A DYNAMICAL SYSTEMS MODEL FOR OPTIMIZING ROTATIONAL GRAZING

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Dedication

This thesis is dedicated to
my Lord and Master, Jesus Christ,
who brought me to Massey to do it.
My prayer is that something that I have done
in these three years
will endure.

Acknowledgments

The lion's share of the thanks goes to my principal supervisor, Professor Graeme C. Wake. Working with you these three years has taught me a lot both about research and about diplomacy. Thank you for regularly giving so generously of your time, for searching out sources of funding, for your constant optimism and encouragement, and for challenging me to mature in every aspect of being a scientist.

Sincere thanks are due also my external supervisors, Dr David G. McCall and Mr Anthony B. Pleasants of AgResearch Whatawhata. Thank you for your enthusiasm for the project and for the personal interest you have taken in me and my work.

Many thanks to Professor John Hodgson of the Department of Plant Science at Massey University—we have appreciated your generous help, interest and valuable advice throughout these three years.

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Abstract

This thesis considers modelling agricultural grazing using dynamical systems. It is in five chapters, some of which have been or will be published in international refereed journals.

The first chapter considers grazing a two-paddock sub-system at low pasture mass in order to maximise herbage conservation and/or herbage intake. For the latter objective, there is an optimal swap-over time which depends on the initial herbage masses and the stocking densities. In general, optimal swap-over gives only small improvements in herbage intake compared to continuous grazing or rotational grazing in which animals spend equal time in each paddock.

The second chapter applies this to comparing continuous, rotational, and optimal grazing strategies over a range of stocking rates. As stocking rate increases optimal rotational grazing can increase herbage intake.

The third chapter deals with grazing a multi-paddock system in order to maximise intake. Animals are shifted at regular time intervals. Stocking rate and average initial herbage have the greatest effect on herbage growth, conservation, and intake. Grazing strategy effects are less significant. However, traditional strategies of rotational grazing perform poorly in some cases, and in these cases a "greedy" grazing strategy can give improved production. The difficulties of finding optimal strategies are discussed.

The fourth chapter examines modelling senescence in grazed grass pasture using a differential-delay equation where senescence rates are explicitly dependent on leaf age. A simple differential-delay model is formulated and appraised by comparison to data from a published grazing experiment. This simple model describes subtle features of pasture dynamics.

The fifth chapter uses this delay model to make a simple comparison between rotational and continuous grazing. The average rate of senescence is higher under rotational grazing and this is exacerbated by delay effects. For this reason, production is likely to be lower under rotational grazing.

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Chapter 1

Introduction

This thesis deals with the problem of optimally feeding grazing animals on pasture. This problem is of interest to agricultural researchers wishing to improve the efficiency of using pasture resources to graze livestock.

On 6 November 1990 the Department of Mathematics (and Statistics) of Massey University held an industrial problem solving workshop as part of its Quantitative Problem Solving Consultancy (QPSC) programme. At this workshop Mr Tony Pleasants of AgResearch Whatawhata presented the problem of optimizing a rotational grazing system.

After the workshop the Department of Mathematics and AgResearch Whatawhata jointly decided to set up a Masters programme for a student to study optimal rotational grazing in agriculture. Dr David McCall and Mr Tony Pleasants from Whatawhata arranged a grant for support of a student to study in the Department of Mathematics of Massey University in 1991, to be supervised by Professor Graeme Wake. I began at Massey in March 1991. Later the same year the project was upgraded to a PhD. This thesis is an account of the research I have undertaken as a result of this joint project.

The first section of this chapter describes the original problem presented by Tony Pleasants at the QPSC workshop. This sets the scene for the work that appears in this thesis. A brief introduction to the biology of grazing follows, and then a review of theoretical studies of grazing. There is then a detailed outline of the raison d'etre and structure of each of chapters 2–6, and finally a summary of the major results.

1.1 Optimisation of a Grazing System[1]

1.1.1 Background

It is usual for farmers to adopt a planned approach to the grazing of farm animals in an attempt to control their intake of pasture. Pasture intake by animals is affected by the amount of pasture on offer, since this is the main factor in the ease of harvest by the animal. It is also affected by the length of time the animals have been grazing the field, since animals tend to avoid grazing pasture fouled by dung and urine. Similarly, the regrowth of pasture after grazing is affected by the amount of pasture left behind after grazing, since the growth rate of pasture is directly affected by the amount of photosynthetic tissue present (Davies 1988).

The amount of pasture on a field or consumed by grazing animals is measured by the weight of dry matter (DM) present in the pasture. Figures are quoted as kg DM per hectare for the amount of pasture present or as kg DM per day for the amount of pasture grazed.

The most common method of controlled grazing is called rotational grazing. Animals are placed in a field until they have grazed the pasture below a certain level of DM per hectare, then moved to the next field. Typically, animals are moved through a sequence of fields, then return to the first field to begin another round of grazing when the first field has recovered pasture mass.

The number of animals on an area of land is called the stocking density and is expressed as animals per hectare.

A farmer running a rotational grazing system with one animal class can control two interrelated factors: the stocking density and the speed of the round of grazing, that is, the number of animals and the time they spend in each field of the rotation. The aim of grazing management may vary, but most commonly it is to maximise the intake of the grazing animals (which maximises their growth rate) over a period of time. We assume this is the case here.

If the farmer moves the animals rapidly through the fields he ensures a high level of intake for the animals, but the animals return to the field grazed relatively quickly. This means that the pasture grazed previously by the animals has only a short time to regrow, and therefore, a reduced amount of dry matter is offered to the animals on the second rotation. This lowers their intake of pasture. Alternatively, if the animals are moved slowly through the fields of the rotation, this ensures higher

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[1] This section is an abridged transcript of the unpublished problem "Optimization of a Grazing System" presented on 6 November 1990 at the QPSC workshop at Massey University by Mr Tony Pleasants of AgResearch Whatawhata.

regrowth by the time they return to the first field, but the intake of the animals is reduced. Consequently they do not grow so big.

The problem a farmer faces can be described thus: he has a fixed area of land with a number of separate fields. He has a group of animals to be grazed on this land. The number of animals is under his control. He knows the amount of pasture DM on each field at the start of the period of grazing. He has a known period of time (typically 100 days) to work the grazing system. How should he choose the times to shift the animals from one field to the next in order to maximise the intake of the animals? He must bear in mind the constraints of the system. Animals need something to eat each day.

1.1.2 Mathematical Description

The important aspects of pasture growth which must be abstracted to deal with the problem being posed are, in our judgement, the following:

(a) It takes leaf to grow leaf, that is, pasture growth rate is dependent on the amount of pasture already present.

