). The equation best describing the data was:

$$DMI = -3.8 + 0.18 (\pm 0.014) HA + 2.29 (\pm 0.278) HM \quad \text{Equation 3}$$

$$(R^2=0.94; \text{rsd}=0.99; P<0.01)$$

where DMI is the herbage DMI (kg DM/cow.d), HA is herbage allowance and HM is herbage mass (t DM/ha).



**Figure 13. Relationship between herbage allowance and herbage DMI for cows grazing irrigated perennial ryegrass-white clover pastures at low mass (○) and medium mass (●) swards (after Wales *et al.* 1999).**

If the goal is to maximise herbage DMI of high producing dairy cows, management must ensure unrestricted pasture quality and quantity, which is only found for short periods of time during the spring. Unrestricted pasture conditions, that is a high herbage allowance also implies low pasture utilisation (herbage DMI/herbage allowance <50%; McGilloway and Mayne 1996). The studies reviewed by Bargo *et al.* (2003) indicate that maximum herbage DMI is achieved when herbage allowance is between 3 to 5 times the DMI, which is in agreement with Gibb (2006). However, even under unrestrictive pasture conditions, the total herbage DMI achieved by high producing dairy cows is still lower than that by cows consuming total mixed rations (Kolver and Muller 1998) or pasture plus supplements (Bargo *et al.* 2002a, b). Because of low pasture utilisation and deterioration of pasture quality at high herbage allowance a practical recommendation is to provide an herbage allowance of 2 times the expected herbage DMI or 25 kg DM/cow.d of herbage allowance when cows are also fed supplements (Bargo *et al.* 2002a). The use of very high herbage allowances might also result in deterioration of

pasture quality as the season progresses because of the increase in residual SH (Peyraud and Delaby 2001).

Gibb (2006) suggests another factor that cannot be ignored and is termed “the relative competitive ability of the animals.” This was demonstrated by Peyraud *et al.* (1996) in an experiment where mixed groups of primiparous and multiparous dairy cows were provided with a range of daily herbage allowances. The overall mean daily herbage DMI achieved by each group showed a curvilinear response to increasing herbage allowance (Figure 14a). However, when the values are plotted for the two classes of animals separately (Figure 14b), although both classes achieved the same level of DMI relative to their LW, when daily herbage allowance was in excess of 80 g OM/kg LW, the primiparous cows were unable to achieve as high a herbage DMI as those of the multiparous cows at lower daily herbage allowance. This difference was more than likely due to the primiparous cows having a significantly lower milk yield (18.3 v. 24.2 kg/d) and therefore energy demand.

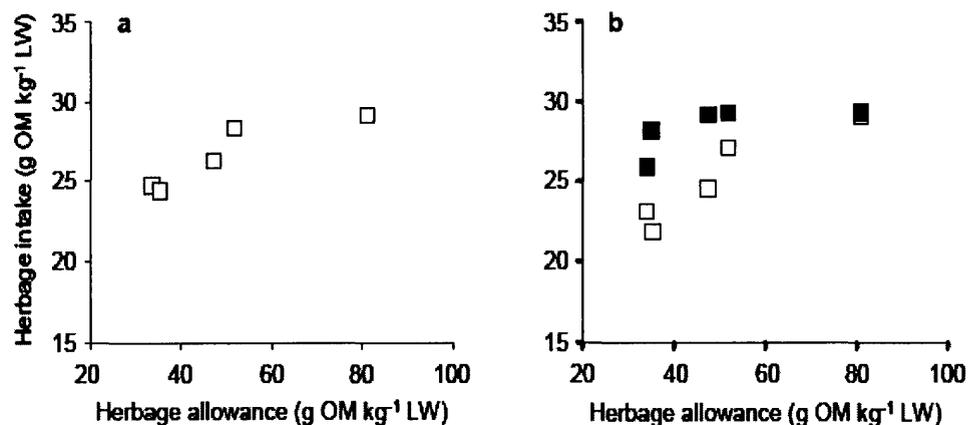


Figure 14. Effect of daily herbage OM allowance on (a) overall mean herbage OM intake within groups of cows and heifers  $\square$  and (b) mean herbage intake by cows  $\blacksquare$  and heifers  $\square$  calculated separately (after Gibb 2006).

### **2.6.2 Nutritive value of herbage**

One of the major difficulties faced by producers is the ability under grazing situations to measure herbage quality. There are several factors that can affect herbage quality and they are highly variable and one may influence the other. However, there is one environmental factor that is relatively constant, and that is the length of the light and dark periods. Of course the duration of these periods change throughout the year but are indeed predictable. Plants seem to have the ability to accumulate carbon that is fixed during photosynthesis which can be used for metabolism during dark periods. These carbon sources are typically in the form of non-structural carbohydrates. Adjusting management practices (grazing intensity, fodder conservation, and supplementation) to utilise this change in carbohydrate levels may improve dairy cow performance or conserved fodder quality (Dillon 2006). The efficient utilisation of grazed grass will require the development of grazing systems designed to maximise daily herbage DMI/cow, while maintaining a greater quantity of high quality herbage over the grazing season.

Wales *et al.* (2005) have suggested that an ideal sward would have a nutrient profile similar to a TMR formulated to provide nutrients in relation to requirements while having the physical characteristics necessary to stimulate rumen function and rumination. A TMR diet offers control over the nutritive characteristics of the diet, when offered in sufficient quantities, it allows animals to approach their potential intake, and can provide the nutrient requirements for high animal performance. Kolver and Muller (1998) compared the nutritive characteristics and animal performance of a pasture diet based on a mixed grass/clover sward and a TMR consumed by early lactation dairy cows. Despite both diets having similar digestibility, there were clear differences in the concentrations of essential nutrients, as well as pasture having lower DM and non structural carbohydrate

concentrations and higher NDF concentrations. In comparison with TMR, cows consuming grazed pasture, even when supplemented with grain, had lower DMI, milk yield, milk protein and fat concentrations, lost more body condition and had lower liveweight. However, there is now strong evidence to show that dairy cattle that are genetically best suited to high concentrate input systems are not best suited to grazing systems, suggesting an interaction between genotype and feeding system (Fulkerson *et al.* 2000; Dillon *et al.* 2006) that may allow producers the capacity to overcome some of the restrictions above for the grazing animal.

The nutritive value of herbage gives an indication of its potential value to grazing animals, but its feeding value (nutritive value x intake) is more important. With fibrous diets, intake is limited by rumen capacity and by the rate of passage of digesta through the rumen (Minson 1982). At high levels of digestibility, Conrad *et al.* (1964) postulated that voluntary intake is controlled more by the energy requirement of the animal and less by the above physical factors, and that intake stabilises at digestibilities above 67%. However, these results were obtained with mixed roughage/concentrate diets and these findings do not apply to herbage diets, where linear responses have been shown up to 83% digestibility (Hodgson 1977). However, digestibility differences in swards are most commonly associated with changes in sward structure, such as SH, and content and distribution of leaf material, sheath, stem or dead material. These differences lead to difficulty in isolating the digestibility effect *per se* from other differences (Dillon 2006).

The DM content of the herbage can have a large effect on herbage intake. Studies with housed cows have shown that below a critical value of 180 g DM/kg, intake is reduced with 1 kg DM, for a reduction in DM content of 40 g/kg (Vérité *et al.* 1970). Lloyd-Davies (1962) found that when water was added to the rumen *per fistulum*, there were no detrimental effects on the intake of forages by sheep, indicating the effects of

water content on herbage intake may be associated with palatability or the large volumes of fresh herbage that need to be processed during ingestion. In cattle intake and eating rate were restricted by water content of grass, but not by external water (Cabrera Estrada *et al.* 2004).

The crude protein (CP) content of herbage varies considerably between species, with legumes being higher than grasses. The nitrogen content of herbage is dependent on the level of fertiliser N applied and soil OM content. Peyraud and Astigarraga (1998) reviewed the effect of fertiliser N on dairy cow performance and showed that in deep and rich soils (10% OM) reducing N fertiliser from 320 kg to almost zero N did not affect milk yield, while CP content of unfertilised swards remained greater than 15 %. In contrast, in soil with low N supply capacity (2% OM) reducing N fertilisation led a reduction in milk yield of 2.5 kg/d and in herbage DMI of 2 kg, while CP content in the herbage fell below 12 %. Therefore, reduced herbage DMI was mostly mediated through reduced CP content of the herbage, while herbage mass and height may also be of influence. To maintain a daily milk production of 0.80 to 0.85 kg of milk protein, Peyraud and Astigarraga (1998) calculated that a daily intake of 3kg of CP is required.

Improvement of animal production from grazed pasture could be achieved through increased use of herbage species or varieties with increased intake and digestibility potential. Plant breeding objectives have mainly focused on increasing DM yield and pest and disease resistance, with little emphasis on factors that affect animal performance. Digestibility is a heritable characteristic and some improvement has resulted from conventional breeding, with further increases likely to result from biotechnological modification. Wales *et al.* (2005) suggested that the use of techniques to genetically modify plants will enable the development of plants with elevated concentration of ruminal undegradable dietary protein and high energy yielding compounds, such as starch

or triacylglycerides. Grazing studies have shown that animals have a strong preference for herbage with high concentrations of soluble carbohydrates (Ciavarella *et al.* 2000). Dairy cows offered pasture with high WSC concentrations will consume more DM and produced more milk than cows fed grasses with lower concentrations in zero-grazing studies (Moorby *et al.* 2001). However Tas *et al.* (2005) found no difference in intake, milk production or milk composition in cultivars of perennial ryegrass differing in WSC. Dillon (2006) suggested that another major objective of grass breeding should be to increase the length of the grass growing season. There appear to be other opportunities to improve herbage DMI by plant breeding by including other species such as Italian ryegrass, or incorporating characteristics from these species into hybrids.

### **2.6.3 Supplementation**

Supplementation can increase animal performance, especially in high producing lactating dairy cows (Bargo *et al.* 2003). On short swards supplementation with concentrates can compensate for the decline in herbage DMI, although herbage substitution (kg of decline in herbage DMI for each kg of concentrate DMI) may increase (Leaver 1986). Grazing efficiency (DMI/h GT) can also decline as supplementation increases and grazing season advances, suggesting that supplemented cattle should be able to maintain productivity while grazing at lower SH than unsupplemented cattle (Gekara *et al.* 2001). Increasing the amount of concentrate reduced GT but did not affect biting rate (Arriaga-Jordan and Holmes 1986; Kibon and Holmes 1987; Rook *et al.* 1994; Bargo *et al.*, 2002a; Gibb *et al.* 2002). Arriaga-Jordan and Holmes (1986) reported that GT was reduced 11 min/kg of concentrate in continuous grazing and 8 min/kg of concentrate in rotational grazing, while biting rate was not affected by the amount of supplementation. Likewise, Rook *et al.* (1994) reported that concentrate supplementation, but not SH, reduced GT 20 min/kg of concentrate. Bite mass decreased as SH decreased, while the

supplementation amount had no effect on bite mass (Rook *et al.* 1994) and the amount but not type of energy supplement (cereal v. beet pulp) reduced GT 8 to 12 min/kg of concentrate by dairy cows grazing ryegrass at two SH (Kibon and Holmes, 1987).

Phillips (1988) concluded that under situations where ample herbage was available, supplementation with grass silage reduced both milk yield and protein yield with variable results on fat yield. Supplementation with grass silage under these conditions resulted in a large reduction in herbage DMI (substitution rates of 0.84 to 1.02 kg OM/kg supplement OM intake). The large substitution effects obtained with the forage supplement appeared to be the result from reduction in GT of approximately 43 minutes/d for each kg of silage DM consumed. In these situations, supplementary forage feeding could result in under-utilization of the grazed grass area and consequent deterioration in sward structure and composition. When herbage availability is low, feeding supplementary forage generally results in increase in DMI and milk production. Corn silage supplementation had a positive effect on milk production when the amount of pasture offered was low (Stockdale 1994). However, where herbage allowance was adequate, supplementation with corn silage reduced herbage DMI and resulted in both similar total DMI and milk production (Holden *et al.* 1995). Substitution rates are generally higher for forage than for concentrate supplementation due to higher forage fill value.

#### **2.6.4 Diet synchrony**

An inevitable side effect of the intake of high quality herbage is that its fermentation in the rumen is unbalanced. There is usually a surplus of N because of the ratio between rumen degradable protein (RDP) and rumen degradable carbohydrates (RDC) being greater than 1.0, resulting in high urinary losses (van Vuuren 1993). The extent of synchronisation between RDP and RDC depends on the nature of the RDC (ie

WSC v. NDF) in the herbage consumed is not fully understood as yet. The knowledge available on how the extent of synchronisation affects microbial protein synthesis is also limited. One option may be to reduce the rumen imbalance after consumption of herbage of high quality by supplementation.

Although it has been suggested that the poor efficiency of N utilisation by dairy cows grazing pasture is in part the result of a poor synchrony between the rates at which the various pasture protein and carbohydrate fractions become available in the rumen (Beever *et al.* 1986; Beever, 1993; van Vuuren 1993; Beever and Cottrill 1994), the benefits of diet synchrony have not been conclusively demonstrated in practice. A renewed interest in the concept of diet synchrony has spawned various attempts to demonstrate its practical importance. These studies have either manipulated the degree of diet synchrony by feeding different sources of N and carbohydrates which differ in their rates of ruminal disappearance, or conversely by supplying the same sources of N and carbohydrates at different times relative to each other *in vitro*.

Trevaskis *et al.* (2004) studied the productivity and rumen status of Friesian cows, grazing short rotation Italian ryegrass (*Lolium multiflorum* cv Concord) pastures in the warm temperate climate of coastal New South Wales, Australia relative to the time of grazing and of feeding cereal-based concentrates. In one experiment, 42 Friesian cows were allocated to one of three groups of 14 cows each and grazed as three separate herds (PM, Synch and ASynch). The provision of the daily allocation of pasture in the morning (AM) and then a higher proportion of cereal-based concentrate in the afternoon (Synch) was predicted to lead to greater nutrient synchrony in the rumen compared to feeding a higher proportion of concentrate in the morning (ASynch). The PM group was a direct comparison with the Synch group of providing the daily allocation of pasture in the morning (AM) or the afternoon (PM). The percentage of cows grazing at 10-min intervals

for 7h from 0700 to 1400h on day 2 of experiment 1 and for 17h from 0700 to 2400h on the last day of experiment 2 was also measured. They found that when grazing activity was expressed as the summation of % cows grazing each hour there was no difference between the groups. However, the diurnal pattern of grazing did appear to differ. The PM group's afternoon grazing activity lasted 39% longer than that observed in the remaining groups at that time, given their daily allocation in the morning.

Supplementing grazing dairy cows can increase overall intake and hence, performance and time spent grazing can be reduced by supplementation such that substitution of pasture for supplement can have a negative affect on pasture utilisation. *There have been very few studies that have investigated the effects of diet synchrony on behaviour and temporal patterns in grazing dairy cows. To improve feed allocation strategies that include supplements, quantification of the effects of synchronisation on grazing behaviour is required.*

### **2.6.5. Integrating information – decision support tools**

Grazing dynamics are the result of complex interactions between animal and sward characteristics. While the sward is being depleted, a decline in IR is partly offset by longer GT. This behaviour may be controlled by nutritional feedback from digestion and nutrient absorption as the quality of the ingested herbage decreases. Models are useful because they help to organize and quantify knowledge about a subject. Scientific investigation normally begins as a conceptual thought model of the factors that influence the behaviour of a system. Traditionally this has led to experimental designs that have kept all factors, except the ones under investigation, constant. Therefore, the effect of imposed treatments is evaluated and therefore to test all factors at the same time would quickly overwhelm resources. Systems analysis offers an alternative to traditional experimental procedures. As the complexity of a system increases, the value of

quantitative systems model increases. Unfortunately, a model is often evaluated based on its predictive ability. However, simulation models can provide useful insights into problems regardless of their predictive ability. Simulation models help by: (1) defining problems, (2) organising thoughts, (3) understanding the data and theory, and (4) making predictions.

Rook and Penning (1991) used a finite Markov chain to study the transition among eating (grazing), ruminating and idling activities of grazing sheep and explored whether these were time-dependent. Only eating activity was found to be sensitive to the preceding length of a given meal. A failing of the Markov model is that it assumes that the transition probabilities between states are constant. However, a grazing animal would be more likely to cease a particular activity if it has been engaged in that activity for a long time. This is in agreement with intake theories based on accumulation of ingesta in the rumen or metabolites in the blood (Forbes 1995). Dutilleul *et al.* (2000) presented a new methodology using time-dependent transitions for chewing behaviour in sheep. This method determined the transition probabilities at each sampling time point, without having to assume that they were independent of the position in time.

Using simple mathematical representations allows the calculation of such things as grazing duration, rotation length and so on (eg Woodward 1998). Rook and Yarrow (2002) constructed models to predict herbage DMI of grazing dairy cows and found that the best fit model accounted for 0.37 of the variance and contained the factor chewing rate while ruminating. Other behaviour variables, eating time, eating jaw movement rate and ruminating time were not significant. However, model performance was generally poor. Including behaviour and rumen fermentation characteristics (eg Williams *et al.* 2005; Bargo and Muller 2005) may improve a model's ability to predict herbage DMI and understanding the interaction between behaviour and rumen fermentation characteristics

would help producers to make better decisions about pasture allocation, rotation length and supplementary feeding. Models of the pasture-animal interface would benefit from including such data to help predict herbage DMI and animal performance. Decision support tools help in decision making for grazing enterprises. Many DST available for dairy enterprises are mainly for ration formulation. There is a lack of DST for grazing dairy cows that help in the allocation of feed. One such tool is called *FeedSmart* (Dobos and Fulkerson 2004) but future improvement is required and inclusion of *quantitative analysis of grazing behaviour will be of significant benefit to simulation models and DST.*

*To develop more efficient grazing systems and improve the prediction of herbage DMI, it is important to understand how the dairy cow grazes and adapts its behaviour throughout the day as sward dynamics change. Therefore, an understanding of why, how, and when animals graze is essential in trying to improve pasture utilisation and the management of livestock. Being aware of the factors that encourage or discourage grazing can help a producer make decisions about pasture rotation, supplementary feeding and stocking density.*

*This review has highlighted the interactions between factors considered as constraints on grazing behaviour of dairy cows are still poorly quantified. To improve management decisions that enhance pasture utilisation and animal performance we still need to understand the following:*

- (1) *how dairy cows behave when SH and length of the grazing session varies within a grazing period and whether this will influence their temporal pattern of behaviour;*
- (2) *how sward dynamics changes as length of the grazing session is altered;*

- (3) *how time of allocation of a fresh pasture and diet synchrony influence the behaviour and temporal patterns of grazing dairy cows;*
- (4) *how SH x GD, time of allocation of fresh pasture and diet synchrony affect the initiation and cessation of feeding.*

*This research thesis is a quantitative analysis of grazing behaviour of dairy cows designed to fill the knowledge gaps outlined above. The following experimental chapters were part of a larger programme of research conducted between 1999 and 2002 and funded by Dairy Australia (DAN 097).*

## CHAPTER 3

# THE EFFECTS OF SWARD HEIGHT AND GRAZING DURATION ON BEHAVIOUR AND INTAKE OF DAIRY COWS GRAZING KIKUYU (*Pennisetum clandestinum*) GRASS PASTURES.

### 3.1 Introduction

The major limitation to cow productivity in pasture-based dairy farm systems is low herbage dry matter intake (DMI). Grazing animals must allocate their time each day to grazing, ruminating, and to activities such as resting, drinking, walking, milking, and sleeping (Walker and Heitschmidt 1989). The time allocated to each of these activities depends on factors including the quantity and quality of available pasture, the animals' physiological state and energy requirements, and the weather. For grazing animals, herbage availability is usually the factor limiting intake.

Under grazing conditions, DMI is the product of intake rate (IR) and grazing time (GT) (Allden and Whittaker 1970). The grazing dairy cow can modify its herbage DMI by adjusting its eating behaviour in terms of GT, bite rate, bite mass, chewing rate, and IR to satisfy its nutritional needs under the circumstances imposed by the sward, management, and the environment. Although there has been substantial progress in the understanding and quantifying of the main mechanisms determining DMI and IR (Ungar 1996), there is still limited understanding of GT and how it interacts with sward characteristics. Changes in the moment (time of grazing new pasture) and length of the grazing session (grazing duration, GD) may induce modifications on IR, selectivity and fermentation patterns (Dougherty *et al.* 1989; Chilibroste *et al.* 1997), as well as herbage DMI and grazing behaviour. Barrett *et al.* (2001) found that, although cows graze throughout the day on swards that were

progressively depleted, as indicative of rotationally grazed paddocks, bite mass declined linearly and intake behaviour was variable. However, where intake was assessed on high quality, undefoliated swards, intake behaviour was similar regardless of the time of day and the immediate previous experience.

The most common forage base for dairy cows in the warm temperate/subtropical regions of Australia is a two-pasture system with ryegrass (*Lolium spp*) in the winter/spring and kikuyu (*Pennisetum clandestinum*) in summer/autumn. Herbage availability (HA) or pre-grazing sward height (SH) can affect DMI, as well as grazing behaviour of ruminants (Wright *et al.* 1990; Peyraud *et al.* 1996). Iason *et al.* (1999) tested the theory that large herbivore foraging assumes that total GT is a key constraint for daily DMI and diet choice and concluded that the interactions between factors considered as constraining foraging behaviour are poorly quantified.

To develop more efficient grazing management systems and to improve the predictability of herbage DMI, it is essential to understand how the cow grazes and adapts its grazing behaviour during the day and to changes in sward condition. The objectives of this experiment were to determine 1) the pattern of behaviour, DMI and IR and 2) the subsequent sward structure of kikuyu pastures when dairy cows strip-grazed at 2 levels of compressed sward height (10 and 13cm) and 5 levels of grazing duration (1, 2, 4, 8 and 15h).

## 3.2 Materials and methods

### 3.2.1 Study location and design

This study was conducted at NSW Department of Primary Industries' Wollongbar Agricultural Institute (28°S, 153°E) in northern NSW from 23 to 25 February 2000, inclusive. Minimum and maximum temperatures were  $25.9 \pm 1.0$  and  $17.7 \pm 0.2$  °C, respectively. The experiment was established using 30 small grazing paddocks. Each treatment grazing paddock was 9m x 45m (405 m<sup>2</sup>) in area, consisting of kikuyu pasture.

To determine the affect of SH on DMI, IR and behaviour, two compressed sward heights were used, as determined by rising plate meter (RPM; Earle and McGowan 1979): namely 10cm (SH10  $10.2 \pm 0.18$  cm; mean  $\pm$  se) and 13cm (SH13;  $12.8 \pm 0.26$  cm). These two sward heights were chosen as being typical for kikuyu pasture management at this time of the year. The amount of pasture on offer at these two SH was calculated from measurements taken using the RPM were  $925 \pm 25$  and  $1186 \pm 48$  kg DM/ha above 5 cm stubble height at the beginning of the experimental period for 10cm and 13cm treatment swards, respectively. The calibration curves were obtained from Reeves *et al.* (1996) and are described in Equations 4 and 5:

$$\text{pre-grazing: } \text{kg DM/ha (above 5cm)} = -1200 + 200 * MR(\text{cm}) \quad \text{Equation 4}$$

$$\text{post-grazing: } \text{kg DM/ha (above 5cm)} = -1400 + 220 * MR(\text{cm}) \quad \text{Equation 5}$$

where  $MR$  = meter reading in cm.

Sward height treatments were prepared by re-grazing the SH10 treatment twice and the SH13 treatment swards once, over a 4.5 leaf/tiller regrowth cycle

(approximately 30 days/regrowth cycle; Reeves *et al.* 1996). This provided less on offer on the SH10 treatment swards but the same area/cow.

To test the effect of GD independently and in combination with SH, 5 grazing durations (namely 1, 2, 4, 8 and 15h after initial introduction to pasture) were used. This created a 2x5 factorial experiment; 2 factors, one with 2 levels of SH and the other with 5 levels of GD. Six multiparous cows were allocated to each treatment combination matched for current milk, milk fat and milk protein production, liveweight, age and parity. After an initial 3d training period, behaviour activity measurements were taken by trained observers over the next 3 consecutive days between 1600 and 0700h (15h). Cows on the shorter GD treatments of 1, 2 and 4h were removed to pastures that had just been grazed to a 5cm stubble height. The kikuyu pasture offered to all experimental cows at the beginning of the experimental period had an ME value of 9.9 MJ/kg DM, 207 g/kg DM CP, 230 g/kg DM ADF, 602 g/kg DM NDF, 0.607 g/kg DM OMD. All cows were supplemented twice-a-day at each milking with a commercial dairy pellet (13.5 MJ ME/kg DM, 180 g/kg DM CP) at the rate of 4 kg/cow.milking. Six cows were removed at the end of each GD treatment within each SH treatment for each replicate (day). Cows were randomly reassigned to treatments at the end of each 15h period based on the criteria described above.

### **3.2.2 Grazing behaviour**

All cows were observed at 20-minute intervals for the first 2h after entering their paddocks at 1600h (after the afternoon milking) and thereafter at 30 minute intervals until 0700h the next day (Hodgson 1982). The choice of 1600h as the start of grazing was based on the knowledge that water soluble carbohydrate content and palatability is at a maximum at that time of the day (Fulkerson and Trevaskis 1997).

Also, during summer, grazing behaviour is influenced by temperature and humidity, therefore to reduce bias due to high daily temperatures on grazing behaviour; cows were offered their pasture allocation from late afternoon. The number of cows grazing, resting and ruminating per treatment group was recorded at these intervals as the total number of cows in each treatment group expressing that activity. Total time spent in an activity for that time interval was then calculated by using the number of cows that were observed in that activity and adjusting for the time interval used (Appendix 1). Night-time activity was determined by the use of a “night scope” (Litton Electronic Devices, Arizona, USA).

### 3.2.3 Herbage intake

Herbage DMI (kg/cow) was calculated from the difference between pre- and post-grazing pasture mass as per Equation 6:

$$HI = (pre - post) * area / cows \quad \text{Equation 6}$$

where *HI* is herbage DMI; *pre* and *post* are the pre- and post-grazing pasture residues (kg DM/ha) measured with the RPM; *area* is the area of the paddock in ha; and *cows* is the number of cows grazing that paddock at that grazing duration. Twenty pre-grazing RPM measurements per paddock were taken each day before cows entered their allocated paddock, while 20 post-grazing RPM measurements per paddock were taken 3h after the last GD treatment.

Intake rate (IR) for each SH x GD treatment was calculated as the ratio of herbage DMI for that SH x GD treatment by the time spent grazing (GT) within that SH x GD treatment for both SH treatments.

### 3.2.4 Sward structure

To determine the effects of SH x GD treatment on sward structure, 20 pre-grazing individual RPM measurements per paddock were recorded on each day before cows entered their allocated paddock, while 20 post-grazing RPM measurements per paddock were taken 3h after the last GD treatment so that pasture had time to recover from treading. These measurements were taken along a diagonal transect within each treatment paddock at approximately 1m apart. For each SH treatment, there were 300 observations from the distribution of heights determined before cows grazed the experimental area. These represent the distribution of sward height after 0h of grazing. The post-grazing data contained 60 observations from the distribution of pasture height for each of the 1, 2, 4, 8 and 15h GD treatments.

### 3.2.5 Statistical analysis

Differences between treatments were tested for significance by ANOVA for a replicated 2x5 factorial design as described by Equation 7. Linear and quadratic trends for SH and GD was also tested.

$$y = \beta_0 + \beta_1x_1 + \beta_2x_2 + \beta_3x_2^2 + \beta_4x_1x_2 + \beta_5x_1x_2^2 + \varepsilon \quad \text{Equation 7}$$

where  $x_1$ ,  $x_2$  and  $x_2^2$  are the main effects of SH and GD, respectively, while  $x_1x_2$  and  $x_1x_2^2$  are the interactions between SH and GD, respectively;  $\beta$  represents the average slope for a response to a change in SH and GD, respectively. The higher order effects such as  $x_2^3$  and so on, were considered insignificant and were included in the error term,  $\varepsilon$

Means  $\pm$  se are presented for each treatment effect and their interaction. Relationships between GD and GT, herbage DMI, IR and pasture depletion were established by fitting linear ( $y=a+bx$ ) and asymptotic equations ( $y=a+br^x$  and  $a+br^x+cx$ ;  $r=e^{-k}$ ). To determine effects of SH and GD on sward structure, linear models for pre-grazing SH were fitted and included terms for paddock and GD effects; the latter term was fitted in order to check for bias in the allocation of paddocks to GD. Grazing duration was not a significant ( $P>0.05$ ) predictor for either set of pre-grazing SH. However, paddocks were found to have significantly different mean pre-grazing SH. The estimates of the paddock effects were subtracted from the observed pre-grazing SH to give SH adjusted so that the mean SH in each paddock was equal to the overall mean pre-grazing SH. Post grazing SH were analysed by a similar model and both GD and paddock accounted for significant ( $P<0.05$ ) levels of variation in SH. The estimated GD and paddock effects were used to calculate the adjusted SH data. Histograms are presented to show the effect of SH and GD on sward structure.

Appendix 1 summarises the data used in this Chapter and Appendix 2 contains the data used to generate Figure 18.

### **3.3 Results**

#### **3.3.1 Effect of SH and GD on behaviour**

The effect of SH and GD on mean ( $\pm$  se) total time spent in an activity (min) is shown in Figure 15. There was a significant ( $P<0.001$ ) effect of SH on mean ( $\pm$  se) total time spent grazing ( $142.2 \pm 4.78$  v.  $187.2 \pm 18.88$  min) but not ( $P>0.05$ ) on mean ( $\pm$  se) total time spent ruminating ( $347.9 \pm 13.87$  v.  $343.5 \pm 13.22$  min) and resting ( $410.1 \pm 12.71$  v.  $419.7 \pm 11.83$  min) over the 15h grazing period for SH10 and SH13 treatments, respectively. Significant linear and quadratic effects due to GD were

found for GT (linear and quadratic  $P < 0.001$ ) and resting (linear  $P < 0.001$ ; quadratic  $P = 0.002$ ). However, only a significant ( $P < 0.001$ ) linear effect of GD on time spent ruminating was found. There was no significant interaction ( $P > 0.05$ ) between SH and GD treatments for any of the behaviour activities.

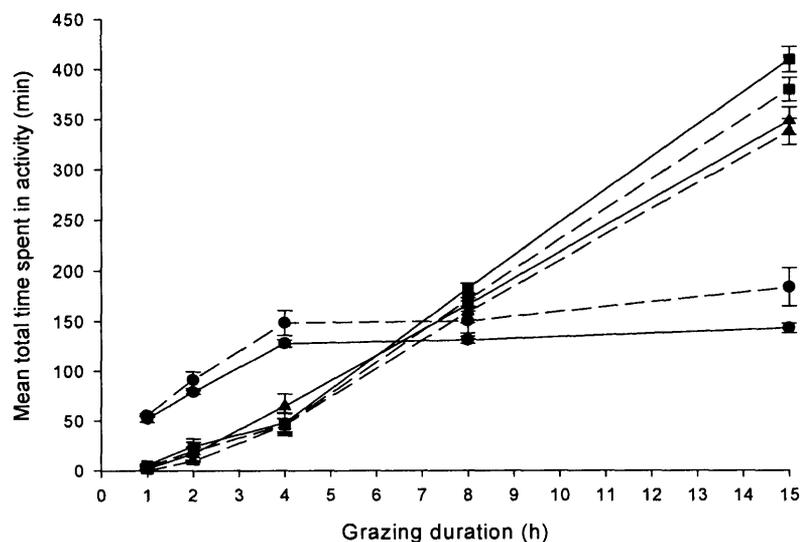
There was a strong asymptotic relationship between GD and GT ( $P < 0.001$ ;  $r^2 = 0.86$ ). There was a significant ( $P = 0.05$ ) difference in asymptote but no significant ( $P > 0.05$ ) difference in the rate parameter between SH treatments. Equation 8 describes the best fit relationship between SH, GD and GT for the pooled SH data.

$$GT = A - 163.5 * 0.64 (\pm 0.053)^{GD} \quad \text{Equation 8}$$

If SH10,  $A = 147.0$ ; SH13,  $A = 166.2$ ;

$r^2 = 0.92$ ; where  $A$  is the asymptote.

Time spent grazing increased by 0.45 h/h GD and reached a maximum at 4h GD, while the length of time spent ruminating and resting mainly increased after the 4h GD treatment (Figure 15).



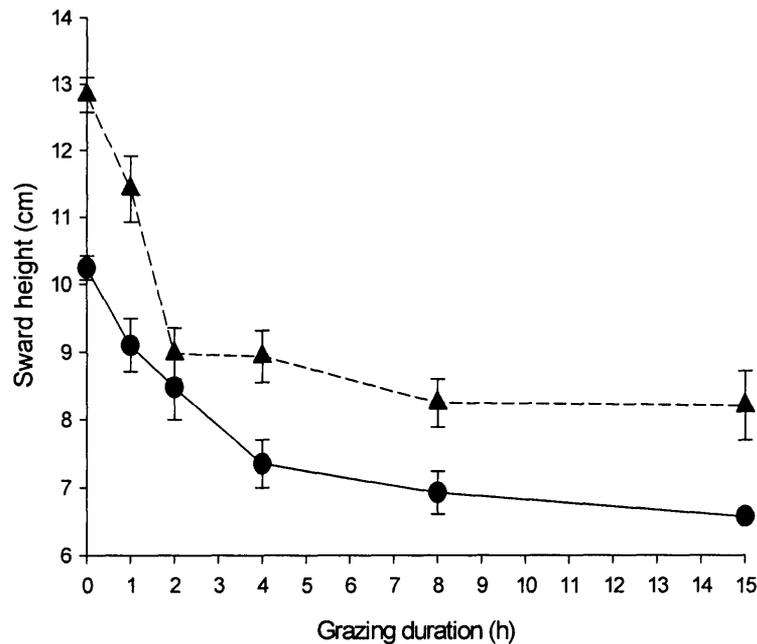
**Figure 15.** Effect of SH (— 10cm; ---- 13cm SH) and length of grazing session (1, 2, 4, 8 and 15 h) on mean ( $\pm$ se) total time (min) spent (a) grazing (●), (b) ruminating (▲) and (c) resting (■) for dairy cows grazing sub-tropical pastures. Vertical bars are  $\pm$ se.

