A DYNAMICAL SYSTEMS MODEL FOR OPTIMIZING ROTATIONAL GRAZING

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Simon James Roy Woodward
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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,

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

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.

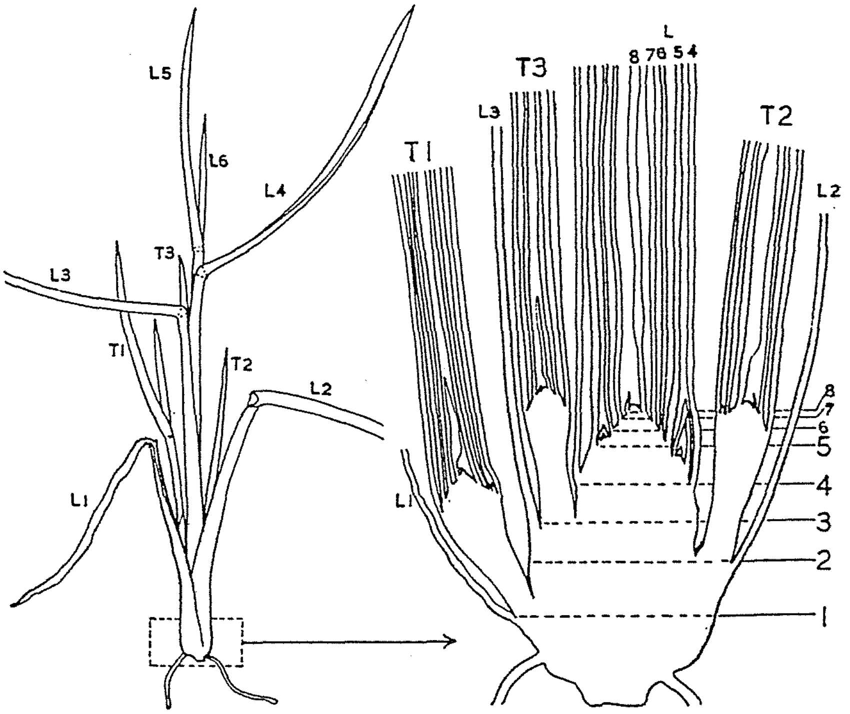

Figure 1.1: Grass shoot after commencement of tillering, and diagrammatic longitudinal section of stem apex (meristem). L1–8 = leaves of main shoot (in order of age). T1–3 = tillers in axils of leaves. Numbers at right indicate nodes of main shoot. From Gill and Vear 1958.

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.

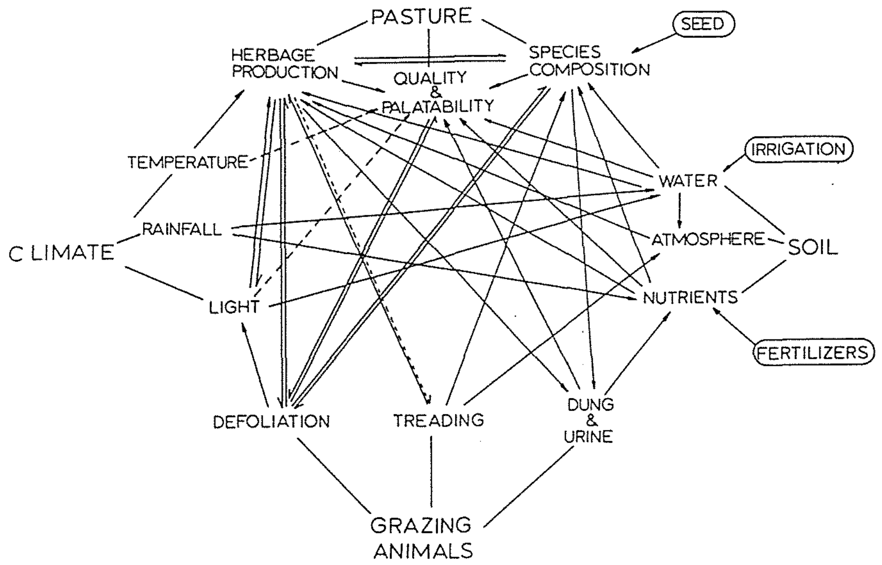

Figure 1.3: A simplified diagram of the interactions between grazing animals and the grazed pasture; only the more important effects are indicated. Soil and climatic factors are included to show how some of the interactions between plants and animals are mediated by, or influenced by, the abiotic environment.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

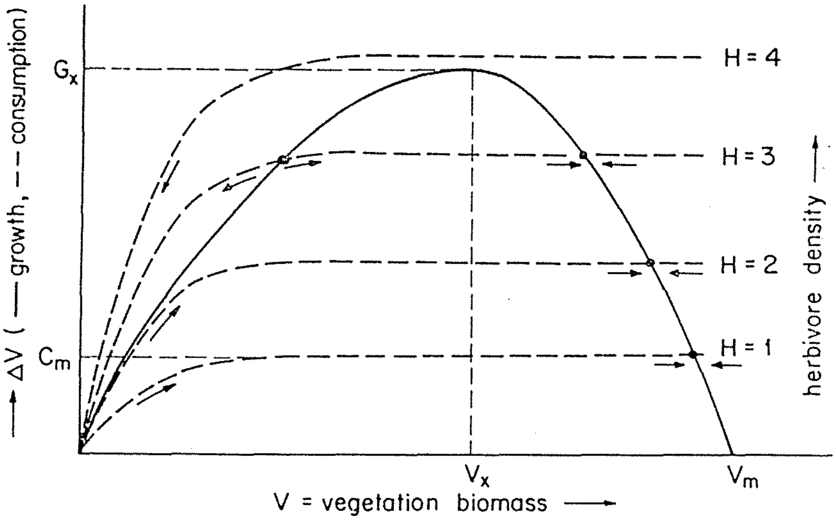

Figure 1.4: Superimposed graphs of growth G (solid line) and grazing C (dotted line) as functions of vegetation biomass V and herbivore density H. G_x = maximum growth rate; V_x = biomass at which growth is maximum; V_m = maximum biomass; C_m = maximum consumption rate when $H = 1$. From Noy-Meir 1976.

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

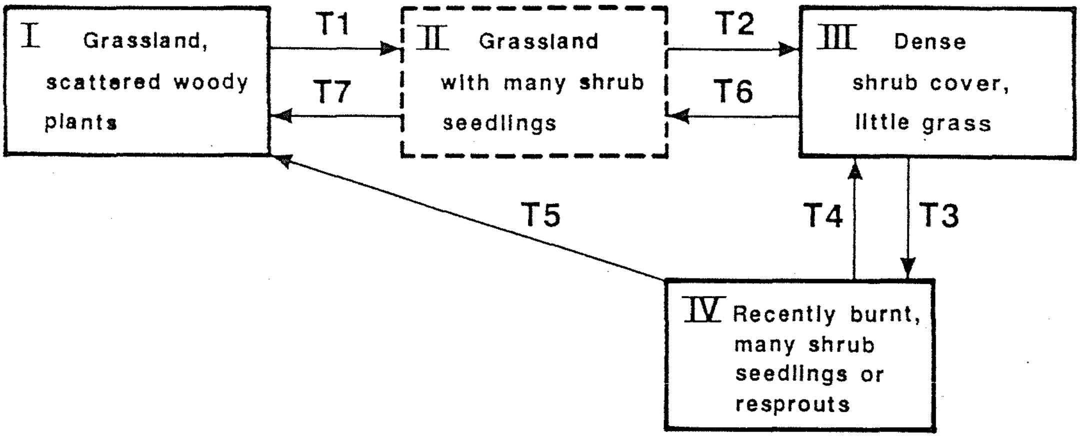

Figure 1.5: State-and-transition representation of semi-arid grassland/woodland in eastern Australia with potential for increase of shrubs. I–IV = botanically distinct states of the rangeland. T1–7 = transitions driven by time, rains, fire, etc. From Westoby et al 1989a.

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).

Part I

Optimizing Rotational Grazing

Chapter 2

A 2-Field Model for Optimizing Rotational Grazing

2.1 Abstract

A simple mathematical model is formulated to describe a simple rotational grazing system of two fields where a mob of animals is grazed first in one field then the other. By using linear functions for the rate of herbage mass accumulation and for the rate of animal herbage intake, this system may be solved explicitly to yield expressions for (1) the total intake per animal over the time period, and (2) the total remaining herbage after grazing. Regarding the swap over time as an optimal control variable, these expressions can be optimised. The results are analysed for various initial conditions including stocking rate, initial biomass in each field, and field area. Comparisons are made with continuous grazing. Extensions to the model are discussed.

2.2 Introduction

This chapter deals with the allocation of pasture to a group of animals to optimize some aspect of production. Ecologists have usually modelled the interaction between plant and herbivore populations using predator-prey theory (eg. Caughley and Lawton 1981), an approach which relies on the mathematics of dynamical systems. It is usual for ecologists to concentrate on the stability of such systems in order to predict population fluctuations and to identify critical sensitivities which may be exploited or managed to achieve certain outcomes (eg. Barlow 1987, Goh et al 1974, Stocker and Walters 1984).

A well known application of this theory to domestic grazing systems is that of

Noy-Meir (1975, 1978b) who suggested that some continuous grazing systems might have two possible steady states. Many agriculturalists (eg. Johnson and Parsons 1985) support this idea that grazing systems may be discontinuously stable, a feature which may be able to be exploited to achieve increased productivity.

There are important differences between ecological systems and agricultural grazing systems. The wild ecosystem is by and large uncontrolled; both herbivore and herbage populations are allowed to fluctuate naturally, and this implicitly requires long time scales. The kinds of controls which are used usually entail some form of harvesting, and often it is movement towards a steady state (sustainable yield) which is desired.

By contrast, in agricultural grazing systems we are often dealing with populations of animals that are intensively managed on discrete fields, most commonly by controlling the animals' access to pasture. The time scales are short, and so stability analysis is not always relevant.

While agricultural systems are of great interest due to their economic importance, they are also, unfortunately, notoriously difficult to perform experiments on. This is due to both the tremendous number of alternatives of possible grazing schedules, and to the dependence of productivity on environmental conditions with significant random variability. In practice, direct measurement is difficult and costly, and the use of frequent cutting to simulate grazing is questionable. Therefore, a theoretical analysis is relevant (Chen and Wang 1988).

Computers have helped alleviate these problems by allowing large numbers of carefully controlled trials to be simulated at low cost (eg. White et al 1983, Christian 1981). Computer models may be very sophisticated and take into account a huge range of extrinsic factors. However, the fundamental cause and effect mechanisms of the system can be obscured by this very sophistication. An analytical approach is required to achieve a thorough mechanistic understanding.

Parsons and Johnson (1986) have provided a good summary of the theoretical understanding of continuous grazing management. Rotational grazing, on the other hand, is still not yet well understood. Experimental results seem contradictory regarding when and whether rotational grazing offers increased production over continuous grazing (eg. Sharrow 1983, Morley 1981, Florez et al 1986).

Morley (1968) and Parsons et al (1988) approached optimizing pasture production in rotational grazing by considering the optimal rest period for fields between being grazed. While an innovative and tractable approach, it avoids the issues of (1) how much herbage is produced during grazing, and (2) how these conclusions may be put together into a practical grazing programme.

Noy-Meir (1976) applied ecological stability theory to a grazing system under rotational management. He made the *a priori* assumption in common with most models of rotational grazing that the rest and grazing intervals should be of fixed length, and compared results using different interval lengths. Noy-Meir principally examined the long term stability of such a system.

Achieving optimum performance from any modelled system must involve some form of mathematical optimization procedure (for instance, as used by Morley 1968 and by Parsons et al 1988). Because agricultural grazing involves intensive control of the herbivore-plant system in order to maximise productivity, this points to the use of optimal control theory, which was developed by engineers who wished to find optimum control schedules for machines. For an example in agricultural economics see Huffaker et al (1989).

Chen (1986) and Chen and Wang (1988) have applied optimal control theory to Johnson and Parsons' (1985) pasture model. Chen (1986) found the theoretical optimal sequence of cuts for a pasture harvested by mowing over a growing season of 273 days. Then Chen and Wang (1988) found the theoretical optimal stocking density (adjusted by the farmer with time) that maximised total animal intake over the same growing season.

The purpose of this paper is to apply a mathematical analysis to a simple rotational grazing situation involving the movement of animals between defined fields. The particular problem of interest involves the optimal control of grazing for animal production where there are no pasture quality constraints. This is the situation in winter and early spring in year-round grazing systems. At this time pasture production limits animal production because the intake potential of animals is greater than net pasture growth. Two common objectives exist in the control of grazing over this period. The first involves pregnant animals where the objective is to optimise conservation of herbage over winter for feeding in early spring after parturition. This strategy maximises milk production in dairy cows (Bryant 1982) and lamb production in ewes (Bircham 1984). The second objective is to maximise animal intake over the entire period, a goal sought by farmers raising animals for slaughter. In the above cases the farmer has a number of fields with given initial herbage cover. The farmer may control the number of animals in the system (the stocking rate), the order of grazing the fields, and the time at which animals are moved between fields.