(b) Plant mass reaches an asymptote.

(c) The greater the plant mass, the more rapid the turnover, or decay, of plant material.

Points (a) and (b) have usually been modelled by the logistic equation,

$$w' = aw(1 - bw) \tag{1.1}$$

where a and b are constants. This has a number of appealing features in this situation.

There is good evidence that the rate of consumption of pasture dry matter by animals is proportional to the amount of pasture dry matter on offer (Hodgson 1985a). It is also dependent on the length of time the animals have been on the pasture, that is, the amount grazed, this being due to the fouling of pasture by dung and urine and the rejection of fouled pasture by the animals. The intake rate of animals will clearly be asymptotic at high levels of pasture mass, but our development is confined to the linear region as a first approximation. There are many practical circumstances for which the response in this region is of great interest.

This gives a simple equation for the rate of pasture consumption per animal, c':

$$c' = kw - q(w_0 - w) \qquad t > t_0,\ w_0 > w \tag{1.2}$$

where t_0 is the time the animals are introduced into the field and w_0 is the herbage cover at that time. The second term, $-q(w_0 - w)$, represents inhibition of grazing due to pasture fouling.

If we assume that there are n animals per hectare in the grazing group, then equations 1.1 and 1.2 can be written as a system,

$$\begin{aligned} w' &= aw(1-bw) - nc' \\ c' &= kw - q(w_0 - w) \end{aligned} \tag{1.3}$$

1.1.3 The Problem[2]

The problem facing the farmer may be summarised as follows: he is given two (or in general f) identical fields, each having initial conditions of $w(0)$ kgDM/ha. He has a group of animals. The animals must be rotated around two (or f) fields over a period of, say, $T = 100$ days. The problem is to find the times t_i between 0 and T, at which the animals must be changed from one field to the next in the sequence so that the intake of pasture mass by the animals c is maximised. This maximisation is subject to the constraints that the level of intake by the animals must never fall below a given level, c'_{min}, that is,

$$\begin{aligned} &\text{find } \ t_1, t_2, t_3 \ldots t_{m-1} \\ &\text{to maximise } \ c(T) \\ &\text{such that } \ 0 \le t_1 \le t_2 \le t_3 \ldots t_{m-1} \le T \\ &\text{and } \ c' \ge c'_{\text{min}} \text{ for all } t. \end{aligned}$$

Note that equations 1.3 apply only to the particular field that is being grazed between t_{i-1} and t_i. At this time only equation 1.1 applies to the other field (or $f-1$ fields) not being grazed.

It is usual to seek integer solutions to this problem. In practice animals are only moved at certain times during the day.

A variation of this problem, important to dairy farmers calving cows in the spring, is to choose the times $t_1, t_2, t_3 \ldots t_{m-1}$ so that the amount of pasture dry matter w on all the fields is maximised at day 100, under the constraint that consumption by cows must be above a given level of consumption, c'_{min}. This provides maximum pasture in the spring when lactation begins, increasing milk yield and profitability.

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[2] A limited version of this problem is briefly considered in Appendix A.

In a full description of the problem all variables except field area and stocking density must be regarded as random, so that equations 1.3 are stochastic. A particular problem is that the variance is likely to increase with the mean of w.

1.2 An Introduction to Grazing Biology[3]

The function of pasture land is to provide year-round low-cost feed for grazing animals such as cattle, sheep and goats. The primary characteristics of a good pasture plant are that it can withstand being grazed and that it produces sufficient quantities of edible organic matter. Unlike natural rangeland, sown pastures are typically dominated by a small number of species (Spedding 1971). The main plants sown in grazed pastures in New Zealand are grasses (*gramineae*) and clovers (*trifolium*).

1.2.1 Grasses and Clovers

Grasses are chosen on the basis of two major features. Firstly, pasture grasses grow particularly fast and produce high-nutrition forage for grazing animals.

Secondly, by virtue of their structure and their growth habit being low to the ground, grasses are extremely well suited to being grazed, and this accounts for their success as pasture plants. The main morphological feature in this respect is the position of the stem apex (growing point) which lies close to the soil surface, well below the level normally reached by the grazing animal (Langer 1990). Figure 1.1 shows the morphology of a young grass plant, illustrating how grass leaves are pushed upwards from the stem apex (or meristem) in the base of the plant.

Grass swards are characterised by a rapid, continuous turnover of plant tissue. Grass leaves have a relatively short lifespan, 5–9 weeks on average, depending on the time of year (Chapman et al 1984). A single tiller (see Figure 1.1) typically has 3–4 actively growing leaves at any one time. New leaves are continually being formed from microscopic apical buds on the meristem. These elongate and push upwards inside the sheath formed by the existing leaves (the "pseudostem") until they appear at the top as new leaves.

Young leaves are very efficient photosynthesisers (unless they have developed in conditions of limited light, water, or nutrients). As a leaf elongates and widens, its

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[3] During 1991 and 1992 I read a special course in the "Biology of Pasture Production and Consumption" supervised by Professor John Hodgson of the Department of Plant Science at Massey University. This provided me with a good background to the biology of agricultural grazing processes which has been very helpful as we have sought to communicate our work to agricultural scientists. An introduction to the biology of grazed pastures is given in this section, culled from my work with Professor Hodgson. It is hoped this will help those unfamiliar with grazing biology to understand this thesis.