Increasing GD significantly ( $P=0.003$ ) increased the proportion of time cows spent grazing (0.5 v. 0.6) for SH10 and SH13 treatments, respectively. Restricting the time that cows were allowed to graze significantly increased ( $P<0.001$ ) GT as a proportion of the total time of access to the swards (0.9 for 1h, 0.7 for 2h, 0.6 for 4h, 0.3 for 8h and 0.2 for 15h). There was no significant interaction ( $P=0.82$ ) between SH and GD.

### **3.3.2 Effect of SH and GD on pasture depletion**

The mean ( $\pm$  se) SH (cm) for the two SH treatments at each GD treatment is shown in Figure 16 (0h is the height taken before the experiment commenced and the other points relate to post-grazing SH after GD treatments commenced). There was a significant ( $P<0.001$ ) effect of SH and a significant ( $P<0.001$ ) linear and quadratic effect due to GD on post-grazing SH. No significant ( $P=0.5$ ) SH x GD interaction was found for post-grazing SH. The SH13 treatment group had significantly ( $P<0.05$ ) higher mean post-grazing SH at 0, 1, 4, 8 and 15h GD treatments, respectively.

The rate of pasture depletion in the first 4h was not significantly ( $P>0.05$ ) different ( $0.7 \pm 0.272$  v.  $1.0 \pm 0.385$  cm/h) between SH10 and SH13, respectively. Thereafter, the rate of pasture depletion was negligible.



**Figure 16.** Effect of SH (10 (—●—) and 13 (---▲---) cm) and length of grazing session (1, 2, 4, 8 and 15h) treatments on post-grazing pasture heights (cm) of kikuyu pastures grazed by dairy cows. Vertical bars are  $\pm$ se.

### 3.3.4 Effect of SH and GD on DMI and IR

The effects of SH and GD treatments on herbage DMI (kg/cow) are shown in Table 1. There was a significant ( $P < 0.001$ ) effect of SH on mean ( $\pm$  se) herbage DMI ( $12.3 \pm 0.44$  v.  $19.6 \pm 0.58$  kg DM/cow.d) for SH10 and SH13 treatments, respectively. There were significant linear ( $P < 0.001$ ) and quadratic ( $P < 0.001$ ) effects due to GD on herbage DMI and there was also a significant ( $P < 0.01$ ) SH x GD interaction. Therefore, the mean change in herbage DMI for a one unit change in SH is dependent on length of grazing session (GD). Herbage DMI for the first 2h after grazing commenced were similar within each SH treatment but there was a significant ( $P < 0.001$ ) difference in herbage DMI between SH treatments at the 1 and 2h GD treatments (Table 1). However, the SH10 treatment cows increased herbage DMI by

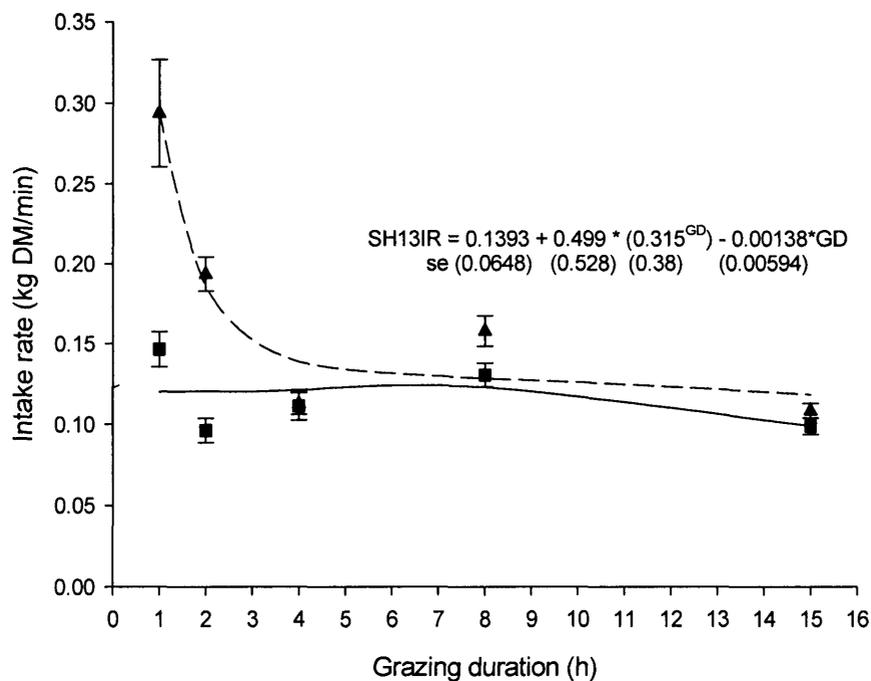
nearly 50% in the next 2h (4h GD treatment), while the SH13 cows appeared to have stabilised their herbage DMI by this time. Both SH treatments had an increase in herbage DMI at 8h GD treatment (Table 1).

**Table 1. Effect of sward height (10 and 13cm) and length of grazing session (1, 2, 4, 8 and 15 h) treatments on herbage dry matter intake (DMI, kg DM/cow) for dairy cows grazing sub-tropical pastures.**

Grazing duration (GD, h)	Sward height (SH, cm)	
	10	13
1	7.7 ( $\pm$ 0.57)	16.4 ( $\pm$ 1.85)
2	7.6 ( $\pm$ 0.60)	17.9 ( $\pm$ 0.98)
4	14.2 ( $\pm$ 1.12)	17.3 ( $\pm$ 1.03)
8	17.1 ( $\pm$ 0.98)	24.6 ( $\pm$ 1.49)
15	14.1 ( $\pm$ 0.74)	20.3 ( $\pm$ 0.86)

The effects of SH and GD on IR (kg DM/min spent grazing) are shown in Figure 17. There was a significant ( $P < 0.001$ ) effect of SH on mean ( $\pm$  se) IR ( $0.115 \pm 0.004$  v.  $0.166 \pm 0.007$  kg DM/min spent grazing) between SH10 and SH13 treatments, respectively. There were also significant linear ( $P < 0.001$ ) and quadratic ( $P = 0.004$ ) effects of GD on IR. There was also a significant ( $P < 0.001$ ) interaction between SH and GD, indicating that the mean change in IR for a one unit change in SH is dependent on the length of the grazing session. Intake rates for the SH10 treatment cows was significantly ( $P < 0.05$ ) lower for the first 2h of grazing than IR for the SH13 treatment cows but were similar thereafter (Figure 17).

Fitting a linear exponential model of the form  $y = a + b*(r^{GD}) + c*GD$  (where  $r = e^{-k}$ ) to these IR data showed that the decline in mean IR was significantly ( $P < 0.05$ ) different between SH treatments (Figure 17). The fit of this model for the SH10 treatment was very poor, while the fit was significant for the SH13 treatment ( $P < 0.001$ ;  $r^2 = 0.58$ ).



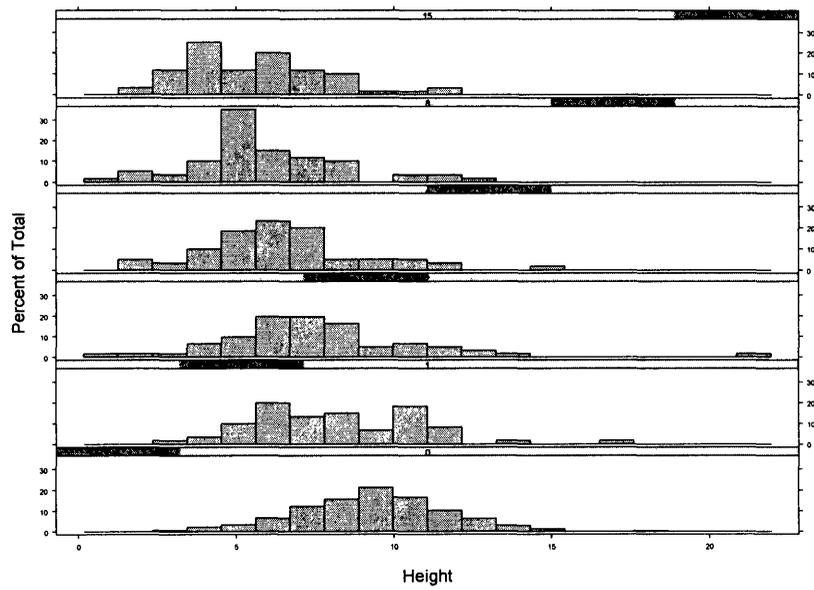
**Figure 17.** Effect of sward height (10 and 13cm) and length of grazing session (1, 2, 4, 8 and 15 h) treatments on intake rate (kg DM/min spent grazing) for dairy cows grazing sub-tropical pastures (SH10 ■ \_\_\_\_ SH13 ▲-----).

### 3.3.5 Effect of SH and GD on sward structure

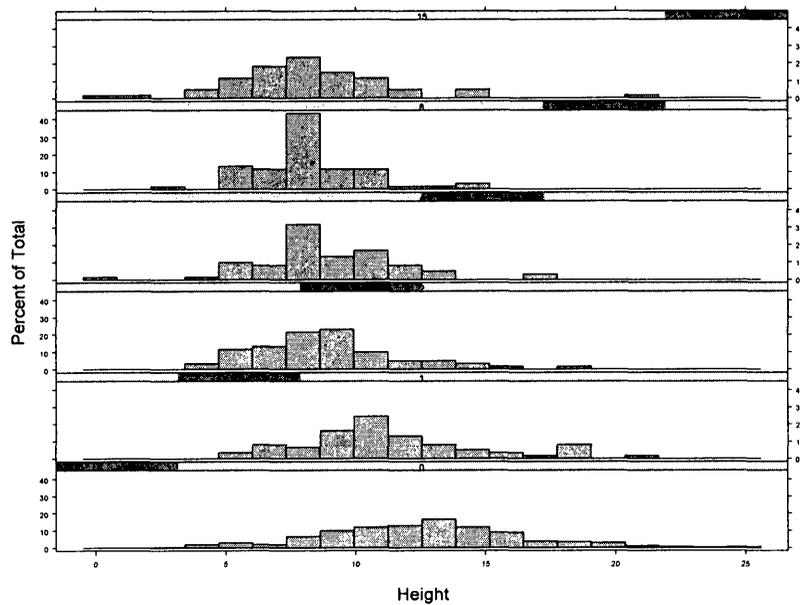
The frequency histograms of SH measurements made for the SH10 and SH13 treatment swards is shown in Figure 18. As GD increased, there was a definite reduction in the mean distribution of pasture height. However the shape of each distribution also seems to change with the exception of the 15h observations. For those data, the shapes of the distributions seem consistent which implies that the paddocks had been grazed evenly by 15h. However, the distributions in-between had different shapes. The right tails of the distributions at 1 and 2h are noticeably heavier than the distribution at 0h. Thus, the cows preferred shorter to taller pasture. However, further inspection reveals that most of the change from 0 to 1h occurs in the mid-range of heights. From 1 to 2h, the change is in the middle to top end of the distribution and after 4h the distribution of SH begins to change evenly.

Therefore, to determine what distribution of SH at the various SH x GD treatments that best describes the sward profile during this experiment further analysis of the data was conducted in Chapter 4 of this current thesis.

(a)



(b)



**Figure 18. Frequency histograms of sward height measurements made in (a) 10cm and (b) 13cm swards at the different length of grazing sessions (from bottom 0, 1, 2, 4, 8 and 15h).**

## 3.4 Discussion

This current study has quantified the relationship between SH and GD in terms of grazing dairy cow behaviour, IR and DMI over a 15h grazing period. Cows grazing swards at the SH10 treatment described in this current study had a reduced DMI and IR as GD increased compared to those cows grazing swards at the SH13 treatment. The SH10 treatment cows did not increase GT in response to the reduction in pasture on offer.

### 3.4.1. Behaviour and pasture depletion

Grazing dairy cow behaviour can be influenced by SH (Wright *et al.* 1990). In this current study, GT was significantly ( $P < 0.001$ ) influenced by SH, such that cows grazing the SH10 treatment swards had a total mean GT that was 45min less than those grazing the SH13 treatment swards over the 15h grazing period. There was no significant ( $P > 0.05$ ) effect due to SH and GD on rumination and idling activities. The relationship between GT and GD was asymptotic for both SH treatments (Figure 15). Time spent grazing increased by 0.45 h/h GD and reached a maximum at 4h GD.

There have been limited studies quantifying the relationship between SH and the length of the grazing session (GD) with GT for dairy cows. Iason *et al.* (1999) found that restricting the time available to graze affected GT such that overnight-restricted sheep grazed for almost the entire available grazing session for fewer, longer bouts with a shorter total daily GT than non-restricted sheep. The behavioural responses to overnight food restriction were able to counteract the reduction in GT only when food availability was high. Barrett *et al.* (2001) found that, although cows graze throughout the day on swards that were progressively depleted, as indicative of rotationally grazed paddocks, bite mass declined linearly and intake behaviour was

variable. Chilibroste *et al.* (1999b) found that a high proportion of the total DM disappeared in the first 2h of grazing for all their treatments. They also concluded that concentrating the grazing session in the afternoon significantly changed the defoliation pattern. This may have been due to either a different sward composition or to a better synchronisation with other components of the diets or both. In this current study, herbage was depleted at a similar rate of 0.85 cm/h irrelevant of SH treatment. Restricting the time available to graze also reinforces preference for high quality swards, even when digestibility is low (Ginane and Petit 2005). Soca *et al.* (1999) found that cows given access to pasture for 6h/d commencing at 1200h had a longer initial grazing meal than those cows restricted to 8h/d commencing at 0600h (120 v. 82min). Gibb *et al.* (1998) has interpreted the increase in afternoon grazing activity as an optimum foraging strategy to harvest pasture with higher concentrations of WSC and DM. In this current study, cows on both SH treatments were introduced to their pastures in the afternoon, therefore reducing any bias due to diurnal variation either WSC or DM. Chapter 5 reports the results of studies to quantify the temporal patterns of behaviour of grazing dairy cows in terms of the different SH x GD combinations.

### **3.4.2 Herbage DMI and IR**

The estimation of herbage DMI has always been a problem. The method chosen in this current study had the least impact when it came to disturbing the cows compared with others eg insensible weight loss. However, estimating herbage DMI by using the RPM can be subject to large error if SH is >20cm or <5cm (Michell 1982). Michell (1982) tested the value of using the RPM to estimate herbage mass of grazed perennial ryegrass-white clover swards and found that the RPM gave reliable estimates below SH of 20cm. On tropical pastures, Reeves (1998) found that herbage DMI estimated using the RPM was not significantly different to those estimated by

other techniques. The estimates of herbage DMI in this current study are close to those estimated by using the equations from SCA (1990).

McGilloway *et al.* (1999) found that herbage DMI for lactating dairy cows on rotationally grazed swards decreased as the level of pasture depletion increased from low to high. They concluded that the primary factor determining herbage DMI as swards were progressively grazed down was SSH, but at a high level of sward depletion, sward bulk density also influences intake/bite. In this current study, mean herbage DMI was significantly ( $P < 0.05$ ) greater for the SH13 treatment cows compared to those on the SH10 treatment.

The IR for the SH13 treatment cows decreased more rapidly than for the SH10 treatment cows during the first 2h after grazing commenced but thereafter IR was similar. The rate of decline in IR was significantly ( $P < 0.05$ ) different between SH10 and SH13 treatments. The differences in IR between the two SH treatments explains most of the difference in herbage DMI between the two SH treatments. This supports the results of Chilibroste *et al.* (1999b) who also found that herbage DMI and IR had stabilised after 2h of grazing for lactating dairy cows strip grazing oats pastures.

The results from this current study have implications for feed allocation systems for grazing dairy cows. To accurately allocate pasture and supplements on a daily basis to grazing dairy cows, knowledge of the relationship between SH and GD is important. Different feed allocation decisions would be necessary when cows graze tall pastures compared to those that graze short pastures. This hypothesis was tested by Fulkerson *et al.* (2005) in two experiments where the effect of accurately allocating feed on a daily basis to lactating Holstein–Friesian dairy cows was assessed. They concluded that accurately allocating supplementary feed to maintain a constant grazing pressure was successful and this would then enable dairy farmers to

decide whether the effort required to allocate feed accurately to dairy cows on a daily basis, is worthwhile.

### **3.4.3 Sward structure**

There are few studies quantifying the effects of SH and GD on sward structure. Generally, a lower proportion of leaf tissue is removed in each bite taken as cows graze down through the profile (Rook 2000). The bite fracture force of herbage increases down the sward profile at a rate that is higher for the taller sward than for the shorter sward. It has also been proposed that a relatively lower resistance to prehension in the short sward compared with the tall sward explains the greater proportionate increase in total defoliation area and DMI corresponding to an increase in herbage available (Tharmaraj *et al.* 2003).

Exploratory analyses of the sward structure results from this current study revealed that grazing dairy cows showed preferences for herbage of a certain height and did not graze at random. It would seem that the cows in this current study preferred pasture of “average height” when first introduced to a sward and then slightly taller pasture during the next 4h and thereafter grazed any height pasture. Gibb (1991) described swards continuously stocked by sheep as “a mosaic of short, frequently grazed areas and tall, infrequently grazed areas”. The grazing treatments outlined in this current study did not create a sward profile as that seen when swards are stocked continuously by sheep and cattle. By 15h GD the sward profiles for both SH treatments in this current study indicated that the paddocks were evenly grazed. This could also be due the grazing dairy cow being driven by the need to utilise as much of the energy gained from herbage for milk production. Therefore, quantifying the distribution that best describes the resultant sward structure from this experiment will help elucidate the foraging strategy followed by cows grazing at the 2 SH

treatments. Chapter 4 of this current thesis further quantifies sward structure in terms of SH and GD on the frequency distribution of sward height.

### 3.5 Conclusions

Dairy cows grazing pastures as described in this current study would be expected to deplete pastures at a rate of 0.85 cm/h and spend about 0.45h/h grazing up to 4h post-introduction. This has implications for herbage utilisation, feed allocation and the grazing of waterlogged pastures because IR is maximised by 4h post-introduction to a new pasture. Although this has yet to be tested directly, there is some evidence that offering different types of supplements at different times of the day does affect milk responses (Trevaskis *et al.* 2004). Also, since >70% of the herbage DMI was achieved by 4h post-introduction in this current study, removing cows after this time from waterlogged pastures would probably have little negative impact on production. However, the time cows are away from pasture would then become critical, as another grazing bout occurs 4h later (ie 8h post-introduction) and this may have subsequent negative impacts on production (Chilibroste *et al.* 2004).

#### *Acknowledgement*

Many thanks to Mr S. Morris, Biometrician, NSW Department of Primary Industries, Wollongbar Agricultural Institute, Wollongbar for analysing the sward structure data presented in Figure 18.

## CHAPTER 4

### THE EFFECT OF SWARD HEIGHT AND GRAZING DURATION ON THE FREQUENCY DISTRIBUTION OF SWARD HEIGHT OF KIKUYU (*Pennisetum clandestinum*) GRASS PASTURES GRAZED BY DAIRY COWS.

#### 4.1 Introduction

Sward height (SH) has a major influence on the ingestive behaviour of cattle grazing pastures (Chapter 2; Wright *et al.* 1990; Hodgson 1985; Alden and Whittaker 1970). In many tropical pastures, there are large differences in the quantity and quality of leaf and the nutritive value of herbage from the top to the base (Stobbs 1973a; 1975). Since leaf in the top layers of the sward is the first to be removed (Waite 1963), the quantity and quality of the diet selected by grazing animals will depend on the intensity of defoliation.

Populations of SH are frequently summarised by the sample mean and standard error. This is most appropriate when the population distribution is approximately symmetrical. In continuously grazed swards, a combination of relatively 'short' and 'tall' patches in pasture are created and maintained by cattle through selective grazing (Edwards *et al.* 1997). This is partly because cattle tend to consume the shorter vegetative herbage and avoid the taller less digestible herbage where leaf material is less accessible (Wallis deVries and Balebout 1994; Laca *et al.* 1994) and areas contaminated by faeces. The relative proportions of 'short' and 'tall' areas are largely affected by management factors such as grazing intensity and the length of the grazing session. Therefore SH frequencies usually show a skewed

distribution and the representation of a single mean sward height is potentially misleading (Gibb and Ridout 1986).

For predictive and modelling purposes it is often desirable to know the frequency distribution of SH or herbage mass under grazing. Gibb and Ridout (1986; 1988) found that frequencies of SH continuously grazed by cattle had a skewed distribution that was better described by a double-normal (DN) distribution than by the single-normal (SN) distribution. The proportion of swards that are occupied by 'short' and 'tall' vegetation and the characterization of these fractions have been previously quantified by using the DN distribution (Fisher *et al.* 1995; Gibb *et al.* 1999; Morris *et al.* 1999). Evidence of bimodality is not always strong and Shiyomi *et al.* (1983; 1984; 1998) and Sanders *et al.* (2003) have suggested that the gamma (G) distribution is a good descriptor of frequency distributions of herbage mass and of SH in swards rotationally grazed by cattle. The three-parameter Weibull (W) distribution has been found to fit SH and mass data in semi-arid short-grass steppe grazed by cattle better than other distributions (Remington *et al.* 1992), while Barthram *et al.* (2005) studying the frequency distribution of SH under sheep grazing, found that the SN and Weibull (W) distributions were inadequate and that the G and log-normal (LN) distributions had the best fits. Therefore, it appears that the distribution that best fits the SH data may alter with management type.

The effects of SH and GD on the frequency distributions of SH in sub-tropical pastures grazed by dairy cows are not known. In Chapter 3 it was found that cows grazing kikuyu at different SH and GD did not graze at random and created a sward structure of the type that is seen when sheep and cattle graze swards continuously. Therefore, the objective of this analysis was to determine the best fit distribution from the following five distributions: gamma, normal, double-normal, log-normal and

Weibull when kikuyu (*Pennisetum clandestinum*) swards were strip-grazed by dairy cows at two different sward heights (10 and 13cm) and at 5 different grazing durations (1, 2, 4, 8, and 15h).

## **4.2 Materials and methods**

### **4.2.1 Study location and experimental design**

The details of the study location and experimental design are given in Chapter 3.

### **4.2.2 Swards and sward height**

Swards were well managed kikuyu and SH treatment differences were prepared as described in Chapter 3. To determine pasture profiles within a SH x GD treatment combination, 20 pre-grazing RPM measurements/paddock were taken each day before cows entered their allocated paddock, while 20 post-grazing RPM measurements per paddock were taken 3h after the last GD treatment so that pasture had time to recover from treading. This gave a total of 60 observations pre- and 60 post-grazing, that is, 120 observations for each SHxGD combination. These measurements were taken along a diagonal transect within each treatment paddock at approximately 30cm apart. For each SH treatment, there were 300 observations from the distribution of heights determined before cows grazed the experimental area. These represent the distribution of pasture height after 0h of grazing. The post-grazing data contained 60 observations from the distribution of pasture height after 1, 2, 4, 8 and 15h of grazing. Only the histograms for the pasture heights post-grazing are presented.

### 4.2.3 Statistical analysis

Before studying the frequency distributions of SH, effects of paddocks were assessed. This was achieved by fitting linear models for pre-grazing SH for the two SH treatments. Terms in the model included paddock and GD. The latter term was fitted to check for bias in the allocation of paddocks to the GD treatments. Grazing duration was not a significant ( $P > 0.05$ ) predictor for either set of pre-grazing SH treatments. However, paddocks were found to have significantly different average pre-grazing SH. The estimates of the paddock effects were subtracted from the observed pre-grazing heights to give heights adjusted so that the average height in each paddock was equal to the overall average pre-grazing height. Post-grazing SH were then analysed by a similar model and both GD and paddock accounted for significant ( $P < 0.05$ ) levels of variation in SH. The estimated GD and paddock effects were used to calculate adjusted data.

Single-normal (SN), double-normal (DN), log-normal (LN), gamma (G) and Weibull (W) distributions were fitted separately to each set of measurements. The SN distribution, also known as the normal distribution, is used in this analysis to avoid confusion with other forms of the normal distribution. It is defined by its mean  $\mu$  and variance,  $\sigma^2$  and has the following density function (Payne 2004):

$$f(x) = \frac{1}{\sigma\sqrt{2\pi}} \exp\left[-\frac{1}{2}\left(\frac{x-\mu}{\sigma}\right)^2\right] = \Phi(x; \mu; \sigma) \quad \text{Equation 9}$$

The DN distribution can be used when an observation may come from either two SN distributions with different means. It can occur when a proportion,  $p$ , of the population is normally distributed with mean  $\mu_1$  and variance,  $\sigma_1^2$  and a proportion  $(1-p)$  is normally distributed with mean  $\mu_2$  and variance,  $\sigma_2^2$ . The distribution is therefore described by five parameters. The density function is:

$$f(x) = p\Phi(x; \mu_1; \sigma_1) + (1-p)\Phi(x; \mu_2; \sigma_2) \quad \text{Equation 10}$$

with mean  $p\mu_1 + (1-p)\mu_2$  and variance  $p\sigma_1^2 + (1-p)\sigma_2^2 + p(1-p)(\mu_1 - \mu_2)^2$ .

The LN distribution assumes that  $\log_e(X)$  has a normal distribution with mean  $\mu$  and variance  $\sigma^2$ , and must have positive skewness. The density function is:

$$f(x) = \frac{1}{x} \Phi(\log(x); \mu; \sigma) \quad \text{Equation 11}$$

with mean,  $\exp(\mu + \sigma^2/2)$  and variance,  $\exp(2\mu + \sigma^2)[\exp(\sigma^2) - 1]$ .

The G distribution is a general empirical distribution described by two parameters,  $k$  (the shape parameter) and  $b$  (the scale parameter), with mean  $k/b$  and variance  $k/b^2$ . The density function is:

$$f(x) = b^k x^{k-1} \frac{e^{-bx}}{\Gamma(k)} \quad \text{Equation 12}$$

where  $\Gamma(k) = \int_0^{\infty} x^{k-1} e^{-x} dx$ ,  $x > 0$ .

The three-parameter W distribution is a generalization of the exponential distribution. The density function is:

$$f(x) = cb^c (x-a)^{c-1} e^{-b(x-a)c} \quad x, b, c > 0 \quad \text{Equation 13}$$

which has mean,  $a + (1/b)\Gamma((c+1)/c)$  and median,  $a + (1/b)(\log 2)^{1/c}$ , where  $c$  is the shape parameter,  $b$  the scale parameter and  $a$  is a location parameter (which allows the minimum theoretical value of the distribution to values other than zero).

For all five distributions, parameter estimates were calculated using the DISTRIBUTION procedure of GENSTAT (7<sup>th</sup> edition, version 7.1.0.198; VSN International, Oxford, UK). The Akaike Information Criterion (AIC) statistic (Akaike 1974) was used to evaluate the fits of the different distributions. The AIC statistic is defined as  $-2(-\log \text{likelihood}) + 2(\text{number of parameters})$ . This statistic gives a single quantitative measure of the fitted theoretical distribution from the observed data.

Lower AIC values indicate a better fit between the observed data and the theoretical distribution than higher AIC values. Appendix 2 contains the data and GENSTAT code.

Also, to highlight any systematic differences between the fitted theoretical density functions and the frequency distributions of sward height observations over the range of data, plots showing differences between the proportions of observed sward heights and the theoretical density functions that fell within the intervals of the observed height data were constructed. One cm sward height intervals were used for both SH treatments. These plots allowed examination of any pattern in the deviances for each SH x GD combination.

### 4.3 Results

The effects of SH and GD on mean  $\pm$  se sward heights for each SH x GD combination are shown in Table 2. The mean  $\pm$  se sward heights for all paddocks and replicates at the GD treatment of zero h were  $10.3 \pm 0.18$  and  $12.8 \pm 0.26$ cm for SH treatments 10cm (SH10) and 13cm (SH13), respectively. The parameter estimates for five theoretical distributions fitted to sward height distributions and coefficients of variation from swards grazed at different durations at SH10 and SH13 treatments are shown in Tables 3 and 4, respectively. The standard deviations changed inconsistently as GD treatment progressed for both SH treatments. However, the SH13 treatment showed the least variability. The SH13 x 4h GD combination could not be fitted for the DN distribution.

**Table 2. Effect of sward height and grazing duration on mean±se pre- and post-grazing heights.**

Sward height (cm)	Grazing duration (h)	Pre-grazing sward height (cm)	Post-grazing sward height (cm)
10	1	10.3±0.39	9.1±0.40
	2	10.0±0.42	8.2±0.40
	4	10.6±0.43	7.4±0.35
	8	10.3±0.43	6.9±0.31
	15	10.0±0.3	6.6±0.3
13	1	12.8±0.69	11.3±0.48
	2	13.1±0.46	9.0±0.38
	4	12.2±0.61	8.9±0.39
	8	13.5±0.56	8.3±0.35
	15	12.6±0.58	8.2±0.51

**Table 3. Parameter estimates for five theoretical distributions fitted to sward height distributions, skewness and coefficients of variation (CV) from swards grazed at different durations with a 10cm target height.  $p$  is the proportion that is 'tall'.**

Distribution	Grazing duration (h)				
	1	2	4	8	15
Single-normal					
$\mu$	9.12	8.14	7.28	6.87	6.55
$\sigma$	3.17	3.02	2.75	2.48	2.35
Double-normal					
$p$	0.37	0.63	0.09	0.24	0.74
$\mu_1$	11.97	9.47	12.55	9.00	7.24
$\sigma_1$	2.87	3.04	4.25	4.18	2.36
$\mu_2$	7.44	5.88	6.77	6.24	4.76
$\sigma_2$	1.83	0.84	1.99	1.40	0.18
Log-normal					
$\mu$	2.15	2.04	1.92	1.87	1.83
$\sigma$	0.35	0.36	0.36	0.36	0.34
Gamma					
$k$	8.49	7.95	7.74	8.00	8.69
$b$	0.93	0.97	1.06	1.16	1.32
Weibull					
$c$	1.93	1.52	1.79	2.33	1.17
$b$	0.38	0.35	0.39	0.46	0.39
$a$	3.30	3.69	2.58	1.32	3.76
skewness	0.62	0.88	1.22	0.95	0.94
CV (%)	33.8	36.9	36.5	34.9	35.0

**Table 4. Parameter estimates for five theoretical distributions fitted to sward height distributions, skewness and coefficients of variation (CV) from swards grazed at different durations with a 13cm target height.  $p$  is the proportion that is 'tall'.**

Distribution	Grazing duration (h)				
	1	2	4	8	15
Single-normal					
$\mu$	11.28	8.87	8.91	8.19	8.18
$\sigma$	3.70	3.13	3.05	2.81	4.12
Double-normal					
$p$	0.17	0.30	No	0.73	0.26
$\mu_1$	17.98	11.05		9.11	12.21
$\sigma_1$	2.48	3.91	fit	2.73	5.66
$\mu_2$	9.92	7.98		5.72	6.84
$\sigma_2$	1.97	2.12		0.81	2.22
Log-normal					
$\mu$	2.38	2.14	2.13	2.05	2.00
$\sigma$	0.30	0.34	0.37	0.34	0.46
Gamma					
$k$	10.57	8.82	8.35	8.73	4.70
$b$	0.94	0.99	0.93	1.06	0.57
Weibull					
$c$	1.62	1.75	2.73	1.68	1.49
$b$	0.32	0.37	0.45	0.37	0.29
$a$	5.60	3.81	0.81	3.55	2.42
skewness	1.10	0.92	0.89	0.64	1.52
CV (%)	32.9	32.8	33.4	33.2	48.5

Table 5 shows the AIC statistics for the five theoretical distributions fitted to SH frequency distributions measured for the SH10 and SH13 and GD of 1, 2, 4, 8 and 15h treatment combinations, respectively. The SN distribution had the poorest fit of the 5 distributions fitted to the SH x GD data. No one distribution fitted all the SH x GD data consistently. However, overall the LN distribution fitted most combinations best.

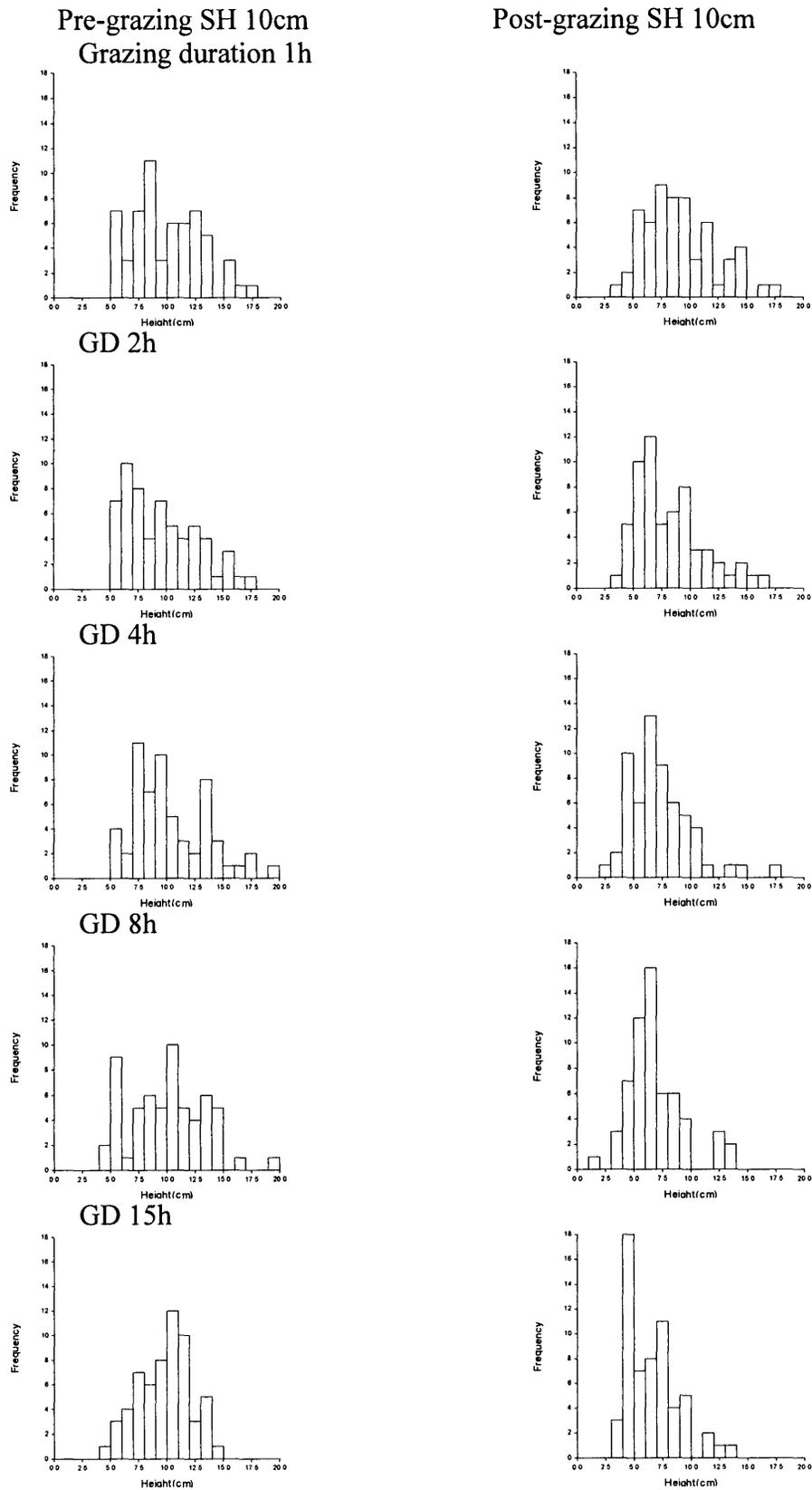
Skewness is a measure of symmetry, or more precisely, lack of symmetry. A distribution, or data set, is symmetrical if it looks the same to the left and right of the centre point. The skewness for a normal distribution is zero, and any symmetric data should have skewness near zero. Negative values for skewness indicate data that are skewed left and positive values for skewness indicate data that are skewed right. By skewed left, the left tail is heavier than the right tail and skewed right means that the right tail is heavier than the left tail. Some measurements have a lower bound and are skewed right.