Whereas Chen and Wang used a relatively complex model (that of Johnson and Parsons 1985) and solved it numerically, our aim in this thesis is to use a greatly simplified model at first, and to explore the behaviour of the optimal solutions of this model analytically. The advantages of this are that the strategic outcomes are found for a large range of parameters simultaneously, and that results will be derived from a mechanistic understanding. When the structure of the simple grazing system is understood, extensions to the model dealing with even more realistic situations will be able to be developed.

2.3 The Model

In this section we describe the assumptions upon which the model is based and the formulation of the model itself in mathematical terms. Taking simple pasture growth and animal intake functions the model is then solved.

2.3.1 Assumptions

(1) Suppose a farmer has 2 fields of area h_1 and h_2 hectares, respectively. At time $t = 0$ days the mass of herbage in the fields is $w_1(0)$ and $w_2(0)$ kg/ha. Assume that a pasture can be adequately represented by a single state variable, the herbage mass.

(2) The farmer wishes to graze a mob of n animals (constant) in these two fields for a total period of T days. This is split between t_1 days in field 1 followed by $T - t_1$ days in field 2. The swapover time t_1 is the point in time at which he or she transfers the animals into field 2.

In this context the two fields consist only a small part of a wider farm system, and alone are not expected to sustain the animals for more than the limited time period we are interested in.

(3) Assume that the rate of pasture accumulation is dependant only on the current herbage mass, and label the pasture accumulation rate function grow(w) (unspecified at this point). Then, in a field i which is being rested (ie. not grazed),

$$\frac{dw_i}{dt} = \text{grow}(w_i) \quad \text{kg/ha/day} \tag{2.1}$$

where w_i kg/ha is the herbage mass in field i.

In general, the net pasture growth function grow(w) will be convex with a single maximum. Figure 2.1 shows some explicit functions which have been used in previous models.

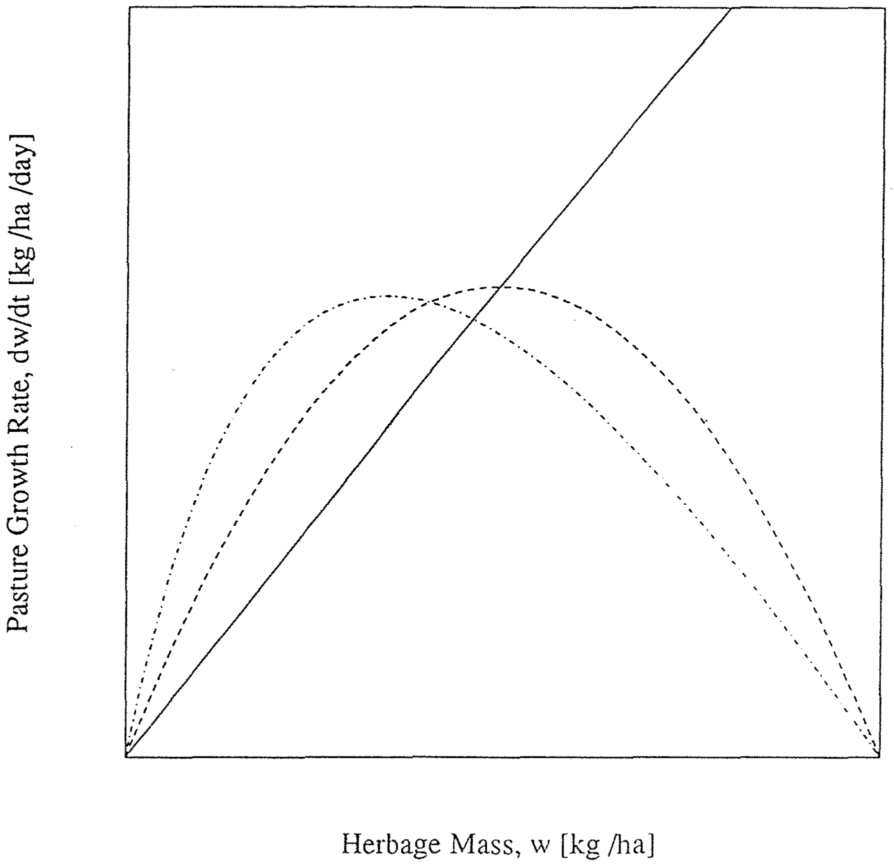

Figure 2.1: Pasture growth rate functions: ———, linear; - - - -, logistic; — · — · —, skewed (after Barlow 1987).

(4) Assume that the intake rate of an animal, dc/dt, depends only on the instantaneous available herbage biomass in the field f being grazed and that the pasture removal rate by the mob is the sum of the intake rates of all of the animals. This implies that animals (1) are non-selective, and (2) do not influence one another's grazing except through a greater or lesser rate of pasture removal. Assume that the effects of treading and fouling can be neglected. We label our animal intake rate function graze(w) (also unspecified) so that the rate of intake of a single animal is,

$$\frac{dc}{dt} = \text{graze}(w_f) \quad \text{kg/an/day} \tag{2.2}$$

where w_f is the pasture mass in the field f being grazed.

The parameter c can be interpreted as the cumulative intake of a single animal over some time period, expressed in kg/an.

The general form of an animal intake function graze(w) is that of a saturation function. Figure 2.2 shows some examples of intake functions from the literature.

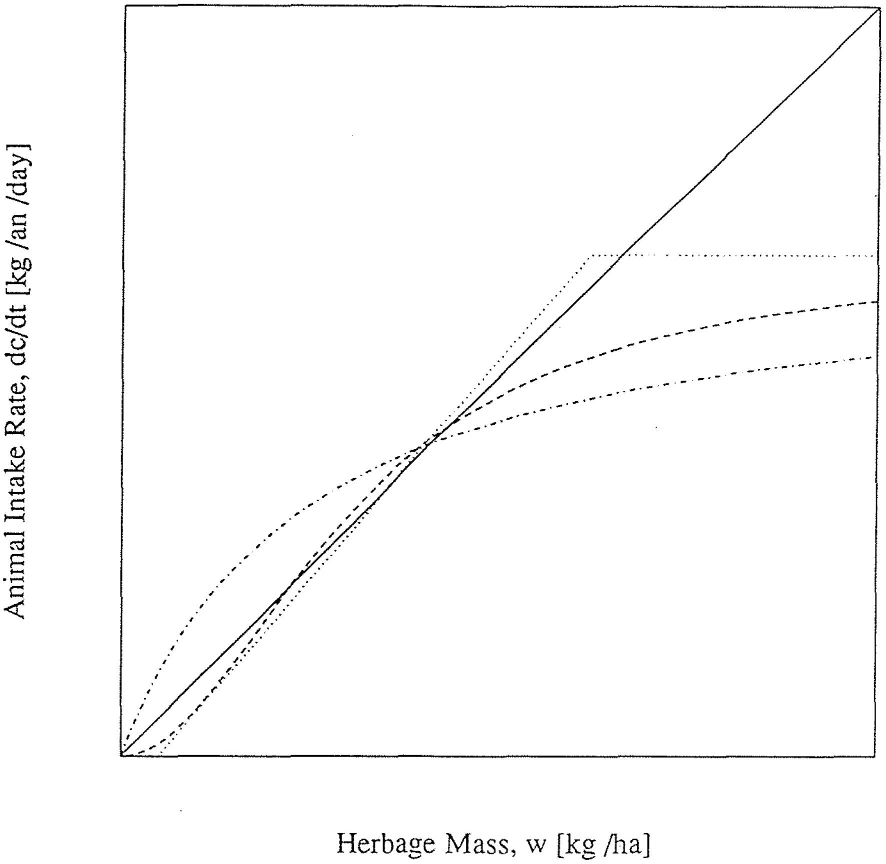

Figure 2.2: Animal intake rate functions: ————, linear; ········, ramped, including an ungrazeable residual (eg. Noy-Meir 1978b); – – – –, sigmoid (eg. Noy-Meir 1978a); – · – · –, Michaelis-Menten (eg. Barlow 1987).

The rate of increase or decrease of biomass in the grazed field is the difference between pasture accumulation and pasture removal by grazing, ie.

$$\frac{dw_f}{dt} = \text{grow}(w_f) - \frac{n}{h_f}\text{graze}(w_f) \tag{2.3}$$

where n/h_f is the stocking density.

Only two major assumptions have been made, namely that the animals' intake rate and the pasture growth rate can be described as the single parameter functions graze(w) and grow(w), respectively. These assumptions have often been made when modelling grazing systems at this level of detail (eg. Noy-Meir 1975) and are considered appropriate for times of the year when pasture is in deficit to potential animal demand and is of uniform high quality. Even so, this type of system can conceptually be extended to multi-compartment grass growth models such as Johnson and Parsons' (1985), if desired.

The three equations 2.1, 2.2, and 2.3 form a dynamical system. Given explicit functions for grow(w) and graze(w), it is theoretically possible to solve the system and predict the changes in c and w with time. In this chapter the two quantities of interest are $c(T)$ kg/an, the total intake per animal over the time 0 to T, and $W(T)$, the total remaining herbage mass at the end of the grazing period, where

$$W(T) = h_1 w_1(T) + h_2 w_2(T) \quad \text{kg.} \tag{2.4}$$

2.3.2 Explicit Functions

In this analysis we have chosen linear functions for grow(w) and graze(w) for simplicity, that is to say, the rate of herbage increase and the rate of animal intake are both proportional to the biomass, ie.

$$\text{grow}(w_i) = a w_i \tag{2.5}$$

$$\text{graze}(w_f) = k w_f \tag{2.6}$$

This simplification will be most appropriate where potential animal demands are greater than net pasture growth and hence herbage mass tends to a low level.

The system of equations 2.1, 2.2, and 2.3 now become

$$\begin{aligned} \frac{dw_i}{dt} &= a w_i \\ \frac{dw_f}{dt} &= a w_f - \frac{n}{h_f} k w_f \\ &= a(1 - m_f) w_f \\ \frac{dc}{dt} &= k w_f \end{aligned} \tag{2.7}$$

where we have chosen the dimensionless "grazing intensity" ratio $m_f = nk/ah_f$ to represent the ratio of maximum grazing rate to maximum pasture growth rate.

m_f is a positive constant for each field f with the following interpretation: if m_f is large, this implies a grazing situation with a stocking density n/h_f high enough that the field will be grazed to extinction unless the animals are moved on. If $m_f = 1$, we have an equilibrium situation where the animals are removing leaf at the same rate that it is being produced. If $m_f < 1$, we have lax grazing where herbage accumulation in field f outstrips removal by grazing.

We do not expect this latter case ($m_f < 1$) to be well represented by the linear growth equation 2.5 since real pastures are limited to a ceiling yield of biomass due to the burdens of leaf ageing and senescence. Thus, any results for $m_f < 1$ are presented here for completeness rather than realism. A lax grazing situation with high pasture mass would require one of the other curves on Figure 2.1, such as the logistic growth equation, to model the real world adequately as well as a saturation intake function such as the "ramped" on Figure 2.2. The actual forms of the functions required are difficult to investigate and have not yet been satisfactorily established.

2.3.3 Parameter Values

Although the mathematical analysis here is theoretical and the qualitative results we derive are not dependent on the actual values of the various parameters and constants, it is desirable to use realistic parameter values when making comparisons between grazing models or with experimental outcomes from the field.

The values used in plotting the figures in this paper are listed in Table 2.1 with the list of symbols.

In the analysis that follows the only restriction on parameter values is that they be greater than or equal to zero.

2.3.4 Solving the Model

At time $t = 0$ we have initial conditions $c(0) = 0$, $w_1(0)$, and $w_2(0)$. Solving equations 2.7 with $f = 1$ and $i = 2$ and applying these initial conditions gives, at some later time t_1,

$$\begin{aligned} w_1(t_1) &= w_1(0)\exp(a(1-m_1)t_1) \\ w_2(t_1) &= w_2(0)\exp(at_1) \\ c(t_1) &= \frac{kw_1(0)}{a(1-m_1)}(\exp(a(1-m_1)t_1)-1) \end{aligned} \tag{2.8}$$

At time $t = t_1$ the farmer moves his or her stock to field 2. So we have $f = 2$, $i = 1$ in equations 2.7. Solving the system again with initial conditions $c(t_1)$, $w_1(t_1)$ and $w_2(t_1)$ at time $t = t_1$ gives the solution at some later time T,

$$\begin{aligned} w_1(T) &= w_1(t_1)\exp(a(T-t_1)) \\ w_2(T) &= w_2(t_1)\exp(a(1-m_2)(T-t_1)) \\ c(T) &= c(t_1) + \frac{kw_2(t_1)}{a(1-m_2)}(\exp(a(1-m_2)(T-t_1))-1) \end{aligned} \tag{2.9}$$

Replacing $c(t_1)$, $w_1(t_1)$ and $w_2(t_1)$ with their values calculated in equations 2.8 gives us the final solution:

$$\begin{aligned} w_1(T) &= w_1(0)\exp(a(1-m_1)t_1)\exp(a(T-t_1)) \\ w_2(T) &= w_2(0)\exp(at_1)\exp(a(1-m_2)(T-t_1)) \\ c(T) &= \frac{kw_1(0)}{a(1-m_1)}(\exp(a(1-m_1)t_1)-1) \\ &\quad + \frac{kw_2(0)\exp(at_1)}{a(1-m_2)}(\exp(a(1-m_2)(T-t_1))-1) \end{aligned} \tag{2.10}$$

Parameter	**Typical value**	**[units]**	**Description**
a	1.4%	[day^{-1}]	pasture 'intrinsic' growth rate
c		[kg an^{-1}]	cumulative per animal intake
$\frac{dc}{dt}$	7.5	[kg an^{-1}day^{-1}]	animal intake rate
$c'_{\min}$	4	[kg an^{-1} day^{-1}]	minimum intake rate
f			number of the field being grazed
h_f	1.0	[ha]	area of the field being grazed
H	2	[ha]	total area of all fields
i			number of a field being rested
k	0.5%	[ha an^{-1}day^{-1}]	proportional animal intake rate
m_f	0-100	[]	'grazing intensity' ratio
n	0-100	[an]	number of animals
t_l	5	[days]	swap over time
$\hat{t}_l$	?	[days]	optimal swap over time
T	10	[days]	length of rotation
w_i	1500	[kg ha^{-1}]	herbage biomass in field i at time t
$\frac{dw_i}{dt}$	20	[kg ha^{-1}day^{-1}]	pasture growth rate
W	3000	[kg]	total biomass at time t in all fields

Table 2.1: Nomenclature, units, and typical parameter values when the model is applied to a mob of 300 kg bulls during the winter on a perennial ryegrass pasture.