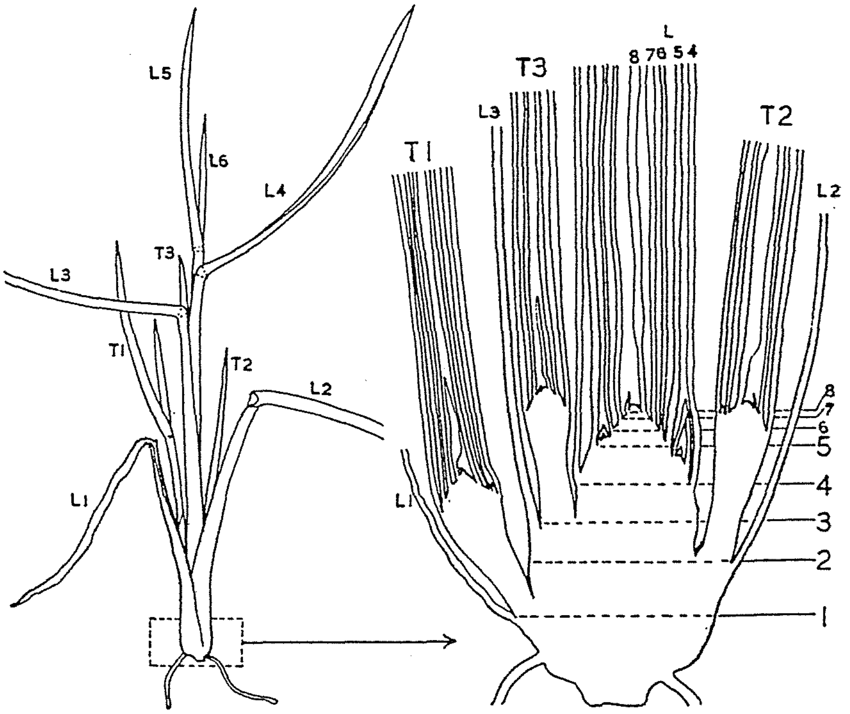

Figure 1.1: Grass shoot after commencement of tillering, and diagrammatic longitudinal section of stem apex (meristem). L1–8 = leaves of main shoot (in order of age). T1–3 = tillers in axils of leaves. Numbers at right indicate nodes of main shoot. From Gill and Vear 1958.

photosynthetic area increases. However, as leaves age they also require a greater quantity of carbon for maintenance processes. In addition, aging leaves decline in photosynthetic ability per square centimetre.

Ultimately, the oldest leaf on the tiller senesces, dies, and decays. Senescence is an in-built degenerative process which triggers death of the leaf even in the absence of outside influences. Senescence is observed as a loss of green chlorophyll from the leaf. Dead leaf is removed by earthworms and the decaying actions of soil microfauna.

Grass also grows by means of "tillering". Tillers are plant units which are produced vegetatively. The apical dome shown on the right-hand side of Figure 1.1 has microscopic buds (protrusions), which, as mentioned above, normally become leaves. However, under favourable conditions, when sufficient light and nutrients are available, the buds may form instead into new tillers.

A mature grass plant may have hundreds of tillers. In a mature sward the tiller density may be as high as 50–60 000 tillers per m^2, each of which typically has from 3–4 actively growing leaves at any one time.

Clovers also have two main features which make them valuable as pasture plants. The first is their high nutritional value and growth rate which make them a valuable

Figure 1.2: An unshaded and undefoliated parent stolon of white clover bearing eight fully expanded leaves (1 = youngest to 8 = oldest). From Robson et al 1989.

source of forage.

The second and more important contribution of clovers in grazed pastures is their ability to “fix” atmospheric nitrogen, that is, to assimilate atmospheric nitrogen into soluble nitrogen compounds within the plant. Ultimately, some of this nitrogen is released into the soil. Because nitrogen is essential to the construction of proteins, the supply of soil nitrogen is a critical factor limiting production of leaf tissue in grasses. This is why the application of nitrogenous fertilisers is often valuable for increasing pasture production. It is for this reason also that mixed grass/clover swards provide some of the highest production pasture in the world.

Many clover species are also well adapted to being grazed, growing vegetatively by means of creepers below the ground or on the soil surface. These stolons (or “rhizomes” if subterranean) are not usually susceptible to grazing, ensuring the longevity of the plant.

1.2.2 The Physiology of Grazing

The main feature of grazing animals that is of interest to us is their daily herbage intake. Intake of herbage contributes to animals’ daily gain in live-weight, which is the quantity of economic interest. Live-weight gain is not directly dependent on the quantity and quality of ingested herbage. The animal itself is a complex system of cycling nutrients. This is especially true of ruminants (eg. sheep and cows) with their complex four-stomach digestion. The first and second stomachs (the rumen and reticulum) contain an enormous pool of bacteria and protozoa. These not only assist in the slow digestion of the cellulose cell walls in ingested herbage but also themselves constitute a significant fraction of the animal's diet.

In this thesis we are not concerned with the details of live-weight gain and animal nutrition (a good introduction to this subject is given by Waghorn and Barry (1987)). We simply assume that live-weight gain, and thus added economic value, increases monotonically with herbage intake.

Animals graze in order to meet their energy and nutritional requirements. Daily herbage intake depends upon the size of the animals' mouths, their rate of biting, intake per bite, and time spent grazing each day. These in turn are affected by the structure of the pasture plants, the digestibility of the grazed leaf and stem parts, and the animals' preference for the various plants or parts of plants on offer. When the pasture level is low, animals have difficulty prehending leaf tissue. Although they will increase their grazing time to some extent in order to compensate, their daily intake will be low. On the other hand, when pasture is high, animals' intake is limited by their ability to ingest forage quickly and by their physiological digestive capacity.

At most times of year, sown pasture in New Zealand is of high quality so herbage digestibility considerations may be neglected. However, this may not be true in drier climates, or in the late spring when there is an accumulation of dead reproductive stem on the pasture. In this thesis we assume that pasture is of a uniform high quality.

Plant-herbivore grazing systems involve complex interactions between several trophic levels, from soil microfauna to large ruminants. Grazing systems are also influenced by related abiotic systems such as soil chemistry and weather. A schematic diagram illustrating the complexity even of intensively managed farmland is given in Figure 1.3. Any quantitative study must naturally deal with only a limited part of this system.

Grazing effects pasture plants in a number of ways. Firstly, removal of leaf means that there is less photosynthetic material available to contribute to the photosynthesis of soluble carbohydrate assimilates. These assimilates are the plants' fuel for maintenance respiration and growth. Secondly, grazing lets more light into the base of the sward, which stimulates the production of tillers and increases the photosynthetic capacity of young developing leaves. Severe grazing may also result in the uprooting of whole plants or tillers, or may cause fatal damage to the meristem.

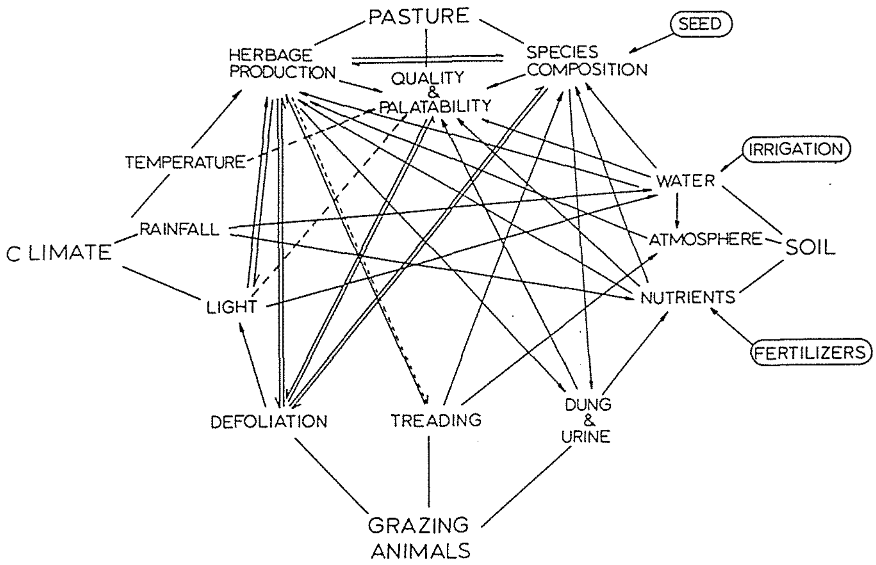

Figure 1.3: A simplified diagram of the interactions between grazing animals and the grazed pasture; only the more important effects are indicated. Soil and climatic factors are included to show how some of the interactions between plants and animals are mediated by, or influenced by, the abiotic environment. From Snaydon 1981.