Sward height data for both SH treatments tended to be positively skewed (Tables 3 and 4, Figures 19 and 20). However, the tendency towards positive skewness was more pronounced for swards in the SH13 treatment. That is, as GD increased the sward profile for the SH13 treatment changed, suggesting cows grazing this SH treatment exhibited different grazing behaviour to those cows grazing the SH13 treatment (Chapter 3). As a result of this skewness, the SN distribution had the poorest fit for both SH x GD treatment combinations (Table 5).

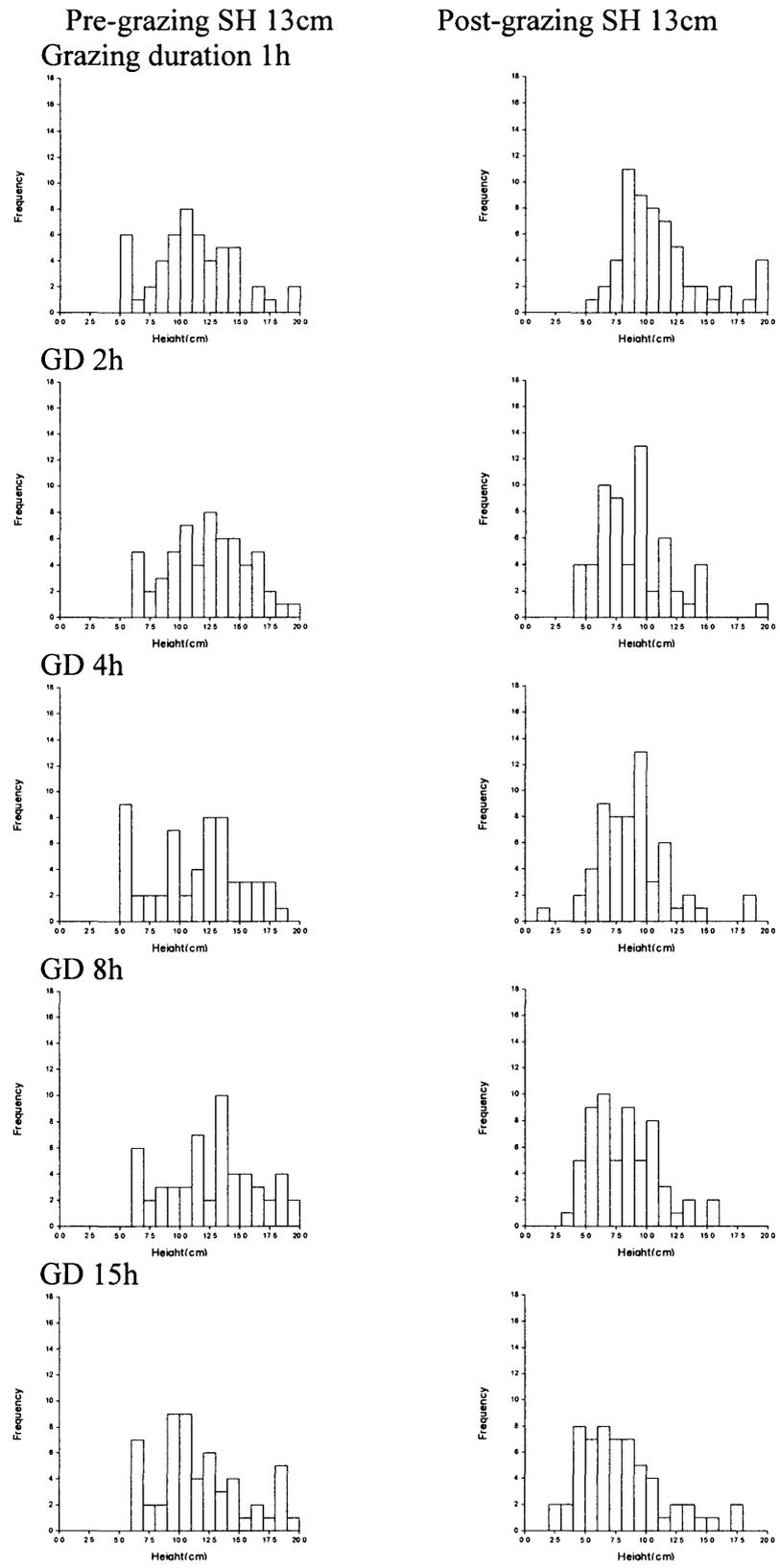
**Table 5. Akaike information statistics for five theoretical distributions fitted to sward height frequency distributions measured at sward heights of 10 and 13cm and grazing durations of 1, 2, 4, 8 and 15h.**

Distribution	Grazing duration (h)				
	1	2	4	8	15
Single-normal					
10cm	20.53	22.68	26.58	33.17	31.62
13cm	37.11	31.03	31.69	20.13	33.88
Double-normal					
10cm	19.89	15.34	19.90	23.19	19.94
13cm	<b>21.23</b>	31.66	*	18.89	22.29
Log-normal					
10cm	<b>14.58</b>	<b>10.75</b>	<b>14.14</b>	26.37	20.91
13cm	22.77	<b>22.69</b>	32.09	<b>12.40</b>	<b>15.11</b>
Gamma					
10cm	14.91	13.08	16.01	<b>22.18</b>	23.19
13cm	26.24	25.40	<b>28.78</b>	13.53	17.95
Weibull					
10cm	16.85	11.56	19.39	32.94	<b>17.70</b>
13cm	25.68	27.79	35.30	13.84	20.61

\* DN distribution could not be fitted to data. Numbers in bold, italics are lowest AIC value for that fit.



**Figure 19. Frequency histograms of pre- and post-grazing sward height measurements made in 10cm swards at different grazing durations (GD = 1, 2, 4, 8 and 15h).**



**Figure 20. Frequency histograms of pre- and post-grazing sward height measurements made in 13cm swards at different grazing durations (GD = 1, 2, 4, 8 and 15h).**

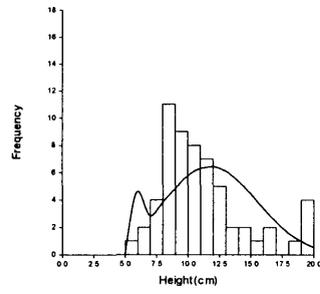
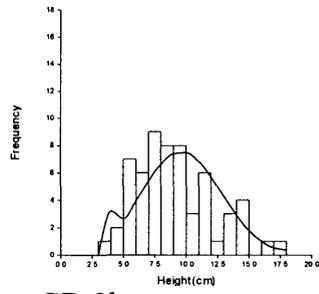
Figures 21 to 25 show the relationships between observed frequency histograms of SH and fitted frequency distributions for each of the 5 distributions fitted to data from each SH x GD combination. The LN distribution best described the distribution of SH for the SH10 treatment at GD treatments of 1, 2 and 4 h, while it best described the distribution of SH for the SH13 treatments at 2, 8 and 15 h (Table 5). The parameter estimates for the LN distribution appeared to be the most stable across SH x GD combinations.

The AIC statistics were compared to the distributions of observed heights in relation to the coefficient of variation. This allows for a comparison of whether the fits change with this measure of variability (Tables 3 and 4). There did not appear to be any relationship between CV (%) and AIC for any of the SH x GD combinations. Also, inspection of the parameter estimates for the mean values indicates that, relative to the other distributions, the SN and LN distributions gave estimates of the mean that were reasonably close to the (Tables 2, 3 and 4).

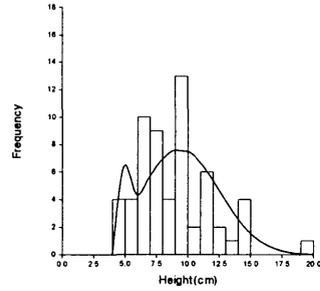
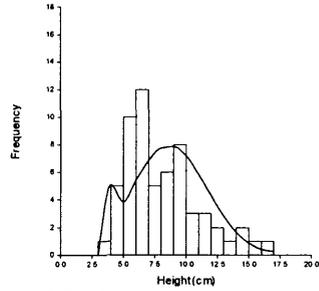
The DN distribution, although it did not fit the height data well for most SH x GD combinations, gives an estimate of the proportion of 'short' and 'tall' components of the sward at each SH x GD combination. The proportion of the sward that is 'short' (p), varied considerably for each SH x GD combination. It was the highest for the 15 and 8h and lowest for the 4h and 1h GD treatments for SH10 and SH13 treatments, respectively (Tables 3 and 4). Thus, as GD progresses the proportion of 'short' and 'tall' components in the sward varied.

Post-grazing SH10  
Grazing duration 1h

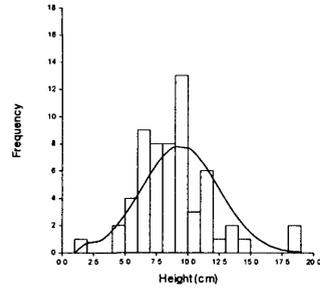
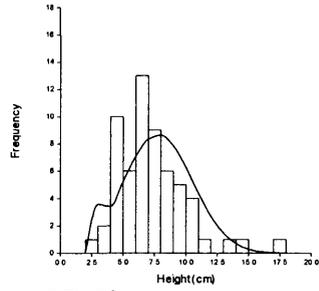
Post-grazing SH13



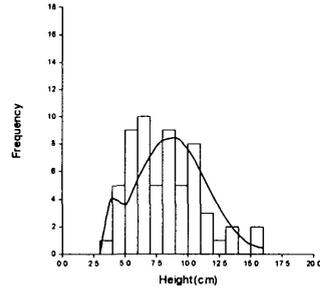
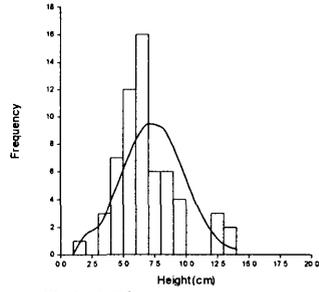
GD 2h



GD 4h



GD 8h



GD 15h

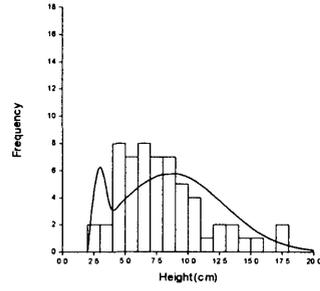
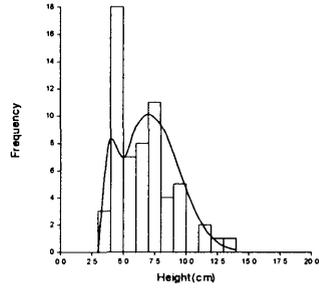
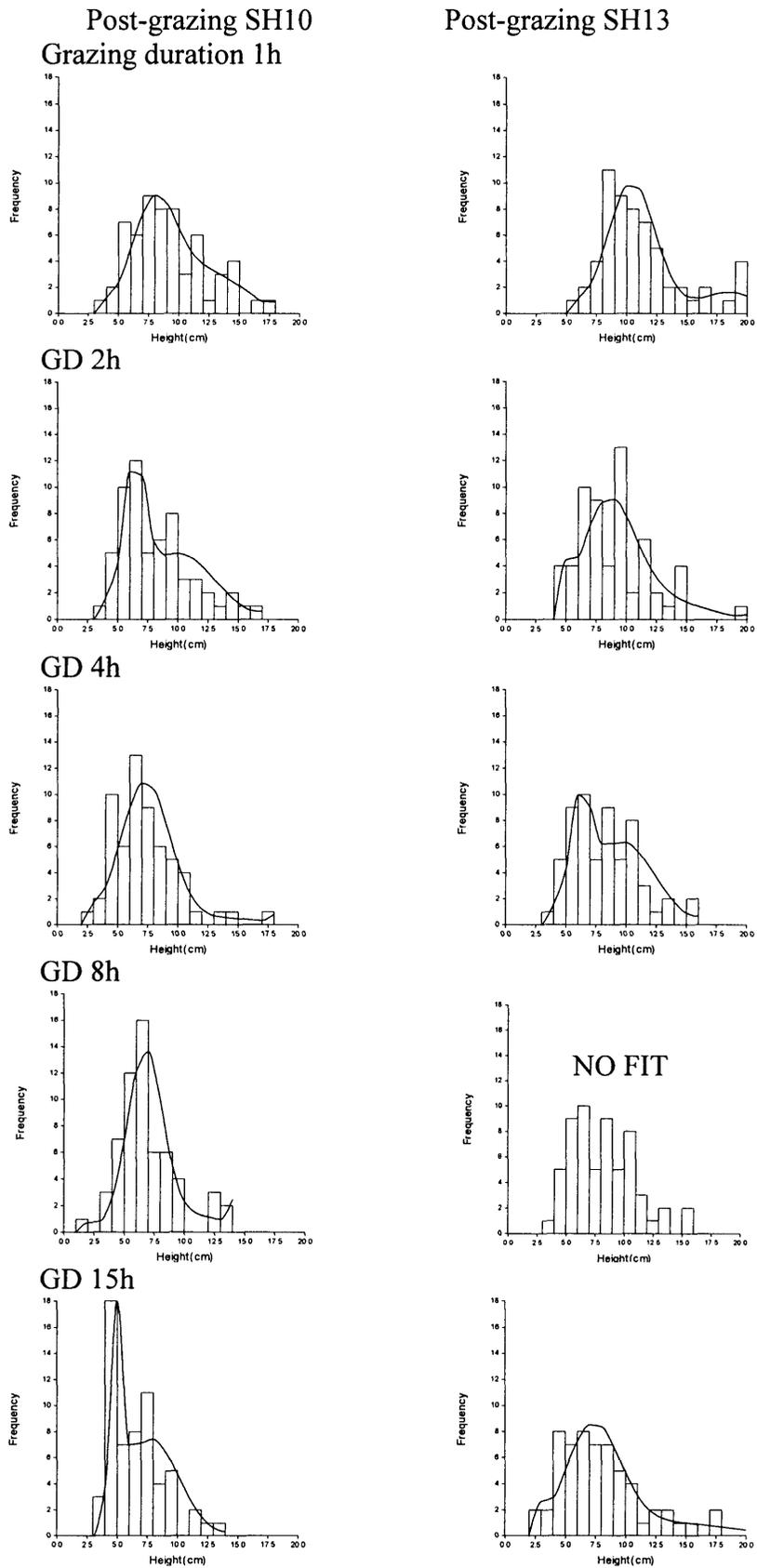
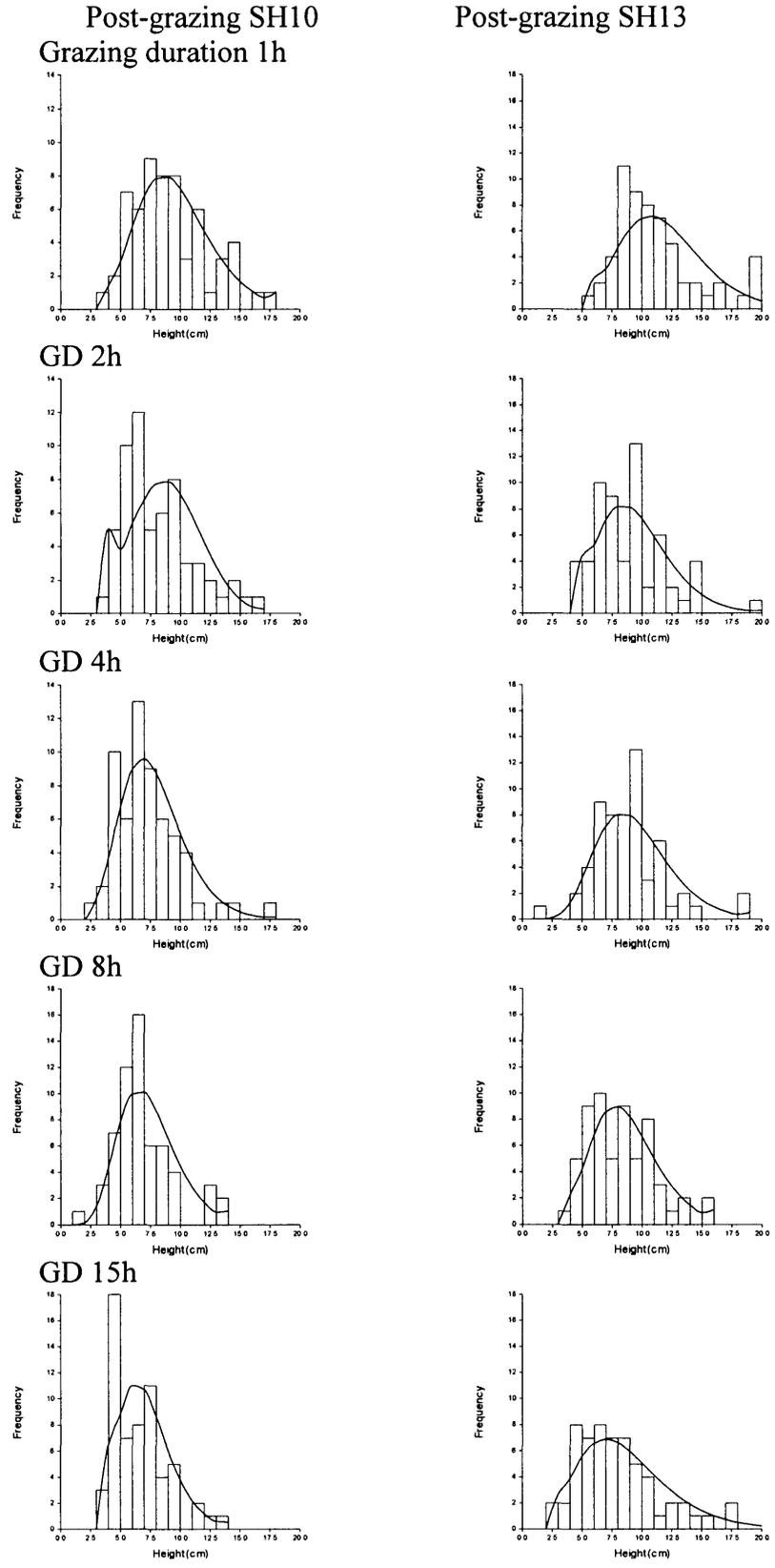


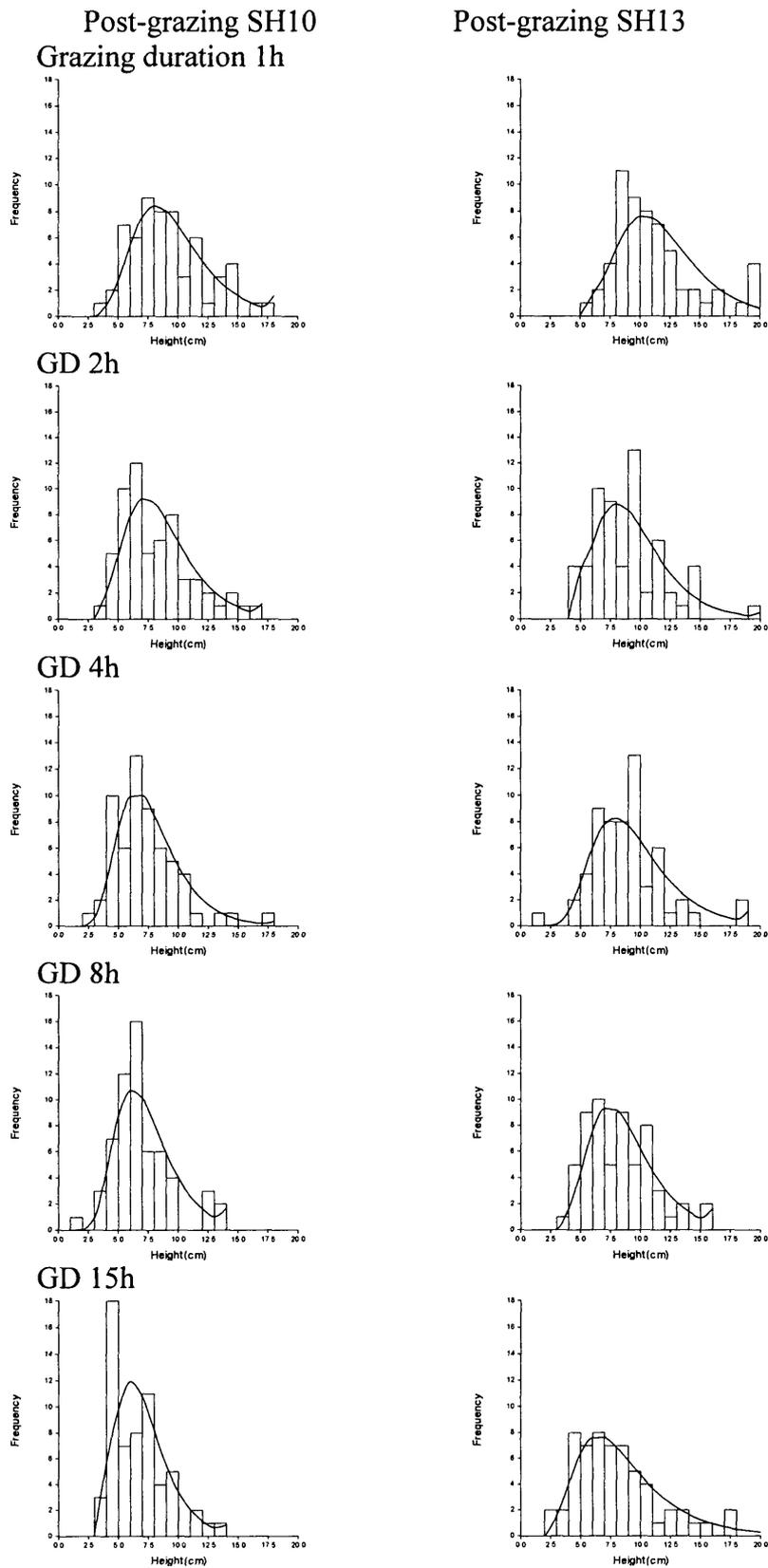
Figure 21. Fit of single-normal distribution to post-grazing sward height frequency distributions for SH 10cm and 13cm at different grazing durations.



**Figure 22. Fit of double-normal distribution to post-grazing sward height frequency distributions for SH of 10cm and 13cm at different grazing durations (SH 13cm x GD 8h – no fit).**



**Figure 23. Fit of gamma distribution to post-grazing sward height frequency distributions for SH of 10cm and 13cm at different grazing durations.**



**Figure 24. Fit of log-normal distribution to post-grazing sward height frequency distributions for SH of 10cm and 13cm at different grazing durations.**

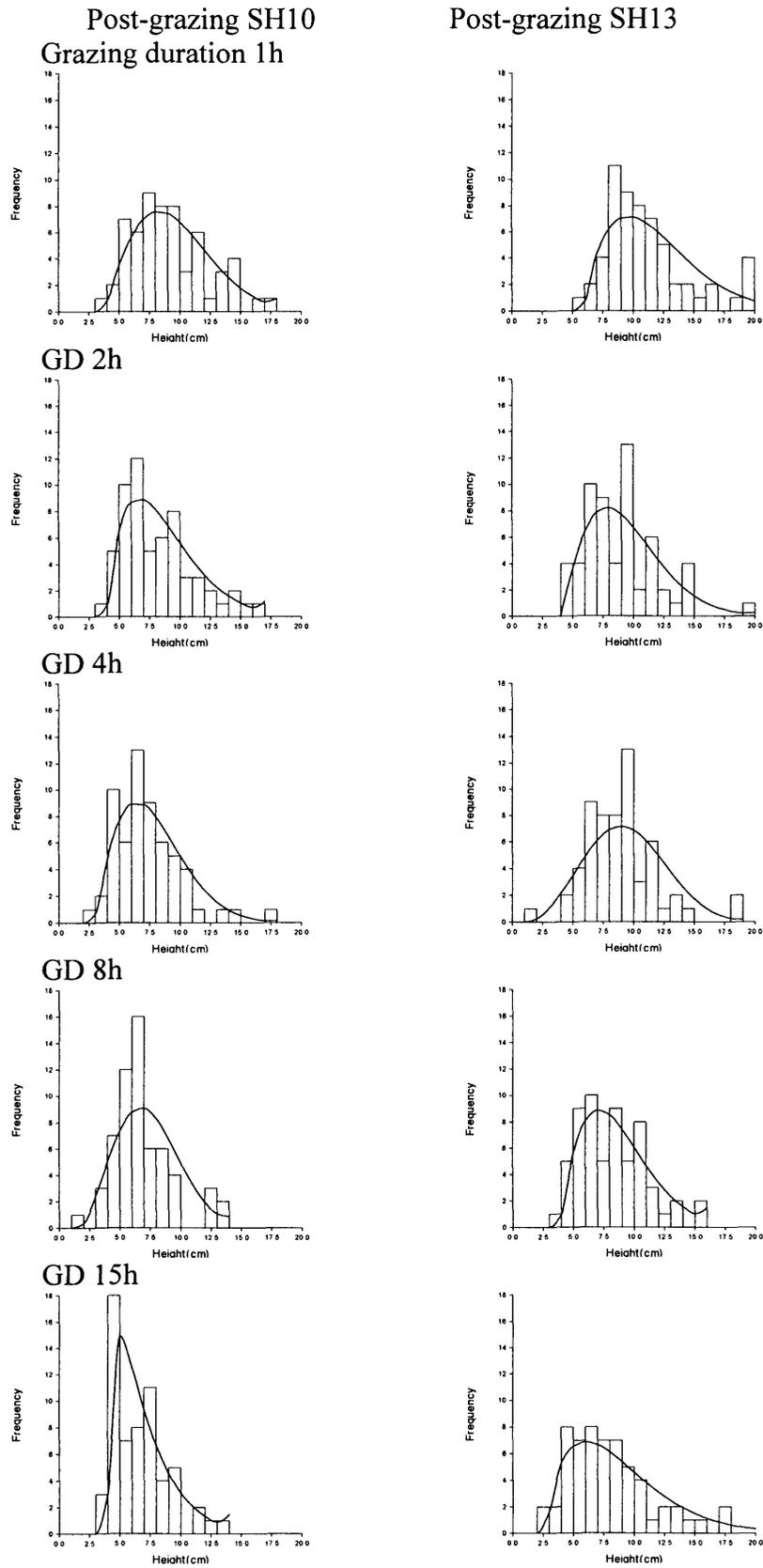


Figure 25. Fit of Weibull distribution to post-grazing sward height frequency distributions for SH of 10cm and 13cm at different grazing durations.

## 4.4 Discussion

This current study quantified the effects of combinations of SH and GD on the frequency distributions of sward height in sub-tropical swards grazed intensely by dairy cows. The results confirm that grazing dairy cows altered their behaviour in response to the different SH and GD combinations. That is, different sward profiles were evident between the two SH treatments for the different GD treatments. The log-normal distribution best fitted most of the sward height data in this current study.

The observation of Gibb and Ridout (1988) that the DN fit was superior to the SN distribution to SH data has been referred to many times as evidence of the heterogeneous nature of swards grazed by cattle. However, its fit does not appear to have been tested in rotationally grazed sub-tropical swards by dairy cows. For cattle the W distribution, like the DN distribution, has only been compared with the SN distribution (Remington *et al.* 1992). The same five distributions as in used in this current study have been compared in swards grazed by sheep (Barthram *et al.* 2005). The present study investigated these distributions in kikuyu based swards grazed intensely by dairy cows at different initial SH with different lengths of GD. The frequency distribution of SH was not described by the SN distribution very well. The fit was particularly poor as GD progressed in the 10cm swards, while the fit improved after 8h GD in 13cm swards. No distribution had a clear and consistent best fit to the data based on the AIC statistics alone.

A potential issue in the fitting of the SN and DN distributions to SH data is that neither distribution can be constrained to fit to positive data only. A large proportion of recorded sward heights may be relatively close to zero; therefore, the mean height may be low relative to the standard deviation. This would result in the left tail of the distribution containing unrealistic negative values if either an SN or a

DN distribution were fitted. The LN, G and W distributions attempt to address this issue. These three distributions are appropriate for fitting to frequency distributions showing positive skewness. The LN distribution is normally distributed on a log-transformed scale rather than the measurement scale. Hence, it can only be fitted to data displaying positive skewness and is not appropriate where data are negatively skewed or have a symmetrical distribution.

The SH data recorded in this current study that showed positive skewness was best fitted with the LN distribution (Figure 24 and Table 5). The two-parameter G distribution used in this current study is described in terms of shape and scale, parameters  $k$  and  $b$ , respectively. When  $k$  is large and  $b = 1$ , this distribution closely approximates a normal distribution, but with the advantage over the normal distribution that it can be fitted to positively skewed data and can be constrained to fit only to positive observations. Tsutsumi *et al.* (2002) showed that  $k$  (the shape parameter) is an index representing the spatial heterogeneity of the herbage mass over the grazing area. The spatial pattern of herbage height can be determined such that if  $k=1$ , the frequency distribution of height follows the exponential distribution, that is, the spatial pattern is random; if  $0 < k < 1$ , the spatial pattern is more heterogeneous than can be accounted for by a random distribution, and as  $k$  approaches 0, spatial heterogeneity increases and if  $k > 1$  the spatial pattern is less heterogeneous than found in a random distribution and as  $k$  increases, heterogeneity decreases. In the case of this current study,  $k$  was similar (and  $> 1$ ) for each GD treatment for 10cm swards, but was highest (10.57) for GD of 1h and lowest (4.70) for GD of 15h. This suggests that there was limited heterogeneity in the 10cm swards, while heterogeneity was more pronounced after 15h GD in the 13cm swards.

The three-parameter version of the W distribution used in this current study and the study by Remington *et al.* (1992), is defined in terms of shape, scale and location parameters ( $c$ ,  $b$  and  $a$ ). When  $c$  is approximately 3.5, the W distribution approximates to a normal distribution. Lower values of  $c$  are associated with positive skewness and higher values with negative skewness. The  $b$  parameter is a scaling factor, which is a measure of the variability in the data. The location parameter,  $a$ , indicates the minimum theoretical value of the distribution. Allowing the location parameter to vary, allows for an improved fit in the left tail of the distribution. The W distribution did not fit the SH distribution data from this current study as well as the LN distribution.

The DN distribution fitted the SH data best when the frequency distribution showed some bimodality (Figure 14 and Table 5). This distribution has the added advantage of being able to take account of both positive and negative skewness and bimodality. The LN distribution best fitted most of the sward height frequency distributions under the conditions described here. Shiyomi *et al.* (1984) suggested that  $p$  was a good indicator for spatial aggregation of herbage mass. This parameter was also useful in describing the spatial heterogeneity of herbage mass in rotationally grazed bahiagrass by beef cattle (Liu and Hirata 1995).

The average variance ( $\sigma^2$  of the SN distribution) for the heights in the 10cm swards was less than that for the 13cm swards (7.7 cm<sup>2</sup> vs. 11.5 cm<sup>2</sup>). This would indicate that there was greater heterogeneity in the 13cm swards. However, the coefficients of variation of both SH treatments were similar at each GD treatment. This indicates that the magnitude of the variability changed with the mean height. Shiyomi *et al.* (1983) found that the more intensely the pasture is grazed by cattle in a rotational grazing system, the more heterogeneous the spatial pattern of herbage

biomass can become. These findings imply that there must be a threshold indicating that the more intensively the sward is grazed the more likely it will become homogeneous.

The preliminary analysis of sward structure conducted in Chapter 3 indicated that the cows in this current study preferred pasture of “average height” when first introduced to a sward and then slightly taller pasture during the next 4h and thereafter grazed any height pasture. This is confirmed from this more detailed analysis. Also, the mosaic of tall and short patches was only seen in the 1h GD treatment for the SH13 treatment (Figure 14). However, this mosaic disappeared by the 15h GD treatment. Therefore, using the DN distribution to describe the swards resulting from intensive grazing over 15h as in this study, may not be valid.

## 4.5 Conclusions

The methodology used in this study provides a useful tool for the description and comparison of the patterns of SH distribution which is created by contrasting initial SH and different lengths of grazing in kikuyu swards grazed by dairy cows. The SH data in this present study did not provide unequivocal evidence for either bimodal or unimodal distributions. Therefore, the data does not give support to any of the above distributions fitted. However, the LN distribution appeared to be the best fit in the majority of cases. The pattern of herbage removal by the grazing dairy cows in this study indicated that there was a difference in the behaviour due to different SH and GD treatments. Therefore, Chapter 5 of this thesis provides further quantification of the behaviour of grazing dairy cows by using spectral analysis to determine cyclic behaviour in terms of SH and GD, time of day allocation of fresh pasture and type of carbohydrate supplement offered.