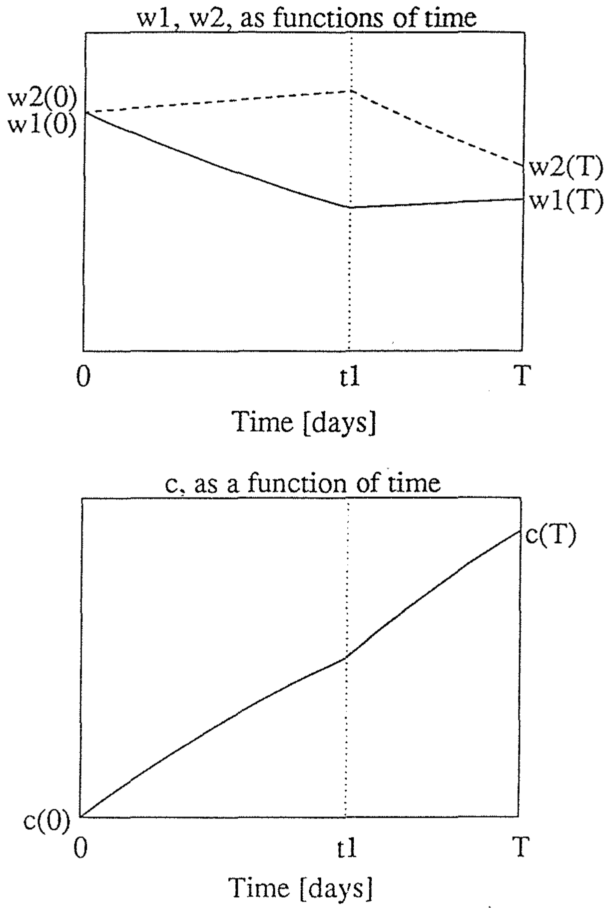

Figure 2.3: Typical course of $w_1(t)$, $w_2(t)$ and $c(t)$ over the grazing period. The dotted line shows the swapover time, t_1, at which the animals are transferred into field 2.

and also from equation 2.4,

$$\begin{aligned} W(T) &= h_1 w_1(T) + h_2 w_2(T) \\ &= h_1 w_1(0) \exp(a(1-m_1)t_1) \exp(a(T-t_1)) \\ &\quad + h_2 w_2(0) \exp(at_1) \exp(a(1-m_2)(T-t_1)) \end{aligned} \tag{2.11}$$

Figure 2.3 shows a typical time course of w_1, w_2 and c over the duration of grazing.

2.4 Results

The objective is to control our grazing system so as to maximise $c(T)$ or $W(T)$. The results derived will (in theory) be valid for any values of the parameters and so may be applied across a wide range of modelled scenarios. Nevertheless it is helpful at this point to choose some parameter values for the sake of visualisation, even though our calculations will not rely on these. We have used the values for a, k and T given

Field 1	Field 2	Total System	
$h_1 = 0.8$	$h_2 = 1.2$	$H = 2.0$	[ha]
$w_1(0) = 1620$	$w_2(0) = 1420$		[kg ha^{-1}]
$h_1 w_1(0) = 1296$	$h_2 w_2(0) = 1704$	$W(0) = 3000$	[kg]
$m_1 = \frac{nk}{ah_1} = 8.93$	$m_2 = \frac{nk}{ah_2} = 5.95$	$M = \frac{nk}{aH} = 3.57$	[ ]
		$n = 20$	[an]

Table 2.2: Two field system used in examples.

Field 1	Field 2	Total System	
$h_1 = 0.8$	$h_2 = 1.2$	$H = 2.0$	[ha]
$w_1(0) = 1500$	$w_2(0) = 1500$	$w(0) = 1500$	[kg ha^{-1}]
$h_1 w_1(0) = 1200$	$h_2 w_2(0) = 1800$	$W(0) = 3000$	[kg]
$m_1 = 8.93$	$m_2 = 5.95$	$M = 3.57$	[ ]
		$n = 20$	[an]

Table 2.3: Two field system with homogeneous initial pasture mass used in examples.

in Table 2.1 and the sample systems in Tables 2.2 and 2.3 for our examples. Note that

$$W(0) = h_1 w_1(0) + h_2 w_2(0) \quad \text{kg} \tag{2.12}$$

is the total initial herbage mass, and

$$M = \frac{nk}{aH}$$

is the grazing intensity over the whole area.

We now consider strategies of management that maximise intake, residual pasture mass, or some combination of these two objectives. Figure 2.4 shows how $c(T)$ and $W(T)$ vary as the control parameter (ie. the swapover time t_1) is varied between 0 and T for a typical scenario. We can see that $c(T)$ is maximised at a local maximum midway through the time period, near $t_1 = 5$ days, and $W(T)$ is maximised at one of the end points, that is, when only one of the fields is grazed for the total $T = 10$ days.

2.4.1 Maximum Residual Herbage

Let us first suppose that the farmer wishes to manage the system to give the maximum amount of herbage remaining after grazing. Conservation of herbage is a

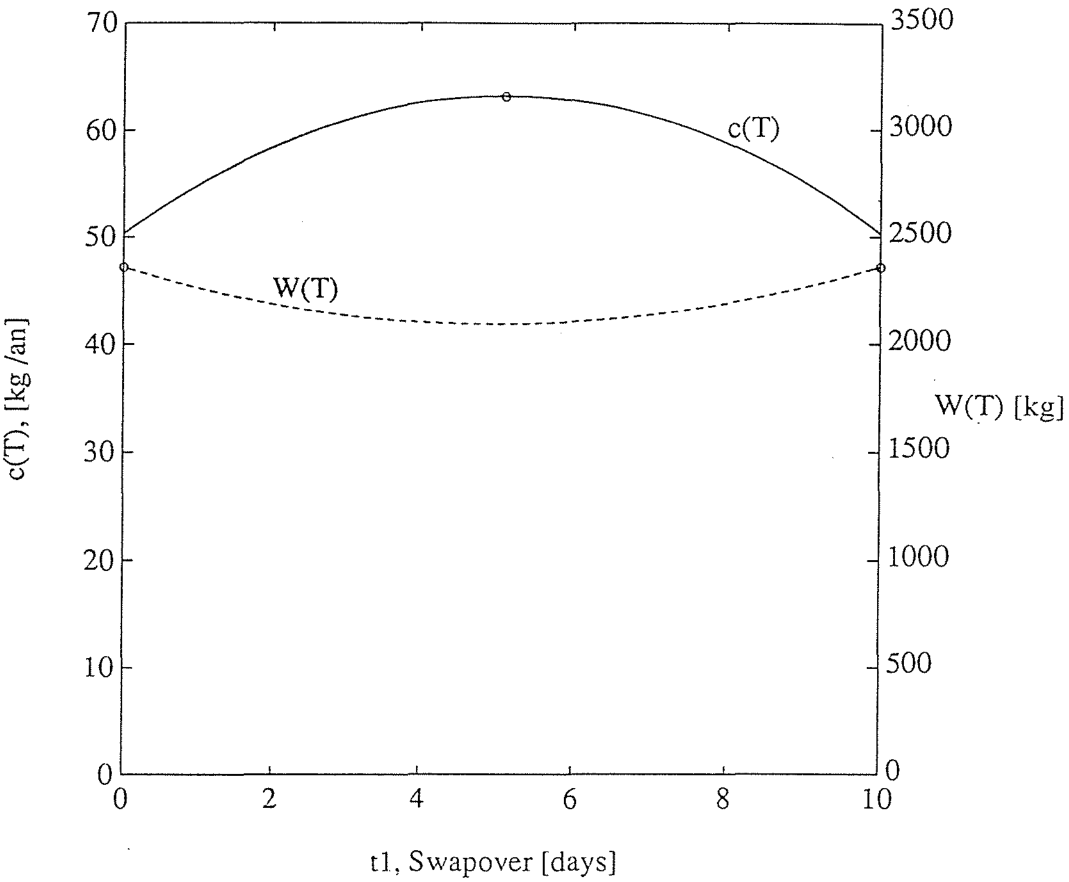

Figure 2.4: Typical changes in $c(T)$ (———) and $W(T)$ (- - - -) achieved by varying t_1, the swapover time. Optimal strategies are marked (o).

common objective of rotational grazing management and may be practiced either to maintain a consistent (but low) supply of feed during a period of slow pasture growth or to accumulate pasture mass in preparation for a future need, especially parturition, when newborn lambs or calves require sufficient feed to allow their rapid weight gain and increased survival chances. From Figure 2.4 we predict that t_1 should be chosen to be at one of the end points of the feasible region. It is easy to show that $\partial^2 W(T)/\partial t_1^2 \geq 0$ for all scenarios. Therefore, the function $W(T)$ has no local maxima, and the maximum residual herbage will indeed always be achieved by choosing the latest or the earliest feasible t_1. The feasible region here is

$$0 \leq t_1 \leq T \tag{2.13}$$

Whether to choose $t_1 = 0$ or $t_1 = T$ can be ascertained by evaluating equation 2.11 with each of these values of t_1 and observing which yields the greater value of $W(T)$. That is, choose $t_1 = 0$ (ie. graze only field 2) if

$$W(T)|_{t_1=0} > W(T)|_{t_1=T} \tag{2.14}$$

ie.

$$\begin{aligned} h_1 w_1(0)\exp(aT) &+ h_2 w_2(0)\exp(a(1-m_2)T) \\ &> h_1 w_1(0)\exp(a(1-m_1)T) + h_2 w_2(0)\exp(aT) \end{aligned} \tag{2.15}$$

If this is not the case, choosing $t_1 = T$ will give the maximum residual herbage, that is, we would choose only to graze field 1.

Example Using the values in Table 2.2, grazing only field 2 gives

$$W(T)|_{t_1=0} = 2343 \text{ kg}$$

and grazing only field 1,

$$W(T)|_{t_1=T} = 2387 \text{ kg}$$

Therefore, maximum herbage is conserved if only field 1 is grazed ($t_1 = T$). This may be a little surprising since we choose to graze the field with the greater initial herbage but can be explained by the reasoning that field 2 is able to achieve greater biomass production due to its larger area, which results in a greater residual bulk of herbage (though not a greater herbage density).

As a comparison, if both fields are grazed equal lengths of time the model predicts a much lower residual herbage mass,

$$W(T)|_{t_1=T/2} = 2090 \text{ kg}$$

This example shows that it is not always possible to determine the optimum strategy intuitively, even in a simple case like this. Conditions such as equation 2.15 are useful in providing quantitative predictions of the consequences of choosing various strategies.

Minimum Intake Constraint

Usually when a farmer wishes to conserve herbage he or she will wish also to ensure that the animals receive some minimum level of feeding. This is relevant when m_1 and m_2 are greater than 1, that is, animals tend to graze to extinction. As seen in Figure 2.4, choosing $t_1 = 0$ or T to maximise $W(T)$ results in a low intake for the animals. It is therefore necessary to set a constraint to ensure that the animals achieve at least a minimal rate of intake. This can be done by requiring that

$$\frac{dc}{dt} \geq c'_{\min} \quad \text{kg/ha/day} \tag{2.16}$$

throughout the period. Since the animals' intake rate is proportional to the available pasture mass, this constraint will be limiting when the pasture mass becomes low, especially at the end of the animals' time in field 1 (time t_1) and the end of the animals' time in field 2 (time T) (cf. Figure 2.3).

In practice it is more appropriate to specify a minimum average intake over some period of several days. In this case the intake on a given day could be lower than this average. While it is possible (though more complicated) to construct such a constraint mathematically, the form of constraint in equation 2.16 is sufficient for our current purposes if it is remembered that c'_{min} is then a conservative minimum requirement.