In the spring, some tillers bear seeds in order to reproduce. The meristem elongates upwards high above the leaves to form an inflorescence (seed bearing stem). Once an inflorescence has formed, the tiller cannot initiate new leaves or tillers because the meristem is no longer active, and will subsequently die. Grazing at this time to remove the inflorescence has the effect of inhibiting seeding. If the pasture grasses are perennial, hard grazing at this time is advantageous, because it prevents the build-up of non-nutritious dead stem on the pasture in the late spring. If the pasture grasses are annuals, however, natural reseeding is often desirable to re-establish the pasture in the subsequent season.

Apart from removal of leaf and stem, animals affect the pasture in a number of other ways including fouling the pasture and treading on the plants. In wet weather, treading also exacerbates waterlogging which can drown the plants. These effects result in additional losses of pasture which do not contribute to the animals' weight gain.

Over 90% of pasture growth is fuelled by photosynthesis, which in turn depends on the amount of photosynthetic leaf tissue in the sward (Robson et al 1988). In the absence of limiting factors such as drought or nutrient deficits, growth is therefore related to the amount of green leaf in the sward. As leaf is constantly being formed, aging and senescing, it is clear that net pasture growth is actually the result of a complex dynamical system and is not dependent on any single sward variable.

1.2.3 Management of Grazing Systems

Agricultural grazing involves the use of pasture to feed farm animals such as cattle, sheep, and goats. The end products are meat, hides, milk, wool, etc., which are important consumer items.

Temperate grass-dominant pastures like those in New Zealand can provide complete year-round nutrition for animals. However, this depends on careful grazing management.

The most basic kind of grazing management is "set stocking", where a set number of animals remain on an area of pasture for a long period of time. A form of this is "continuous grazing", in which an area of pasture is grazed continuously through time, although in this case the number of animals may not be constant. In this thesis we will use the terms interchangeably.

In continuous grazing, the stocking density is important as it determines the productivity of the system (in terms of animal intake and live-weight gain). If too many animals are put on the pasture, it will be grazed to extinction and the animals will subsequently not be able to get enough to eat to maintain their condition. On the other hand, if too few animals are grazed, the pasture may grow tall and become clumpy. The animals then avoid the clumps, which consist of older, less palatable leaf. This decline in pasture quality seriously reduces the efficiency of production.

This implies that if continuous grazing is to efficiently carry animals over a long period of time, the farmer must adjust the stocking density to keep the leaf cover near the value at which pasture growth is maximised. Leaf cover is usually expressed as square metres of leaf per square metre of ground, that is, the "leaf area index" (LAI). An excellent summary of grazing physiology is given by Parsons and Johnson (1986).

Tissue flows in continuously grazed swards are near equilibrium, changes over time being due to weather and the plants' annual reproductive cycles. That is, new leaf growth is approximately balanced by losses due to grazing and senescence (plus other secondary losses due to insects, treading, plant disease, fouling, etc.).

Another form of grazing management in contrast to continuous grazing is "intermittent grazing". This term implies that any given area of pasture is grazed intermittently. This is generally achieved by means of fences dividing the farm into multiple paddocks. At any one time, one or more paddocks are grazed and the remainder are rested.

A common type of intermittent grazing is "rotational grazing", where a group of animals is rotated through a sequence of paddocks over a period of time. The length of this time is called the "rotation length". In this thesis the terms "intermittent grazing" and "rotational grazing" are used interchangeably, because we examine non-standard forms of intermittent grazing for which convenient terminology does not exist. At the same time, the term "intermittent grazing" is not commonly used except in technical discussions. "Rotational grazing" is a more convenient and familiar term.

Rotational grazing is practiced for a number of different purposes at different times of year. The possible aims of rotational grazing are outlined in section 4.2 and include control of spring reproductive growth, maximising stocking rate, and conservation of herbage *in situ* to meet future demands, especially those due to parturition (birth of lambs/calves).

The stocking density (animals per hectare being grazed) in a real rotational grazing system is always sufficiently high that the pasture level in the paddock being grazed will decline. Immediately after grazing, a rotational paddock typically has a low level of pasture.

During the regrowth period, the young leaves have high photosynthetic ability because of the high levels of light reaching the base of the sward. The extra light may also stimulate rapid tillering. Therefore, regrowth is initially rapid (Davies 1988). As the sward approaches ceiling yield (the maximum pasture mass at which new growth balances net losses in the absence of grazing animals) the average age of leaves in the sward increases and the rate of senescence begins to catch up with the growth rate. Photosynthesis is then less efficient due to leaves shading one another. Ideally, the animals will return to graze the paddock before pasture quality declines and senescence rates become too high. The optimal time of regrazing has been the topic of several theoretical studies (Morley 1968, Parsons and Penning 1988).

Clearly, rotational grazing is a far more dynamic process that continuous grazing, with sward variables fluctuating markedly over time, and the physiology of continuous and rotationally grazed swards is therefore quite different (Parsons et al 1988a). By considering models of continuous and rotational grazing, this thesis seeks to provide fundamental comparisons between pasture dynamics under each of these two grazing systems.

1.3 A Review of Grazing Modelling

Compared to some other areas of biological modelling, the development of mathematical modelling of agricultural grazing has been slow. This is both because agricultural systems are complex, spanning several trophic levels from soil chemistry and microfauna to large grazing ruminants (Caughley and Lawton 1981), and also because agricultural systems are driven by forces which are themselves complex and unpredictable, particularly weather. As a result, the main modelling tool in agriculture has been computer simulation.

However, because of the economic importance of agricultural systems and the increasingly scientific approach to control of these systems, applications of mathematical techniques to problems in agricultural production and ecology are appearing. This review introduces some of the significant contributions of mathematical modelling to the study of problems in agricultural grazing.