## CHAPTER 5

# SPECTRAL ANALYSIS OF DAIRY COW GRAZING BEHAVIOUR PATTERNS RELATIVE TO SWARD HEIGHT AND TIME OF ALLOCATION OF PASTURE AND CARBOHYDRATE SUPPLEMENTS.

### 5.1 Introduction

The cyclical pattern of grazing activity by cattle and sheep is well documented. Cattle and sheep graze 4 to 5 times in each 24h with the longest and most intense periods occurring in the early morning and between late afternoon and dusk. When the daytime temperature exceeds their thermal comfort zone, cows tend to increase their night grazing and graze less during the day. Interspersed between the periods of grazing are periods of idling/resting and ruminating.

Understanding the factors that affect grazing behaviour and the resultant behaviour patterns will help in the development of more efficient feed allocation systems and may also help in developing an understanding of how both behavioural and physiological processes control feeding (Fulkerson *et al.* 2005). Trevaskis *et al.* (2004) found no difference in grazing activity when expressed as the summation of % cows grazing each hour but the diurnal pattern appeared to differ. Therefore, two treatments may show no differences in their mean values, but their transient behaviour may be significantly different. For example, animals within one treatment may respond slowly to deviations from their mean values, while animals on another treatment may respond rapidly. Thus, depending on the purpose of the treatment, one response may be more preferable than another and a simple comparison of the treatment means may well mask any cyclic differences.

Murphy *et al.* (1983) characterized rumination patterns of sheep and goats by a least squares fitting of rumination time (min/h) to a cosine equation. However, this approach ascribes all rumination activity to a single wavelength and a simple sinusoidal shape. Although the daily rumination profile appeared to be cyclical, it may consist of other wave components of differing frequencies. Stroup *et al.* (1987) discussed experimental design issues associated with investigating feed intake of animals in feedlots and highlighted the inadequacies of the analysis of designs such as Latin squares, crossover etc using standard ANOVA procedures. The ANOVA procedure for row-column designs assumes that there is no row x column interaction. Using the traditional ANOVA procedure on data sets with substantial row x column interaction will produce biased estimates of treatment means and inflated estimates of experimental error. To overcome this problem, Stroup *et al.* (1987) suggested the use of finite Fourier transformations and spectral analysis to account for the cyclic variation in feed intake data for feedlot fed cattle.

Deswysen *et al.* (1993) using Fourier analysis noted differences in grazing cyclicity among heifers with different pedigrees for milk production and also found that individual heifers exhibited different complex rhythm components for both time spent eating and ruminating. Seman *et al.* (1997) found that spectral analysis was valuable in describing grazing behaviour when comparing steers grazing either endophyte infected or endophyte free tall fescue pastures. Spectral analysis was also used to relate dietary quality and herbage species to the behaviour of grazing steers (Seman *et al.* 1999) and to determine the differences in feeding and lying behaviour of steers in feedlots (Wilson *et al.* 2005).

Investigating the underlying cyclical responses to changes in feed allocation using spectral analysis may help in designing improved feed allocation systems for

grazing animals. Therefore, the objectives of this current study were to utilise spectral analysis to examine the rhythmic patterns of hourly grazing, ruminating and resting activities and to relate such patterns to the effects of SH and GD, the timing of allocation of pasture and carbohydrate supplements among grazing dairy cows.

## **5.2 Materials and Methods**

### **5.2.1 Behaviour relative to SH and GD (Chapter 3)**

The protocol for the experimental design and collection of the behaviour data from Chapter 3 is explained in detail in that chapter. Briefly, 6 cows were randomly allocated to one of 2 SH x 5 GD treatments on kikuyu pastures over a 15h grazing period (1600h to 0700h) for 3 days (replicates). Cows were observed at 20-minute intervals for the first 2 hrs after entering their paddocks at 1600h and thereafter at 30 minute intervals until 0700h the next day. Time spent in an activity was calculated as described in Chapter 3 of this thesis. This study was also a pilot study for Trevaskis *et al.* (2004).

### **5.2.2 Grazing behaviour relative to time of fresh pasture and carbohydrate supplements allocation (Trevaskis *et al.* 2004)**

Trevaskis *et al.* (2004) studied the productivity and rumen status of Friesian cows grazing short rotation Italian ryegrass (*Lolium multiflorum* cv Concord) pastures in the warm temperate climate of coastal New South Wales, Australia relative to the time of grazing and of feeding cereal-based concentrates. In their second experiment, 42 Friesian cows were allocated to one of three groups of 14 cows each and grazed as three separate herds (PM, Synch and ASynch). The provision of the daily allocation of pasture in the morning and then a higher proportion of cereal-based concentrate in the afternoon (Synch) was predicted to lead to greater nutrient synchrony in the rumen

compared to feeding a higher proportion of concentrate in the morning (ASynch). The PM group was a direct comparison with the synch group of providing the daily allocation of pasture in the morning or the afternoon. Cows had access to their daily allocation of pasture for only 1 day with the interval between grazing based on pasture regrowth rate and related to the time taken for three new leaves/tiller to regrow (Fulkerson and Donaghy 2001) with the actual grazing interval varying from 12 to 35 days. Each group was grazed separately over a 10-day adjustment period followed by a 21-day experimental period.

As part of the 2 experiments, Trevaskis *et al.* (2004) measured the percentage of cows grazing at 10-min intervals for 7h from 0700 to 1400h on day 2 of experiment 1 and for 17h from 0700 to 2400h on the last day of experiment 2. Data from experiment 2 has been analysed in this current study. The data were converted to time spent grazing (min/h) over the 17h measurement period by using the method described in Chapter 3 of this thesis.

### 5.2.3 Spectral analysis

Spectral analysis refers to the decomposition of the total sum of squares of a time series into components due to periodicities at each of several discrete frequencies, as well as the interpretation of these components. The total variance of the spectral data is partitioned into sums of squares for the different cyclical components. These cyclical components are identified by Fourier frequencies ( $\omega=2\pi/n$ ) with a total of  $n/2$  frequencies, where  $n$  is the number of observations in the time series. For each Fourier frequency, an ordinate or sum of squares is calculated as follows:

$$I(\omega) = \left[ \left\{ \sum_{t=1}^n y_t \cos(\omega t) \right\}^2 + \left\{ \sum_{t=1}^n y_t \sin(\omega t) \right\}^2 \right] / n \quad \text{Equation 14}$$

where  $I(\omega)$  is the ordinate owing to each Fourier frequency ( $\omega$ ) and  $n$  is the number of observations in the time series.

Ordinates or “normalised amplitudes” are plotted v. cycle length (h) on a periodogram. The periodogram was developed to model “hidden periodicities”. The spectrum of a time series can display more complex behaviour when there may be several cycles with different periods. The spectrum is more correctly called the power density function; it is a function of frequency and represents the contribution to the variance of the time series of components with varying frequency. The area under the spectral density function is the total variance of the time series. Significant ordinates are identified using an  $F$ -test to determine whether the coefficients of the sine and cosine functions are equal to zero, and no significant cycle is detected (Fuller 1976).

Spectra for the two SH grazing treatments described in Chapter 3 of this thesis were compared by generating a composite ordinate,  $\bar{I}(\omega)$  which was computed from the ordinates of each SH grazing treatment at each Fourier frequency, or:

$$I(\omega) = r^{-1} \sum_{k=1}^r I_k(\omega) \quad \text{Equation 15}$$

where  $r$  is the number of cows and  $I_k(\omega)$  is the ordinate of the  $k^{\text{th}}$  series at frequency  $\omega = 2\pi / n$  (Diggle 1990).

To compare grazing behaviour spectra averages,  $\bar{I}_1(\omega)$  and  $\bar{I}_2(\omega)$  based on  $r_1$  and  $r_2$  cows in these averages, the following ratio was calculated:

$$R(\omega) = \frac{I_1(\omega)}{I_2(\omega)} \quad \text{Equation 16}$$

with an  $F$  distribution with  $2r_1$ ,  $2r_2$  degrees of freedom (Diggle 1990). The ratio was plotted with the critical upper and lower  $F$ -values indicating significant, point-wise differences when the ratios exceeded the  $F$  boundaries (see Figure 5.3(c)). Differences

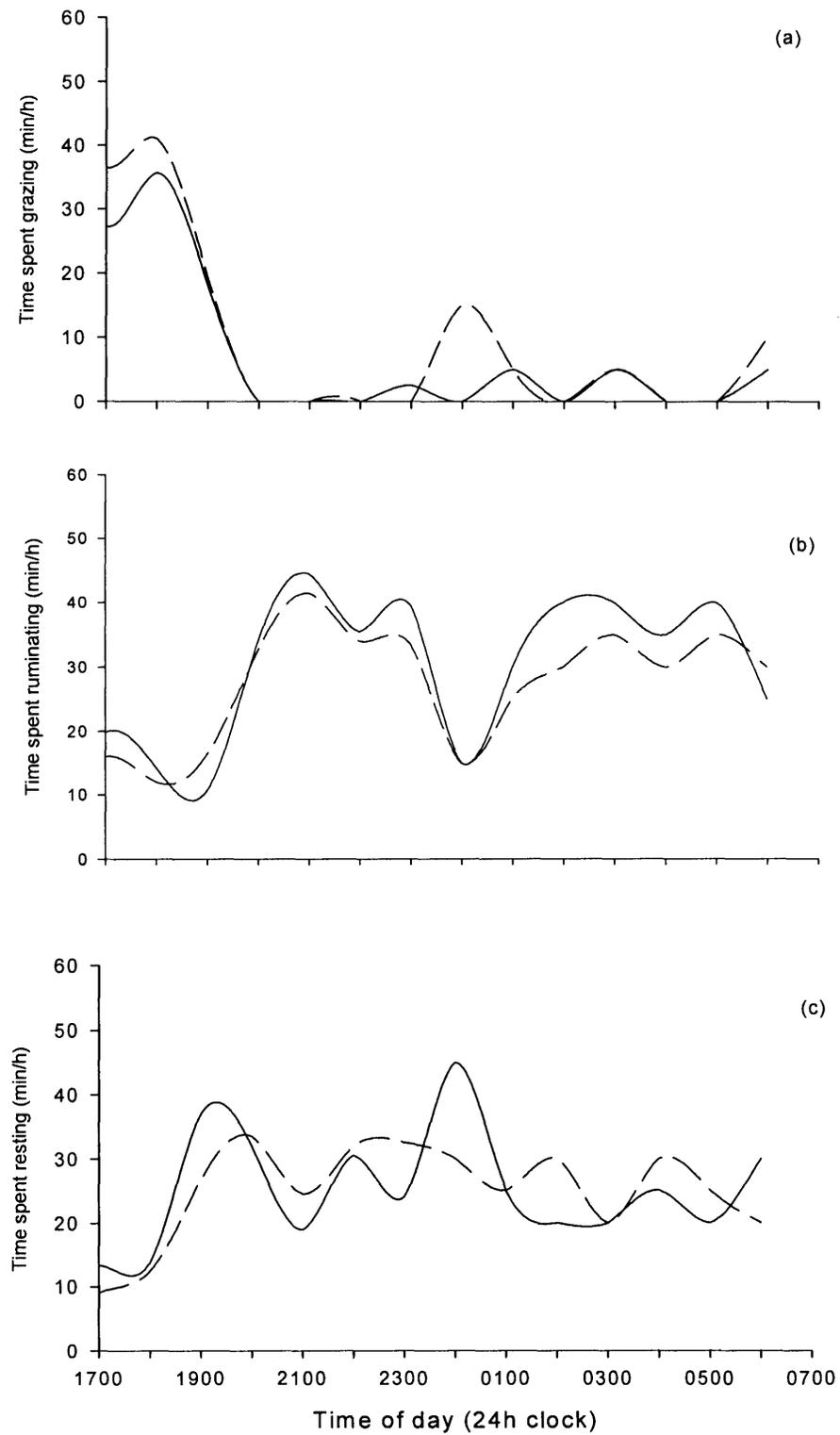
between two entire spectra were tested using maximum and minimum  $R(\omega)$  (Diggle 1990), and the probabilities for the  $F$  distribution for this test were calculated with the *FDIST* function within Microsoft Excel spreadsheet package (Microsoft Corp., Redmond, WA, USA).

Spectral analysis was conducted using GENSTAT for Windows 7<sup>th</sup> edition release 7.1 (Payne 2004). The same analysis was repeated for the grazing behaviour data of Trevaskis *et al.* (2004). Appendix 3 lists the GENSTAT code used to conduct the spectral analysis on the two data sets and summarises the behaviour data for the two experiments.

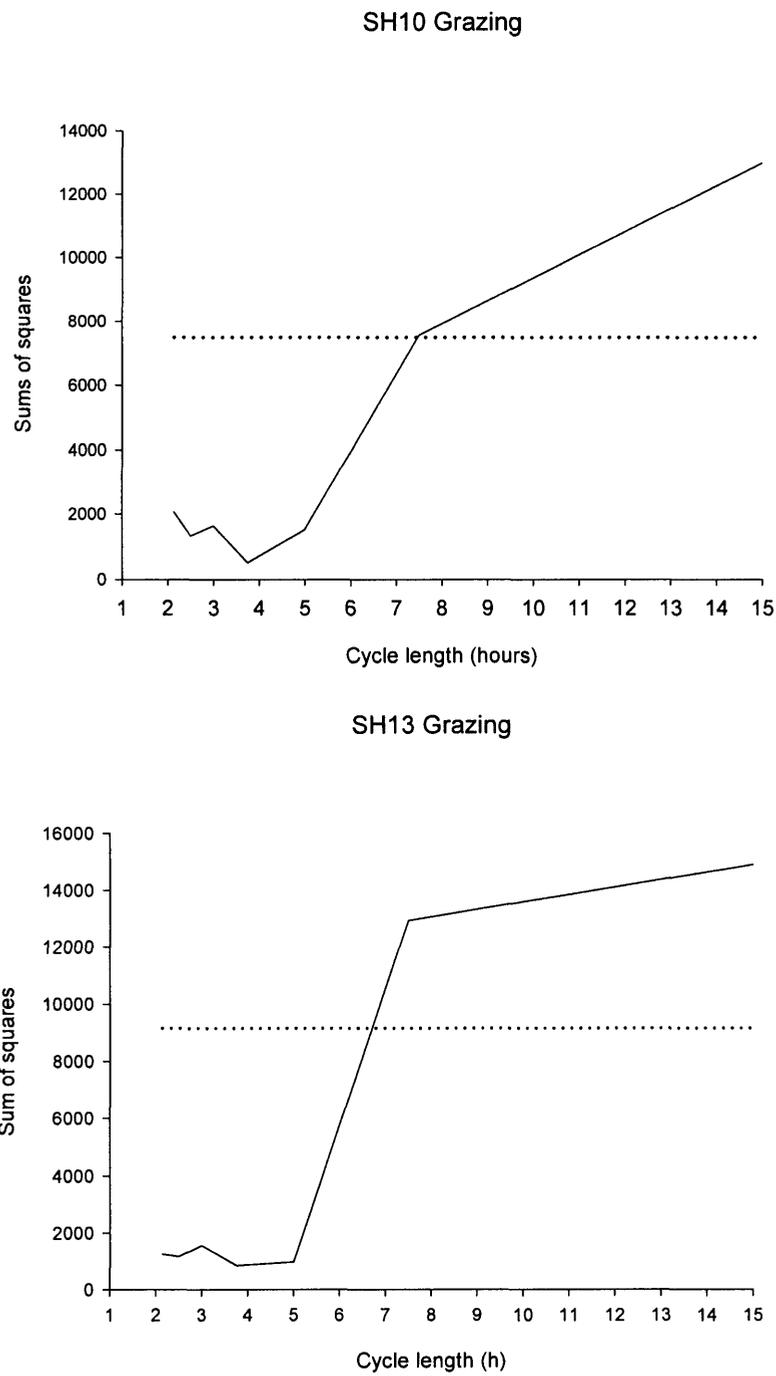
## 5.3 Results

### 5.3.1 Temporal behaviour patterns – Chapter 3 data

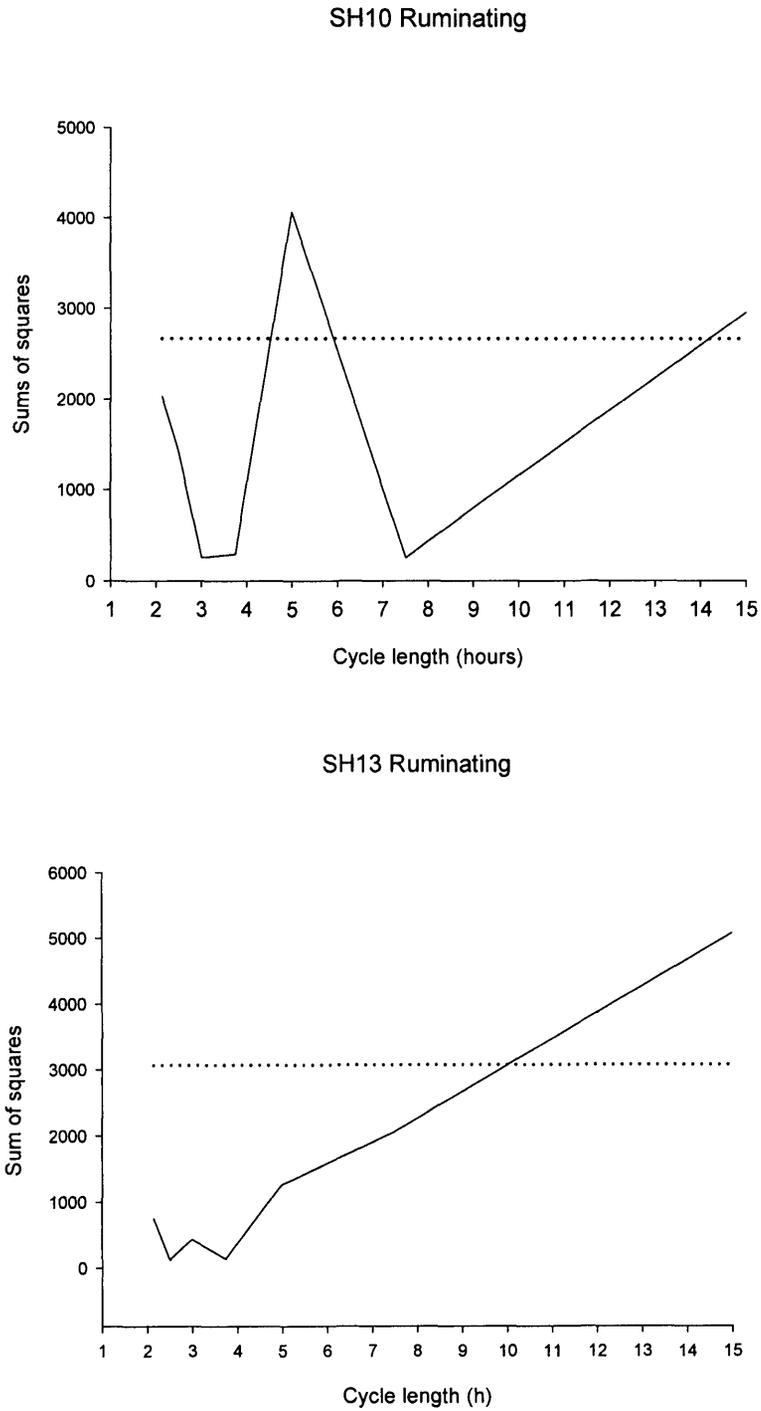
Figure 26 shows the pattern of time spent (a) grazing, (b) ruminating and (c) resting for cows in the experiment reported in Chapter 3 of this thesis. Figures 27 to 29 are periodograms where the averaged ordinates for each SH treatment over the 3 days (replicates) are plotted against cycle length. Cycle lengths that significantly contribute to cyclicity are identified by exceeding the  $F$  critical value ( $P < 0.05$ ). In the 10cm SH treatment cows exhibited cycling occurring with cycle lengths of 7.5h and 15h. Cows grazing the 13cm SH treatment followed the same cycling characteristics with the 7.5h cycle being significant ( $P < 0.05$ ). Cows grazing in the 10cm SH treatment had a significant ( $P < 0.05$ ) cycle length for ruminating at 5h, while there were no significant ( $P > 0.05$ ) short ruminating cycle lengths found for the 13cm SH treatment cows. Cows in both treatments exhibited similar resting cycles, with a significant cycle at 7.5h.



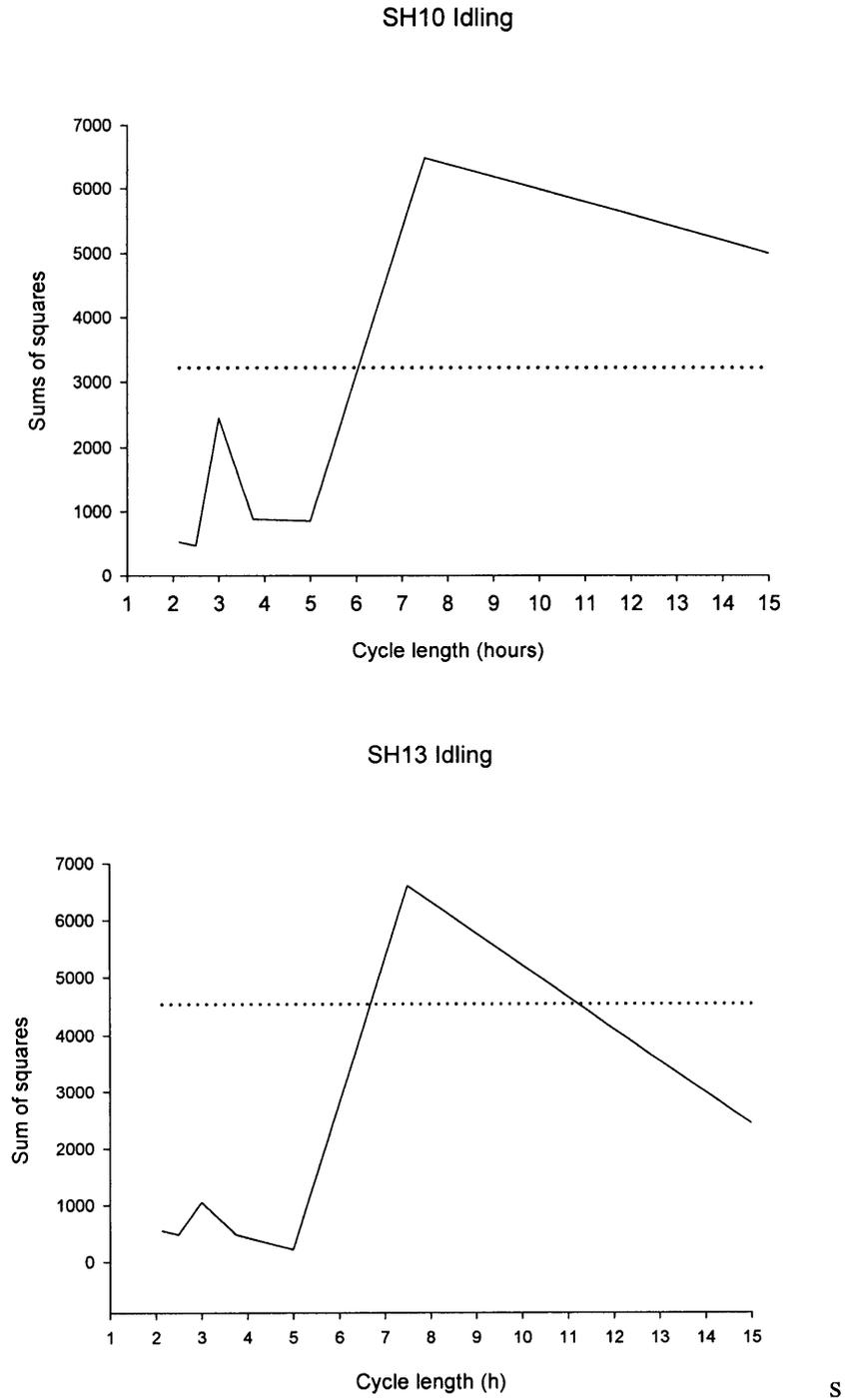
**Figure 26. Effect of SH (10 \_\_\_\_ v 13cm ----) on time spent (min/h) (a) grazing, (b) ruminating and (c) resting from 1600h to 0700h by dairy cows grazing kikuyu pastures.**



**Figure 27. Periodograms of grazing behaviour for cows grazing kikuyu pastures at either a SH of 10cm or 13cm (..... approx F at  $P < 0.05$ ).**

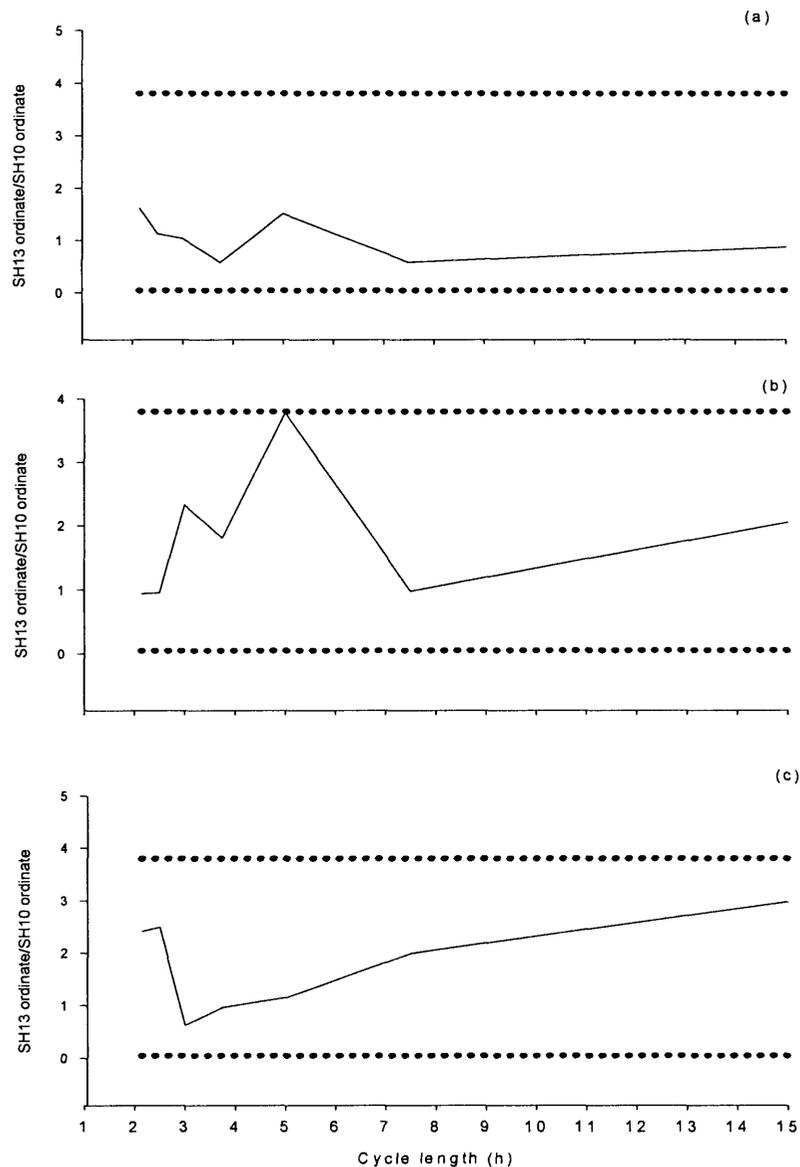


**Figure 28. Periodograms of ruminating behaviour for cows grazing kikuyu pastures at either a SH of 10cm or 13cm (..... approx F at  $P < 0.05$ ).**



**Figure 29. Periodograms of resting (idling) behaviour for cows grazing kikuyu pastures at either a SH of 10cm or 13cm (..... approx F at P<0.05).**

The ratio of ordinates,  $\bar{I}_{13}(\omega) : \bar{I}_{10}(\omega)$  and the 5% and 95% critical values,  $F_{(2rSH13, 2rSH10)}$  were examined to determine if cyclicity differed between the treatments. These are illustrated in Figure 30. The ratio did not exceed the critical values for any of the behaviour characteristics measured. However, there was almost a difference in the ratio at a cycle length of 5h for ruminating between the two treatments.

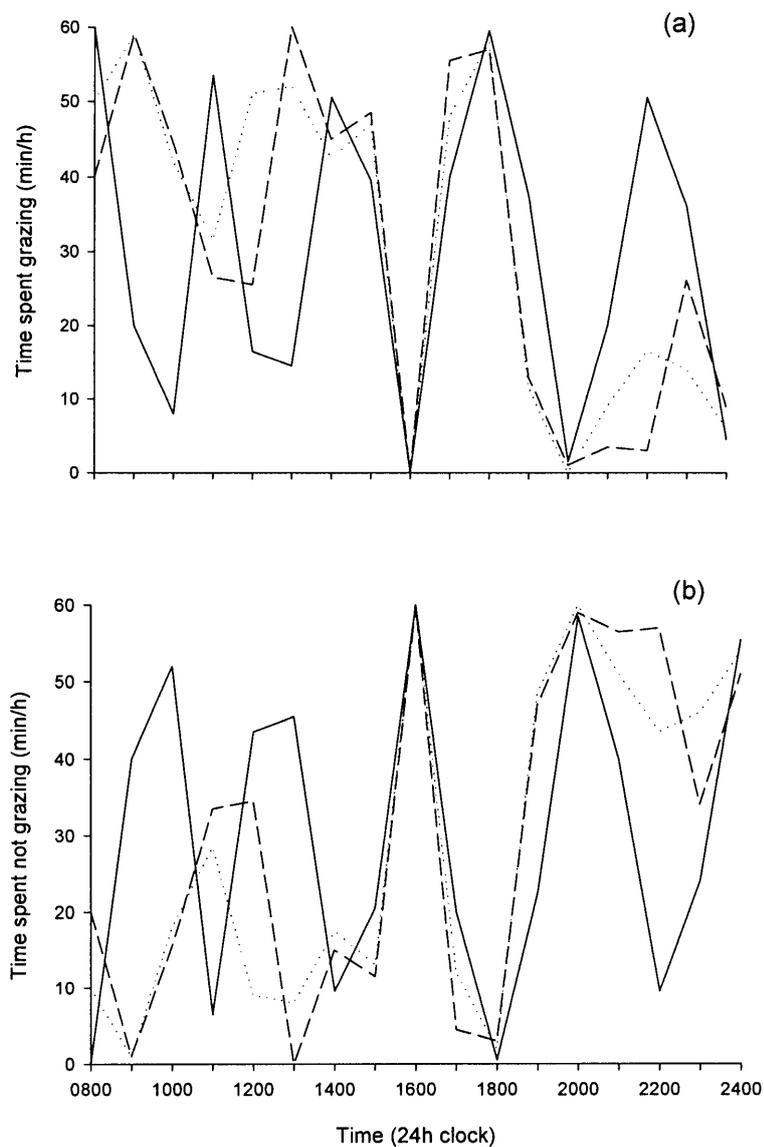


**Figure 30. Ratio of ordinates at each cycle length for (a) grazing, (b) ruminating and (c) resting (idling) activities by dairy cows grazing kikuyu pastures at an initial SH of 10cm and 13cm and associated upper and lower critical F values (.....,  $\alpha = 0.05$ ) from 1600h to 0700h.**

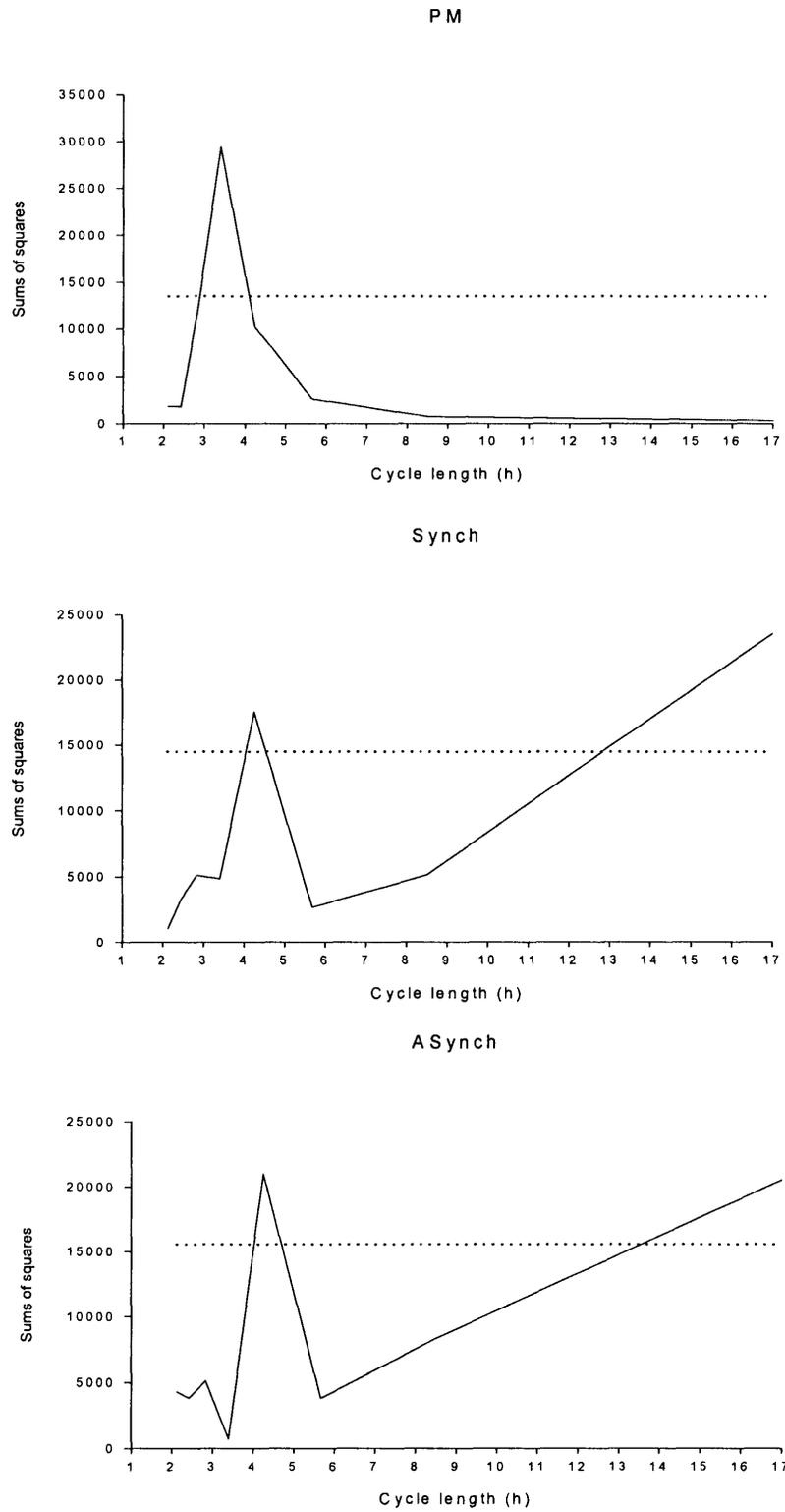
### **5.3.2 Temporal behaviour patterns – Trevaskis *et al.* (2004)**

Figure 31 shows the pattern of time spent (min/h) grazing and not grazing for cows in PM, Synch and ASynch groups in experiment 2 reported by Trevaskis *et al.* (2004). Total grazing times for the 3 groups were similar (944 min ASynch, 926 Synch and 912 PM). However, the PM group's grazing activity between 1600 and 2400 was 39% longer than the Synch and ASynch groups at the same time. Cows in the PM group spent less time grazing immediately after the morning milking than those in the ASynch and Synch groups. This was probably more than likely due to more pasture being available to the latter two groups at this time. The PM group's grazing pattern appeared "out of phase" with the other two groups pattern before 1600h. There are two distinct peaks of grazing activity for the PM group after 1600h compared to only one for the other two groups.