From equations 2.7, $dc/dt = kw_f$. So we require

$$\left.\frac{dc}{dt}\right|_{t=t_1} = kw_1(t_1) = kw_1(0)\exp(a(1-m_1)t_1) \geq c'_{\text{min}}$$

and

$$\left.\frac{dc}{dt}\right|_{t=T} = kw_2(T) = kw_2(0)\exp(at_1)\exp(a(1-m_2)(T-t_1)) \geq c'_{\text{min}} \tag{2.17}$$

These can be rearranged to give limits on the swapover times t_1 which may be chosen if the minimum intake level in equation 2.16 is to be achieved:

$$\frac{1}{m_2 a}\ln\left(\frac{c'_{\text{min}}}{kw_2(0)\exp(a(1-m_2)T)}\right) \leq t_1 \leq \frac{1}{(1-m_1)a}\ln\left(\frac{c'_{\text{min}}}{kw_1(0)}\right) \tag{2.18}$$

Example Returning to the previous example, consider the effect of requiring at least a minimum daily intake of

$$c'_{\text{min}} = 4 \text{ kg/an/day}$$

Then as well as condition 2.13 we are limited to values of t_1 which satisfy

$$1.4 \leq t_1 \leq 6.4 \text{ days}$$

from condition 2.18. Clearly $t_1 = T$ cannot now be chosen because the minimum intake constraint would be violated and the animals' condition would not be maintained. The best strategy will instead be to choose one of the end points of condition 2.18. To determine which, compare

$$\begin{aligned} W(T)|_{t_1=1.4} &= 2209 \text{ kg} \\ W(T)|_{t_1=6.4} &= 2122 \text{ kg} \end{aligned}$$

Therefore the best strategy to maximise residual herbage while providing a minimal diet is to choose $t_1 = 1.4$ days. It is interesting that whereas for the unconstrained question we chose to graze only field 1, we now choose to graze mostly field 2.

It should be noted that for high values of $c'_{\min}$ the interval in equation 2.18 vanishes and so it is not possible to find a swapover time t_1 which can satisfy the constraint in equation 2.16. This is due to the unrealistic expectations put upon the grazing system. One would need to graze fewer animals to remedy this.

Maximum number of animals allowed to achieve minimal intake

If a minimum intake rate $c'_{\min}$ is desired, the swapover time t_1 must be within the interval given by equation 2.18. For this to be possible the interval in equation 2.18 must exist, that is,

$$\frac{1}{m_2 a} \ln\left(\frac{c'_{\min}}{k w_2(0) \exp\left(a(1-m_2)T\right)}\right) \leq \frac{1}{(1-m_1)a} \ln\left(\frac{c'_{\min}}{k w_2(0)}\right) \tag{2.19}$$

If the number of animals is too great this will be impossible. Using $n = m_1 h_1 a/k = m_2 h_2 a/k$ we can rearrange equation 2.19 to give the maximum number of animals. Using B and C as dummy variables, let

$$B = \frac{a h_2}{2k}\left(1 - \frac{1}{aT}\ln\left(\frac{c'_{\min}}{k w_2(0)}\right)\right) + \frac{a h_1}{2k}\left(1 - \frac{1}{aT}\ln\left(\frac{c'_{\min}}{k w_1(0)}\right)\right)$$

and

$$C = \frac{a^2}{k^2} h_1 h_2\left(1 - \frac{1}{aT}\ln\left(\frac{c'_{\min}}{k w_2(0)}\right)\right)$$

Then equation 2.19 will be satisfied if and only if the number of animals,

$$n \leq B + \sqrt{B^2 - C}$$

This result assumes a grazing pressure sufficient that m_1, m_2 are both greater than 1.

Example Consider again the example in Table 2.3. If the farmer requires $c'_{\min} =$ 4 kg/animal/day to be the minimum intake rate, we then derive from the above formula that ($B = 15.4$, $C = 41.3$)

$$n \leq 29 \text{ animals}$$

to satisfy condition 2.16.

Which field to graze first?

A final question to consider in this section is whether greater herbage may be conserved if the two fields are grazed in one or the other order. Specifically, which field should be grazed first?

When there is no minimum intake constraint the optimal strategy is to graze only one field, as chosen by condition 2.15, so the question of which field to graze first is not relevant. However, it may be necessary to graze both fields to satisfy a minimum intake constraint if one exists.

When a minimum intake is specified there is a constraint on the possible choices of the swapover time as described by condition 2.18. If field 2 is to be grazed first we derive a similar expression limiting t_1, where t_1 is now the time spent in field 2:

$$\frac{1}{m_1 a} \ln\left(\frac{c'_{\text{min}}}{k w_1(0) \exp(a(1-m_1)T)}\right) \leq t_1 \leq \frac{1}{(1-m_2)a} \ln\left(\frac{c'_{\text{min}}}{k w_2(0)}\right)$$

The optimal strategy lies at one of the constraint limits. There is no simple *a priori* method to determine which of these four strategies will be optimal in a given case, so we must compare the predicted results from the model using each strategy in turn:

(1) Graze field 1 first, for $t_1 = \frac{1}{m_2 a} \ln\left(\frac{c'_{\text{min}}}{k w_2(0) \exp(a(1-m_2)T)}\right)$ days.

(2) Graze field 1 first, for $t_1 = \frac{1}{(1-m_1)a} \ln\left(\frac{c'_{\text{min}}}{k w_1(0)}\right)$ days.

(3) Graze field 2 first, for $t_1 = \frac{1}{m_1 a} \ln\left(\frac{c'_{\text{min}}}{k w_1(0) \exp(a(1-m_1)T)}\right)$ days.

(4) Graze field 2 first, for $t_1 = \frac{1}{(1-m_2)a} \ln\left(\frac{c'_{\text{min}}}{k w_2(0)}\right)$ days.

Example As before, with $c'_{\text{min}} = 4$ kg/an/day. Compare the results for each of the 4 strategies above.

Strategies (1) and (2); graze field 1 first:

$$\begin{aligned} (1)\ W(T)|_{t_1=1.4} &= 2209 \text{ kg} \\ (2)\ W(T)|_{t_1=6.4} &= 2122 \text{ kg} \end{aligned}$$

Strategies (3) and (4); graze field 2 first:

$$\begin{aligned} (3)\ W(T)|_{t_1=3.2} &= 2139 \text{ kg} \\ (4)\ W(T)|_{t_1=8.3} &= 2187 \text{ kg} \end{aligned}$$

So strategy (1) is the optimum in this scenario.

Comparison with Continuous Grazing

Rotational grazing is sometimes advocated as a means to conserve herbage. In continuous grazing herbage conservation is not possible except by removing animals from the system. Using this methodology we can compare the results from these two strategies theoretically.

If $w_1(0) = w_2(0)$, the two fields can be combined to make one field of size H hectares and initial herbage mass $W(0)/H$ kg/ha. Then the grazing intensity ratio is M and the residual herbage mass at time T is,

$$W_c(T) = W(0)\exp(a(1-M)T)$$

The minimum intake constraint will be satisfied if

$$\left.\frac{dc}{dt}\right|_{t_1=T} = k\frac{W_c(T)}{H} = k\frac{W(0)}{H}\exp(a(1-M)T) \geq c'_{\text{min}}$$

For this we require

$$n \leq \frac{aH}{k}\left(1 - \frac{1}{aT}\ln\left(\frac{c'_{\text{min}}H}{kW(0)}\right)\right)$$

Example Take the example in Table 2.2 with $w_1(0) = w_2(0) = 1500$ kg/ha. Combining the two fields gives one field of area 2 hectares and initial mass 1500 kg/ha. We require $n \leq 30$ animals to satisfy a minimum intake requirement of $c'_{\text{min}} = 4$ kg/an/day for continuous grazing. This being met since $n = 20$ animals, we calculate the residual herbage from continuous grazing to be

$$W_c(T) = 2093 \text{ kg}$$

The two field rotation system requires $n \leq 29$ animals to satisfy this same minimum intake (see section 2.4.1 for method). Testing the four rotational strategies gives the optimum strategy to be (1) $W(T)|_{t_1=0.8} = 2211$ kg, that is, to graze field 1 first and swap over into field 2 at $t_1 = 0.8$ days. By comparison, $W(T)|_{t_1=5} = 2104$ kg. Therefore, a significant improvement in $W(T)$ is achieved by using the optimal rotational strategy over the continuous strategy in this case. It is possible, however, that this improvement would be masked by random variability in practice.

2.4.2 Optimal Animal Intake

An alternative objective is to find the swapover time $\hat{t}_1$ which gives the maximum cumulative intake per animal, $c(T)$. Mathematically, the maximum of $c(T)$ shown in Figure 2.4 is located by setting the partial derivative of equation 2.10 equal to zero, ie.

$$\begin{aligned}\frac{\partial c(T)}{\partial t_1} &= kw_1(0)\exp\left(a(1-m_1)t_1\right)\\ &\quad+\frac{kw_2(0)\exp(at_1)}{1-m_2}\left(\exp\left(a(1-m_2)(T-t_1)\right)-1\right)\\ &\quad-kw_2(0)\exp\left(at_1\right)\exp\left(a(1-m_2)(T-t_1)\right)\\ &= kw_2(0)\exp\left(at_1\right)\\ &\quad\times\left[\frac{w_1(0)}{w_2(0)}\exp(-m_1at_1)-\frac{1-m_2\exp(a(1-m_2)(T-t_1))}{1-m_2}\right] \qquad (2.20)\\ &= 0 \text{ for extrema.}\end{aligned}$$

It is reasonable to assume that the first factor, $kw_2(0)\exp(at_1)$, is non zero and so we can rearrange equation 2.20 to give

$$(1-m_2)r\exp\left(-m_1a\hat{t}_1\right)=1-m_2\exp\left(a(1-m_2)(T-\hat{t}_1)\right) \qquad (2.21)$$

where $r=w_1(0)/w_2(0)$, the ratio between the initial herbage masses. In Table 2.2, $r=1620/1420=1.14$. Then if $W(0)$ is as defined in equation 2.12, the original herbage masses may be recovered by

$$\begin{aligned}w_1(0) &= rW(0)/(h_1r+h_2)\\ w_2(0) &= W(0)/(h_1r+h_2)\end{aligned}$$

Equation 2.21 has a unique solution $\hat{t}_1$ corresponding to a maximum of $c(T)$. While equation 2.21 gives the mathematical optimum of $c(T)$, this must be constrained by condition 2.13 to give a feasible swapover time. The maximum intake per animal is then achieved by swapping the animals over at this t_1. Unfortunately, it is not possible to obtain an explicit expression for $\hat{t}_1$. Because of this, graphical methods are used to show how it depends on the other parameters.

The Relationship of $\hat{t}_1$ to T

By rearranging equation 2.21 to give

$$T=\hat{t}_1+\frac{1}{a(1-m_2)}\ln\left(\frac{1}{m_2}-r\frac{1-m_2}{m_2}\exp\left(-m_1a\hat{t}_1\right)\right) \qquad (2.22)$$

we may get a feel for how $\hat{t}_1$ depends on T. Figure 2.5 shows two graphs of $T(\hat{t}_1)$, one for $r>1$ and one for $r<1$. The dotted lines on these graphs show the location of the physical constraints and of two simple bounds to $T(\hat{t}_1)$. Since it is not possible to find the exact $\hat{t}_1$ explicitly, it may be useful to have these linear bounds which

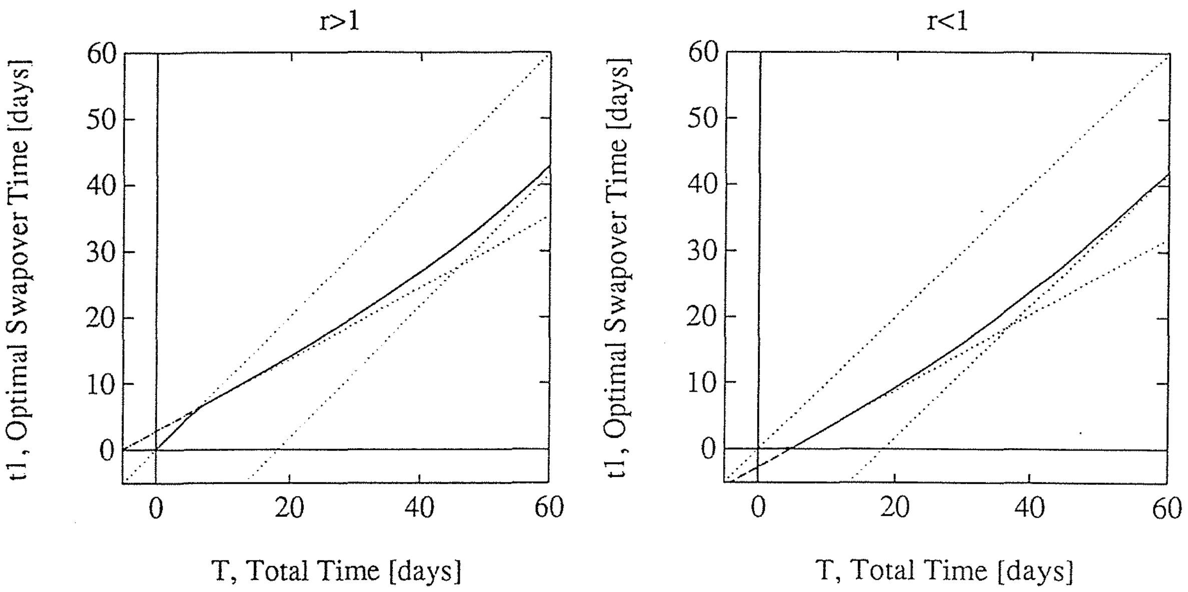

Figure 2.5: Optimal t_1 against T for the two cases $r < 1$ and $r > 1$ from equation 2.22. ————, optimum constrained by constraint 2.13; – – – –, solution to equation 2.21 where this violates constraint 2.13; ·········, constraint 2.13 and bounds as described in section 2.4.2.

allow a good approximation. The bounds shown are derived and explained later in this section.