1.3.1 Simple Dynamical Models

In the 1950's and 1960's a major debate among agricultural scientists concerned the relative merits of continuous vs rotational grazing methods. Even by 1960 influential agriculturalists such as the legendary C.P. McMeekan had realised that grazing method was not the most important factor influencing farm production, as expounded in his keynote address to the 1960 International Grassland Congress at Massey University, New Zealand (McMeekan 1960).

Nevertheless, agriculturalists who had some mathematical background soon contributed to the debate. A formative paper is that of F.H.W. Morley (1968). Brougham (1956) had fitted logistic curves to field measurements of pasture mass. Morley used these curves to analyse the optimal resting time between successive grazings of a single paddock in a rotational grazing system.

The logistic growth model is described by the differential equation

$$w'(t) = aw(t)(1 - w(t)/w_{max}) \quad \text{kgDM/ha/day} \tag{1.4}$$

where $w'(t)$ is the instantaneous rate of pasture growth, $w(t)$ is the pasture mass at time t, a is the maximum specific growth rate, and w_{max} is the ceiling yield. The maximum growth rate is achieved when $w = w_{max}/2$ and is $aw_{max}/4$ kgDM/ha/day. If the initial pasture mass $w(0)$ is given, equation 1.4 has solution

$$w(t) = \frac{w(0)w_{max}}{w(0) + (w_{max} - w(0))\exp(-at)} \quad \text{kgDM/ha} \tag{1.5}$$

which is a typical sigmoid growth function. Equation 1.5 is due to Thornley (1990) and is a more convenient form than that used by Brougham.

In this thesis we initially adopt a linear growth function,

$$w'(t) = aw(t) \quad \text{kgDM/ha/day}$$

in chapters 2 and 3. This is justified at low pasture mass (Brougham 1955). A logistic growth function is used in chapter 4.

If equation 1.5 describes the regrowth of a sward, then the maximum average rate of regrowth, and thus the optimal time of regrazing, will occur when

$$\begin{aligned} \frac{d(w(t)/t)}{dt} &= 0 \\ \Rightarrow \quad w(0) + (1 - at)(w_{max} - w(0)) \exp(-at) &= 0 \end{aligned}$$

the solution of which can be obtained numerically. In this way, Morley (1968) showed that average pasture growth rate in the time period between successive grazings of a paddock could be maximised if the length of spelling was between 6 and 9 weeks, depending upon the time of year. Morley also used rule of thumb calculations to show that a relatively small number of paddocks was sufficient for a useful rotational grazing scheme.

Morley's method of concentrating attention on maximising pasture growth in a single paddock under intermittent grazing was followed in subsequent studies (eg. Noy-Meir 1976, Parsons and Penning 1988). The assumption is that all other paddocks in the system may then be treated similarly and an optimal rotational grazing strategy constructed. This assumption is one which this thesis sets out to challenge.

Other simple models used by agriculturalists include that of McCall et al (1986), who successfully used a negative exponential function to model the decline in standing pasture mass during grazing. This assumes that animal intake rate is proportional to the instantaneous herbage mass and herbage growth and senescence during grazing are negligible, that is,

$$w'(t) = -knw(t) \quad \text{kgDM/ha/day}$$

where n is the number of animals and k is the relative per animal removal rate (hectares/animal/day). Solving this gives

$$w(t) = w(0) \exp(-knt) \quad \text{kgDM/ha}$$

from which several rough rules of grazing management were derived.

There is an affinity between these simple pasture models and simple economic models of profit and cost. Since agriculture is an economic as well as an ecological activity, several studies have combined simple economic and grazing models to make predictions about, for instance, economically optimal stocking rates (eg. Wright and Pringle 1983, Workman and Fowler 1986). Economic considerations are often essential if one is to define what is meant by "optimal" in any given situation, and future grazing modelling efforts will need to keep this in mind.

These models have been motivated by particular problems in agricultural management. For this reason they rest on simple biological assumptions and have proved useful because of their simple forms. However, when using them one needs to keep in mind the assumptions under which the model is valid. For simple models, this may be a restrictive subset of the real situations one would like to analyse. Therefore, more descriptive models are required.

1.3.2 Plant-Herbivore Models

In 1975 Imanuel Noy-Meir published a paper in the *Journal of Ecology* which was to influence all subsequent work in the field of grazing modelling. Noy-Meir introduced a dynamical systems approach to modelling herbivore-pasture systems. His approach rested on an area of mathematics which was already extremely well developed; the "predator-prey" models used in theoretical ecology (eg. May 1981).

Caughley and Lawton (1981) provide an overview of the theory of modelling grazing systems in this way. Several other modellers have applied this theory to agricultural grazing systems. For example: Caughley (1982) examined the theory of a single herbivore grazing a mixed species pasture; Barlow (1987) studied the influence of pasture-eating pests on grazing productivity; and Walker et al (1981) examined the ecology of grazing in semi-arid environments. These are all theoretical studies. However, their application in agricultural science has been slight, perhaps because such papers have not been written with practical agricultural problems in mind or because the underlying models have been unacceptably simplistic to agriculturalists (even while the analysis has been sophisticated).

Because Noy-Meir presented his results in a form that was accessible to agricultural scientists, his work has gained wide acceptance. Noy-Meir's analysis was similar to that which is commonly used to study interactions between populations in uncontrolled ecosystems, except that in his model the herbivore density was held constant. The approach of theoretical ecologists is then to look for equilibrium states where the herbivore and vegetation populations are balanced so that the sizes of both are stable.

Noy-Meir modelled the rate of accumulation of grazed pasture as

$$V' = G(V) - HC(V) \tag{1.6}$$

where $G(V)$ is the rate of herbage growth in the absence of grazing at herbage biomass V, H is the density of animals, and $C(V)$ is the rate of herbage intake by a single animal unit (ie. $H = 1$) at herbage biomass V (Noy-Meir 1975). Using this model, he showed that in some grazing systems, depending on the form of the response functions G and C (see Noy-Meir 1978a), there could be two stable steady states of plant biomass at a given herbivore density; one at low herbage biomass