Figure 32 shows the periodograms where the ordinates for each treatment are plotted against cycle length. Cycle lengths that significantly contributed to cyclicity are identified by exceeding the F critical value ( $P < 0.05$ ). The PM treatment cows exhibited significant grazing cycling ( $P < 0.05$ ) at a cycle length of 3.4h, while ASynch and Synch treatment cows had significant cycles at 4.25 and 17h. That is, PM cows grazed every 3.4h, while the cows from the other treatments grazed every 4.25h within the 17h grazing period.

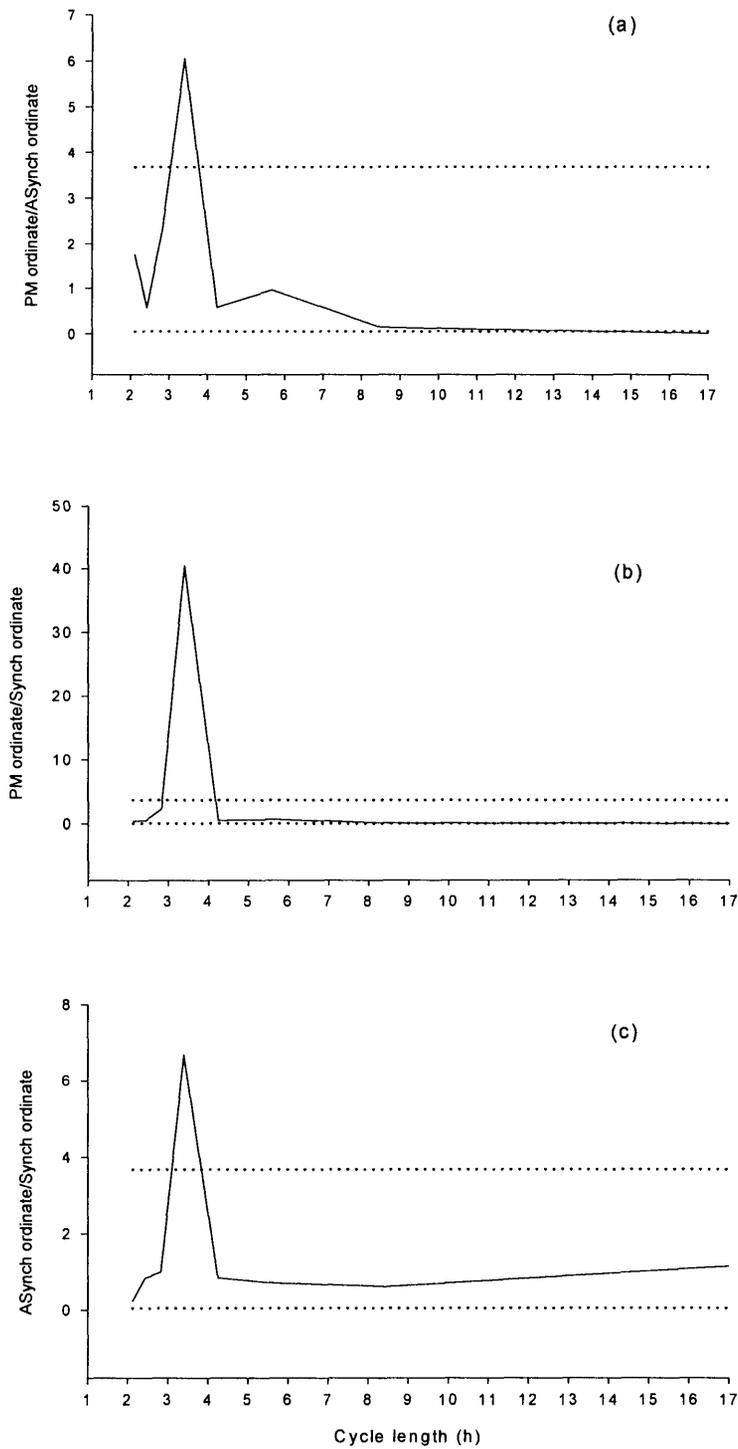


**Figure 31.** Effect of time of allocation of fresh grazing area and carbohydrate feeding on time spent (min/h) (a) grazing and (b) not grazing of dairy cows grazing annual ryegrass pastures 0700 to 2400h on the last day of experiment 2 of Trevaskis *et al.* (2004). \_\_\_ PM; ..... Synch; ---- ASynch



**Figure 32. Periodograms of grazing behaviour for cows grazing annual ryegrass pastures for treatments PM, Synch and ASynch from Trevaskis *et al.* (2004) (..... approx F at  $P < 0.05$ ).**

The ratio of ordinates,  $\bar{I}_{PM}(\omega) : \bar{I}_{Synch}(\omega)$ ,  $\bar{I}_{PM}(\omega) : \bar{I}_{ASynch}(\omega)$  and  $\bar{I}_{ASynch}(\omega) : \bar{I}_{Synch}(\omega)$  and the 5% and 95% critical values,  $F_{(2rPM, 2rSynch)}$ ,  $F_{(2rPM, 2rASynch)}$  and  $F_{(2rASynch, 2rSynch)}$  were examined to determine if cyclicity differed between the treatments (Figure 33). The ratio exceeded the critical values at a cycle length of 3.4h for PM/ASynch, PM/Synch and ASynch/Synch ratios. The difference in the ratios was greatest when comparing PM against Synch treatments (Figure 33(b)). Figure 33 shows that the major difference between the PM and ASynch and PM and Synch grazing behaviour occurred because the PM cows followed a significantly dominant grazing cycle of 3.4h. The difference between Synch and ASynch grazing cyclicity based on the ratio of ordinates is small but significant ( $P < 0.05$ ).



**Figure 33. Plot of ratio of ordinates for (a) PM/ASynch, (b) PM/Synch, (c) ASynch/Synch. Where the ratio exceeds the upper or lower critical F ( $P < 0.05$ ) boundaries, differences exist in grazing cyclicality.**

## 5.4 Discussion

The results of this current study show that spectral analysis is a robust and useful technique to analyse behaviour data collected from grazing dairy cows under the management described in this study. It was also useful in highlighting cyclicity in behaviour when cows grazed kikuyu pastures at different initial SH and revealed significant differences in grazing cycles when cows were allocated fresh pasture areas either after morning milking or after the afternoon milking or different carbohydrate sources.

Seman *et al.* (1999) found that spectral analysis revealed differences in behaviour of steers grazing forages of differing proportions of alfalfa and tall fescue as they defoliated the pastures. Deswysen *et al.* (1993) noted differences in grazing cyclicity among heifers with different pedigrees for milk production. Spectral decomposition of the Chapter 3 behaviour data indicated that there were no significant differences in behaviour activities measured between SH treatments based on the ratio of ordinates (Figure 30). This is confirmed by inspection of Figure 27 which shows a similar pattern of behavioural activity for the Chapter 3 experiment. An extra grazing bout did occur around 8h after grazing began for the 13cm treatment cows. Hence, the periodogram analysis indicated a significant cycle at 7.5h for this treatment (Figure 27).

In their original paper, Trevaskis *et al.* (2004) found that the total time spent grazing (summation of % cows grazing at each hour) was not different between the 3 groups. The herbage DMI of individual cows, as estimated from alkane technology, was also not significantly different ( $15.3 \pm 2.1$  kg DM/cow.d), however, there was a significantly higher dry matter digestible intake (DDMI) in the PM group compared with the 2 other groups ( $13.6 \pm 1.0$  v.  $11.0 \pm 0.5$  %DM). Spectral decomposition

revealed that cows in the PM treatment had a significantly ( $P < 0.05$ ) different grazing cycle every 3.4h compared to the cows from Synch and ASynch groups having a grazing cycle every 4.25h over the 17h measurement period. The grazing activity of the PM group was “out of phase” with the other two groups between morning and afternoon milking times but was then “in phase” after the afternoon milking (Figure 31).

Shifting the time of feed delivery away from milking time increases daily feeding time and alters feeding and lying patterns in stall fed dairy cows (DeVries *et al.* 2005). Champion *et al.* (1994) noted that grazing sheep followed an 8h cycle length and that 6, 8 and 12h are all harmonics of a 24h day. Orr *et al.* (2001) found that cows that were given their fresh allocation in the morning had initial meal duration of  $\approx 2$ h, while cows given their fresh allocation after afternoon milking grazed less in the period between morning and afternoon milking times. At these times of the day, cows are on depleted pastures and thus their IR would be constrained. Cows in the PM group of Trevaskis *et al.* (2004) experiment 2 had two distinct peaks of grazing activity in the period between morning and afternoon milking times, while the cows given their allocation in the morning showed a more continuous pattern of grazing during this period.

The small but significant difference in the ratio of ordinates between Synch and ASynch groups indicates that there was a difference in grazing activity between these two groups. There has been no studies conducted comparing behaviour between synchronous and asynchronous diets in grazing dairy cows. More research is required to determine if any real difference in behaviour does exist when these types of diets are given to grazing dairy cows and in combination with allocation of fresh pasture at different times of the day.

Because of the way the behaviour data were collected in the experiments analysed in this current study, it was not possible to determine individual cow cyclic variation within treatments. Deswysen *et al.* (1993) found that individual heifers can exhibit different complex rhythm components for both time spent eating and ruminating. However, Seman *et al.* (1999) found no significant differences between individual animals within a treatment when using spectral analysis to relate dietary quality and herbage species to the behaviour of grazing steers. Stroup *et al.* (1987) recommended that consideration of the variations in cyclic behaviour be part of the experimental design when investigating aspects of feed intake.

## 5.5 Conclusions

The results of this current study indicate that spectral analysis can be used to determine the extent to which behaviour patterns are unique and whether these patterns can be altered by SH and GD, timing of allocation of fresh pasture and carbohydrate supplement. Total grazing time alone may not reflect differences in grazing behaviour, but spectral analysis revealed that SH did not influence grazing and resting cycles (7.5h) but did affect rumination cycle (5h for 10cm). It also showed that cows offered a fresh pasture after afternoon milking have a different grazing pattern than those offered their fresh pasture after morning milking. The PM cows repeat their grazing behaviour every 3.4h while the AM cows will repeat theirs every 4.25h. However, shifting the time of delivery of carbohydrate supplements does not appear to modify grazing behaviour. Results using spectral analysis offer additional information to aid in studying grazing behaviour. More research is required to investigate if any real differences do occur between diet synchrony and asynchrony on grazing behaviour of dairy cows and if these differences influence other aspects eg pasture composition, quality, selection, rumen fermentation and animal performance.

## CHAPTER 6

### TIME-DEPENDENT TRANSITION PROBABILITIES IN BEHAVIOUR OF GRAZING DAIRY COWS.

#### 6.1 Introduction

The factors that control and limit herbage DMI by grazing dairy cows are still not fully understood. Herbage DMI of grazing cows is determined by a complex interaction of factors (Arnold and Dudzinski 1978) including periods of non-grazing of various durations. With an ad libitum feed supply, circadian patterns develop and day length is a primary determinant of when animals eat. Major grazing periods correspond to sunrise and sunset in free-ranging animals, and are determined by the timing of feeding in housed animals (Arnold *et al.* 1981). The time spent eating will also depend on the age, size, breed and physiological state of the animal, among other factors (Arnold 1985; Penning *et al.* 1995).

Rook and Penning (1991) used a finite Markov chain to study the transition among eating (grazing), ruminating and idling activities of grazing sheep and explored whether these were time-dependent. Only eating activity was found to be sensitive to the preceding length of a given meal. A failing of the Markov model is that it assumes that the transition probabilities between states are constant. However, a grazing animal would be more likely to cease a particular activity if it has been engaged in that activity for a long time. This is in agreement with intake theories based on accumulation of ingesta in the rumen or metabolites in the blood (Forbes 1995). Dutilleul *et al.* (2000) presented a new methodology using time-dependent transitions for chewing behaviour in sheep. This method determined the transition

probabilities at each sampling time point, without having to assume that they were independent of the position in time.

To understand the effects of pasture and supplement allocation on the behaviour and performance of grazing dairy cows, models describing the time-dependent transition of behaviour would be useful. Therefore, the aim of this current study was to utilise the methodology of Dutilleul *et al.* (2000) to determine the time-dependent probabilities in behaviour of grazing dairy cows using behaviour data from Chapter 3 of this thesis and of Trevaskis *et al.* (2004). The Chapter 3 experiment was designed to investigate the effects of SH and GD on behaviour and the Trevaskis *et al.* (2004) experiments were designed to investigate the effects of time of day and the type of carbohydrate supplement on dairy cow performance, rumen fermentation parameters and behaviour.

## **6.2 Materials and Methods**

### **6.1.1 Grazing behaviour data**

The protocol for the experimental design and collection of the behaviour data from Chapter 3 is explained in detail in that chapter and the experimental protocols for the Trevaskis *et al.* (2004) study is briefly described in Chapter 5 of this thesis.

### **6.2.2. Time-dependent transition probabilities**

The terminology and methodology of Dutilleul *et al.* (2000) has been used throughout this chapter. Within ‘time-dependent transition probabilities’ are incorporated three types of probabilities: (1) the probabilities of being in a given state, (2) the probabilities of staying in the same state, and (3) the probabilities of changing of state, although being in a given state is not a transition *per se*. These probabilities are calculated at multiples of a ‘sampling interval’ ( $\Delta t$ ) in discrete time, from the raw

data collected in continuous time. That is, the initial time the animal enters the state in question, the final time the animal leaves that state for another one, and the next state (Slater 1978). In this current study the sampling interval was defined by using the actual interval during the data collection period – 30 min for Chapter 3 data and 10 min for Trevaskis *et al.* (2004) behaviour data. The calculation of all three types of time-dependent transition probabilities is based on estimating the probability of an event by the corresponding observed relative frequency. Transition probabilities were estimated at different sampling time points without having to assume that they were independent of the position in time - stationarity assumption (Fagen and Young 1978) and that the dependence of the current state of behaviour on past states extended only over one time interval - Markovian assumption (Priestley 1981). Thus, a 'binary response' was given the value 1 if the event of interest was observed at the sampling time point considered, and 0, otherwise. Depending on the type of time-dependent transition probability, the event of interest was: being in a given state at time  $t$ , being in the same state at times  $t$  and  $t+\Delta t$ , or changing of state from time  $t$  to time  $t+\Delta t$ , where  $\Delta t$  denotes the length of the sampling interval. In the case of probability of being in a given state, the event of interest is a single event, whereas in the cases of probability of staying in the same state and probability of changing state, it combines two events and consists of their intersection. Thus, the probabilities of staying in the same state and changing state are not conditional probabilities, but unconditional probabilities of the intersection ( $\cap$ ) of two events. These conditional probabilities at time  $t+\Delta t$  may be obtained by dividing the unconditional same state probability and changing state probability at time  $t+\Delta t$  by the probability of being in a given state of the conditioning state at time  $t$ , when strictly positive.

Because they are time-dependent, the probabilities of changing state indicate the moments at which changes of state occurred in time, whereas the probabilities being in a given state represent the likelihood of an animal being in a given state as a function of time. The probabilities of being in a given state are autocorrelated, that is, the likelihood of an animal being in a state at time  $t$  is correlated with the likelihood of it being in that state at times  $t \pm \Delta t$ ,  $t \pm 2\Delta t$ , etc. They are also cross-correlated, that is, the likelihood of an animal being in a state at time  $t$  is correlated with the likelihood of it being in a different state at times  $t$ ,  $t \pm \Delta t$ ,  $t \pm 2\Delta t$  etc.

If the sampling interval is too short, the probabilities of being in a given state and staying in the same state will be identical, leading to redundancy. However, if it is too long, a large number of changes of state will be missed in the calculation of probabilities of changing state, leading to lack of sufficiency (Hurnik and Mullen 1981). In time series notation, the probability of being in state  $a$  at time  $t$ , from initial grazing of the day in this current study is denoted:

$$BSa_t = P(\text{state } a \text{ at time } t) \quad (a=1, \dots, s), \quad \text{Equation 17}$$

where BS is being in a given state;  $P$  denotes the classical probability measure;  $s$  is the states that  $a$  belongs to.

Probabilities of staying in state  $a$  from time  $t$  to time  $t + \Delta t$  are denoted:

$$SSa_t = P(\text{state } a \text{ at time } t \cap \text{state } a \text{ at time } t + \Delta t) \quad (a=1, \dots, s) \quad \text{Equation 18}$$

where SS is staying in same state.

Probabilities of changing of state - leaving state  $a$  for state  $b$  from time  $t$  to time  $t+\Delta t$ ,

$$CSab_t = P(\text{state } a \text{ at time } t \cap \text{state } b \text{ at time } t+\Delta t) \quad (a,b=1, \dots, s; a \neq b) \quad \text{Equation 19}$$

where CS is changing state.

The steady-state transition probabilities were also calculated for both data sets (see Appendix 4).

## 6.3 Results

### 6.3.1 Time-dependent transition probabilities

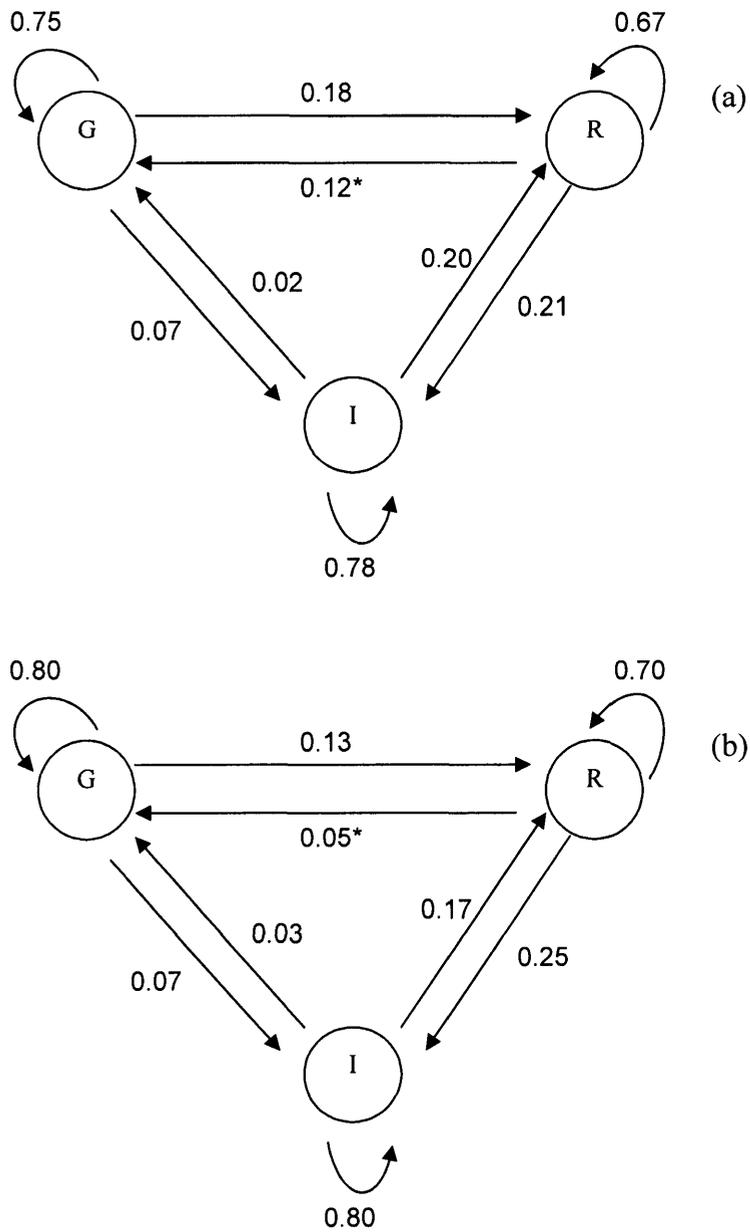
#### 6.3.1.1 Chapter 3 behaviour data

The transition probabilities calculated for the behaviour data from Chapter 3 are shown in Figure 34. The probability of being in a given state of grazing, ruminating and idling were [0.37 0.31 0.32] and [0.49 0.25 0.26] for SH10 and SH13 treatments, respectively. Thus, the likelihood of dairy cows in the SH13 treatment being in the grazing state was about twice the likelihood of them either being in ruminating or idling states.

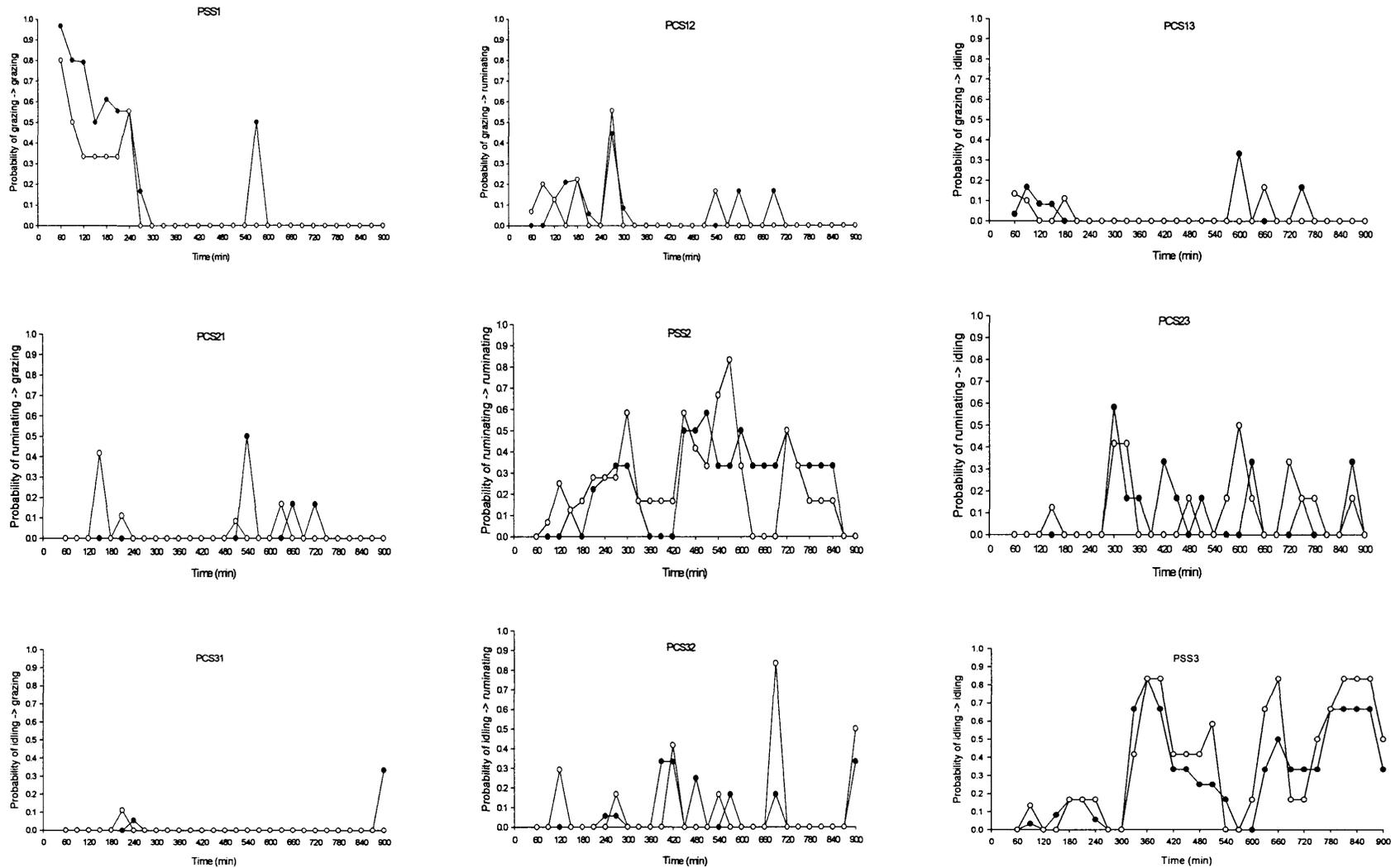
The large probability of staying in same state values suggests that cows tend to remain a relatively long time in the same state, thus inducing dependence among consecutive observations. The largest difference between SH treatments in the probabilities of changing a state was between ruminating (previous state)  $\rightarrow$  grazing (current state) (0.12 SH10 v. 0.05 SH13). That is, cows in the SH10 treatment were twice as likely to move from the ruminating state to the grazing state as those cows in the SH13 treatment.

Steady-state probabilities (see Appendix 4 for method of calculating) were [0.21 (grazing) 0.37 (ruminating) 0.42 (idling)] and [0.16 0.35 0.49] for treatments SH10 and SH13, respectively. That is, as time progresses, there was a 21% chance of finding SH10 treatment being in the grazing, while there was a 16% chance of finding SH13 treatment cows being in the grazing state. The probabilities of finding cows in either the ruminating state or idling state were similar for either SH treatment as time within the activity progressed.

The time-dependent transition probabilities of staying in a state and changing of state for both SH treatments are shown in Figure 35. The likelihood of the herd moving from idling → grazing (PCS31) and its converse for both SH treatments was very unlikely as the length of the idling session progressed. An interesting result was the relatively low likelihood of transition from ruminating → grazing (PCS21) for both SH treatments. This could have implications on what mechanism initiates grazing.



**Figure 34. Transition diagrams for the Markov model of dairy cows grazing (a) SH10 and (b) SH13 treatment swards of kikuyu over a 15h period (G=grazing state, R=ruminating state, I=idling state).**



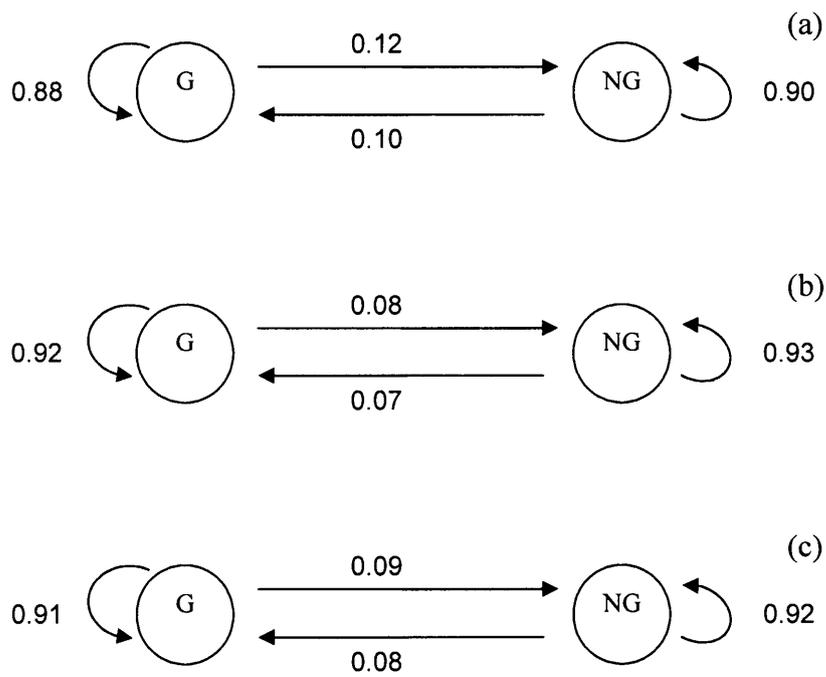
**Figure 35. Time-dependent transition probabilities of staying in a state (diagonal) and changing of state (off-diagonals) for dairy cows grazing kikuyu pastures at an initial sward height of 10cm (○) and 13cm (●). State 1=grazing; state 2=ruminating; state 3=idling (PSS1=probability of staying in state 1; PCS12=probability of transition from state 1 to state 2).**

### 6.3.1.2 *Trevaskis et al. (2004) behaviour data*

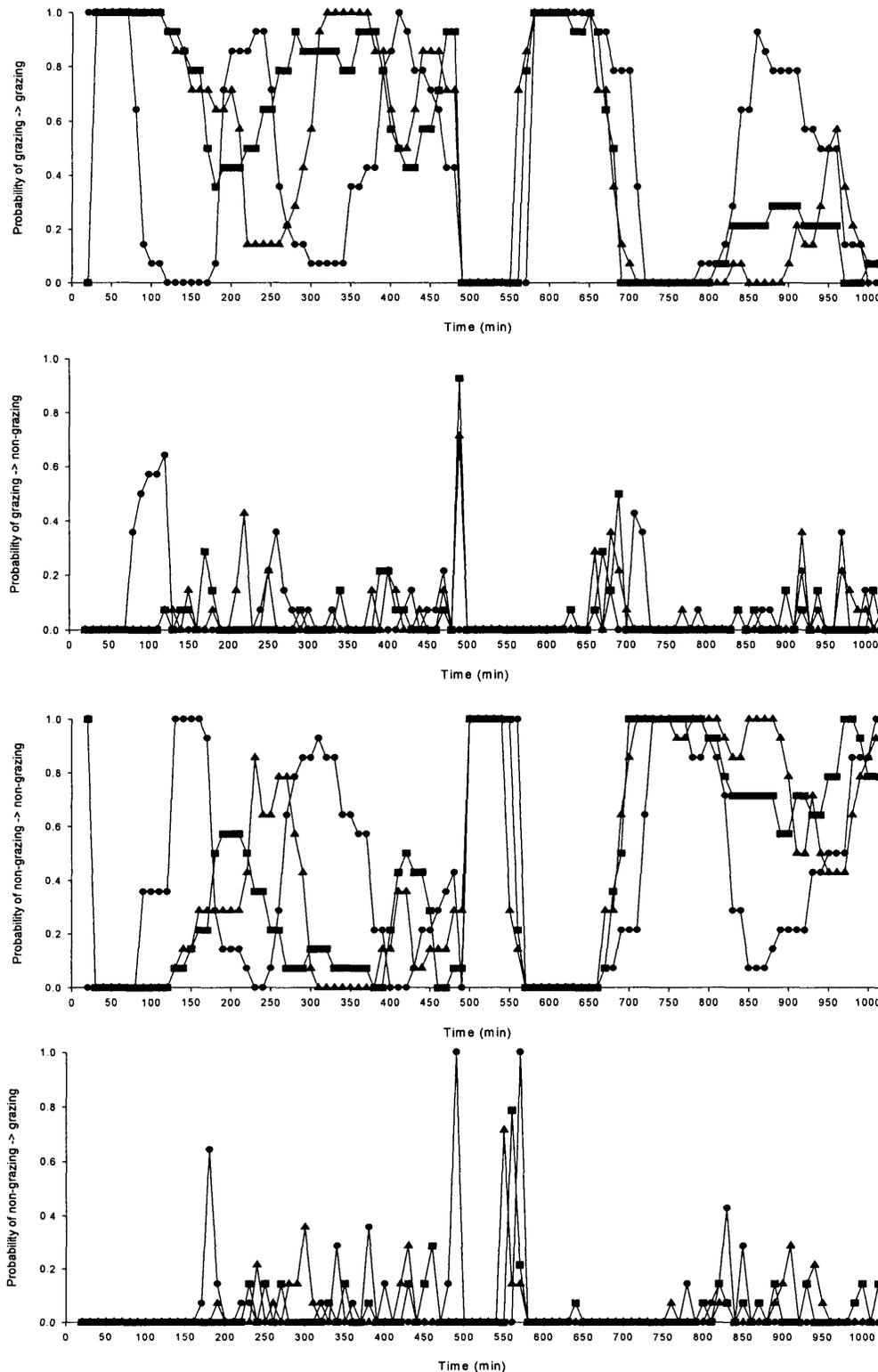
The transition probabilities calculated for the behaviour data from Trevaskis *et al.* (2004) are shown in Figure 36. The overall probabilities of being in a given state shows that on average, the likelihood of dairy cows grazing when offered their fresh pasture after afternoon milking (PM) was similar to the likelihood of cows offered their fresh pasture after morning milking (Synch and ASynch) [0.5 v. 0.53 v. 0.51]. The likelihood that cows were in the non-grazing state was also similar for each treatment group [0.5 v. 0.47 v. 0.49], PM, Synch and ASynch respectively. There were no differences between treatment groups in the probability of changing state.

Steady-state probabilities (see Appendix 4 for method of calculating) were [0.45 (grazing) 0.55 (non-grazing)], [0.47 0.53] and [0.47 0.53] for PM, Synch and ASynch, respectively.

The time-dependent transition probabilities of staying in a state and changing of state for treatment groups are shown in Figure 37. The overall likelihood of the herd moving from non-grazing → grazing for all 3 treatment groups was low. However, cows in the PM group had a higher likelihood of changing from non-grazing → grazing state while the other 2 groups had a higher likelihood of changing from grazing → non-grazing state just before the afternoon milking (500min). All 3 groups had a high likelihood of changing state from non-grazing → grazing after afternoon milking.