The physical constraints are given in equation 2.13 and are the lines $\hat{t}_1 = 0$ and $\hat{t}_1 = T$, respectively, on Figure 2.5. The conditions necessary to satisfy these constraints are also derived later in this section.

The heavy curve on Figure 2.5 is defined by equation 2.22 and gives the optimal $\hat{t}_1$ as a function of T for an arbitrary set of parameters. The shape of this curve depends non-linearly on r, m_1 and m_2.

Bounds on $\hat{t}_1$

Since the optimal $\hat{t}_1$ to maximise $c(T)$ cannot be found explicitly from equation 2.21, it is useful to find limits inside which $\hat{t}_1$ is known to lie. These give us a good approximation to where the optimum is.

The bound shown in Figure 2.5 as the steep dotted line to the right of the optimal solid curve is found by letting $m_1 a\hat{t}_1 \to \infty$ in equation 2.22. Notice that the right hand side increases monotonically with $\hat{t}_1$ to the asymptote

$$T = \hat{t}_1 + \frac{\ln(1/m_2)}{a(1-m_2)}$$

This gives the bound

$$\hat{t}_1 > T - \frac{\ln(1/m_2)}{a(1-m_2)} \tag{2.23}$$

which is close to the exact solution at large T and m_2.

A second bound is obtained by linearization of $T(\hat{t}_1)$ near $\hat{t}_1 = 0$. This bound will be close to the exact solution for low values of T.

As preliminaries, we differentiate equation 2.22 to get

$$\frac{\partial T}{\partial \hat{t}_1} = \frac{(1/r)\exp(m_1 a \hat{t}_1) - 1 + m_1 + m_2}{(1/r)\exp(m_1 a \hat{t}_1) - 1 + m_2}$$

and

$$\frac{\partial^2 T}{\partial \hat{t}_1^2} = \frac{-(m_1^2 a/r)\exp(m_1 a \hat{t}_1)}{\left[(1/r)\exp(m_1 a \hat{t}_1) - 1 + m_2\right]^2}$$

From these we get (assuming $m_2 > 1$),

$$\left.\frac{\partial T}{\partial \hat{t}_1}\right|_{\hat{t}_1=0} \geq 0, \quad \left.\frac{\partial T}{\partial \hat{t}_1}\right|_{\hat{t}_1\to\infty} \to 1, \quad \text{and} \quad \frac{\partial^2 T}{\partial \hat{t}_1^2} < 0$$

From these and equation 2.22 we now have,

$$\begin{aligned}
T|_{\hat{t}_1=0} &= \frac{1}{a(1-m_2)}\ln\left(\frac{1}{m_2} - r\frac{1-m_2}{m_2}\right) \\
\left.\frac{\partial T}{\partial \hat{t}_1}\right|_{\hat{t}_1=0} &= \frac{((1/r)-1) + m_1 + m_2}{((1/r)-1) + m_2} \\
\left.\frac{\partial T}{\partial \hat{t}_1}\right|_{\hat{t}_1\to\infty} &\to 1 \\
\frac{\partial^2 T}{\partial \hat{t}_1^2} &< 0
\end{aligned} \tag{2.24}$$

Because of the latter, any tangent to $T(\hat{t}_1)$ is a bound of the function, including the tangent at $\hat{t}_1 = 0$,

$$T \leq T|_{\hat{t}_1=0} + \hat{t}_1 \cdot \left.\frac{\partial T}{\partial \hat{t}_1}\right|_{\hat{t}_1=0} \tag{2.25}$$

Inverting gives the bound

$$\hat{t}_1 \geq \left(T - T|_{\hat{t}_1=0}\right) \div \left.\frac{\partial T}{\partial \hat{t}_1}\right|_{\hat{t}_1=0} \tag{2.26}$$

where the relevant values can be calculated from results 2.24.

In Figure 2.5 this bound is represented by the less steep dotted line which touches the solid/dashed curve at $\hat{t}_1 = 0$.

Example As in Table 2.2, $r = 1.14$, $m_1 = 8.93$, $m_2 = 5.95$, $a = 0.014$ per day, and $T = 10$ days. Then the bounds from equations 2.23 and 2.26 are

$$\hat{t}_1 > -15.7$$

and

$$\hat{t}_1 \geq 4.6$$

respectively. The former is not very helpful in this case, but the latter is quite close to the optimum, since T is fairly small. Numerically calculated, the true optimum in this case is $\hat{t}_1 \approx 4.7$ days.

Constraint Violations on $T(\hat{t}_1)$

When optimising $c(T)$ the mathematical maximum is found by solving equation 2.21. This solution does not always satisfy constraint 2.13, as observed on Figure 2.5 when the solid curve leaves the feasible region $0 \leq \hat{t}_1 \leq T$. In this case we have shown a dashed curve on the figure.

The conditions for this constraint to be violated can be derived as follows. Firstly, we find that $\hat{t}_1 < 0$ only if $r \leq 1$, and when

$$T < \frac{1}{a(1-m_2)} \ln\left(\frac{1}{m_2} - r\frac{1-m_2}{m_2}\right)$$

(by putting $\hat{t}_1 = 0$ into equation 2.22).

Secondly, $\hat{t}_1 > T$ only if $r > 1$, and when

$$\frac{1}{a(1-m_2)} \ln\left(\frac{1}{m_2} - r\frac{1-m_2}{m_2}\exp\left(-m_1 a T\right)\right) < 0$$

(by putting $\hat{t}_1 = T$ into equation 2.22). This simplifies to

$$T < \frac{\ln(r)}{m_1 a}$$

By corollary, if $r \leq 1$ then the solution to equation 2.21 will always satisfy $\hat{t}_1 \leq T$, and if $r \geq 1$ then it will always satisfy $\hat{t}_1 \geq 0$. If $r = 1$, the solution to equation 2.21 is always feasible.

Example In the previous example we had $r = 1.14$. In this case $\hat{t}_1 > T$ if

$$T < 1.0 \text{ days}$$

T is much larger than this so spurious solutions to equation 2.21 do not occur. If T was 0.5 days however, we should ignore the solution $\hat{t}_1$ and graze only field 1 ($\hat{t}_1 = T$).

Two Identical Fields

In general, all of the parameters could take any non-negative value. Because of difficulties involved in finding the optimal solutions and analysing their dependence on the various parameters, we start by assuming that the two fields are identical, that is,

$$\begin{aligned} h_1 &= h_2 = H/2 \\ w_1(0) &= w_2(0) = W(0)/H \end{aligned}$$

Then

$$\begin{aligned} r &= 1 \\ m_1 &= m_2 = 2M \end{aligned}$$

where $M = nk/aH$.

Using $H = 2$ ha and $W(0) = 3000$ kg, Figure 2.6 shows how the optimum shifts as different numbers of animals are grazed in a typical system, from $n = 1$ to 500 bulls.

At stocking densities less than 100 an/ha the optimum is near to 5 days, which would be the usual strategy adopted by a farmer grazing animals on 2 identical fields. In practice, farmers use stocking densities higher than this only with very short grazing durations.

Considerably lower intake would be achieved by choosing $t_1 = 0$ or $t_1 = T$. This is to be expected, since only half of the total area is then grazed. Clearly this is a poorer strategy than continuous grazing. However, is even the optimum strategy poorer than continuous grazing? Since $w_1(0) = w_2(0)$ it is possible to test this hypothesis.

Comparison with Continuous Grazing

If instead of dividing the H ha of land into 2 fields the farmer leaves it as a single field and grazes the animals on it for T days, their intake is, from equation 2.8,

$$c_c(T) = \frac{kw(0)}{a(1-M)}(\exp(a(1-M)T) - 1)$$

where $w(0) = W(0)/H$ kg/ha. In this case the farmer exercises no control over grazing.

Figure 2.7 shows how intake per animal varies as a function of the number of animals for three strategies: (1) continuous, (2) equal time rotation, and (3) optimal swapover time rotation. This graph shows that for identical fields not only

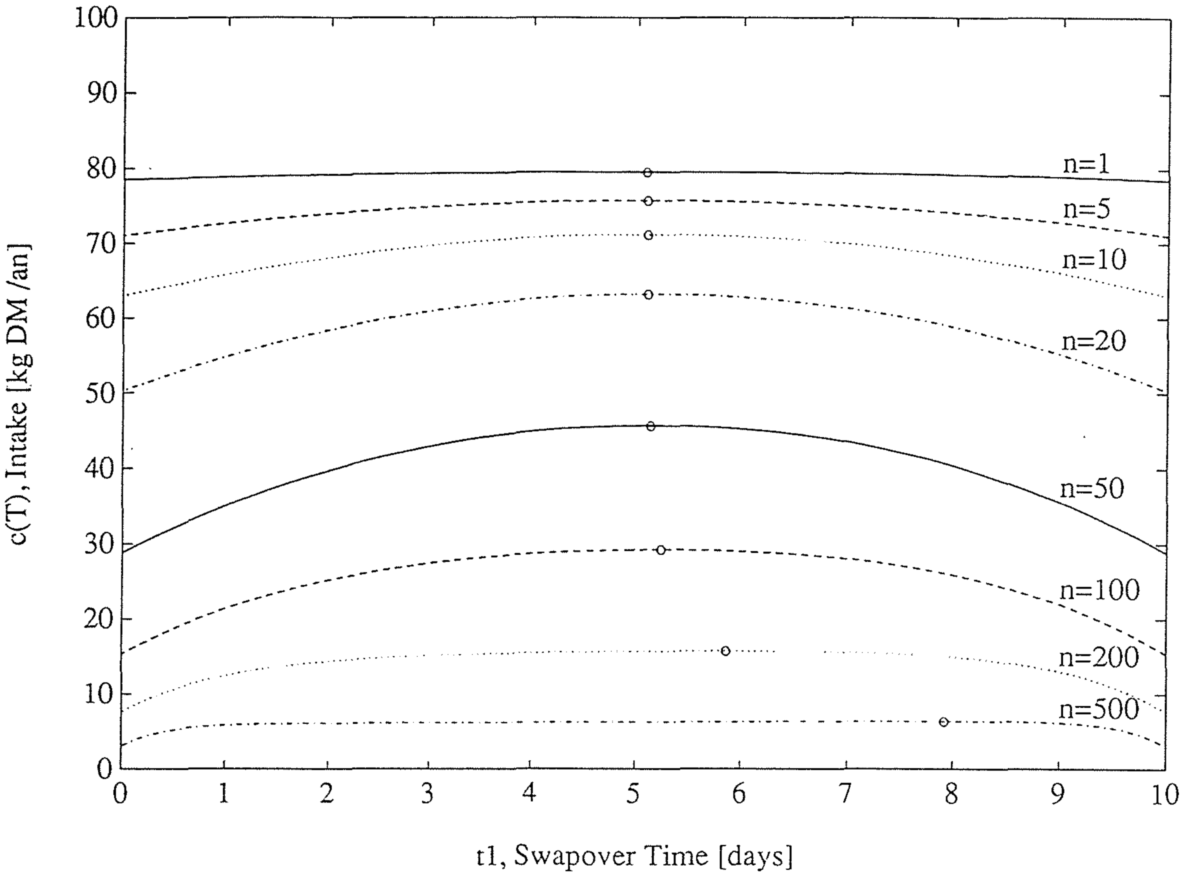

Figure 2.6: Intake $c(T)$ against t_1 for identical fields, ie. $r = 1$ and $h_1 = h_2$ (equal sized fields with uniform initial herbage mass). Each curve corresponds to a different number of animals n as shown. Optimal strategies in each case are marked (o).

is the optimal strategy no better than the usual strategy of $t_1 = 5$, but neither is it significantly better than the continuous strategy. The differences increase as stocking rate gets large, but even if n can feasibly be as large as 600 animals, the optimal strategy provides only 5% more intake per animal than the continuous strategy.

It should be noted that to completely optimise the two field rotational treatment we also need to calculate the optimal field sizes, h_1 and h_2, which may not turn out to be ideally equal. We have assumed the division $h_1 = h_2$.