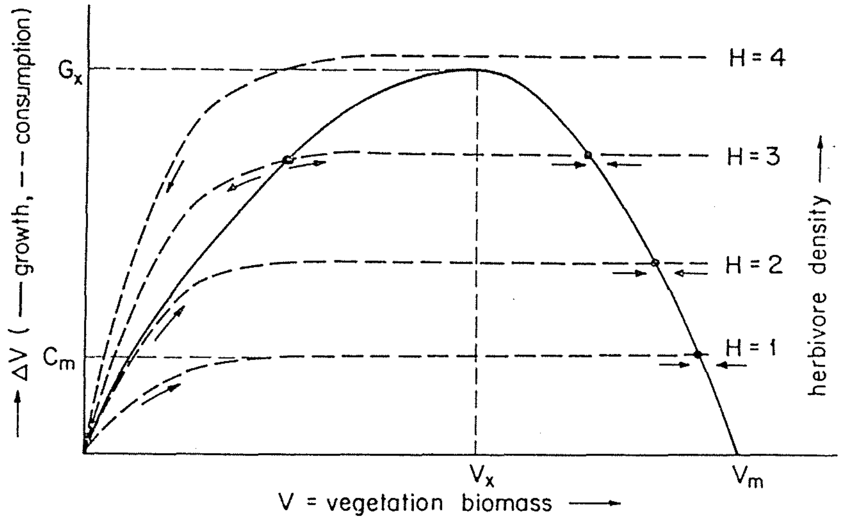

Figure 1.4: Superimposed graphs of growth G (solid line) and grazing C (dotted line) as functions of vegetation biomass V and herbivore density H. G_x = maximum growth rate; V_x = biomass at which growth is maximum; V_m = maximum biomass; C_m = maximum consumption rate when $H = 1$. From Noy-Meir 1976.

and one at high herbage biomass (Noy-Meir 1975). This he termed "discontinuous stability". Figure 1.4 shows typical response curves of growth rate (solid line) and rate of herbage removal by grazing at different stocking rates (dotted lines). Steady states (both unstable and stable) occur where these curves cross.

So influential was this paper that agriculturalists began to look for ways to drive agricultural grazings systems towards the theoretical high herbage steady state in order to increase productivity. One suggestion was that rotational grazing might achieve this (Noy-Meir 1976). In certain special situations this was found to be theoretically possible. However, pasture variables in real grazing systems exhibit a high degree of unpredictable variation due to climatic and other effects, and so "discontinuous stability" has rarely been observed in practice.

While equilibrium analysis might be useful in studying continuous grazing, it is not naturally applicable to rotational grazing where pastures are periodically disturbed by the introduction or removal of animals. A central theme of this thesis is to construct models that deal more happily with the switching inherent in rotational grazing. Unfortunately this takes us onto new ground where many classical results concerning stability are not applicable.

1.3.3 Simulation

By the late 1970's the rise of computer modelling was already having considerable impact on agricultural science, as shown by the fact that the 1981 book *Grazing*

Animals edited by F.H.W. Morley devoted an entire chapter to computer simulation models of grazing systems (Christian 1981). Computer simulation models have proved appropriate for modelling many specific agricultural problems. Some examples of the purposes for which simulation models have been constructed are: to predict grazing pasture productivity (Shiyomi et al 1983); to schedule irrigation (Baars et al 1976); to schedule spring grazing (Buckmaster and Parker (in press)); to examine forage dynamics (Blackburn and Kothmann 1989); and to model pasture fouling (Hirata et al 1991). These models typically have a large number of equations with simple (often linear) relationships between the many state variables. Because they have been constructed to accurately model specific problems, they often require complex input information such as temperature and rainfall data. For these reasons, computer simulation models are often limited in their applicability and do not seem to have contributed much to general theories of grazing.

We have tried to avoid excess complexity in this thesis and have favoured simple analytical methods in the hope of being able to provide simple rules of thumb for grazing management.

In the mid-80's plant growth modellers I.R. Johnson and J.H.M Thornley and agronomist A.J. Parsons developed a general purpose model grazed grass pasture (Johnson and Thornley 1983, Johnson and Parsons 1985a). This was a mechanistic model of grass pasture biology with five compartments for different age classes of leaf and differential rates of removal of leaves of different ages depending on animal preference. Being both multi-purpose and mechanistic, this model became the new standard for modelling grazing (eg. Chen 1986, Chen and Wang 1988) although Noy-Meir's much simpler model is still adequate for many purposes (eg. Huffaker at al 1989).

The "Johnson and Parsons" model is a dynamical system of 13 non-linear equations (Johnson and Parsons 1985a). However, this system is relatively intractable to analytical methods and computer simulation is necessary in practice. The authors of this model have used it for a number of theoretical studies into grazed pasture dynamics; to study seasonal production (Johnson and Parsons 1985b), rotationally grazed sward dynamics (Parsons and Penning 1988), and comparisons between continuous and rotational grazing (Parsons et al 1988). Many important hypotheses concerning grazing theory have come out of these studies.

1.3.4 Optimal Control, State-and-Transition, and Stochastic Modelling

The models that have been most effective in providing decision support for farm managers are those which have been formulated to answer specific questions. Indeed, with the increasing emphasis on economic outputs from science, agricultural science will increasingly be forced to address specific commercial problems. These problems often entail some form of optimisation.

It is not surprising therefore that optimal control theory is finding applications in agriculture. From the point of view of optimising grazing, several studies deserve mention. Two are due to J.L. Chen and Q. Wang of Shanghai, China. Using Johnson and Parsons' model, Chen and Wang applied optimal control theory to examine the optimal cutting and optimal continuous grazing strategies that maximised the quantity of herbage harvested annually (Chen 1986, Chen and Wang 1988). Hendy (1992) used similar methods to determine the optimal rate of feeding sheep to maximise their annual wool growth.

Similarly, Huffaker et al (1989) addressed a problem in agricultural economics raised by a specific piece of legislation in the United States. They used Noy-Meir's model (equation 1.6) to formulate an optimal control problem where stocking rate must be controlled to maximise the profitability of grazing a leased rangeland. In this case the profit from animal productivity was offset by penalties for ecological damage to the rangeland. This gives an example of how ecological and economic objectives can be addressed simultaneously using a modelling approach.

These applications of optimal control theory have provided formulations of the problems presented which are solvable by existing methods in control theory, but again often fail to offer simple maxims for day to day management. Our aim in this thesis is to model in such a way as to allow simple generalisations to be derived from our results in order to bridge the gap between theoretical and practical aspects of agricultural science.