**Figure 36. Transition diagrams for the Markov model of (a) PM, (b) Synch and (c) ASynch treatment groups of Trevaskis *et al.* (2004) over a 17h period (G=grazing state, NG= not grazing state).**



**Figure 37.** Time-dependent transition probabilities of staying in a state and changing of state for dairy cows grazing annual ryegrass pastures between 0700 and 2400h on the last day of experiment 2 for treatments PM (●), Synch (■) and ASynch (▲) (calculated from Trevaskis *et al.* 2004).

## 6.4 Discussion

The time-dependent probabilities calculated in this current study shows that the likelihood of finding the herd in the grazing state is reduced as the length of the grazing session increases, irrespective of SH treatment, time of day a fresh pasture break is offered and when a carbohydrate supplement is offered. This is the first use of this method for grazing dairy cows and appears to be a robust method to detect differences between treatments.

The Markov model for the SH behaviour data indicated that the likelihood of the herd grazing decreased by more than 60% for both SH treatments in the first 4.5h after grazing commenced. However, by the same time the likelihood of either ruminating or idling had only decreased by around 40% for either SH treatment. The transition probabilities for grazing did not reach steady state until around 8.5h after grazing commenced, while the steady state was reached at around 5h for ruminating and idling for both SH treatments. This supports the results of Rook and Penning (1991) who found that eating (grazing) was a time-dependent process controlled by some satiety mechanism such as a build up of metabolites in the blood or the increasing physical fill of the rumen. It also supports their conclusion that an animal would be more likely to cease a particular activity if it has been engaged in that activity for a long time.

Analysis of the Trevaskis *et al.* (2004) behaviour data using the Markov model found that the transition probabilities of the herd being in either the grazing or non-grazing states for the PM treatment reached steady state by 5h after grazing commenced, while that for the Synch and ASynch treatment reached steady state by 4h. Thus, the PM treatment herd would have spent more time grazing than cows within the other two treatments, as found by Trevaskis *et al.* (2004).

Soca *et al.* (1999) found that if the grazing session was divided into 2h (1230-1430) and 4h (1630-2030) these cows (T3) had a probability of being in the grazing state of 0.81. This was at the expense of a lower rumination and resting time. Cows grazing for 8h (T1; 0630-1430) and for 6h (T2; 0830-1230 and 1630-1830) had similar probabilities of being in the grazing state (0.57 v. 0.59). The first grazing bout was significantly longer in the T3 cows (120 min) than in T1 and T2 (82 and 94 min, respectively). This needs to be tested further to determine how herbage DMI can be increased by implementing aspects of behaviour into grazing management.

The time of allocation of carbohydrate source did not result in any differences in the either the Markov model transition probabilities or the time-dependent transition probabilities between Synch and ASynch groups (Figure 33). However, the ASynch group did move from grazing → non-grazing and the converse after approximately 4h once grazing had commenced compared to 3h for the Synch group. This may have been due to changes in rumen fermentation characteristics as described by Trevaskis *et al.* (2004) and Williams *et al.* (2005).

Dutilleul *et al.* (2000) concluded that the time-dependent transition probabilities were useful in determining the effects of season on within-day variations in the chewing behaviour of housed sheep. They also found that their time-dependent transition probabilities supported the notion that an animal should be more likely to cease a particular activity if it has been engaged in that activity for a long time. The use of time-dependent probabilities in this current study found that cows remain in the grazing state for the first 4.5h after grazing commenced, irrespective of SH treatment. Also, calculation of the time-dependent probabilities has helped in determining when the herd starts and ceases grazing and what characteristics contribute to the initiation of the herd moving from the grazing state to a non-grazing state and vice versa.

A major criticism of using time-dependent transition probabilities is the need to choose a length of the sampling interval that avoids redundancy and sufficiency. Rook and Penning (1991) started with 1min records of the grazing behaviour of sheep before grouping them into 5min intervals to find the predominant activity in each interval and to overcome timing errors between sets of recording equipment. Dutilleul *et al.* (2000) used sampling intervals of 1min for eating, ruminating and idling activities in housed sheep. In this current study, the Chapter 3 data had a sampling interval of 30min, while the sampling interval for the Trevaskis *et al.* (2004) data was 10min. There is a possibility that the 30min sampling interval may have missed some events that could have improved the estimation of the time-dependent transition probabilities. However, since grazing continued for around 4.5h in both SH treatment groups and was consistent over the 3 days, a smaller sampling interval may not have been any more informative in this case. The 10min interval used in the Trevaskis *et al.* (2004) experiment was chosen based on the results of Chapter 3 as it was thought, at the time, that a 30min sampling interval may have been too long for the objectives of that study.

It is the duration of the activity and hence the time to move to a new activity that are important. Presumably a diet which fills the rumen rapidly (high IR) or has a rapid release of nutrients (increased metabolic satiety signals with fast rate of digestion) would have higher time-dependent probabilities of transition from one state to the next. Further use of this technique to test such hypotheses is required.

## 6.5 Conclusions

Time-dependent transition probabilities of behaviour of grazing dairy cows is a useful technique to determine the effects of SH and GD, allocation of a fresh pasture break (time of day) and type of carbohydrate supplement. The calculation of these supported the notion that an animal would be more likely to cease a particular activity if it

has been engaged in that activity for a long time. This also supports feed intake theories based on accumulation of ingesta in the rumen or metabolites in the blood. Further research is required to determine how time of day of allocation of pasture and carbohydrate influences behaviour. Including time-dependent transition probabilities that are linked to patterns of rumen fermentation would help improve our understanding of how rumen fermentation characteristics influence behaviour and herbage DMI. The calculation of the time-dependent probabilities can also help in determining how length of a grazing session affects aspects of grazing management and also aspects of the substitution effect.

## CHAPTER 7

### GENERAL DISCUSSION

#### 7.1 Introduction

The research studies reported in this thesis were part of a larger research programme entitled “The effect of carbohydrate supplements on N utilisation and on the digestibility of pastures grazed by dairy cows” (DAN097) funded by Dairy Australia between 1999 and 2002. The principle objective of this project was to determine the most appropriate supplementation strategy for dairy cows grazing various pasture types in terms of total feed response. Included in DAN097 were research studies designed to answer questions on whether synchronisation of N and energy in the rumen improves the efficiency of microbial protein synthesis in grazing dairy cows fed different sources of carbohydrate supplements, what are the characteristics of carbohydrate sources that synchronise with the N coming from pasture and does time of day grazing and supplementing affect synchrony and rumen microbial protein synthesis?

To help predict the availability of nutrients from pasture in the rumen so that supplements can be fed at appropriate times when energy and N are synchronised, knowledge of the temporal patterns of behaviour of grazing dairy cows is required. Chapter 3 of this thesis was designed to quantify the effect of SH and GD on patterns of behaviour in grazing dairy cows. The results from Chapter 3 were then used to help design the experiments reported in Trevaskis *et al.* (2004) and Trevaskis (2003). One of the major issues with a research programme such as DAN097 is how can the knowledge gained from the project be transferred to producers and their advisers? One approach is to quantify the behaviour data generated within DAN097. Such an analysis would not only improve our understanding of the mechanisms involved but also more readily allow

transfer of critical information to clients about the pasture-animal interface. As part of this larger project, the DST *FeedSmart* (Dobos and Fulkerson 2004) was developed to improve feed allocation decision making.

Grazing behaviour is governed by a variety of plant, animal and environmental factors. An understanding of why, how, and when animals graze is essential in trying to improve pasture utilisation and the management of livestock. Being aware of the factors that encourage or discourage grazing can help a producer make decisions about pasture rotation, supplementary feeding and stocking density.

## **7.2 Quantification of the effects of SH and GD on IR, herbage DMI, grazing behaviour and sward dynamics**

The time required to obtain adequate nutrients is highly dependent on sward factors such as SH, availability, condition and quality of the herbage. Also, understanding the factors that influence IR and GT will improve our understanding of intake (Forbes 1995). Total herbage DMI and diet selection at grazing are mediated by the different foraging strategies that result from the integration by dairy cows of short (meal size, duration and interval between meals) - and long (body energy stores) -term information, suggesting a complex, but an important and interesting research subject.

Chapter 3 of this thesis quantified the relationship between SH and GD in terms of behaviour of grazing dairy cows. Grazing time was significantly ( $P < 0.05$ ) higher for the SH13 cows compared to the SH10 cows (187 v. 142 min) over the 15h grazing period. Time spent grazing had an asymptotic relationship with GD, such that GT increased by 0.45h/h up to a maximum of 4h GD. Irrespective of SH treatment, cows received 70% of their total herbage DMI within the first 4h of GD. Therefore, knowing that cows will graze intensively for the first 4h and receive around 70% of their herbage DMI within this time is valuable information for issues such as waterlogged pastures and supplementary

feeding. Other research (eg Soca *et al.* 1999) has found that dairy cows given access to pasture for 6h/d commencing at 1200h had a longer initial grazing meal than those cows restricted to 8h/d commencing at 0600h (120 v. 82min). It was also found that 60% of the herbage DMI was achieved within the first 2h of initial grazing.

Mean herbage DMI over the 15h grazing period in this current study was also significantly ( $P<0.05$ ) higher for the SH13 cows compared to the SH10 cows (19.6 v. 12.3 kg DM/cow). The rate of decline of IR was significantly ( $P<0.05$ ) faster for SH13 cows than for the SH10 cows. Most of this decline in IR occurred in the first 2h after grazing commenced, thereafter IR was similar for both SH treatments.

Knowing that IR decreases more rapidly on taller swards than on shorter swards also has implications for management decisions such as when to supplement. Because IR remains relatively constant on shorter swards compared to taller swards, timing of supplementary feeding becomes critical to ensure that GT and hence herbage DMI are not affected. This raises the questions of when is the best time to supplement grazing dairy cows, and what are the best supplements to feed that will enhance GT and also herbage DMI. Chapters 5 and 6 of this current thesis quantified temporal patterns and the time-dependent transition probabilities of behaviour in grazing dairy cows to help answer these questions. Trevaskis *et al.* (2004) and Trevaskis (2003) investigated aspects of time of day allocating fresh pasture and type of supplement offered on rumen parameters, grazing behaviour and performance of dairy cows.

Time spent grazing in this current study increased as SH increased. This appears to be contrary to other results which found that show grazing animals compensate for less pasture availability by increasing GT (eg Allden and Whittaker 1970; Ungar and Noy-Meir 1988). Under the grazing management used in this current study, strip-grazing, this may not be the case. A lactating dairy cow is being driven by the requirements to fulfil its

genetic potential to produce milk, especially in early lactation. The compensatory effect appears to be found mainly in continuous grazing systems and may not be relevant to either strip or rotational grazing systems, because the entire area is available to be grazed (Bailey *et al.* 1996). Sward height is the major constraint on bite mass in temperate pastures, with the effect primarily on bite depth rather than bite area (Rook 2000).

The effect of SH and GD on sward dynamics was studied in Chapter 4 of this thesis. It is interesting to note that no one particular distribution of the 5 distributions fitted to the data consistently explained the sward dynamics under the grazing management system used in this current study. However, the double normal distribution would appear to be the most appropriate mathematical description when both tall and short SH are present in the sward. Under the grazing management used in this current study and at the SH and GD treatments imposed, the “mosaic” of tall and short swards as seen under continuous grazing management did not eventuate. Therefore, further research using more SH treatments in conjunction with GD is necessary to understand sward dynamics better. Knowing the dynamics of sward depletion as cows graze will help improve in the allocation of supplements and also improve intake and animal performance.

The opportunity to sample pastures at the various GD treatments for quality was not undertaken in this current study. Therefore, further research investigating the effects of SH and GD on grazing behaviour would benefit from such data being collected. This will help answer some of the questions on initiation and cessation of grazing.

### **7.3 Quantification of effects of SH and GD, time of allocation of pasture and type of carbohydrate supplement on temporal patterns of grazing behaviour**

The temporal pattern of grazing, ruminating and idling activity is fairly consistent over the course of a day, despite the interruption due to milking. During the hours of darkness the cow performs alternating periods of idling and ruminating. However, after returning to pasture after morning milking the cow has a relatively short grazing meal of approximately 90min followed by alternating periods of ruminating and idling. By late morning the cow has a second grazing meal of approximately 150min in length followed by more periods of ruminating and idling. After the afternoon milking the majority of the remaining time until dusk is spent grazing (Gibb 2006).

One issue with reporting the treatment effects on behavioural activities is that many research articles have only reported the mean of that activity. Two treatments may show no differences in their mean values, but their transient behaviour may be significantly different. For example, animals within one treatment may respond slowly to deviations from their mean values, while animals on another treatment may respond rapidly. Thus, depending on the purpose of the treatment, one response may be more preferable than another and a simple comparison of the treatment means may well mask any cyclic differences. Therefore, the aim of quantifying the effects of SH and GD, time of allocation of pasture and type of carbohydrate supplement on temporal patterns of behaviour was to utilise spectral analysis as a technique to determine if differences occurred due to the various perturbations to the “normal” temporal pattern.

Chapter 3 data were subjected to spectral decomposition to determine if SH significantly affected the temporal pattern of behaviour. Cows on the SH13 treatment swards did return to grazing about 4-5h after their first initial grazing bout whereas the SH10 treatment cows did not. Spectral decomposition found that both treatments had

significant cycle lengths at 7.5h for grazing and resting (idling) activities but there was no difference in grazing and idling activities between the two SH treatments. However, SH10 cows had a significantly different cycle length of 5h compared to 15h for SH13 cows for ruminating activity. The significance of this difference is difficult to explain but is probably due to the SH13 cows having more pasture available and being able to return to grazing 4-5h later than the SH10 cows, hence affecting cyclicity of rumination.

Time of day allocating a fresh pasture area is known to affect animal performance however there is limited information on how this affects temporal patterns of behavioural activity. Trevaskis *et al.* (2004) found that although the total time spent grazing between the three experimental groups of cows was not significantly different the cows allocated their fresh pasture after afternoon milking (PM) had a higher GT in the afternoon than those cows allocated fresh pasture after morning milking (AM). This was probably because the cows in the AM group had little pasture available at this time, as their total GT when allocated their fresh pasture was similar to the PM cows. Similar GT were found for cows offered a carbohydrate supplement to be in synchrony with pasture N availability in the rumen (Synch) and those that were offered their carbohydrate supplement to be asynchronous for N and energy in the rumen (ASynch).

Since the mean total time spent grazing was not different, Chapter 5 of this thesis investigated the affect of allocating fresh pasture at different times of the day and offering different types of carbohydrate supplements on the temporal patterns of behaviour in grazing dairy cows using spectral analysis. Spectral analysis of similar data has been used successfully before (eg Wilson *et al.* 2005; Seman *et al.* 1999). Using this technique on behavioural data from animals fed under different management scenarios has found differences in temporal patterns of behaviour. For example, Wilson *et al.* (2005) used spectral analysis to determine why “normal” and “stressed” feedlot animals did not differ

in intake and growth rate after 70d. Spectral decomposition found that the “normal” treatment animals had an 8h cycle while the “stressed” animals modified their feeding patterns to have a 4h cycle, thus compensating for any reduction in intake due to stress.

In this current study, temporal patterns of grazing behaviour did differ between the AM and PM treatment groups, such that the PM group had a significant cycle at 3.4h while the AM group had a significant cycle at 4.25h. However, temporal patterns of behaviour between the ASynch and Synch groups did not differ. The PM group had a 39% larger GT than the AM groups due to their longer GT after afternoon milking and that the longest GT for both groups was at this time. This has been attributed to the increased DM and WSC content of herbage at this time (Orr *et al.* 2001). Also, the temporal pattern of grazing by the two groups was “out of phase” after morning milking, but was “in phase” after the afternoon milking. This supports previous research by Orr *et al.* (2001) who found similar results. The temporal patterns of behaviour of the ASynch and Synch groups were very similar.

Therefore, SH under the management conditions described in this current study did not affect the temporal patterns of grazing and idling behaviour but did affect rumination behaviour. Also, PM grazing generates a different temporal pattern of behaviour compared to AM grazing, but diet synchrony does not. Further research is required to determine the reasons why diet synchrony does not change temporal patterns of behaviour.

## **7.4 Quantification of effects of SH and GD, time of allocation of pasture and type of carbohydrate supplement on the time-dependent probabilities of grazing behaviour**

To further understand how SH and GD, time of allocation of pasture and type of carbohydrate supplement influence behaviour in grazing dairy cows the data from Chapter 3 and 5 were analysed to determine the time-dependent transition probabilities using the technique described by Dutilleul *et al.* (2000). Knowing time-dependent transition probabilities of behaviour would help in determining time of the day to offer supplements. For example, if there is a high likelihood that animal will move from the grazing state to the ruminating state, supplementation may not be of benefit. However, if there is a high likelihood that an animal will change state from ruminating to grazing this may enhance supplementation. Such combinations need to be confirmed.

Analysis of the time-dependent transition probabilities incorporates three types of probabilities: the probabilities of (1) being in a given state, (2) staying in the same state, and (3) changing state, although being in a given state is not a transition *per se*. These probabilities are calculated at multiples of a 'sampling interval' in discrete time, from the raw data collected in continuous time ie the initial time the animal enters a state, the state in question, the final time the animal leaves the state for another one, and the other state.

In the case of the probability of being in a given state, the event of interest is a single event, whereas in the cases of the probability of staying a state and the probability of changing state combine two events and consists of their intersection. Thus, the probabilities of staying in a state and those for changing state are not conditional probabilities, but unconditional probabilities of the intersection of two events. Because they are time-dependent, the probabilities of changing state indicate the moments at which

changes of state occur in time, whereas the probabilities of being in a state represent the likelihood of an animal being in a given state as a function of time.

The results obtained in this current study are in agreement with Rook and Penning (1991) who found that an animal would be more likely to cease a particular activity if it has been engaged in that activity for a long time. The authors also put forward some intake control theories to support their statement, and the results of this current study appear to confirm this. Only eating activity was found to be sensitive to the preceding length of a given meal.

This data could be included into decision support tools such as *FeedSmart* (Dobos and Fulkerson 2004). The Markov modelling approach is being used to help in analysing and understanding decision making processes in areas such as dairy cow replacement, optimal length of leys, productive lifespan of sows, dairy herd health, and growth rates of organic steers (Kristensen and Jorgensen 2000; Lien *et al.* 2003; Plá *et al.* 2003; Østergaard *et al.* 2003; Nielsen *et al.* 2004). Further research using the Markov modelling approach to quantify behaviour of grazing dairy cows appears warranted.

## **7.5 Practical implications, conclusions and perspectives**

The results of this current thesis have highlighted through quantification of SH in combination with GD that dairy cows allocated their fresh pasture after afternoon milking will consume >70% of their herbage DMI within the first 4h, irrespective of SH treatment. Cows grazing taller swards returned to graze about 4h later probably because of more pasture being available. The pattern of grazing exhibited would allow the prediction of pasture N availability which can be synchronised with readily fermentable carbohydrates (eg concentrates). In terms of practical use of these results, the effect of SH on GT is of particular interest. Since dairy cows have consumed >70% of their herbage DMI by 4h GD, is it worthwhile moving the cows onto a fresh allocation after this time?

Would this increase DMI and milk production? Dalley *et al.* (2001) tested this hypothesis and found that there was no increase in either DMI or milk production when cows were offered a new allocation more frequently during the day. However, to test this properly requires more than just shifting cows more frequently in a day. Knowing the time-dependent probabilities of what state a cow is currently in and what the probability is that the cow will move to another state would be important to test this hypothesis.

When fresh pasture was allocated after afternoon milking (PM), cows exhibited a modified pattern of grazing behaviour compared to those cows allocated fresh pasture after morning milking (AM). Grazing was “out of phase” between the two groups after AM milking but returned to be “in phase” after PM milking. However, there was no difference in patterns of grazing behaviour when diets were either synchronised for N and energy release in the rumen or unsynchronised. More research is required to investigate other combinations of synchrony and time of day allocation for dairy cows grazing pasture to fine tune the decision making process involved in supplementation and grazing management.

Quantifying the time-dependent probabilities for the three types of probabilities described in this current thesis will help improve our understanding of how grazing is initiated and how it ends. There is limited information for dairy cows grazing pasture on what is the likelihood that cows will be in either the grazing or any other state. Knowing these time-dependent probabilities can help improve in the decision making process involved in maximising herbage DMI.

One method of using the results from this current thesis is in the “minimal total discomfort” (MTD) hypothesis discussed by Forbes (2005). An index of MTD can be calculated knowing the energy required, energy supplied and IR. The MTD can also be calculated for NDF, CP and other factors and hence, the total MTD can be calculated.

Further research into how the MTD and various states of activity correlate would be worthwhile. Another aspect for future research is to combine behaviour activities with rumen fermentation characteristics in a model to help determine the mechanisms determining intake and associated behaviour activities.

The decision support tool *FeedSmart* allows the user to more precisely allocate pasture and supplements based on daily calculations of feed available and feed required. Understanding how the dairy cow adapts its behaviour under different management scenarios will help improve herbage utilisation and hence, milk production.

The issue of what constitutes a suitable sampling interval for behaviour studies, that is length of interval between observations, has been the subject of many research studies. The time interval between observations chosen in the SH X GD experiment was 20min, while Trevaskis *et al.* (2004) chose 10min. Previous research has used automatic data collection devices to measure eg jaw movements. These instruments do increase the resolution, however, the opportunity to utilise such instruments in the studies used in this thesis was unavailable. Therefore, repeating aspects of these experiments utilising such instruments and analysing using the techniques described would be worthwhile.

The studies in this current thesis have identified a number of future research needs. These include aspects of genetic merit and type of supplementation and time of allocation of fresh pasture, as well as improving our understanding of what circumstances initiates the change from one state to another during the grazing session. This would have to include measurements of rumen parameters for animals in the various states. *The consequences of the behavioural adaptations to constraints during grazing on ruminal characteristics and on the digestive process must be investigated. These advances will contribute to improving grazing and feeding management systems.*

**BIBLIOGRAPHY**

- Albright, J.L. and Avare, C.W. (1997) The behaviour of cattle. CAB International, Cambridge, UK.
- Akaike, H. (1974) A new look at statistical model identification. *IEEE Transactions of Automatic Control*, AU-19, pp. 716–722.
- Allden, W.G. and Whittaker, A.M.C. (1970) The determinant of herbage intake by grazing sheep: the interrelationship of factors influencing herbage intake and availability. *Aust. J. Agric. Res.* **21**, 755–766.
- Arnold, G.W. (1985) Regulation of forage intake. In: *Robert J. Hudson and Robert G. White (eds). Bioenergetics of wild herbivores*. CRC Press, Boca Raton, FL., pp. 81-101.
- Arnold, G.W., Wallace, S.R. and Rea, W.A. (1981) Associations between individuals and home-range behaviour in natural flocks of three breeds of domestic sheep. *Applied Animal Ethology*. **7**, 239-257.
- Arnold, G.W. and Dudzinski, M.L. (1978) The Ethology of Free-ranging Domestic Animals. Elsevier, Amsterdam, 198 pp.
- Arriaga-Jordan, C.M. and Holmes, W. (1986) The effect of concentrate supplementation on high yielding dairy cows under two systems of grazing. *J. Agric. Sci. (Camb.)* **107**, 453–461.
- Baile, C.A. and McLaughlin, C.L. (1987) Mechanisms controlling feed intake of ruminants. *J. Anim. Sci.* **64**, 915-922.
- Bailey, D.W., Gross, J.E., Laca, E.A., Rittenhouse, L.R., Coughenour, M.B., Swift, D.M., Sims, P.L. (1996) Mechanisms that result in large herbivore grazing distribution patterns. *J. Range Manage.* **49**, 386–400.
- Baker, R.D., Le Du, Y.L.P. and Alvarez, F. (1981) The herbage intake and performance of set-stocked suckler cows and calves. *Grass and Forage Science* **36**, 201–210.
- Bao, J., Giller, P.S. and Kett, J.J. (1992) The effect of milk production level on grazing behaviour of Friesian cows under variable pasture conditions. *Irish Journal of Agricultural and Food Research*. **31**, 23-33.
- Bargo, F. and Muller, L.D. (2005) Grazing behaviour affects daily ruminal pH and NH<sub>3</sub> oscillations of dairy cows on pasture *J. Dairy Science*. **88**, 303-309.

- Bargo, F., Muller, L.D., Kolver, E.S. and Delahoy, J.E. (2003) Invited review: Production and digestion of supplemented dairy cows on pasture *J. Dairy Science*. **86**, 1-42.
- Bargo, F., Muller, L.D., Delahoy, J.E. and Cassidy, T.W. (2002a) Performance of high producing dairy cows with three different feeding systems combining pasture and total mixed rations *J. Dairy Science*. **85**, 2948-2963.
- Bargo, F., Muller, L.D., Delahoy, J.E. and Cassidy, T.W. (2002b) Milk response to concentrate supplementation of high producing dairy cows grazing at two pasture allowances *J. Dairy Science*. **85**, 1777-1792.
- Barrett, P.D., Laidlaw, A.S., Mayne, C.S. and Christie, H. (2001) Pattern of herbage intake rate and bite dimensions of rotationally grazed dairy cows as sward height declines. *Grass and Forage Science*. **56**, 362-373.
- Barthram, G.T., Duff, E.I., Elston, D.A., Griffiths, J.H., Common, T.G. and Marriott, C.A. (2005) Frequency distributions of sward height under sheep grazing. *Grass and Forage Science*. **60**, 4-16
- Barthram, G.T. and Grant, S.A. (1984) Defoliation of ryegrass dominated swards by sheep. *Grass and Forage Science*. **39**, 211-219.
- Barthram, G.T. (1980) Sward structure and the depth of the grazing horizon. *Grass and Forage Science*. **36**, 130-131.
- Bazely, D.R. (1988) Foraging behaviour of sheep (*Ovis aries* L.) grazing on swards of perennial ryegrass (*Lolium perenne* L.). Ph.D. thesis. Oxford University, U.K.
- Beever, D.E. and Cottrill, B.R. (1994) Protein systems for feeding ruminant livestock: a European assessment. *J. Dairy Science*. **77**, 2031-2043.
- Beever, D.E. (1993) Characterisation of forages: appraisal of current practice and future opportunities. In: *Recent advances in animal nutrition*. Nottingham University Press, Loughborough, UK. pp. 3-17.
- Beever, D.E. Dhanoa, M.S. Losada, H.R. Evans, R.T. Cammell, S.B. France, J. (1986) The effect of forage species and stage of harvest on the processes of digestion occurring in the rumen of cattle. *British Journal of Nutrition*. **56**, 2, 439-454.
- Black, J.L. and Kenney, P.A. (1984). Factors affecting diet selection by ' sheep. II. Height and density of pasture. *Aust. J. Agric. Res.* **35**, 565-578.
- Burlison, A.J., Hodgson J. and Illius A.W. ( 1991 ) Sward canopy structure and the bite dimensions and bite weight of grazing sheep. *Grass and Forage Science*. **46**, 29-38.

- Cabrera Estrada, J.I., Delagarde, R., Faverdin, P., et al. (2004) Dry matter intake and eating rate of grass by dairy cows is restricted by internal, but not external water. *Animal Feed Science and Technology*. **114**, 59-74.
- Campbell, J.B., Stringam, E. and Gervais, P. (1969) Pasture activities of cattle and sheep. *Can. Dept. of Agric. Publ.* **1315**, 105-112 (Chap 12).
- Cangiano, C.A., Galli, J.R., Pece, M.A., Dichio, L. and Rozsypalek, S.H. (2002) Effect of liveweight and pasture height on cattle bite dimensions during progressive defoliation. *Aust. J. Agric. Res.* **53**, 541 – 549.
- Chacon, E. and Stobbs, T.H. (1976) Influence of progressive defoliation of a grass sward on the eating behaviour of cattle. *Aust. J. Agric. Res.* **27**, 709-727
- Champion, R.A., Rutter, S.M., Penning, P.D. and Rook, A.J. (1994) Temporal variation in grazing behaviour of sheep and the reliability of sampling periods. *Applied Animal Behaviour Science*. **42**, 99–108.
- Charnov, E.L. (1976) Optimal foraging, the Marginal Value Theorem. *Theor. Popul. Biol.* **9**, 129–136.
- Chilibroste, P., Gibb, M. and Tamminga, S (2005) Pasture and animal performance. In: *J. Dijkstra, J.M. Forbes and J. France (eds). Quantitative Aspects of Ruminant Digestion and Metabolism, 2<sup>nd</sup> edition*. CAB International, pp. 681-706.
- Chilibroste, P., Soca, P., Mattiauda, D.A. and Bentancurt, O. (2004) Incorporation of short term fasting in grazing and feeding management strategies cattle: an integrated approach In: *J. Pizarro (ed). Proceedings of II International Symposium "Grassland Ecophysiology and Grazing Ecology"*. Curitiba, Parana Brazil.
- Chilibroste, P., Williams, B.A., Tamminga, S. and Calabro, S. (1999a) The use of cumulative gas production technique to characterize changes in the fermentation characteristics of rumen contents following variable periods of starvation and grazing in dairy cows. *Animal Science*. **69**, 647-655.
- Chilibroste, P., Soca, P. and Mattiauda, D.A. (1999b) Effect of the moment and length of the grazing session on: 1. milk production and pasture depletion dynamics. In: *Moraes, A., Nabinger, C., Carvalho, P.C., Alvez, S.J. and Lustosa, S.B. Agosto. (eds) Proceedings of international Symposium "Grassland Ecophysiology and Grazing Ecology"*. Curitiba. Brasil. pp. 295-298
- Chilibroste, P., Tamminga, S., and Boer, H. (1997) Effect of length of grazing session, rumen fill and starvation time before grazing on dry matter intake, ingestive

- behaviour and dry matter rumen pool sizes of grazing lactating dairy cows. *Grass and Forage Science*. **52**, 249-257.
- Christie, H., Mayne, C.S., Laidlaw, A.S., Patterson, D.M. and McGilloway, D.A. (2000) Effect of sward manipulation and milk yield potential on herbage intake of grazing dairy cows. In: Rook, A.J. and Penning, P.D. (eds.) *Grazing management: the principles and practice of grazing, for profit and environmental gain, within temperate grassland systems: proceedings of the British Grassland Society Conference held at the Cairn Hotel, Harrogate, 29 February-2 March 2000*. BBSRC Institute of Grassland and Environmental Research, Aberystwyth. Occasional Symposium British Grassland Society no. 34. pp. 79-84
- Ciavarella, T. A., Dove, H., Leury, B. J. and Simpson, R. J.(2000) Diet selection by sheep grazing *Phalaris aquatica* L. pastures of differing water-soluble carbohydrate content. *Aus. J. Agric. Res.* **51**, 757-764.
- Clark, D.A., and Kanneganti, V.R. (1998) Grazing management systems for dairy cattle. In: J. H. Cherney and D. J. R. Cherney (eds.) *Grass for Dairy Cattle*. CAB International. pp. 331
- Clarke, J.L., Welch, D. and Gordon, I.J. (1995) The influence of vegetation pattern on the grazing of heather moorland by red deer and sheep. I. The location of animals on grass/heather mosaics. *Journal of Applied Ecology*. **32**, 166–176.
- Conrad, H.R., Pratt, A.D. and Hibbs, J.W. (1964) Regulation of feed intake in dairy cows. I. Change in importance of physical and physiological factors with increasing digestibility. *J. Dairy Sci.* **47**, 54-62.
- Cosgrove, G.P. (1997) Grazing behaviour and forage intake. In: J.A. Gomide (ed). *Int. Symp. On Animal production under Grazing, Vicosa, Brazil. 4-6 Nov. 1997*. Dep. Zootecnia, Univ. Federal de Vicosa, Vicosa, Brazil. pp. 59-80.
- Curll. M.L. and Davidson, J.L. (1983) Defoliation and productivity of a *Phalaris*-subterranean clover sward, and the influence of grazing experience on sheep intake. *Grass and Forage Science*. **38**, 159-167.
- Dalley, D.E., Roche, J.R., Moate, P.J. and Grainger, C. (2001) More frequent allocation of herbage does not improve the milk production of dairy cows in early lactation. *Aust. J. Exp. Agric.* **41**, 593–599.