Different Sized Fields, $w_1(0) = w_2(0)$

Now consider the effect of changing the size of the fields. If the total amount of land H is fixed, then $h_1 + h_2 = H$. Then

$$\frac{nk}{am_1} + \frac{nk}{am_2} = \frac{nk}{aM}$$

ie.

$$\frac{1}{m_1} + \frac{1}{m_2} = \frac{1}{M}$$

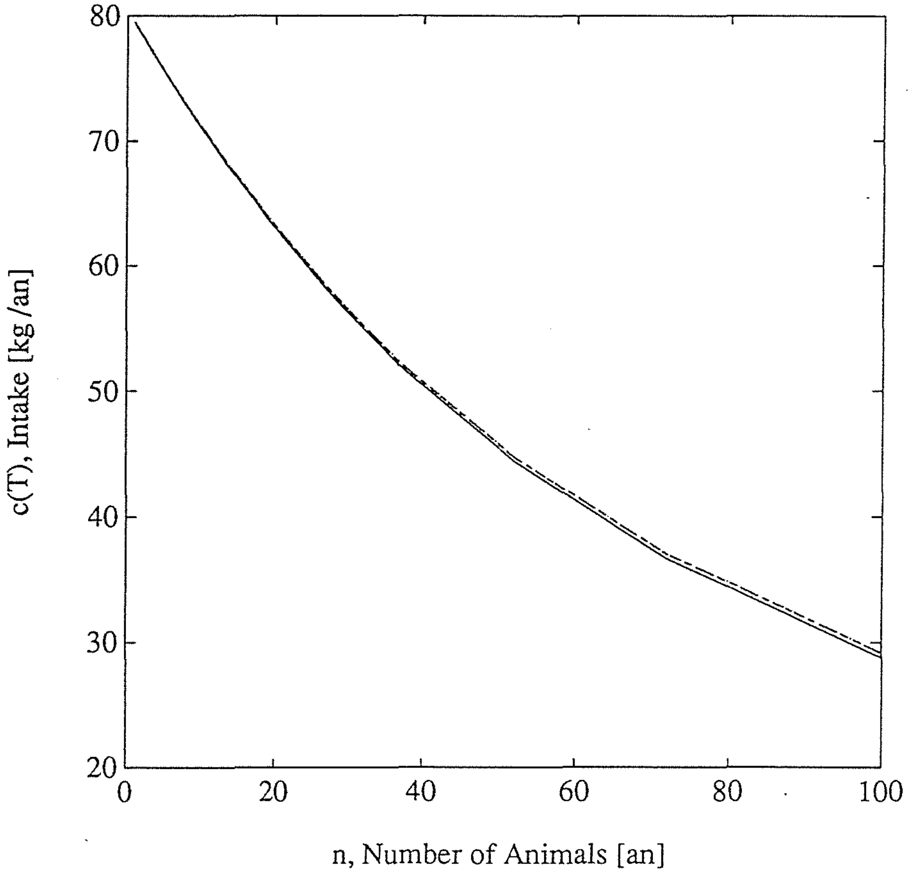

Figure 2.7: Comparison of grazing managements in identical fields, ie. $r = 1$ and $h_1 = h_2$ (equal sized fields with uniform initial herbage mass); ————, continuous grazing; – – – –, optimal rotational strategy; – · – · –, equal time rotation (partially obscured by optimal rotation curve).

Since we are considering the case where $r = 1$, the optimum $\hat{t}_1$ described by equation 2.21 will always lie in the feasible region given by equation 2.13 (see results earlier in this section).

Figure 2.8 shows how the optimal choice of t_1 depends on m_1 and m_2, and Figure 2.9 shows the corresponding optimal $c(T)$. The dotted lines in Figure 2.9 are lines of constant stocking rate, that is, constant M.

From Figure 2.8, notice that there are two qualitatively different situations. The first is where M is less than about 60. This would be the case in most practical scenarios since it corresponds to

$$n/H = aM/k \leq 110 \text{ animals/ha}$$

In this case, the optimal swapover time is determined by the ratio of the sizes of the fields, $r = h_1/h_2$, and changes in stocking rate affect only the animals' intake, not the optimal strategy.

The other case is where M is greater than 60. This corresponds to a situation

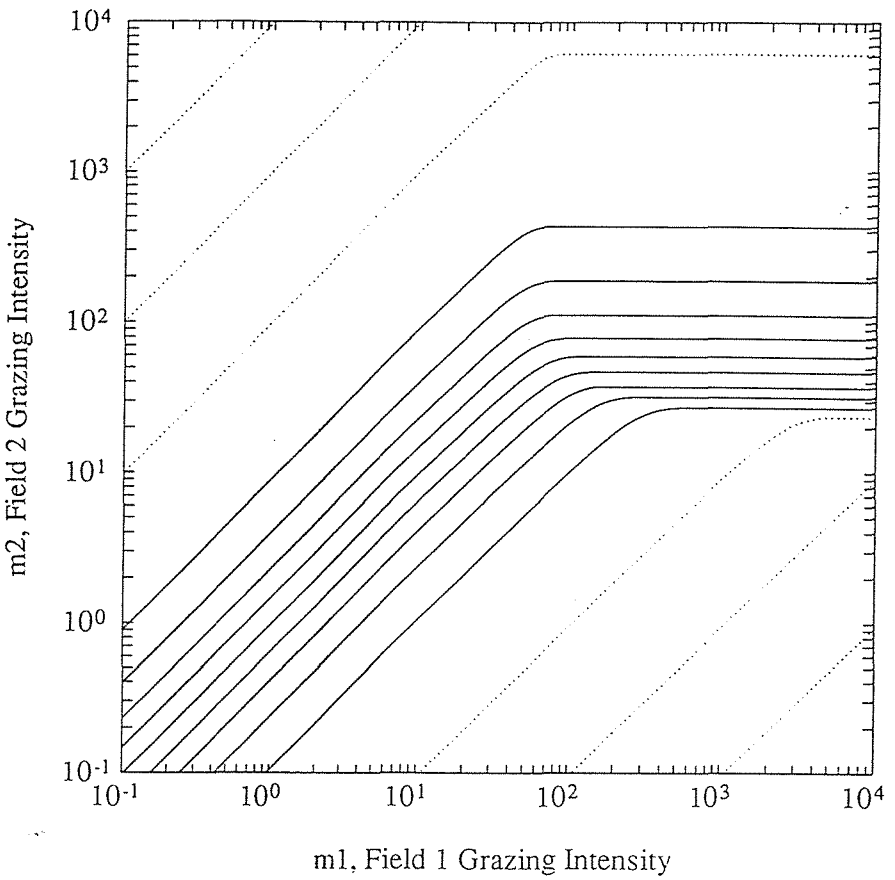

Figure 2.8: Optimal t_1 when $r = 1$ (uniform initial herbage masses). ———, contours of optimal t_1=1, 2, 3 ... 9 days; ·········, contours of optimal t_1=0.001, 0.01, 0.01, 9.9, 9.99, and 9.999 days.

of extremely high stocking rate where the pasture is grazed to extinction in a short time. In this case there is an advantage to be gained by detaining the animals in field 1, and thus allowing some extra production in field 2 prior to swapover. Since the lines of constant $\hat{t}_1$ are horizontal in this region, the optimal swapover time is determined solely by m_2 (since field 1 is considered a holding area or "sacrifice field") and is near

$$\hat{t}_1 \approx T + \frac{\ln(m_2)}{a(1 - m_2)}$$

(which is one of the bounds on the optimum derived earlier in this section).

Earlier we noted that to properly optimise the rotational strategy, attention must be paid to both swap over time and field sizes. The consequence of Figure 2.9 is that the division of field sizes is not significant provided the optimal swapover time is used. Because the lines of optimal $c(T)$ are parallel to the lines of constant M, optimal intake is shown to be completely determined by stocking rate. This also shows that there is little latitude for grazing strategy to increase intake once stocking rate is determined.

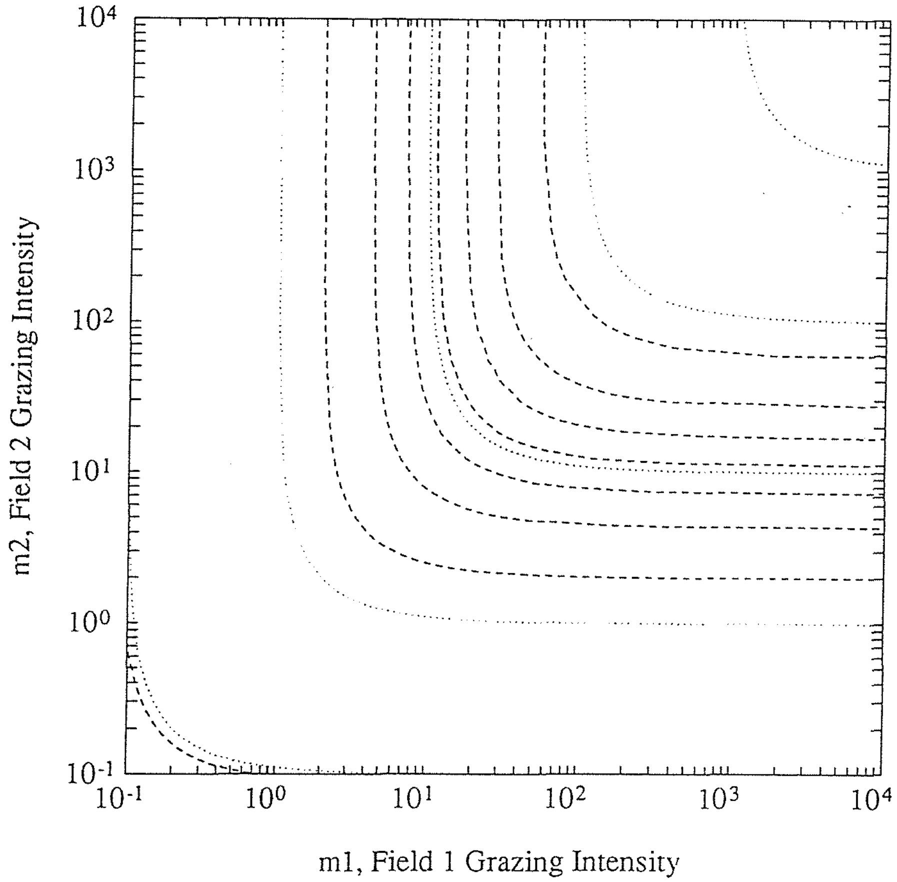

Figure 2.9: Optimal $c(T)$ when $r = 1\cdot$ (uniform initial herbage masses) corresponding to the optima in Figure 2.8. – – – –, contours of optimal $c(T)$=10, 20 ... 80 kg/animal; ········, lines of constant M, proportional to stocking rate.

Figure 2.9 shows that when $r = 1$, it is not important which field is grazed first, and that no further advantage may be gained in terms of animal intake by adjusting the field sizes over and above that achieved when the fields are of equal size.

Equal Sized Fields with $w_1(0) \neq w_2(0)$

Apart from size, the other important difference between the two fields which may influence the choice of t_1 is their initial herbage cover. This can be reduced to the consideration of the parameter r as noted in equation 2.21. So far we have only examined cases where $r = 1$.

Figure 2.10 shows how $\hat{t}_1$ varies with r when $m_1 = m_2$. Figure 2.11 shows the corresponding optimal $c(T)$, and $c(T)|_{t_1=T/2}$.

As r increases from 1 we see that a greater intake $c(T)$ will be achieved by increasing the length of time the animals spend in field 1 as opposed to field 2. At high stocking rate this effect is moderated since the animals will consume most of the herbage mass in a short time anyway. However, some advantage is gained at

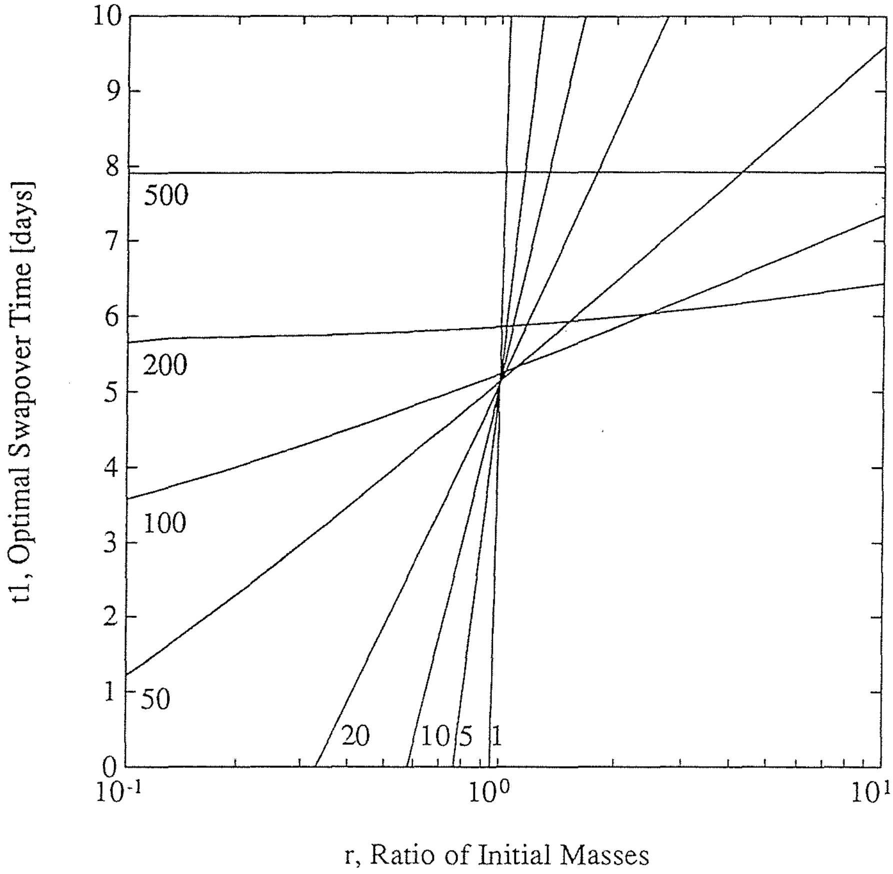

Figure 2.10: Optimal t_1 when $h_1 = h_2$ (equal sized fields); ———, optimal t_1 against r for n=1, 5, 10, 20, 50, 100, 200 and 500 animals, respectively.

high stocking rate by holding the animals in field 1 even after the herbage level has been reduced to near zero, as mentioned before, in order that field 2 may accumulate a little more leaf before the animals are grazed there.