Another tool which offers a simple method for the synthesis of qualitative ecological information with quantitative modelling is the "state-and-transition" framework (Westoby et al 1989a,b). The idea is that a system (such as a grassland, for example) might have a number of ecologically distinct states. Figure 1.5 is an example of such a system. States are either stable or unstable. If the system is in an unstable state, it will gradually evolve towards more ecologically stable "advanced" states unless disturbed. On the other hand, if the system is already in a stable state, natural events or human controls such as grazing, fire, disease, rain, or drought are required to push the system to new states. From an agricultural point of view, some states

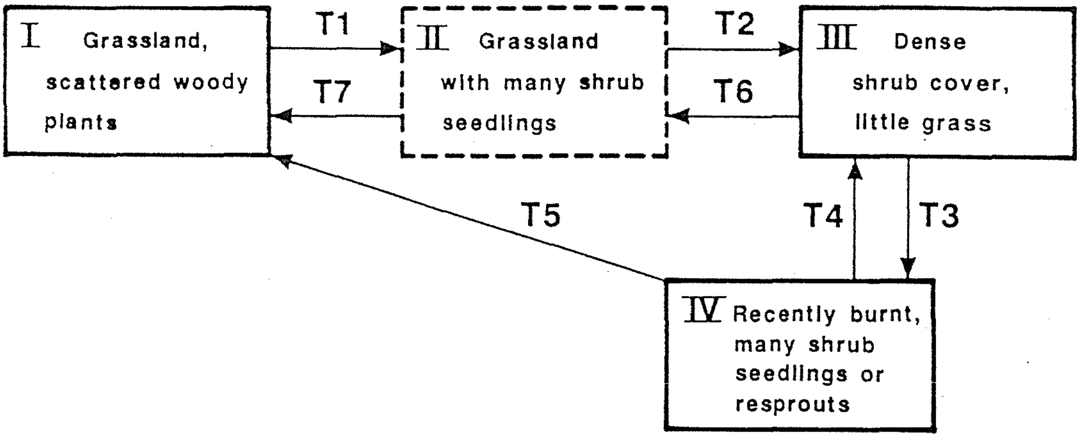

Figure 1.5: State-and-transition representation of semi-arid grassland/woodland in eastern Australia with potential for increase of shrubs. I–IV = botanically distinct states of the rangeland. T1–7 = transitions driven by time, rains, fire, etc. From Westoby et al 1989a.

are more desirable than others because they allow greater agricultural productivity.

This is analogous to a dynamical system having a number of stable steady states where a perturbation might push the system from one equilibrium to another. The state-and-transition framework may be the ideal tool to marry ecological descriptions of the states of an ecosystem with the theoretical conditions necessary for their stability.

Lastly, the ability to handle random variation is becoming increasingly important in many areas of modelling. Because agricultural systems are complex and are driven by unpredictable forces (such as the weather) there is always an element of risk in agricultural management. There are theories of stochastic processes and risk management which may be tapped to deal with this (Hertzler 1991). Work in this area is currently rudimentary, including probabilistic models of grass growth (Gross 1988) and the grazing behaviour of sheep (Rook and Penning 1991), but more substantial techniques are being developed to deal with uncertainty (Pleasants et al (in press a,b)).

1.3.5 Summary

This brief survey is intended to highlight some of the important developmental steps in grazing modelling and to name some of the central figures. It also provides a context for understanding the contribution of this thesis. Our models are mathematically and biologically simple compared to many of the approaches we have described above. This is because of a desire to preserve the ability to derive simple rules of thumb from the results. Even though these rules of thumb may only be applicable under limiting assumptions, they constitute a positive contribution to the understanding of the theory of grazing, and in particular, of rotational grazing.

This thesis is exploratory in nature, as it examines problems which have not previously been approached in a systematic theoretical manner. This has meant some latitude in choosing what will be studied and we have been guided by the need to tackle current problems in agricultural practice in New Zealand. There are many directions we have not taken—now that we have suggested this approach to studying rotational grazing we hope that future mathematicians will be encouraged to further explore this important subject.

1.4 Outline of Thesis[4]

1.4.1 Chapter 2[5]

The central theme of this thesis is the optimal grazing of a rotational grazing system similar to that described in the original problem in section 1.1.

The most fundamental feature of rotational grazing management is the shifting of animals between fields. Because full-scale rotational grazing systems are complicated, we begin by examining the effect of changing the time at which animals are shifted between fields on their intake and on herbage conservation. To do this, a model of a two-field grazing system is constructed where a group of n animals grazes first one field and then a second field for a total of T days, being swapped between fields at time t_1. The growth and intake response functions are linear as a first approximation, which is reasonable when pasture mass is low. The optimal values of t_1 that maximise (1) herbage conserved *in situ* and (2) total animal intake are analysed. The results are presented in this chapter and chapter 3.

This has a similar flavour to the study of Morley (1968) in finding optimal rest times for paddocks between successive grazings, and as in Morley's study, the optimum could not be obtained as a simple formula—numerical solutions were required. This is a simple methodology that may be used to analyse real world problems.

The obvious extensions are to increase the number of fields in the system, to formulate the system to include multiple rotations where each field is visited more than once, and to consider how more realistic growth and grazing functions may

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[4] As each of chapters 2, 3 and 5 are available in international journals, their published form has been preserved here. This is to save the reader the effort of searching these chapters for additional material that has not appeared in print elsewhere. All other sections are unique to this thesis.

[5] Chapter 2 has been published in *Agricultural Systems* (Woodward et al 1993). In this thesis the published appendix has been assimilated into the text.

be included, or to assess if indeed the choice of these functions is critical. Some of these extensions have been explored in later chapters. A brief exploration into extending the linear model to describe grazing a sequence of paddocks is described in appendix A. Another possible refinement would be to consider the effect of time variation in the pasture growth rate.

1.4.2 Chapter 3[6]

While the two field model presented in chapter 2 is rudimentary, some intriguing conclusions are suggested. In addition, it is easy to see how ideas in practical grazing management can be represented by this model. By using the two field model to model simple continuous, rotational, and optimal grazing managements, we are able to present our results as a direct comparison of herbage intake from the three grazing managements over a range of stocking rates, as a field experiment might do. This has the advantage of revealing the practical results implied by the theory as well as making the work more accessible to agricultural scientists.

This "experiment" considers spending different lengths of time in each field, which field to graze first, fields being of different sizes, and fields having different initial herbage masses. This highlights the large number of factors at a farmer's control in designing a rotational grazing policy.

This brief chapter shows how results from a very simple modelling study can be presented in such a way as to highlight the practical implications. On the other hand, one must be careful not to gloss over the assumptions that are made and thus give one's audience a false confidence in the results, which may, after all, be valid only within a limited context.

1.4.3 Chapter 4[7]

Field studies suggest that productivity is relatively independent of grazing strategy, being more strongly influenced by stocking rate and animal factors (McMeekan 1960). Nevertheless, there are still a large number of variables at a farmer's control in rotational grazing, the effects of which have not yet been fully investigated.