- Dalley, D.E., Roche, J.R., Grainger, C. and Moate, P.J. (1999) Dry matter intake, nutrient selection and milk production of dairy cows grazing rainfed perennial pastures at different herbage allowances in spring *Aust. J. Exp. Agric.* **39**, 923-931.
- Delaby, L., Peyraud, J.L. and Delagarde, R. (2001) Effect of the level of concentrate supplementation, herbage allowance and milk yield at turn-out on the performance of dairy cows in mid lactation at grazing. *Animal Science*. **73**, 171–181.
- Demment, M.W. and van Soest, P.J. (1985) A nutritional explanation for body size patterns of ruminant and non-ruminant herbivores. *The American Naturalist*. **125**, 641-672.
- Demment, M.W. and Laca, E.A. (1993) The grazing ruminant: models and experimental techniques to relate sward structure and intake. In: *Proceedings 7th World Conference on Animal Production*, Edmonton, Alberta, Canada June 28 - July 2, 1993. Volume 1. World Conference on Animal Production, Edmonton, Canada: pp. 439-461.
- Deswysen, A.G., Dutilleul, P., Godfrin, J.P. and Ellis, W.C. (1993) Nycterohemeral eating and ruminating patterns in heifers fed grass or corn silage: Analysis by finite Fourier transform. *J. Animal Science*. **71**, 2739–2747.
- DeVries, T.J., von Keyserlingk, M.A.G. and Beauchemin, K.A. (2005) Frequency of feed delivery affects the behaviour of lactating dairy cows. *J. Dairy Science*. **88**, 3553-3562.
- Diggle, P. (1990) *Time Series: A Biostatistical Introduction*. Clarendon Press, Oxford, pp.117-124.
- Dillon, P., Berry, D.P., Evans, R.D., Buckley, F. and Horan, B. (2006) Consequences of genetic selection for increased milk production in European seasonal pasture based systems of milk production. *Livestock Science*. **99**, 141-158
- Dillon, P. (2006) Achieving high dry-matter intake from pasture with grazing dairy cows. In: *A. Elgersma, J. Dijkstra and S. Tamminga (eds.), Fresh Herbage for Dairy Cattle*, pp. 1-26.
- Dobos, R.C. and Fulkerson, W.J. (2004) A database program to assist in the allocation of pasture and supplements to grazing dairy cows. *Environmental Modelling and Software*. **19**, 581–589

- Dougherty, C.T., Bradley, N.W., Cornelius, P.L. and Lauriault, L.M. (1989) Short-term fasts and the ingestive behaviour of grazing cattle. *Grass and Forage Science*. **44**, 295-302.
- Dove, H. and Mayes, R.W. (1996) Plant wax components: A new approach to estimating intake and diet composition in herbivores. *J. Nutr.* **126**, 13-26.
- Doyle, P.T., Carter, D.J., Speijers, E.J., Plaisted, T.W., Hetherington, R.E. and Love, R.A. (1996) Changes in the amount and nutritive characteristics of annual pastures from late spring to autumn on the south coast of Western Australia. *Aust. J. Exp. Agric.* **36**, 791-801.
- Dumont, B. and Petit, M. (1998) Spatial memory of sheep at pasture. *Applied Animal Behaviour Science*. **60**, 43-53.
- Dumont, B., Dutrone, A. and Petit, M. (1998) How readily will sheep walk for a preferred forage? *J. Animal Science* **76**, 965-971.
- Dumont, B., D'hour, P. and Petit, M. (1995) The usefulness of grazing tests for studying the ability of sheep and cattle to exploit reproductive patches of pastures. *Applied Animal Behaviour Science*. **45**, 79-88.
- Dutilleul, P., Deswysen, A.G., Fischer, V. and Maene, D. (2000) Time-dependent transition probabilities and the assessment of seasonal effects on within-day variations in chewing behaviour of housed sheep. *Applied Animal Behaviour Science*. **68**, 13-37
- Earle, D.F. and McGowan, A.A. (1979) Evaluation and calibration of an automatic rising plate meter for estimating dry matter yield of pasture *Australian Journal of Experimental Agriculture and Animal Husbandry*. **19**, 337-343.
- Edwards, G.R., Newman, J.A., Parsons, A.J. and Krebs, J.R. (1997) Use of cues by grazing animals to locate food patches: an example with sheep. *Applied Animal Behaviour Science*. **51**, 59-68.
- Fisher, G.E.J., Roberts, D.J. and Dowdeswell, A.M. (1995) The manipulation of grass swards for summer-calving dairy cows. *Grass and Forage Science*. **50**, 424-438.
- Forbes, J.M. (2005) Voluntary feed intake and diet selection. In: *J. Dijkstra, J.M. Forbes and J. France (eds). Quantitative Aspects of Ruminant Digestion and Metabolism, 2<sup>nd</sup> edition*. CAB International, pp. 607-625.

- Forbes, J.M. (1995) Voluntary food intake and diet selection in farm animals. CAB International, Oxon, UK.
- Forbes, J.M., Jackson, D.A., Johnson, C.L., Stockill, P. and Hoyle, B.S. (1987) A method for the automatic monitoring of food intake and feeding behaviour of individual cows kept in a group. *Research and Development in Agriculture*. **3**, 175-180.
- Fulkerson, W.J., McKean, K., Nandra, K.S. and Barchia, I.M. (2005) Benefits of accurately allocating feed on a daily basis to dairy cows grazing pasture. *Aust. J. Exp. Agric.* **45**, 331–336.
- Fulkerson, W.J. and Donaghy, D.J. (2001) Plant-soluble carbohydrate reserves and senescence-key criteria for developing an effective grazing management system for ryegrass-based pastures: a review. *Aust. J. Exp. Agric.* **41**, 261-275.
- Fulkerson, W.J., Hough, G., Goddard, M. and Davison, T. (2000) The productivity of Freisian cows: effect of genetic merit and level of concentrate feeding. Final report, DAN082, Dairy Research and Development Corporation, Melbourne, Australia.
- Fulkerson, W.J. and Trevaskis, L. (1997) Limitations to milk production from pasture. In: *Corbett, J.L., Choct, M., Nolan, J.V. and Rowe, J.B. (eds.) Recent Advances in Animal Nutrition in Australia 1997*. University of New England, Armidale, Australia. pp. 159-165.
- Fulkerson, W.J. and Slack, K. (1994) Management of *Lolium perenne*/*Trifolium repens* pastures in the subtropics. II. Effect of summer defoliation, irrigation duration, seedbed preparation and pasture type *Aust. J. Agric. Res.* **45**, 721 – 728.
- Fuller, W.A. (1976) *Introduction to Statistical Time Series*. Wiley Publishing, New York, pp. 282-284.
- García, S.C. (2000) Systems, component, and modelling studies of pasture-based dairy systems in which the cows calve at different times of the year. PhD Thesis, Massey University, New Zealand.
- Gekara, O.J., Prigge, E.C., Bryan, W.B., Schettini, M., Nestor, E.L. and Townsend, E.C. (2001) Influence of pasture sward height and concentrate supplementation on intake, digestibility and grazing time of lactating beef cows. *J. Anim. Sci.* **79**, 745-752.
- Gibb, M.J. (2006) Grassland management with emphasis on grazing behaviour. In: *A. Elgersma, J. Dijkstra and S. Tamminga (eds.), Fresh Herbage for Dairy Cattle*, pp. 141-157.

- Gibb, M.J., Huckle, C.A. and Nuthall, R. (2002) Effects of level of concentrate supplementation on grazing behaviour and performance by lactating dairy cows grazing continuously stocked grass swards. *Animal Science*. **74**, 319-335.
- Gibb, M.J., Huckle, C.A. and Nuthall, R. (2000) Effect of temporal pattern of supplementation on grazing behaviour and herbage intake by dairy cows. In: *Rook, A.J. and Penning, P.D. (eds.) Grazing management: the principles and practice of grazing, for profit and environmental gain, within temperate grassland systems: proceedings of the British Grassland Society Conference held at the Cairn Hotel, Harrogate, 29 February-2 March 2000*. BBSRC Institute of Grassland and Environmental Research, Aberystwyth. Occasional Symposium British Grassland Society no. 34. pp. 91-96
- Gibb, M.J., Huckle, C.A., Nuthall, R. and Rook, A.J. (1999) The effect of physiological state (lactating or dry) and sward surface height on grazing behaviour and intake by dairy cows. *Applied Animal Behaviour Science*. **63**, 269-287.
- Gibb, M.J., Huckle, C.A. and Nuthall, R. (1998) Effect of time of day on grazing behaviour by lactating dairy cows. *Grass and Forage Science*. **53**, 41-46.
- Gibb, M.J., Huckle, C.A., Nuthall, R. and Rook, A.J. (1997) Effect of sward surface height on intake and grazing behaviour by lactating Holstein Friesian cows. *Grass and Forage Science*. **52**, 309-321.
- Gibb, M.J., Huckle, C.A., Nuthall, R. and Penning, P.D. (1996) Can grazed pasture meet the needs of the high genetic merit dairy cow? In: *Grass and forage for cattle of high genetic merit: British Grassland Society winter meeting, Great Malvern, November 1996*. British Grassland Society, Reading.
- Gibb, M.J. (1991) Differences in the vertical distribution of plant material within swards continuously stocked with cattle. *Grass and Forage Science*. **46**, 339-342.
- Gibb, M.J. and Ridout, M.S. (1988) Application of double normal frequency distributions fitted to measurements of sward height. *Grass and Forage Science*. **43**, 131-136.
- Gibb, M.J. and Ridout, M.S. (1986) The fitting of frequency distributions to height measurements on grazed swards. *Grass and Forage Science*. **41**, 247-249.
- Ginane, C. and Petit, M. (2005) Constraining the time available to graze reinforces heifers' preference for sward of high quality despite low availability. *Applied Animal Behaviour Science*. **94**, 1-14.
- Gong, Y., Hodgson, J., Lambert, M.G. and Gordon, I.L. (1996) Short term ingestive behaviour of sheep and goats grazing grasses and legumes. 1. Comparison of bite

- weight, bite rate and bite dimensions for forages at two stages of maturity. *N.Z. J. Agric. Res.* **39**, 63-73.
- Gross, J.E., Hobbs, T.N. and Wunder, B.A. (1993a) Independent variables for predicting intake rate of mammalian herbivores: Biomass density, plant density or bite size? *Oikos*. **68**, 75-81.
- Gordon, I.J. (1995) Animal based techniques for grazing ecology research. *Small Ruminant Research*. **16**, 203-214.
- Gross, J.E., Demment, M.W., Hobbs, N.T., Spalinger, D.A. and Wunder, B.A. (1993b) Functional response of herbivores in feed-concentrated patches: Tests of a mechanistic model. *Ecology*. **74**, 778-791.
- Harvey, A. and Orr, R.J. (1996) Dietary preference of sheep for grass and clover at contrasting sward surface heights. *Br. Soc. Anim. Sci.*, Winter Meeting p. 161.
- Hodgson, J. and Brookes, I.M. (1999) Nutrition of grazing animals. In: *White, J. and Hodgson, J. (eds) New Zealand pasture and crop science*. Oxford University Press, Auckland.
- Hodgson, J., Clark, D.A. and Mitchell, R.J. (1994) Foraging behaviour in grazing animals and its impact on plant communities. *Forage quality, evaluation, and utilization*. American Society of Agronomy, Inc., Crop Science Society of America, Inc., and Soil Science Society of America, Inc., Madison, Wisconsin, USA: pp. 796-827.
- Hodgson, J. (1985) The control of herbage intake in the grazing ruminant. *Proceedings of the Nutrition Society*. **44**, 339-346.
- Hodgson, J. (1982) Ingestive behaviour. In: *Leaver, J. D. (ed.) Herbage intake handbook*. Reading, British Grassland Society. pp. 113-138.
- Hodgson, J. (1977) Factors limiting herbage intake by the grazing animal. In: *Proceedings international meeting on animal production from temperate grassland, Dublin, June, 1977*. Irish Grassland and Animal Production Association, Tuam, pp. 70-75.
- Hughes, T.P., Sykes, A.R., Poppi, D.P. and Hodgson, J. (1991) The influence of sward structure on peak bite force and bite weight in sheep. *Proceedings of the New Zealand Society of Animal Production*. **51**, 153-158.
- Iason, G.R., Mantecon, A.R., Sim, D.A., Gonzalez, J., Foreman, E., Bermudez, F.F. and Elston, D.A. (1999) Can grazing sheep compensate for a daily foraging time constraint? *J. Animal Ecology*. **68**, 87-93.
- Illius, A.W., Gordon, I.J., Elston, D.A. and Milne, J.D. (1999) Diet selection in goats: a test of intake-rate maximization. *Ecology*. **80**, 1008-1018.

- Illius, A.W. and Hodgson, J. (1996) Progress in understanding the ecology and management of grazing systems. In: *J. Hodgson and A.W. Illius (eds.) The Ecology and Management of Grazing Systems*. CAB International.
- Illius, A.W., Gordon, I.J., Milne, J.D. and Wright, W. (1995) Costs and benefits of foraging on grasses varying in canopy structure and resistance to defoliation. *Functional Ecology*. **9**, 894-903.
- Illius, A.W. and Gordon, I.J. (1987) The allometry of food intake in grazing ruminants. *J. Animal Ecology*. **56**, 989-999.
- Jamieson, W.S. and Hodgson, J. (1979) The effect of daily herbage allowance and sward characteristics upon ingestive behaviour and herbage intake of calves under strip-grazing management. *Grass and Forage Science*. **34**, 261-271.
- Kellaway, R. and Porta, S. (1993) Feeding concentrates supplements for dairy cows. Dairy Research and Development Corporation, Melbourne, Australia.
- Kibon, A. and Holmes, W. (1987) The effect of height of pasture and concentrate composition on dairy cows grazed on continuously stocked pastures. *J. Agricultural Science*. **109**, 293-301.
- Kolver, E.S. and Muller, L.D. (1998) Performance and nutrient intake of high producing Holstein cows consuming pasture or a total mixed ration *J. Dairy Science*. **81**, 1403-1411.
- Krebs, J.R. and McCleery, R.H. (1984). Optimization in behavioural ecology. In: *J. R. Krebs and N. B. Davies (eds.) 'Behavioural Ecology, an Evolutionary Approach'*. 2nd Edn. Blackwells: Oxford. pp. 91-121.
- Kristensen, A.R. and Jorgensen, E. (2000) Multi-level Markov processes as a framework for herd management. *Annals of Operations Research*. **94**, 69-89.
- Krysl, L.J. and Hess, B.W. (1993) Influence of supplementation on behaviour of grazing cattle. *J. Anim. Sci.* **71**, 2546-2555.
- Laca, E.A., Ungar, E.D. and Demment, M.W. (1994) Mechanisms of handling time and intake rate of a large mammalian grazer. *Applied Animal Behaviour Science*. **39**, 3-19
- Laca, E.A., Demment, M.W., Distel, R.A. and Griggs, T.C. (1993) A conceptual model to explain variation in ingestive behaviour within a feeding patch. *Proceedings of 17<sup>th</sup> International Grassland Congress*, pp. 710-712

- Laca, E.A., Ungar, E.D., Seligman, N. and Demment, M.W. (1992) Effects of sward height and bulk density on bite dimensions of cattle grazing homogeneous swards. *Grass and Forage Science*. **47**, 91-102.
- Leaver, J.D. (1986) Effect of supplements on herbage intake and performance. In: *J. Frame (ed.) Grazing. Occasional Symp. No. 19.*, British Grassland Society, Berkshire, U.K., pp. 79-88.
- Leaver, J.D. (1985) Milk production from grazed temperate grassland. *J. Dairy Research*. **52**, 313-344.
- Lien, G., Kristensen, A.R., Hegrenes, A. and Hardaker, J.B. (2003) Optimal length of leys in an area with winter damage problems. *Grass and Forage Science*. **58**, 168-177.
- Lippke, H. (2002) Estimation of forage intake by ruminants on pasture. *Crop Science*. **42**, 869-872.
- Liu, S and Hirata, M. (1995) Spatial distribution of herbage mass in bahiagrass (*Paspalum notatum* Flugge) pasture under grazing, resting and mowing. *J. Japan. Grassl. Sci.* **40**, 457-470.
- Lloyd Davies, H. (1962) Intake studies in sheep involving high fluid intake. *Proceedings of the Australian Society of Animal Production*, **4**, 167-171.
- Mayne, C.S., and Wright, I.A. (1988) Herbage intake and utilization by the grazing dairy cow. In: *P. C. Garnsworthy (ed.). Nutrition and Lactation in the Dairy Cow.* Butterworths, London. pp. 280-293.
- McGilloway, D.A., Cushnahan, A., Laidlaw, A.S., Mayne, C.S. and Kilpatrick, D.J. (1999) The relationship between level of sward height reduction in a rotationally grazed sward and short-term intake rates of dairy cows *Grass and Forage Science*. **54**, 116-126.
- McGilloway, D.A. and Mayne, C.S. (1996) The importance of grass availability for the high genetic merit dairy cow. In: *P. C. Garnsworthy, J. Wiseman, and W. Haresign (eds.). Recent Advances in Animal Nutrition.* Nottingham University Press, UK. p. 135
- Michell, P (1982) Value of the rising plate meter for estimating herbage mass of grazed perennial ryegrass-white clover swards. *Grass and Forage Science*. **37**, 81-87.
- Moorby, J.M., Miller, L.A., Evans, R.T., Scollan N.D., Theodorou M.K. and MacRae J.C. (2001) Milk production and N partitioning in early lactation dairy cows offered perennial ryegrass containing a high concentration of water soluble carbohydrates.

- In: *Proceedings of the British Society of Animal Science 2001*. British Society of Animal Science, Penicuik, p. 6.
- Morris, C.D., Derry, J.F. and Hardy, M.B. (1999) Effect of cattle and sheep grazing on the structure of Highland Sourveld swards in South Africa. *Tropical Grasslands*. **33**, 111–121.
- Murphy, M.R., Baldwin, R.L., Ulyatt, M.J., and Koong, L.J. (1983) A quantitative analysis of rumination patterns. *J. Anim. Sci.* **56**, 1236-40.
- Newman, J.A., Parsons, A.J., Thornley, J.H.M. and Penning, P.D., (1995) Optimal diet selection by a generalist grazing herbivore. *Functional Ecology*. **9**, 255-268.
- Newman, J.A., Penning, P.D., Parsons, A.J., Harvey, A. and Orr, R.J. (1994) Fasting affects intake behaviour and diet preference of grazing sheep. *Animal Behaviour*. **47**, 185-193.
- Nicol, A.M. (1987) Livestock feeding on pasture. *New Zealand Society of Animal Production*. Occasional Publication No. 10.
- Nielsen, B.K., Kristensen, A.R. and Thamsborg, S.M. (2004) Optimal decisions in organic steer production – a model including winter feed level, grazing strategy and slaughtering policy. *Livestock Production Science*. **88**, 239-250.
- Orr, R.J., Cook, J.E., Champion, R.A. and Rook, A.J. (2004) Relationships between morphological and chemical characteristics of perennial ryegrass varieties and intake by sheep under continuous stocking management. *Grass and Forage Science*. **59**, 389-398.
- Orr, R.J., Rutter, S.M., Penning, P.D. and Rook, A.J. (2001) Matching grass supply to grazing patterns for dairy cows. *Grass and Forage Science*. **56**, 352-361
- Østergaard, S., Sorensen, J.T. and Houe, H. (2003) A stochastic model simulating milk fever in a dairy herd. *Preventative Veterinary Medicine*. **58**, 125-143.
- Parsons, A.J., Newman, J.A., Penning, P.D., Harvey, A. and Orr, R.J. (1994) Diet preference of sheep: effects of recent diet, physiological state and species abundance. *J. Animal Ecology* **63**, 465-478.
- Payne R.W. (2004) *The Guide to Genstat 7.1, Part 2: Statistics*. Oxford: VSN International Limited.
- Penning, P.D., Parson, A.J., Orr, R.J., Harvey, A. and Champion, R.A. (1995) Intake and behaviour responses in sheep, in different physiological states, when grazing monocultures of grass or white clover. *Applied Animal Behaviour Science*. **45**, 63-78.

- Penning, P.D., Parsons, A.J., Orr, R.J. and Hooper, G.E. (1994) Intake and behaviour responses by sheep to changes in sward characteristics under rotational grazing. *Grass and Forage Science*. **49**, 476-486.
- Penning, P.D., Parsons, A.J., Orr, R.J. and Treacher, T.T. (1991) Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. *Grass and Forage Science*. **46**, 15-28.
- Penning, P.D., Parsons, A.J., Hooper, G.E. and Orr, R.J. (1989) Responses in ingestive behaviour by sheep to changes in sward structure. In: *Proceedings of the XVI International Grassland Congress*, 4-11 October 1989, Nice, France. Association Francaise pour la Production Fourragere, Versailles, France: pp. 791-792.
- Penning, P.D. and Hooper, G.E. (1985) An evaluation of short term weight changes in grazing sheep for estimating herbage intake. *Grass and Forage Science*. **40**, 79-84.
- Petit, M. and Bechet, G. (1995) Grass intake and grazing behaviour of dry and suckling ewes according to sward height. *Annales de Zootechnie*. **44** suppl, 250.
- Peyraud, J.L., and Delaby, L. (2001) Ideal concentrate feeds for grazing dairy cows responses to supplementation in interaction with grazing management and grass quality. In: *P. C. Garnsworthy and J. Wiseman (eds.). Recent Advances in Animal Nutrition*. Nottingham University Press, UK. p. 203
- Peyraud, J.L. and Astigarraga, L. (1998) Review of the effect of nitrogen fertilisation on the chemical composition, intake, digestion and nutritive value of fresh herbage: consequences on animal nutrition and N balance. *Animal Feed Science and Technology*. **72**, 235-259.
- Peyraud, J.L., Comeron, E.A., Wade, M.H. and Lemaire, G. (1996) The effect of daily herbage allowance, herbage mass and animal factors upon herbage intake by grazing dairy cows. *Annales de Zootechnie*. **45**, 201-217.
- Phillips, C.J.C. (1992) Photoperiod. In: *Phillips, C.J.C. and Piggitt, D. (eds.) Farm animals and the environment*. CAB International, Wallingford, pp: 131-141.
- Phillips, C.J.C. (1988) The use of conserved forage as a supplement for grazing dairy cows. *Grass and Forage Science*. **43**, 215-230.
- Plá, L.M., Pomar, C. and Pomar, J. (2003) A Markov decision sow model representing the productive lifespan of herd sows. *Agricultural Systems* **76**, 253-272.
- Poppi, D.P., Hughes, T.P. and L'Huillier, P.J. (1987) Intake of pasture by grazing ruminants. In: *Livestock Feeding on Pasture*. NZ Soc. Anim. Prod. Occ. Pub. No. 10. Ruakura Agric. Centre, Hamilton, NZ. p. 55

- Prache, S., Gordon, I.J. and Rook, A.J. (1998) Foraging behaviour and diet selection in domestic herbivores. *Annales de Zootechnie*. **47**, 335-345.
- Prache, S. (1997) Intake rate, intake per bite and time per bite of lactating ewes on vegetative and reproductive swards. *Applied Animal Behaviour Science*. **52**, 53-64.
- Prache, S. and Petit, M. (1995) Influence of maturity of the sward on the bite mass of lactating ewes. *Annales de Zootechnie*. **44** suppl, 108.
- Provenza, F.D. and Balph, D.F. (1990) Applicability of diet-selection models to various grazing challenges ruminants encounter. In: *Hughes, R.N. (ed). Behavioural Mechanisms of Food Selection*. NATO ASI Series, Volume G 20, Springer-Verlag, Berlin, Germany. Pp. 423-459.
- Pulido, R.G. and Leaver, J.D. (2001) Quantifying the influence of sward height, concentrate level and initial milk yield on the milk production and grazing behaviour of continuously stocked dairy cows. *Grass and Forage Science*. **56**, 57-67
- Reeves, M (1998) Milk production from kikuyu (*Pennisetum clandestinum*) grass pastures. PhD Thesis, The University of Sydney, Australia.
- Reeves, M., Fulkerson, W.J. Kellaway, R.C. and Dove, H. (1996) A comparison of three techniques to determine the herbage intake of dairy cows grazing kikuyu (*Pennisetum clandestinum*) pasture. *Aust. J. Expt. Agric.* **36**, 23-30.
- Remington, K.K., Bonham, C.D. and Reich, R.M. (1992) Blue Grama-Buffalograss responses to grazing – a Weibull distribution. *Journal of Range Management*. **45**, 272–276
- Roguet, C., Prache, S. and Petit, M. (1998) Feeding station behaviour of ewes in response to forage availability and sward phenological stage. *Applied Animal Behaviour Science*. **56**, 187–201.
- Rook, A.J. and Yarrow, N.H. (2002) Incorporating grazing behaviour measurements in models to predict herbage intake by grazing dairy cows. *Grass and Forage Science*. **57**, 19–24
- Rook, A.J. (2000) Principles of foraging and grazing behaviour. In: *A. Hopkins (ed). Grass: Its Production and Utilisation*. Blackwell Science, Boston, MA, USA. pp. 229
- Rook A.J. and Huckle C.A. (1995) Synchronization of ingestive behaviour by grazing dairy cows. *Animal Science*. **60**, 25–30.

- Rook, A.J., Huckle, C.A. and Penning, P.D. (1994) Effects of sward height and concentrate supplementation on the performance of spring calving dairy cows grazing grass/white clover swards. *Applied Animal Behaviour Science*. **40**, 101–112.
- Rook, A.J. and Penning, P.D. (1991) Stochastic models of grazing behaviour in sheep. *Applied Animal Behaviour Science*. **32**, 167-177.
- Sanders, I., Topp, C.F.E., Swain, D., Wilson, L. and McRoberts, N. (2003) Modelling seasonal changes in spatial heterogeneity of sward height in grass-clover and grass only swards. In: *Seventh BGS Research Conference, Aberystwyth, 1–3 September 2003*. Reading, UK: British Grassland Society. pp. 41–42
- SCA (Standing Committee on Agriculture) (1990). Feeding Standards for Australian Livestock. Ruminants. (CSIRO Aust., Melbourne.)
- Seman, D.H., Stuedemann, J.A. and Hill, N.S. (1999) Behaviour of steers grazing monocultures and binary mixtures of alfalfa and tall fescue *J. Animal Science*. **77**, 1402–1411.
- Seman, D.H., Stuedemann, J.A. and Anderson, J.E. (1997) Spectral analysis of bovine grazing behaviour on *Neotyphodium coenophialum* infested tall fescue *Applied Animal Behaviour Science*. **54**, 73-87
- Shiyomi, M., Okada, M., Takahashi, S. and Tang, Y.H. (1998) Spatial pattern changes in aboveground plant biomass in a grazing pasture. *Ecological Research*. **13**, 313–322.
- Shiyomi, M., Akiyama, T. and Takahashi, S. (1984) A spatial pattern model of plant biomass in grazing pasture II. *Journal of Japanese Society of Grassland Science*. **30**, 40–48.
- Shiyomi M., Akiyama T. and Takahashi S. (1983) A spatial pattern model of plant biomass in grazing pasture I. *Journal of Japanese Society of Grassland Science*. **28**, 373–382.
- Soca, P., Chilibroste, P. and Mattiauda, D. (1999) Effect of the moment and length of the grazing session on: 2. Grazing time and ingestive behaviour. In: *Moraes, A., Nabinger, C., Carvalho, P.C., Alvez, S.J. and Lustosa, S.B. Agosto. (eds.) Proceedings of international Symposium “Grassland Ecophysiology and Grazing Ecology”*. Curitiba. Brasil. pp. 295-298

- Spalinger, D.E. and Hobbs, N.T. (1992) Mechanisms of foraging in mammalian herbivores: New models of functional response. *The American Naturalist*. **140**, 325-348.
- St-Pierre, N.R. (2001) Integrating quantitative findings from multiple studies using mixed model methodology. *J. Dairy Science*. **84**, 741–755.
- Stakelum, G. (1986a) Herbage intake of grazing dairy cows. 1. Effect of autumn supplementation with concentrates and herbage allowance on herbage intake. *Irish J. Agric. Res.* **25**, 31–40.
- Stakelum, G. (1986b) Herbage intake of grazing dairy cows. 3. Effect of herbage mass, herbage allowance and concentrate feeding on the herbage intake of dairy cows grazing on mid-summer pasture. *Irish J. Agric. Res.* **25**, 179–189.
- Stakelum, G. (1986c) Herbage intake of grazing dairy cows. 3. Effects of herbage mass, herbage allowance and concentrate feeding on the herbage intake of dairy cows grazing on midsummer pasture. *Irish J. Agric. Res.* **25**, 179–189.
- Stobbs, T. H. (1975). Factors limiting the nutritional value of grazing tropical pastures for beef and milk production. *Tropical Grasslands*. **9**, 141-150.
- Stobbs, T.H. (1973a) The effect of plant structure on the intake of tropical pastures. 1. Variation in the bite size of grazing cattle. *Aust. J. Agric. Res.* **24**, 809–819.
- Stobbs, T.H. (1973b) The effect of plant structure on the intake of tropical pastures 2. Differences in sward structure, nutritive value, and bite size of animals grazing *setarza anceps* and *chlorzs ga yana* at various stages of growth. *Aust. J. Agric. Res.* **24**, 821–829.
- Stockdale, C.R. (2000a) Levels of pasture substitution when concentrates are fed to grazing dairy cows in northern Victoria. *Aust. J. Exp. Agric.* **40**, 913-921.
- Stockdale, C.R. (2000b) Differences in body condition and body size affect the responses of grazing dairy cows to high-energy supplements in early lactation. *Aust. J. Exp. Agric.* **40**, 903–911.
- Stockdale, C.R. (1994) Persian clover and maize silage. I. Silage as a supplement for lactating dairy cows offered herbage of different quality. *Aust. J. Agric. Res.* **45**, 1751-1765.
- Stroup, W.W., Nielsen, M.K. and Gosey, J.A. (1987) Cyclic variation in cattle feed intake data: Characterization and implications for experimental design. *J. Animal Science*. **64**, 1638-1647.

- Tas, B.M., Taweel, H.Z., Smit, H. J., Elgersma, A., Dijkstra, J. and Tamminga, S. (2005) Effects of perennial ryegrass cultivars on intake, digestibility, and milk yield in dairy cows. *J. Dairy Sci.* **88**, 3240-3248.
- Tharmaraj, J., Wales, W.J., Chapman, D.F. and Egan, A.R. (2003) Defoliation pattern, foraging behaviour and diet selection by lactating dairy cows in response to sward height and herbage allowance of a ryegrass-dominated pasture. *Grass and Forage Science.* **58**, 225-238.
- Trevaskis, L.M., W.J. Fulkerson, W.J. and Nandra, K.S. (2004) Effect of time of feeding carbohydrate supplements and pasture on production of dairy cows. *Livestock Production Science.* **85**, 275-285.
- Trevaskis, L.M. (2003) Improving the utilisation of pasture nitrogen by ruminants. PhD Thesis, Faculty of Veterinary Science, University of Sydney.
- Tsutsumi, M., Shiyomi, M., Sato, S. and Sugawara, K. (2002) Use of gamma distribution in aboveground biomass of plant species in grazing pasture. *Grassland Science* **47**, 615-618.
- Ungar, E.D. (1996) Ingestive behaviour. In: *Hodgson, J. and Illius, A.W. (eds.). The Ecology and Management of Grazing Systems.* CAB INTERNATIONAL, Wallingford, Oxon OX10 8 DE, UK. pp. 185-218
- Ungar, E.D. and Noy-Meir, I. (1988) Herbage intake in relation to availability and sward structure: Grazing processes and optimal foraging. *J. Applied Ecology.* **25**, 1045-1062.
- Vallentine, J.F. (2001) *Grazing Management.* Academic Press, 525 B Street, Suite 1900, San Diego, CA 92101-4495. 2001. ISBN 0-12-710001-6
- Van Vuuren, A.M. (1993) *Digestion and nitrogen metabolism of grass fed dairy cows.* PhD Thesis. Wageningen Agricultural University.
- Van Vuuren, A.M., Van der Koelen, C.J. and Vroons-de Bruin, J. (1986) Influence of level and composition of concentrate supplements on rumen fermentation patterns of grazing dairy cows. *Netherlands Journal of Agricultural Science* **34**, 457-467.
- Vérité, R., Journet, M., Flechet, J., et al., (1970) Influence de la teneur en eau et de la déshydratation de l'herbe sur sa valeur alimentaire pour les vaches laitières. *Annales de Zootechnie*, **19**, 255-268.
- Wade, M.H., Peyraud, J.L., Lemaire, G. and Comeron, E.A. (1989) The dynamics of daily area and depth of grazing and herbage intake of cows in a five-day paddock

- system. In: *Proceedings 16<sup>th</sup> International Grassland Congress, Nice, France*. pp. 1111-1112.
- Waite, R. (1963) Grazing behaviour. In: *Worden, A.N., Sellers K.C. and Tribe, D.E. (eds.) Animal health, production and pasture*. London: Longmans, pp.286-309.
- Wales, W.J., Stockdale, C.R. and Doyle, P.T. (2005) Plant and sward characteristics to achieve high intake in ruminants. In: *Murphy, J.J. (ed.) Utilisation of grazed grass in temperate animal systems: proceedings of a satellite workshop of the XXth International Grassland Congress, Cork, Ireland, July 2005*. Wageningen Academic Publishers, Wageningen, pp. 37-47.
- Wales, W.J., Williams, Y.J. and Doyle, P.T. (2001) Effect of grain supplementation and the provision of chemical or physical fibre on marginal milk production responses of cows grazing perennial ryegrass pastures *Aust. J. Exp. Agric.* **41**, 465–471.
- Wales, W. J., Doyle, P. T., Stockdale, C. R. and Dellow, D. W. (1999) Effects of variations in herbage mass, allowance, and level of supplement on nutrient intake and milk production of dairy cows in spring and summer. *Aust. J. Exp. Agric.* **39**,119–130.
- Walker, J.W. and Heitschmidt, R.K. (1989) Some effects of a rotational grazing treatment on cattle grazing behavior. *J. Range Manage.* **42**, 337-342.
- Wallis de Vries, M. F. and Dalebout, C. (1994) Foraging strategy of cattle in patchy grassland. *Oecologia* **100**, 98–106.
- Williams, Y.J., Wales, W.J., Doyle, P.T., Egan, A.R. and Stockdale, C.R. (2005) Effects of grain or hay supplementation on the chewing behaviour and stability of rumen fermentation of dairy cows grazing perennial ryegrass-based pasture in spring. *Aust. J. Exp. Agric.* **45**, 1519-1528.
- Wilson, S., Dobos, R.C. and Fell, L.R. (2005) Spectral analysis of feeding and lying behaviour of cattle kept under different feedlot conditions. *Journal of Applied Animal Welfare Science.* **8**, 13-24
- Woodward, S.J.R. (1998) Bite mechanics of cattle and sheep grazing grass-dominant swards. *Applied Animal Behaviour Science.* **56**, 203–222.
- Wright, I. A., Whyte, T. K. and Osoro, K. (1990) The herbage intake and performance of autumn-calving beef cows and their calves when grazing continuously at two sward heights. *Animal Production.* **51**, 85–92.