Graze which field first?

From Figure 2.11 we can again explore the question of which field to graze first, now in terms of whether to graze that with greater or lesser initial herbage cover first. As the graph is closely symmetrical, we conclude that it is not important which field is grazed first, provided the optimal t_1 is used. The dotted lines on Figure 2.11 corresponds to the intake when the non-optimal strategy $t_1 = T/2$ is used. This strategy gives a much lower intake than the optimal strategy when the fields start with very different quantities of herbage.

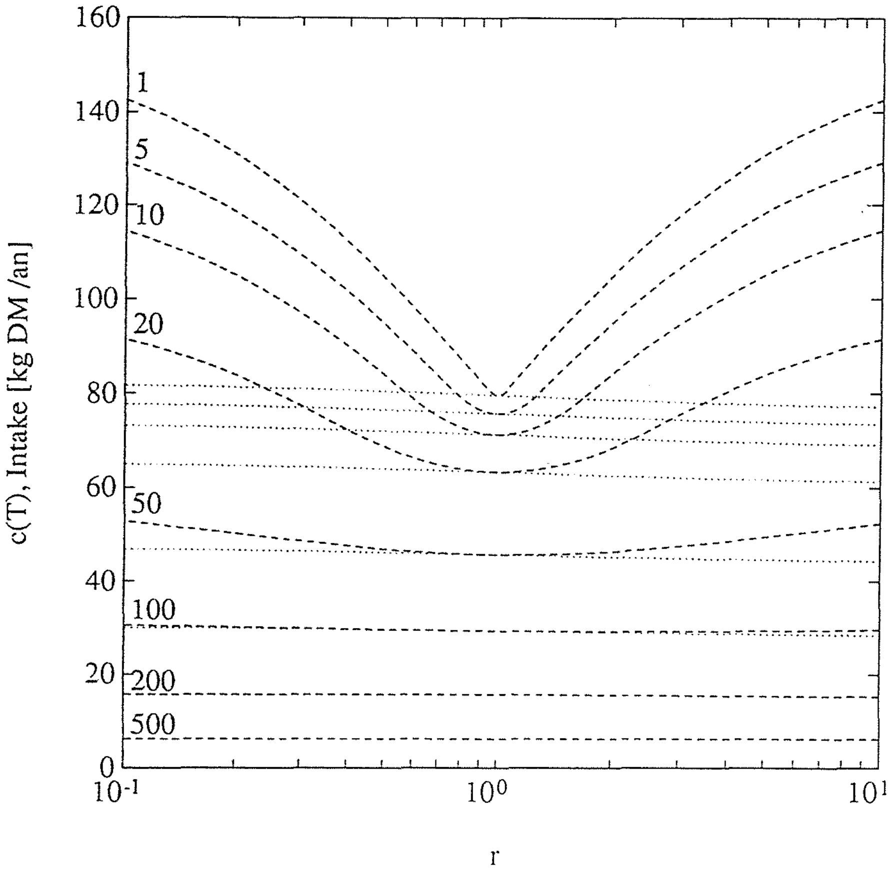

Figure 2.11: Optimal $c(T)$ when $h_1 = h_2$ (equal sized fields) corresponding to the optima in Figure 2.10; – – – –, optimal $c(T)$ against r for n=1, 5, 10, 20, 50, 100, 200 and 500 animals, respectively; ·········, corresponding $c(T)$ when the non-optimal $t_1 = T/2$ strategy is used.

2.4.3 Optimal Compromise

We have looked at the scenarios where the farmer wishes to maximise either the residual herbage $W(T)$ or the per animal intake $c(T)$. In many cases it is desirable to achieve some sort of compromise between these objectives. A possible way of approaching this is to note that the total intake of the mob in kg is, from equation 2.10,

$$\begin{aligned} nc(T) &= \frac{nk}{a}\frac{w_1(0)}{1-m_1}(\exp\left((1-m_1)at_1\right)-1) \\ &\quad +\frac{nk}{a}\frac{w_2(0)\exp(at_1)}{1-m_2}(\exp((1-m_2)a(T-t_1))-1) \\ &= h_1w_1(0)\frac{m_1}{1-m_1}(\exp((1-m_1)at_1)-1) \\ &\quad +h_2w_2(0)\frac{m_2\exp(at_1)}{1-m_2}(\exp((1-m_2)a(T-t_1))-1) \end{aligned}$$

Similarly, the net gain of herbage mass *in situ* (also in kg) over the time period is, from equation 2.11,

$$\begin{aligned} W(T) - W(0) &= [h_1 w_1(0) \exp(a(1-m_1)t_1) \exp(a(T-t_1)) \\ &\quad + h_2 w_2(0) \exp(at_1) \exp((1-m_2)a(T-t_1))] \\ &\quad - [h_1 w_1(0) + h_2 w_2(0)] \end{aligned}$$

These two expressions represent the output of the pasture system in terms of animal intake and herbage production respectively. We desire to maximise some weighted sum of these, with the weighting factor α $(0 \leq \alpha \leq 1)$ being chosen to reflect the relative importance of feeding the animals and conserving herbage. We therefore construct a composite output function,

$$J = \alpha n c(T) + (1-\alpha)(W(T) - W(0))$$

which is optimised with respect to t_1 as before:

$$\begin{aligned} \frac{\partial J}{\partial t_1} &= \alpha n \frac{\partial c(T)}{\partial t_1} + (1-\alpha) \frac{\partial W(T)}{\partial t_1} \\ &= 0 \text{ for optimum.} \end{aligned} \tag{2.27}$$

Differentiating and simplifying, using the fact that $h_1 m_1 = h_2 m_2 = nk/a$, this is equivalent to

$$\begin{aligned} 0 &= w_1(0) \exp\left((1-m_1)at_1\right)[\alpha - (1-\alpha) \exp\left(a(T-t_1)\right)] \\ &\quad + \frac{\alpha w_2(0) \exp\left(at_1\right)}{1-m_2} [m_2 \exp\left((1-m_2)a(T-t_1)\right) - 1] \\ &\quad + (1-\alpha) w_2(0) \exp\left(at_1\right) \exp\left((1-m_2)a(T-t_1)\right) \end{aligned} \tag{2.28}$$

Solving this formula for $\hat{t}_1$ gives both maximal and minimal choices of t_1. To find the absolute maximum value of J over the range $0 \leq t_1 \leq T$ it is necessary to evaluate J at $t_1 = 0$, at $t_1 = T$, and at all the values of t_1 which satisfy equation 2.28 to find the one which gives the maximum output.

$\alpha = 0$ is equivalent to maximising $W(T)$ and $\alpha = 1$ is equivalent to maximising $c(T)$ but apart from these a marginal (eg. monetary) value attached to $c(T)$ and $W(T)$ is necessary in order to determine the appropriate value of α to maximise a given objective.

2.5 Discussion

This chapter has approached the question of optimizing grazing management from two points of view. These are maximising conservation of herbage for feeding at a later time and maximising the cumulative intake of grazing animals over a defined time period.

2.5.1 Conservation of Herbage

Analysis of this model shows that conservation of herbage is achieved almost at the direct expense of animal intake. Herbage production is of a much smaller magnitude than herbage removal by grazing over a short time period such as that considered here. As expected, rotational grazing is shown to be superior to continuous grazing for the purpose of conserving herbage in the examples considered. This is mainly because it allows restriction to animal intake, rather than because it promotes greater herbage growth.

For the case when fields are of different initial pasture mass or of different sizes, the order in which fields are grazed affects optimal herbage conservation (section 2.4.1). However, the optimal strategy for grazing two particular fields for herbage conservation depends in a non-trivial way on a range of factors including initial pasture mass, field size, minimum intake requirements, and stocking rate. Because of this, no simple guidelines can be given.

The consideration of maintaining a minimum intake level for the animals has been dealt with in two ways. The first is by setting a minimum daily intake for each animal, which if violated forces transfer of the animals into the next field. The second method considered was optimisation of a composite measure of herbage conservation and animal intake.

2.5.2 Maximising Animal Intake

A simple rotation gives a small advantage over set stocking in maximising animal intake (Figure 2.7). The results support claims by Bryant (1990a, 1990b) based on field observations that different systems of rotational grazing operating at moderate stocking rate have little effect on the intake of cows over a period of time.

Under heavy stocking, however, pasture considerations become limiting and appropriate management may give improved production, as suggested by McMeekan (1960). Our analysis supports qualitatively different management at high stocking rates (Figures 2.8 and 2.10). The trend towards spending a greater proportion of the time in the first field as stocking rate increases adds weight to the practice adopted by some farmers of sacrificing one field. This allows other fields to accumulate greater pasture mass in order to benefit the system as a whole.

There has been some debate as to whether rotational grazing can achieve higher production than continuous grazing management in practice (eg. Florez et al 1986, Morley 1981). Experiments comparing continuous with rotational managements have given ambiguous results. However, there is a fundamental fallacy in the design of many experiments comparing these strategies. In general, the rotation length and number of fields are chosen arbitrarily (albeit based on experience). Usually animals spend equal lengths of time in each field. However, the philosophy of controlled management does not claim that any control is superior to no control (eg. that in general any rotational treatment will increase performance relative to a corresponding continuous one) but rather that the *optimal* control policy will perform better than no control, or at least no worse, in the case where no control turns out to be the optimal policy. The simple system modelled here is ideal for such comparisons.

At moderate stocking rates, and equal field area and initial herbage mass, animal intake is maximised when the fields are grazed for equal lengths of time (Figure 2.6). This is intuitively reasonable and is the strategy generally adopted by farmers. However, pasture consumption is relatively insensitive to timing of shift about the optimum in a two field system (Figure 2.6). This indicates some latitude for farmers which may be important in practical situations where flexibility is required.

At moderate stocking rates, when two fields are different in size but have equal initial herbage mass, the optimal strategy is to graze the larger field for a longer period of time (Figure 2.8). Reversing the order of grazing the fields does not give a significant increase in animal intake. Provided the optimal strategy is used, it is not important how the total area is divided into two fields. It follows from this that we can not achieve significant increase in animal intake from a two field division over and above set stocking (Figure 2.9). This suggests that little can be gained in terms of production by altering the sizes of existing fenced fields.

When the two fields are of the same size but of unequal initial mass and are grazed at moderate stocking rate, the optimum strategy to maximise intake is to graze the fields for time lengths in proportion to their masses (Figure 2.10). Much greater animal intake is achieved by following this rather than an equal time policy. This is because at low pasture mass such as considered here, non-nutritional pasture availability factors limit intake. This is relevant to practical systems which normally graze fields for equal time intervals but rotate stock through a series of unequal mass fields.

2.5.3 Limitations of the Model

By describing the grazing of farm animals in terms of linear functions this analysis has been able to deal with only the local effects of grazing systems. However, empirical evidence suggests that the linear hypothesis holds well locally for animal intake (McCall et al 1986). While linearity does not hold for net pasture growth, especially at high levels of biomass, linearity can be regarded as approximately true over a range of herbage mass 500–1300 kgDM/ha (see Bircham and Hodgson 1983). This is within the range of pasture mass at which many practical systems operate.

It was found that production from different managements did not differ greatly, as shown in Figure 2.7. This may be due to this assumption of exponential pasture growth. When more realistic growth models are used, production from the different managements may diverge. Also, as the system is extended to encompass multiple fields and rotations, it may be that these small differences will compound, giving a more significant advantage when the optimal treatment is used.

Chapter 3

Use of a 2-Field Model of Continuous and Rotational Grazing to Compare Herbage Consumption

3.1 Abstract

A simple mathematical model (the linear dynamical system presented in chapter 2) is constructed to predict herbage consumption by grazing animals. This model is used to compare three grazing methods over a range of stocking rates at low pasture mass. The grazing methods compared are: continuous grazing (CTS), rotational grazing with equal time intervals (EQ), and rotational grazing where the time of shift is optimal for maximising intake (OPT). The rotational methods are the simplest possible, the land being subdivided into two fields, each of which is grazed once. The order of grazing the fields is also considered.