Rotational grazing is practised with a number of different aims in mind depending on the time of year. These are summarised in section 4.2. Our main interest in this

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[6] Chapter 3 was presented as a poster at the *XVII International Grassland Congress* held in Palmerston North, New Zealand in February 1993, and has been accepted for publication in the Congress Proceedings (Woodward et al (in press a)).

[7] Chapter 4 has been submitted to *Agricultural Systems* for publication (Woodward et al (in press b)).

thesis is in maximising animals' herbage intake. For meat animals such as bull beef this is equivalent to maximising their productivity.

The optimal use of multi-paddock grazing systems is an extremely complicated management problem. Complicating factors include the unreliability of the weather, different fertility between paddocks, seasonal variation in pasture production, the huge number of possible management schedules, and the possibilities of fertiliser application and supplementary feeding with hay, silage, or grains.

In practice, feed budgets are determined beforehand, and a grazing strategy is then devised to meet this budget (Milligan et al 1987). The size of paddocks are usually predetermined by existing fences used to separate areas of different pasture fertility (Bryant and Sheath 1987). Animals usually visit paddocks in simple sequence and are moved on to the next paddock either after a predetermined time of grazing or when the herbage mass in the paddock grazed falls below a predetermined minimum level. Rotational grazing is thus often characterised by (1) the number of paddocks and (2) the "rotation length", that is, the length of time between successive visits to the same paddock.

Alternatively, decisions about where (and how) next to feed the animals are made "dynamically" from day to day depending on the condition of the pasture. This includes decisions to apply fertiliser, to use supplementary feeds, or to sell animals in order to remove pressure from the system.

Chapter 4 examines one aspect of multi-paddock grazing management: the sequence in which paddocks are grazed. The objective in mind is to maximise the intake of a group of animals. Herbage conservation *in situ* and pasture production are also considered.

Again, a simple dynamical system is used, similar to that of Noy-Meir (1975). Because of the long rest periods associated with rotational grazing, a logistic growth function is adopted, since pasture mass might approach ceiling yield. In this case the linear function used previously to model grazing over short time periods would be invalid. The model considers a system of $m = 1$ to 20 paddocks grazed by a group of animals over $T = 60$ days in winter and early spring. The sequence in which paddocks are grazed is determined according to four strategies, one of which is continuous grazing. Total intake, herbage remaining, and pasture grown are calculated. An algorithm is presented for determining the optimal sequence of fields to maximise intake.

1.4.4 Chapter 5[8]

All theoretical studies of grazing require an appropriate model of pasture biology under grazing. Depending upon the particular problem being addressed, the model may be extremely simple (eg. McCall et al 1986) or extremely complex (cf. the simulations models discussed in section 1.3.3). Additional complexity is only worthwhile if it increases the descriptive power of the model. In many circumstances complexity is counterproductive because it introduces unnecessary additional assumptions about processes that are not well understood. This in turn leads to unpredictability in the behaviour of the model.

Many models of pasture growth under grazing ignore the delay between leaf formation and leaf death (eg. Noy-Meir 1975). In some contexts this assumption is pragmatically acceptable. However in the study of rotational grazing one would like to include the consideration of senescence in an explicit form in order to determine whether intermittent grazing can increase pasture utilisation by reducing losses due to senescence. For this reason we consider a simple addition to models like that of Noy-Meir (1975), which explicitly treats the delay inherent in pasture dynamics.

Chapter 5 describes a differential-delay model of grazed pasture dynamics formulated for the purpose of studying this problem.

1.4.5 Chapter 6

There have been suggestions that the fluctuations in the rate of leaf death due to intermittent defoliation would offer scope for improved production if it were not for the increased detrimental effects of treading and fouling associated with high stocking densities such as are typically found in rotational grazing systems (Parsons 1988).

Chapter 6 uses the differential-delay model of grazed pasture described in chapter 5 to make a simple comparison of intake and senescence under continuous and rotational grazing over a range of rotation lengths. By also simulating the system using an equivalent non-delay model, the effects of delayed senescence are immediately observed. It is found that the delay between tissue formation and death in grazed pasture increases the average rate of senescence when rotational grazing management is used. Therefore, it is likely that rotational grazing could not significantly outperform continuous grazing in practice in terms of animal intake.

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[8] Chapter 5 has been accepted for publication in *Mathematical Biosciences* (Woodward and Wake (in press)).

1.5 Main Results

The main results obtained in this thesis are:

- Rotational grazing allows herbage conservation because it restricts animal intake. Conservation *in situ* is maximised when the animals receive their minimum feasible level of feeding (chapter 2).
- Continuous grazing maximises intake when pasture growth is in surplus to animal requirements (chapter 4).
- In general, rotational grazing does not increase intake. In addition, animals' herbage intake under rotational grazing is likely to be poor unless the rate of rotation is carefully synchronised to the pasture growth rate (chapter 4).
- When pasture is unevenly distributed in a multi-paddock system, a "greedy" grazing strategy can give higher intake than continuous grazing or rotational grazing in which animals are rotated through a fixed sequence of paddocks (chapter 4).
- Increasing the number of paddocks in a system while other variables remain unchanged reduces intake (chapter 4).
- Grazing management has only a minor effect on productivity (ie. intake and pasture grown) in comparison to stocking rate and average initial pasture (chapter 4).
- There is a unique optimal time at which to swap animals between paddocks. This depends on the initial herbage masses, the sizes of the paddocks and the number of animals, but is non-trivial to calculate. (chapter 2).
- Optimal swapover gives increased animal intake when the size or herbage cover differs significantly between fields, or when the stocking rate is high. Otherwise, the optimal intake is not significantly greater than that achieved under continuous grazing or rotational grazing where animals spend equal time in each paddock (chapters 2 and 3).
- Under high stocking rates it is optimal to graze the first field for a longer time in order to allow the second (and subsequent) fields to accumulate mass prior to grazing (chapter 2). In this case it is optimal to graze the paddock with least grass first (chapter 3). This result is counter-intuitive.

- The instantaneous rate of senescence is lower in swards under regrowth than in grazed swards at the same herbage mass (chapter 5). However the average rate of senescence in rotationally grazed swards is higher than that in continuously grazed swards due to the higher average herbage mass in rotationally grazed swards. (chapter 6).
- Changes in standing pasture mass account for the major fluctuations observed in rates of pasture loss by ingestion and senescence in intermittently grazed swards (chapter 6).
- A model of pasture accumulation and loss which ignores the delay between leaf formation and senescence is likely to underestimate overall pasture losses due to senescence in intermittently grazed pasture (chapter 6).