## **APPENDIX 1.**

### **Data for Chapter 3 analyses**

**Table A1.1 Behaviour data for Chapter 3 – SH 10cm**

time = time of day (24h clock); graz = number of cows grazing; rum = number of cows ruminating; rest = number of cows resting

time	Grazing duration															Total number of cows		
	1h			2h			4h			8h			15h			graz	rum	rest
	graz	rum	rest	graz	rum	rest	graz	rum	rest	graz	rum	rest	graz	rum	rest	graz	rum	rest
16:20	6	0	0	6	0	0	6	0	0	6	0	0	6	0	0	30	0	0
16:40	4	1	1	6	0	0	6	0	0	5	0	1	6	0	0	27	1	2
17:00	5	1	1	2	1	2	4	1	2	5	0	1	6	0	0	22	3	6
17:30				2	2	2	3	1	1	2	2	2	3	1	2	10	6	7
18:00				3	1	2	4	1	1	2	1	2	2	1	3	11	4	8
18:30							3	2	2	4	0	1	2	2	2	9	4	5
19:00							4	2	0	3	1	2	4	1	1	11	4	3
19:30							3	2	1	3	1	2	2	2	3	8	5	6
20:00							1	5	0	1	5	0	0	6	0	2	16	0
20:30										0	3	3	0	5	1	0	8	4
21:00										0	1	5	0	3	3	0	4	8
21:30										0	2	4	0	2	4	0	4	8
22:00										0	1	5	0	2	3	0	3	8
22:30										0	3	3	0	3	3	0	6	6
23:00										0	3	3	0	2	4	0	5	7
23:30										0	2	4	0	3	3	0	5	7
0:00										0	1	5	1	3	2	1	4	7
0:30													0	4	2	0	4	2
1:00													0	5	1	0	5	1
1:30													0	3	3	0	3	3
2:00													1	2	3	1	2	3
2:30													0	1	5	0	1	5
3:00													0	3	3	0	3	3
3:30													1	2	4	1	2	4

4:00	0	2	4	0	2	4
4:30	0	2	4	0	2	4
5:00	0	3	3	0	3	3
5:30	0	2	4	0	2	4
6:00	0	2	4	0	2	4
6:30	0	3	3	0	3	3
7:00	1	3	2	1	3	2

---

**Table A1.2 Behaviour data for Chapter 3 – SH 13cm**

time = time of day (24h clock); graz = number of cows grazing; rum = number of cows ruminating; rest = number of cows resting

time	Grazing duration															Total number of cows		
	1h			2h			4h			8h			15h			graz	rum	rest
	graz	rum	rest	graz	rum	rest	graz	rum	rest	graz	rum	rest	graz	rum	rest	graz	rum	rest
16:20	6	0	0	6	0	0	6	0	0	6	0	0	6	0	0	30	0	0
16:40	6	0	0	6	0	0	6	0	0	5	0	1	6	0	0	29	0	1
17:00	6	0	0	4	0	2	4	0	2	5	0	1	5	0	1	24	0	6
17:30				3	1	2	4	0	1	3	1	2	4	0	2	14	2	7
18:00				4	1	1	3	2	1	3	0	2	4	2	1	14	5	5
18:30							3	2	1	5	0	0	2	1	3	10	3	4
19:00							5	1	1	3	2	1	5	1	1	13	4	3
19:30							4	1	1	3	0	3	3	1	2	10	2	6
20:00							1	3	2	0	5	1	0	5	0	1	13	3
20:30										0	4	2	0	4	2	0	8	4
21:00										0	3	3	0	1	5	0	4	8
21:30										0	1	5	0	2	4	0	3	9
22:00										0	3	3	0	3	3	0	6	6
22:30										0	2	4	0	3	3	0	5	7
23:00										0	2	4	0	5	1	0	7	5
23:30										0	2	4	0	4	2	0	6	6
0:00										0	3	3	0	3	3	0	6	6
0:30													2	2	2	2	2	2
1:00													1	4	1	1	4	1
1:30													1	3	2	1	3	2
2:00													0	2	3	0	2	3
2:30													0	3	3	0	3	3
3:00													0	3	3	0	3	3
3:30													1	2	3	1	2	3

4:00	0	2	4	0	2	4
4:30	0	3	3	0	3	3
5:00	0	3	3	0	3	3
5:30	0	4	2	0	4	2
6:00	0	1	5	0	1	5
6:30	1	2	3	1	2	3
7:00	1	2	3	1	2	3

---

## **APPENDIX 2.**

### **GENSTAT code and data for Chapter 4 analyses**

## **A2.1 GENSTAT code for fitting the 5 distributions**

```
"fit SH10 GD 1h data (g11)"
factor [levels=(4,6,8,10,12,14,16,18)] g11; decimals=0
table [classification=g11;values=1,9,15,16,9,4,4,2] g11c
distribution [distribution=normal] g11c
distribution [distribution=gamma] g11c
distribution [distribution=lognormal] g11c
distribution [distribution=weibull] g11c
distribution [distribution=dnvunequal;print=monitoring] g11c
distribution [distribution=dnvequal] g11c

"fit g12"
factor [levels=(4,6,8,10,12,14,16,18)] g12; decimals=0
table [classification=g12;values=1,15,17,14,6,3,3,1] g12c
distribution [distribution=normal] g12c
distribution [distribution=gamma] g12c
distribution [distribution=lognormal] g12c
distribution [distribution=weibull] g12c
distribution [distribution=dnvunequal] g12c
distribution [distribution=dnvequal] g12c

"fit g13"
factor [levels=(4,6,8,10,12,14,16,18)] g13; decimals=0
table [classification=g13;values=3,16,22,11,5,1,1,1] g13c
distribution [distribution=normal] g13c
distribution [distribution=gamma] g13c
distribution [distribution=lognormal] g13c
distribution [distribution=weibull] g13c
distribution [distribution=dnvunequal] g13c
distribution [distribution=dnvequal] g13c

"fit g14"
factor [levels=(3,5,6,8,10,11,13,14)] g14; decimals=0
table [classification=g14;values=1,8,24,12,9,1,3,2] g14c
distribution [distribution=normal] g14c
distribution [distribution=gamma] g14c
distribution [distribution=lognormal] g14c
distribution [distribution=weibull] g14c
distribution [distribution=dnvunequal] g14c
distribution [distribution=dnvequal] g14c

"fit g15"
factor [levels=(4,6,8,9,11,12,14,14)] g15; decimals=0
table [classification=g15;values=17,11,13,10,5,2,1,1] g15c
distribution [distribution=normal] g15c
distribution [distribution=gamma] g15c
distribution [distribution=lognormal] g15c
distribution [distribution=weibull] g15c
distribution [distribution=dnvunequal] g15c
distribution [distribution=dnvequal] g15c

"fit g21"
factor [levels=(7,10,13,15,18,20,23)] g21; decimals=0
table [classification=g21;values=6,21,18,6,3,5,1] g21c
distribution [distribution=normal] g21c
distribution [distribution=gamma] g21c
distribution [distribution=lognormal] g21c
```

```

distribution [distribution=weibull] g21c
distribution [distribution=dnvunequal] g21c
distribution [distribution=dnvequal] g21c

"fit g22"
factor [levels=!(6,8,10,12,14,16,18,19)] g22; decimals=0
table [classification=g22;values=8,19,17,8,3,4,0,1] g22c
distribution [distribution=normal] g22c
distribution [distribution=gamma] g22c
distribution [distribution=lognormal] g22c
distribution [distribution=weibull] g22c
distribution [distribution=dnvunequal] g22c
distribution [distribution=dnvequal] g22c

"fit g23"
factor [levels=!(3,5,8,10,13,16,18,19)] g23; decimals=0
table [classification=g23;values=1,2,15,27,10,3,0,2] g23c
distribution [distribution=normal] g23c
distribution [distribution=gamma] g23c
distribution [distribution=lognormal] g23c
distribution [distribution=weibull] g23c
distribution [distribution=dnvunequal] g23c
distribution [distribution=dnvequal] g23c

"fit g24"
factor [levels=!(5,6,8,10,11,13,14,16)] g24; decimals=0
table [classification=g24;values=4,17,9,13,9,4,2,2] g24c
distribution [distribution=normal] g24c
distribution [distribution=gamma] g24c
distribution [distribution=lognormal] g24c
distribution [distribution=weibull] g24c
distribution [distribution=dnvunequal] g24c
distribution [distribution=dnvequal] g24c

"fit g25"
factor [levels=!(4,8,12,16,20,24,28)] g25; decimals=0
table [classification=g25;values=4,30,17,6,2,0,1] g25c
distribution [distribution=normal] g25c
distribution [distribution=gamma] g25c
distribution [distribution=lognormal] g25c
distribution [distribution=weibull] g25c
distribution [distribution=dnvunequal] g25c
distribution [distribution=dnvequal] g25c

```

Note that GENSTAT requires a factor be set that contains the heights and a table containing the frequencies of these heights. That is, for g11 there is 1 at 4cm, 9 at 6cm, 15 at 8cm and so on.

## A2.2 GENSTAT code to generate figures in Chapter 4.

```

variate
[values=0,3.2,2.63,3.95,5.37,6.62,7.38,7.47,6.84,5.68,4.27,2.91,1.79,
1,0.51,0.38] g11f
& [values=3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18] g11h
& [values=3,4,5,6,7,8,9,10,11,12,13,14,15,16,17,18] lim11
pen 1;method=monotonic; symbol=0; thickness=2.5
axes 1; xtitle='Height (cm)';ytitle='Frequency';ylower=0.0;
yupper=14.0; xlower=0.0;xupper=20
dgraph [window=1; key=0] g11f;g11h
DHISTOGRAM [WINDOW=1; KEY=0; limits=lim11; screen=keep] hpost11

```

This code uses the data from Tables A1.1 and A1.2 below. This code was repeated for the other variables listed below.

**Table A2.1 Data for pre-grazing sward height measurements for SH 10cm and 13cm treatments at GD of 1, 2, 4, 8 and 15h.**

hpre11 = SH 10cm GD 1h; hpre12 = SH 10cm GD 2h; hpre13 = SH 10cm GD 4h; hpre14 = SH 10cm GD 8h; hpre15 = SH 10cm GD 15h  
hpre21 = SH 13cm GD 1h; hpre22 = SH 13cm GD 2h; hpre23 = SH 13cm GD 4h; hpre24 = SH 13cm GD 8h; hpre25 = SH 13cm GD 15h

hpre11	hpre12	hpre13	hpre14	hpre15	hpre21	hpre22	hpre23	hpre24	hpre25
6.5	5.5	5	4.5	4.5	8.5	6	7.5	6	6
7	6	6	4.5	6	9	8	8.5	6	6
7	6	6	5.5	6	9	8.5	9	8	6
7.5	6.5	7.5	5.5	6	9.5	9.5	10	9	6.5
7.5	6.5	7.5	6	6.5	9.5	9.5	10	9.5	8
7.5	7	7.5	7	7	10	10	10	10	9
8	7	8	7.5	7	10	11	10	11.5	10
8.5	7	9	7.5	7.5	10	11	10.5	11.5	10
8.5	8	9	8	8	10.5	11	11	12	10
9	9	9	9	8	10.5	11	12	13	10
9	9	9.5	9	8.5	11	11.5	12.5	13	10
10	9.5	9.5	9	8.5	11	13	12.5	13.5	10.5
10.5	10	9.5	9	9.5	12.5	13	12.5	13.5	10.5
10.5	10	9.5	9.5	9.5	13.5	14	13	14.5	11

11.5	10	9.5	10.5	9.5	14	14.5	13.5	14.5	12
13	10	10	10.5	9.5	14.5	14.5	13.5	15.5	12
14	10.5	11	10.5	10.5	15	15	14	16.5	14
14	10.5	13.5	11.5	11.5	20	15	14	17	14.5
14	11	13.5	12.5	11.5	21.5	16	14.5	20.5	15
15.5	11.5	14	13.5	12.5	26.5	17	16.5	21	19.5
5.5	13	6	6	6.5	5	6	5.5	6	6
6	5	6.5	7.5	8	6	8	6	11	6
6	6	6.5	7.5	8	6	8.5	6	12	6
6	6.5	7.5	10.5	8	8	8.5	6	12	10
7.5	6.5	7.5	11	8.5	8.5	10	6.5	13.5	11
8	7	7.5	11	8.5	11.5	11	10	13.5	12
9	7	7.5	11.5	9	12	12	11.5	14	12.5
9	7.5	8	12	10	12.5	12	12.5	14	14
9	7.5	8.5	12	10	13.5	12.5	12.5	14	14.5
9	7.5	8.5	12.5	10.5	15	12.5	13.5	14.5	17
9	7.5	9	13	10.5	15	12.5	14	15.5	17
9	8	9	13	10.5	16.5	12.5	15	15.5	17.5
10.5	8	10	13.5	11	17	13	16	15.5	18.5
11	8	10	13.5	11.5	18	13.5	16.5	16.5	18.5
11	9	10	14	12	20	13.5	17	17.5	18.5
11.5	9.5	10.5	14	12	20.5	13.5	17.5	18.5	19
12	10.5	10.5	14.5	12.5	22.5	14	18.5	18.5	21.5
12	11	11	15	13.5	23	15	20.5	19.5	23
12.5	11.5	11	15	14	23.5	16.5	26.5	19.5	23
13	13	11.5	15	15	25.5	20.5	28	21	23.5
6	14	7.5	6	8	26	6	5.5	6	7.5

6	6	7.5	6	8.5	6	6	6	7	9
6	6	9.5	6	10	6	6	6	7	9.5
8	7	11.5	6	10	6	9.5	6	7.5	10
8.5	8.5	12	6	10.5	6.5	11	6	8.5	10
9.5	10	13	9	10.5	8	11	6.5	9	10.5
9.5	12	13	9	11	10	12	7.5	9.5	11
10.5	12	13.5	9.5	11	10.5	13	9.5	10.5	11
11.5	12.5	14	10	11	11	14	9.5	10.5	11
12	13	14	10	11	11	15	11.5	11.5	11
12.5	13	14	10	11	11	15.5	12	12	11.5
12.5	13.5	14	10.5	11.5	11.5	15.5	12.5	13.5	12.5
13	13.5	14.5	10.5	11.5	11.5	16	12.5	13.5	12.5
13	13.5	14.5	10.5	11.5	12	17	13.5	13.5	12.5
13.5	14.5	15	11	12	12	17	14	14.5	12.5
14	15.5	15.5	11.5	12	13	17	14.5	17.5	13
15.5	16	16.5	13.5	13	13	17.5	16	18.5	14
16	16	17.5	14.5	13.5	14	18	16	18.5	14.5
16.5	16.5	18	16.5	13.5	14	19	17.5	22	15.5
17.5	18	19.5	20	14	14.5	20	17.5	23.5	18.5

**Table A2.2 Data for post-grazing sward height measurements for SH 10cm and 13cm treatments at GD of 1, 2, 4, 8 and 15h.**

hpost11 = SH 10cm GD 1h; hpost12 = SH 10cm GD 2h; hpost13 = SH 10cm GD 4h; hpost14 = SH 10cm GD 8h; hpost15 = SH 10cm GD 15h  
hpost21 = SH 13cm GD 1h; hpost22 = SH 13cm GD 2h; hpost23 = SH 13cm GD 4h; hpost24 = SH 13cm GD 8h; hpost25 = SH 13cm GD 15h

hpost11	hpost12	hpost13	hpost14	hpost15	hpost21	hpost22	hpost23	hpost24	hpost25
5	3.2	4.1	4.1	3.2	6.4	6.4	5.9	3.2	2.7
5.5	5.5	4.5	4.5	4.1	7.3	6.4	5.9	4.1	2.7
6.4	5.5	5	4.5	4.1	7.3	6.4	7.3	4.5	4.1
6.4	5.9	5	5	4.1	7.7	7.7	7.7	5.9	5.5
6.4	5.9	5.5	5.5	4.1	8.2	7.7	7.7	5.9	5.5
6.8	6.4	5.9	5.5	4.5	8.2	8.6	8.2	5.9	5.9
6.8	6.4	5.9	5.5	4.5	8.2	8.6	8.2	5.9	5.9
7.3	6.4	5.9	5.5	4.5	8.6	9.1	8.2	5.9	6.4
7.3	6.4	5.9	5.5	4.5	8.6	9.1	8.6	6.4	6.4
7.7	6.4	6.4	5.9	5.5	8.6	9.5	8.6	6.4	6.4
7.7	6.4	6.4	5.9	5.9	8.6	9.5	9.1	6.4	6.4
8.2	6.8	6.4	6.4	6.4	9.1	9.5	9.1	6.4	6.8
8.6	6.8	6.4	6.4	6.4	9.1	10	9.1	6.4	7.3
9.1	7.3	6.4	6.8	6.8	10	10.5	9.5	6.4	7.3
9.1	7.7	6.8	6.8	6.8	10	11.4	9.5	6.8	7.3
10.5	7.7	7.3	7.3	7.3	10.9	11.4	10.5	6.8	8.2
10.5	7.7	7.3	7.3	7.7	10.9	11.8	10.5	6.8	8.2
10.9	8.2	7.7	7.7	8.2	11.4	11.8	11.8	8.2	9.1
11.4	9.5	10.5	8.6	8.2	11.4	12.3	12.3	8.6	10
11.4	10	10.5	8.6	8.2	12.3	13.6	13.2	13.2	10.5
3.2	10.5	2.7	3.6	4.1	5.9	4.5	1.8	5	3.2
4.5	4.1	3.6	3.6	4.5	6.8	5	5.5	6.8	5.5
5.5	4.5	4.1	3.6	4.5	7.3	5.5	6.4	7.3	7.7

5.5	4.5	5	4.1	5	8.2	5.9	6.4	7.7	8.2
5.5	5	5	4.5	5	8.2	6.4	7.7	8.2	8.2
5.9	5.5	5	5	5	9.1	6.4	7.7	8.6	8.2
5.9	5.5	5	5.5	5.9	9.1	6.8	8.2	9.1	9.5
6.4	5.5	6.8	5.9	5.9	9.1	6.8	8.6	9.5	10
7.3	5.9	6.8	6.4	6.4	10.9	6.8	8.6	9.5	10.5
7.7	5.9	7.3	6.4	6.4	11.4	6.8	9.1	10.5	10.9
7.7	6.4	7.3	6.8	7.3	11.8	7.3	9.5	10.5	10.9
8.2	6.8	7.3	6.8	7.3	12.7	7.3	10	10.5	11.8
8.2	6.8	7.7	8.2	7.7	13.2	7.7	11.8	10.9	12.3
8.2	7.7	8.2	8.2	7.7	13.2	7.7	11.8	10.9	13.6
8.6	8.2	8.2	9.5	8.6	14.5	8.6	11.8	11.4	13.6
10	8.2	8.6	9.5	9.1	15	9.5	11.8	11.8	14.1
10	9.5	9.1	10	9.1	16.4	11.4	13.2	12.7	15.5
11.4	9.5	9.5	12.3	9.5	16.8	11.4	15	13.2	17.3
11.8	10.9	10	13.2	11.4	19.5	12.7	18.2	15.5	17.3
16.4	11.4	10.9	13.6	13.6	20	14.5	18.6	15.9	24.1
5.9	13.2	3.6	1.8	3.2	21.8	4.5	4.1	4.5	3.2
7.3	4.1	4.1	5.5	3.2	8.2	5	4.5	5	4.1
7.7	5.9	5.5	5.9	4.5	8.2	5.5	5.9	5.5	4.1
8.2	6.4	6.4	5.9	4.5	9.1	5.5	6.4	5.9	4.5
8.6	8.2	6.4	6.4	4.5	10	6.8	6.4	5.9	4.5
9.1	8.2	6.4	6.4	5	10.5	7.3	6.4	5.9	5
9.5	8.6	6.8	6.4	5.5	10.5	7.3	6.4	7.3	5
9.5	9.1	6.8	6.4	5.9	10.5	7.7	6.8	7.7	5
10	9.1	7.7	6.4	5.9	10.9	8.2	6.8	7.7	5.5
11.4	10	7.7	6.4	6.4	10.9	9.1	6.8	8.2	5.9

11.4	10	8.2	6.8	6.4	11.4	9.1	7.3	8.2	6.4
12.3	10.5	8.6	6.8	7.3	11.8	9.5	7.7	8.2	6.8
13.2	11.4	8.6	7.3	7.3	11.8	9.5	7.7	8.2	6.8
13.6	11.8	9.1	7.7	7.7	12.3	10	9.5	8.6	7.3
13.6	12.3	9.5	7.7	7.7	12.3	10	9.5	9.1	7.7
14.1	12.7	10.9	8.6	7.7	12.7	10.9	9.5	10	7.7
14.1	14.1	11.8	8.6	9.1	15.5	14.1	9.5	10.5	8.2
14.1	15	13.6	9.5	10	18.6	14.5	10	10.5	8.6
14.5	15.9	14.1	12.3	11.8	19.1	14.5	10.5	10.9	9.1
17.3	16.8	17.3	12.7	12.3	19.5	19.1	11.4	11.4	12.3

## **APPENDIX 3**

### **GENSTAT code and behaviour data for Chapter 5**

### **A3.1 GENSTAT code to conduct spectral analysis of behaviour data from Chapter 3**

```
"Spectral analysis for SH 10cm - grazing"
calculate dgr11=difference(tgraz11)
CORRELATE [PRINT=auto] dgr11; autocorrelations=grlacl;test=grlt1
print grlt1
BJIDENTIFY [GRAPH=high;WINDOWS=8"!(5...8)"] tgraz11
calc grl11=mvrep(tgraz11-mean(tgraz11);0)
fourier [print=transform] grl11; transform=lowat1; itransform=lowbt1;
periodogram=lowpt1
```

```
"Spectral analysis for SH 13cm - grazing"
calculate dgrh1=difference(tgrazh1)
CORRELATE [PRINT=auto] dgrh1; autocorrelations=grhacl;test=grht1
print grht1
BJIDENTIFY [GRAPH=high;WINDOWS=8"!(5,6,7,8)"] tgrazh1
calc grh11=mvrep(tgrazh1-mean(tgrazh1);0)
fourier [print=transform] grh11; transform=hiat1; itransform=hibt1;
periodogram=hipt1
```

```
"Spectral analysis for SH 10cm - resting"
calculate drest11=difference(trest11)
CORRELATE [PRINT=auto] drest11; autocorrelations=restlt1;test=restltal
print restltal
BJIDENTIFY [GRAPH=high;WINDOWS=8"!(5...8)"] trest11
calc restl11=mvrep(trest11-mean(trest11);0)
fourier [print=transform] restl11; transform=rlat1; itransform=rlbt1;
periodogram=rlpt1
```

```
"Spectral analysis for SH 13cm - resting"
calculate dresth1=difference(tresth1)
CORRELATE [PRINT=auto] dresth1; autocorrelations=restht1;test=resthtal
print resthtal
BJIDENTIFY [GRAPH=high;WINDOWS=8"!(5...8)"] tresth1
calc resth11=mvrep(tresth1-mean(tresth1);0)
fourier [print=transform] resth11; transform=rhat1; itransform=rhbt1;
periodogram=rhpt1
```

```
"Spectral analysis for SH 10cm - ruminating"
calculate drum11=difference(trum11)
CORRELATE [PRINT=auto] drum11; autocorrelations=ruml1;test=ruml1al
print ruml1al
BJIDENTIFY [GRAPH=high;WINDOWS=8"!(5...8)"] trum11
calc ruml11=mvrep(trum11-mean(trum11);0)
fourier [print=transform] ruml11; transform=rulat1; itransform=rulbt1;
periodogram=rulpt1
```

```
"Spectral analysis for SH 13cm - ruminating"
calculate drumh1=difference(trumh1)
CORRELATE [PRINT=auto] drumh1; autocorrelations=rumht1;test=rumhtal
print rumhtal
BJIDENTIFY [GRAPH=high;WINDOWS=8"!(5...8)"] trumh1
calc rumh11=mvrep(trumh1-mean(trumh1);0)
fourier [print=transform] rumh11; transform=ruhat1; itransform=rubht1;
periodogram=rubpt1
```

**Table A3.1 Behaviour data from Chapter 3 for spectral analysis in Chapter 5**

tgrazl1 = time spent grazing at SH 10cm; truml1 = time spent ruminating at SH 10cm; trestl1 = time spent resting at SH 10cm; tgrazh1 = time spent grazing at SH 13cm; trumh1 = time spent ruminating at SH 13cm; tresth1 = time spent resting at SH 13cm

tgrazl1	truml1	trestl1	tgrazh1	trumh1	tresth1
52.6667	2.66667	5.33333	55.3333	0	4.66667
27.25	13.25	19.75	36.5	9	16
35.6667	13.6667	14.3333	41	12.3333	12
18	37	10.6667	19.3333	26.6667	16.3333
0	32	34	0	33.5	32.5
0	19	44.5	0	24.5	41.5
0	30.5	35.5	0	32	34
2.5	24	39.5	0	32.5	33.5
0	45	15	15	30	15
5	25	30	5	25	25
0	20	40	0	30	30
5	20	40	5	20	35
0	25	35	0	30	30
0	20	40	0	25	35
5	30	25	10	20	30

### **A3.2 GENSTAT code to conduct spectral analysis of behaviour data from Trevaskis et al. (2004)**

```
"Spectral analysis for PM"
calculate dgrh1=difference(minhpm)
CORRELATE [PRINT=auto] dgrh1; autocorrelations=grhacl;test=grht1
print grht1
BJIDENTIFY [GRAPH=high;WINDOWS=!(5...8)] minhpm
calc grh11=mvrep(minhpm-mean(minhpm);0)
fourier [print=transform] grh11; transform=hiat1; itransform=hibt1;
periodogram=hipt1

"Spectral analysis for ASYNCH"
calculate dresth1=difference(minhasyn)
CORRELATE [PRINT=auto] dresth1; autocorrelations=restht1;test=resthta1
print resthta1
BJIDENTIFY [GRAPH=high;WINDOWS=!(5...8)] minhasyn
calc resth11=mvrep(minhasyn-mean(minhasyn);0)
fourier [print=transform] resth11; transform=rhat1; itransform=rhbt1;
periodogram=rhpt1

"Spectral analysis for SYNCH"
calculate drumh1=difference(minhsyn)
CORRELATE [PRINT=auto] drumh1; autocorrelations=rumht1;test=rumhta1
print rumhta1
BJIDENTIFY [GRAPH=high;WINDOWS=!(5...8)] minhsyn
calc rumh11=mvrep(minhsyn-mean(minhsyn);0)
fourier [print=transform] rumh11; transform=ruhat1; itransform=ruhbt1;
periodogram=ruhpt1
```

**Table A3.2 Behaviour data from Trevaskis *et al.* (2004) for spectral analysis in Chapter 5**

minhpm = time spent grazing for PM group; minhsyn = time spent grazing for ASynch group; minhsyn = time spent grazing for Synch group

minhpm	minhsyn	minhasyn
60	50	40
20	59	59
8	42	44.5
53.5	31.5	26.5
16.5	51	25.5
14.5	52	60
50.5	42.5	45
39.5	47	48.5
0	0	0
40	48	55.5
59.5	58	57
37.5	11.5	13
1.5	0	1
20	9	3.5
50.5	16.5	3
36	14	26
4.5	6	9

## APPENDIX 4

### Solving steady-state probabilities

#### A4.1 Markov chains

A Markov chain is a special type of discrete-time stochastic process. To simplify, assume that at any time, the discrete-time stochastic process can be in one of a finite number of states labelled  $1, 2, \dots, s$ , such that:

$$P(X_{t+1} = i_{t+1} | X_t = i_t, X_{t-1} = i_{t-1}, \dots, X_1 = i_1, X_0 = i_0) = P(X_{t+1} = i_{t+1} | X_t = i_t) \text{ Equation A4.1}$$

Equation A4.1 says that the probability distribution of the state at time  $t+1$  depends on the state at  $t(i_t)$  and does not depend on the states the chain passed through on the way to  $i_t$ , at time  $t$ .

In this current study of Markov chains, there is further assumption that for all states  $i$  and  $j$  and all  $t$ ,  $P(X_{t+1}=j|X_t=i)$  is independent of  $t$ . Thus:

$$P(X_{t+1} = j | X_t = i) = p_{ij} \text{ Equation A4.2}$$

where  $p_{ij}$  is the probability that given the system is in state  $i$  at time  $t$ , it will be in a state  $j$  at time  $t+1$ . If the system moves from state  $i$  during one period to state  $j$  during the next period, a **transition** from  $i$  to  $j$  has occurred. The  $p_{ij}$  are often referred to as the **transition probabilities** for the Markov chain.

Equation A4.2 implies that the probability law relating the next period's state to the current state does not change, or remains stationary, over time. For this reason, A4.2 is often called the *Stationarity Assumption*.

#### A4.2 *n-step transition probabilities*

The question of interest here is: If a Markov chain is in state  $i$  at time  $m$ , what is the probability that  $n$  periods later the Markov chain will be in state  $j$ ? Thus:

$$P(X_{m+n} = j | X_m = i) = P(X_n = j | X_0 = i) = P_{ij}(n) \quad \text{Equation A4.3}$$

where  $P_{ij}(n)$  is called the *n-step probability* of a transition from state  $i$  to  $j$ .

This equation is also known as the *Chapman-Kolomogorov equation*.

#### A4.3 *Solving discrete-time Markov chains*

In Chapter 6 of this thesis two transition probability matrices (TPM) are available. To show how to solve these matrices as a discrete-time Markov chain, the TPM from SH10 (Chapter 3 data) is used as example. These solutions were lifted from the Connexions module m10835.pdf, available at <http://cnx.org/content/m10835/latest/> (accessed 11<sup>th</sup> October 2006).

Recall that the single step TPMs for the data from Chapter 3 data are:

$$SH10 = \begin{bmatrix} 0.75 & 0.18 & 0.07 \\ 0.12 & 0.67 & 0.21 \\ 0.02 & 0.20 & 0.78 \end{bmatrix}$$

$$SH13 = \begin{bmatrix} 0.80 & 0.13 & 0.07 \\ 0.05 & 0.70 & 0.21 \\ 0.03 & 0.17 & 0.80 \end{bmatrix}$$

These are clearly ergodic Markov chains. The computation for this was performed using MATLAB. There are four different ways of calculating the state probabilities using MATLAB.

*A4.3.1 Multiplying the TPM by a matrix containing the initial state probability vector.*

For example, say the initial state probability vector is  $p(0)=[0.1 \ 0.2 \ 0.1]$ . The evolution of the state probability vector for many transitions can be calculated by repeated applications of the Chapman-Kolomogorov equations.

```
EDU>> SH10=[0.75 0.18 0.07;0.12 0.67 0.21;0.02 0.2 0.78]
```

```
SH10 =
```

```
    0.7500    0.1800    0.0700  
    0.1200    0.6700    0.2100  
    0.0200    0.2000    0.7800
```

```
EDU>> p0=[0.1 0.2 0.1]
```

```
p0 =
```

```
    0.1000    0.2000    0.1000
```

```
EDU>> p1=p0*SH10
```

```
p1 =
```

```
    0.1010    0.1720    0.1270
```

```
EDU>> p2=p1*SH10
```

```
p2 =
```

```
    0.0989    0.1588    0.1422
```

```
EDU>> p3=p2*SH10
```

```
p3 =
```

```
    0.0961    0.1527    0.1512
```

and so on.

#### A4.3.2 Raising the TPM to higher powers

This can also be achieved by raising the TPM to higher and higher powers until all the entries in each column are identical to the other entries in the same column.

```
EDU>> SH10^20
```

```
ans =
```

```
0.2119 0.3693 0.4188
0.2109 0.3694 0.4197
0.2103 0.3694 0.4202
```

```
EDU>> SH10^21
```

```
ans =
```

```
0.2116 0.3693 0.4191
0.2109 0.3694 0.4197
0.2105 0.3694 0.4201
```

```
.
.
.
```

```
EDU>> SH10^50
```

```
ans =
```

```
0.2109 0.3694 0.4197
0.2109 0.3694 0.4197
0.2109 0.3694 0.4197
```

#### A4.3.3 Using the normalisation equation

A third method for determining the steady-state probabilities is to treat the problem as one of solving the set of linear equations represented by  $\pi P = \pi$ . However,  $P$  is a stochastic matrix (each of its rows sums to 1) and hence is singular. We need one other independent equation in the  $\pi_i$ s to go with any  $m - 1$  of the  $m$  equations from  $\pi P = \pi$ .

Fortunately, we always have one: the normalisation equation  $\sum_{i=1}^m (\pi_i) = 1$ .

To implement this method, first replace any column  $i$  (for instance, the last column, representing the equation for  $\pi_m$ ), with 1s, corresponding to the normalisation equation.

Following is the MATLAB code to achieve this.

```
EDU>> P1=SH10
```

```
P1 =
```

```
0.7500  0.1800  0.0700
0.1200  0.6700  0.2100
0.0200  0.2000  0.7800
```

```
EDU>> P1(:,3)=[1 1 1]'
```

```
P1 =
```

```
0.7500  0.1800  1.0000
0.1200  0.6700  1.0000
0.0200  0.2000  1.0000
```

Create the  $m \times m$  identity matrix with the  $i$ th diagonal element replaced by 0.

```
EDU>> J=diag([1 1 0],0)
```

```
J =
```

```
1  0  0
0  1  0
0  0  0
```

Solve the system of linear equations  $\pi (P1 - J) = (0, 0, \dots, 0, 1, 0, \dots, 0)^T$  where  $P1$  is SH10 with the  $i$ th column replaced by 1s.  $J$  is the diagonal matrix with 1s along the diagonal except for a 0 in the  $i$ th diagonal element, and the vector on the left-hand side is all 0's except for a 1 in the  $i$ th component.

```
EDU>> pi=[0 0 1]/(P1-J)
```

```
pi =
```

```
0.2109  0.3694  0.4197
```

#### A4.3.4 Eigenvalues of $\pi P = \pi$

Yet another way to solve for the steady state probability vector is based on the realization that  $\pi P = \pi$  implies  $\pi$  is a left eigenvector of  $P$ , with eigenvalue 1. Hence, another way of finding  $\pi$  is to find the left eigenvector corresponding to an eigenvalue of 1. In MATLAB, `[v,d] = eig(A)` returns a square matrix  $v$  whose columns are the right eigenvectors of the square matrix  $A$ , plus a diagonal matrix  $d$  of the eigenvalues of  $A$ . That is,  $d(i,i)$  is the eigenvalue corresponding to the right eigenvector  $v(:,i)$ . There are two problems. One, we want left, not right, eigenvectors of  $P$ . This is easy to get around, by noting that a left eigenvector of  $P$  is a right eigenvector of  $P^T$ , the transpose of  $P$ , for the same eigenvalues.

The second minor difficulty is that if  $\pi$  is an eigenvector, then  $a\pi$  is, too, for any nonzero constant  $a$ . We cannot predict how MATLAB will scale the eigenvectors. However, since the steady-state probabilities must sum to one, we can normalize each element of the eigenvector corresponding to the eigenvalue 1 by dividing by the sum of the elements in the eigenvector to obtain the steady-state probability vector.

The MATLAB code for this follows.

```
EDU>> [v,d]=eig(SH10')
```

```
v =
```

```
-0.3529 -0.7344 0.3216  
-0.6182 0.0583 -0.8108  
-0.7024 0.6762 0.4891
```

```
d =
```

```
1.0000    0    0  
    0 0.7221    0  
    0    0 0.4779
```

```
EDU>> pi=v(:,1)/sum(v(:,1))
```

```
pi =
```

```
0.2109
```

```
0.3694
```

```
0.4
```