The model predicts (1) that at low stocking rates the CTS treatment allows greater intake per head than the rotational treatments in the case where the fields initially have unequal herbage masses, and similar intake in other cases; (2) that at moderate stocking rates intake is similar under all treatments; and (3) that at high stocking rates intake from OPT is greatest, followed by EQ, with CTS giving the lowest intake, although treading and fouling effects were not considered. The model also predicts that greater intake is achieved if the field with lower pasture mass (kg dry matter) is grazed first.

3.2 Introduction

It is of interest to determine whether rotational grazing can increase production over continuous grazing. Field trials are costly and are complicated by unpredictable variations in the environment, while theoretical studies are limited in the accuracy with which they can describe such a complex system as grazing (eg. Morley 1968, NoyMeir 1976, Parsons et al 1988). For this reason, it has not yet been conclusively established when or whether rotational grazing management can give greater herbage intake than continuous grazing (Grant et al 1988, Wheeler 1962).

Our aim is to mathematically model grazing to provide a basis for quantitative comparison of different grazing strategies and the optimisation of any particular strategy. While simplification is necessary, the results nevertheless provide insight into the mechanics and management of real grazing systems.

3.3 Methods

When pasture mass is low, the rates of pasture growth and pasture disappearance under grazing have been shown to be approximately exponential (Brougham 1955, McCall et al 1986). Extending this, the rate of accumulation of herbage, $dw(t)/dt$, in a field of area h hectares being grazed by n animals is the difference between the rate of pasture growth (incorporating loss by senescence) and the rate of removal by grazing. At time t these rates are proportional to the herbage mass, $w(t)$ kgDM/ha. That is,

$$\begin{aligned} \frac{dw(t)}{dt} &= aw(t) - nkw(t)/h \\ &= (a - nk/h)w(t) \quad \text{kgDM/ha/day} \end{aligned}$$

where a and k are constants. This single equation can be used to model both continuously grazed fields and complex intermittent grazing systems of many fields provided that the assumption of exponential growth remains valid.

As a first step to comparing herbage consumption from continuous and rotational grazing, we consider the simplest possible rotational system: two fields of area h_1, h_2 and initial herbage mass $w_1(0)$, $w_2(0)$. Mathematical details are given in chapter 2. The specific situation modelled is grazing 300 kg bulls on perennial ryegrass pasture in winter and early spring, when pasture growth rates are approximately constant (We use a growth rate of $a = 1.4\%$ per day and a relative intake rate of $k = 0.5\%$ (kg/animal)/(kg/ha)/day). The total pasture area is $H = 2$ ha, divided into two fields, the average initial grazeable herbage cover is 1200 kg/ha, and the animals are to be grazed for a total of $T = 10$ days.

We conduct a theoretical experiment comparing herbage intake from this simple pasture system under traditional methods of continuous (CTS) and rotational (EQ) grazing as well as under a new approach to optimal rotational grazing (OPT). The OPT treatment is defined as that in which animals are transferred between fields at the time that maximises their herbage intake. Methods for determining these optimal times are described in chapter 2. This is complicated in full-scale grazing systems.

Herbage consumption from the three treatments is compared for (a) two identical fields, (b) two fields of different size but equal initial pasture mass, and (c) two fields of equal size with unequal initial pasture mass. The effect of revisiting the fields is not examined in this study, although the methodology used here may be easily adapted to incorporate this.

Following McMeekan's (1956) suggestion that animal production is most powerfully determined by stocking rate, we consider a range of stocking rates. Here, "stocking rate" refers to n animals over the total area of the two fields, H. A herbage allowance of at least 6 kg/animal/day over ten days would require a short term stocking rate of no more than 20 animals/ha. However, the two fields are intended to represent only a small part of a total grazing system. They are not thought of as able to feed the animals for more than the short time period considered, so consideration of higher stocking rates is reasonable.

At each stocking rate we calculate the total intake per animal (kg/animal) under each grazing strategy using the methods described in chapter 2. Since the fields may have different initial herbage mass and different sizes, rotational grazing strategies must consider both in which order and for how long to graze the fields. So we compare four treatments of rotational grazing under each stocking rate:

OPT1,2 : graze field 1 first, swapover at the optimal time.

OPT2,1 : graze field 2 first, swapover at the optimal time.

EQ1,2 : graze field 1 first, swapover at time= $T/2$ days.

EQ2,1 : graze field 2 first, swapover at time=$T/2$ days.

In the continuous grazing treatment, animals are free to graze both fields at any time. We assume that animals always graze where the pasture is longest. This means that they first graze the field with greater initial herbage (in kg/ha) until both fields have equal herbage. This theoretically occurs at

$$t = (h_1/nk) \ln (w1(0)/w2(0)) \quad \text{days}$$

After this time they graze the whole pasture area for the remainder of the T days. This assumption allows us to calculate intake per animal under the CTS treatment.

3.4 Results

The results of the study are presented in Figure 3.1. This shows the predicted per animal intake from the five treatments, each expressed as a percentage of the intake from the CTS treatment. In Figure 3.1(a) the fields are identical in size and initial pasture, so the order of grazing is not important, and the "1,2" and "2,1" suffixes are omitted.

3.5 Discussion

This study is designed to demonstrate a novel new approach to optimizing grazing based on simple mechanistic relationships. The qualitative results obtained from this kind of mathematical model are independent of the values of the parameters. The conclusions drawn are applicable to any situation that could be reasonably modelled in this way.

At low stocking rates, CTS gave intake as great as rotational grazing, and sometimes provided greater intake, as in Figures 3.1(b) and 3.1(c). This is because continuous grazing management allows unrestricted grazing.

At higher stocking rates, the advantage of using a rotational strategy increased, up to a 6–8% increase in intake over the CTS treatment. However, the effects of treading and fouling were not taken into account. In practice, these may reduce or reverse the advantage in herbage consumption because of pasture deterioration (Gammon 1978).

Most experimenters graze fields for equal lengths of time (the EQ treatment). Our results show that this is not optimal, and in cases where rotational grazing is viable, intake is increased by an appropriate choice of swapover time, even when the fields are initially identical.

The success of this simple model in showing how intake can be increased shows that there is considerable scope for the use of better designed management strategies for the improvement of grazing production.

The current model is approximate, since exponential growth is clearly limited in its applicability over a wide range of pasture masses, but refinement to more realistic growth functions (eg. logistic, Michaelis-Menten) and to more complex grazing systems is conceptually easy, and introduces only a few technical complications. It

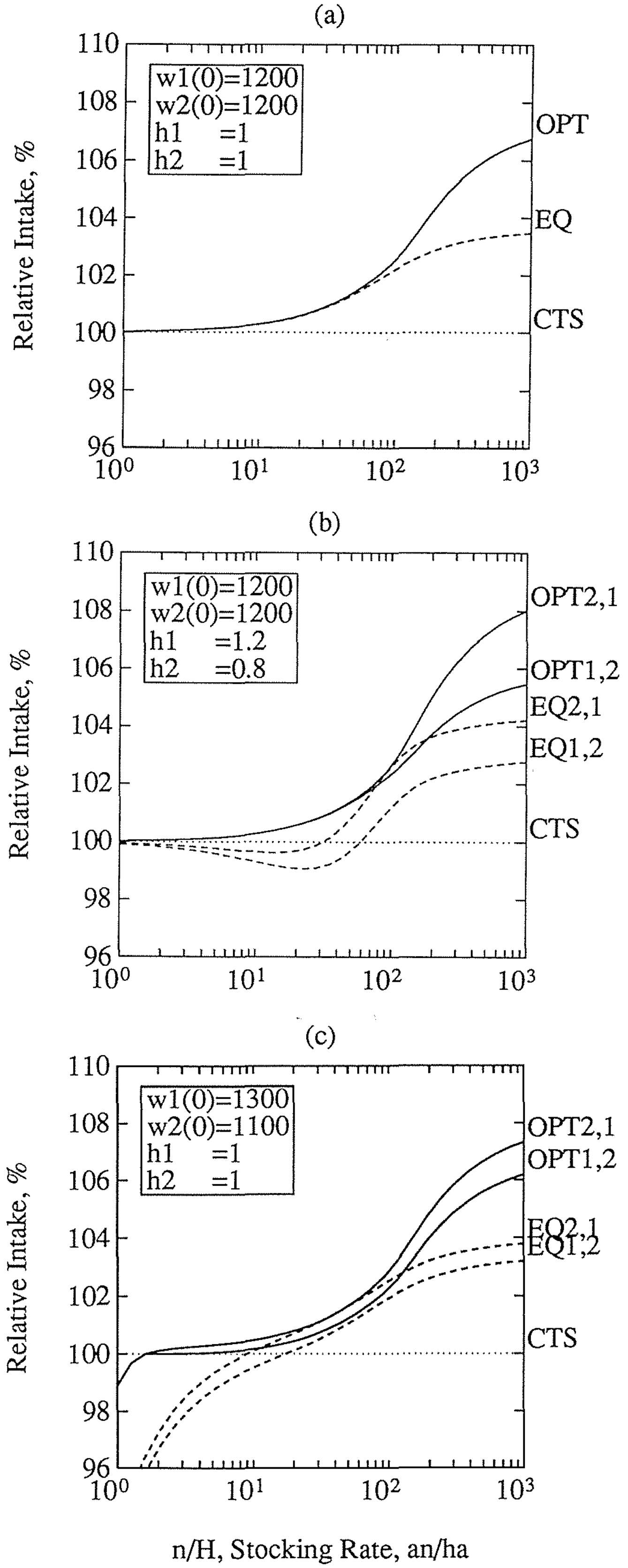

Figure 3.1: Comparison of herbage consumption from the OPT and EQ treatments relative to the CTS treatment, on two fields with (a) equal area and mass, (b) unequal area, and (c) unequal initial mass. $w_1(0)$ and $w_2(0)$ are the initial grazeable herbage masses of the fields in kg/ha. h_1 and h_2 are the areas of fields in ha.

is expected that similar improvement in herbage consumption could be demonstrated for these cases.

A surprising result was that where the fields initially differed in their size and/or pasture mass, it was optimal to graze first the smaller field or that with less pasture mass. This was due to the greater gain in pasture production from resting the larger area or greater herbage field for an additional period prior to the swap over. However, this result was highly dependent on our assumption of linear pasture growth, so was valid only at low pasture mass.

Chapter 4

The Discrete-Time Multi-Paddock Grazing Problem

4.1 Abstract

A general model of rotational grazing is constructed where in each of P consecutive time periods a mob of animals grazes one of m paddocks. The optimal grazing sequence is that which maximises their total herbage intake and satisfies the physical constraints of the grazing system. Total herbage intake is compared for four grazing strategies: continuous grazing, strict cyclic rotation, greedy rotation, and optimal rotation. A branch-and-bound algorithm is used to find the global optimum strategy. A 100 hectare system is simulated carrying 300–400 dairy cows for 60 days in late winter and early spring with a range of subdivisions and grazing durations to ascertain the effectiveness of the different strategies in maximising intake.

It is shown that (1) continuous grazing maximises intake when pasture growth is in surplus to animal requirements, (2) that animals' herbage intake under rotational grazing is likely to be poor unless the rate of rotation is carefully synchronised to the pasture growth rate, (3) that grazing management makes little difference to productivity in comparison to stocking rate and average initial pasture, and (4) that there is no reason to expect subdivision of land to increase productivity unless reasons such as pasture trampling on wet soil mitigate against long grazing durations. Greedy rotational grazing is found to increase herbage intake on multi-paddock systems with an initially inhomogeneous distribution of pasture.

4.2 Introduction

A major aim of grazing management is to improve animal production by controlling the allocation of pasture. Advantages can occur either by allowing more animals to be carried or by improving per animal performance. Objectives of management at any point in time vary depending on the potential intake rate of the animals relative to the current pasture growth rate (Sheath et al 1987).

Rotational grazing is a grazing management tool which offers a number of potential benefits if used appropriately at certain times of year. For example, in winter, when pasture growth rate is typically less than potential animal intake rate, an objective of grazing management is to maximise herbage conservation *in situ* (Sheath et al 1987). Careful rotational grazing at this time can increase herbage conservation (McMeekan 1956). This maintains a reserve of pasture ahead of the herd at all times, allowing animals to winter without losing body condition (Bryant 1990a), and transfers the maximum amount of herbage into spring when marginal animal production responses to extra pasture are greatest (eg. Smeaton and Rattray 1984).

Winter rotational grazing is also widely practised to limit animal intake in order to maximise stocking rate (Bryant 1984, Clark et al 1986). For example, McMeekan and Walshe (1963) found that rotational grazing required 5–10% greater stocking rate than continuous grazing for optimal production and also yielded twice as much conserved herbage (by cutting).

Arguments for rotational grazing extend to benefits in maximising pasture growth rates over the farm (eg. Harris 1983) and rotational grazing can also be practised to maximise the intake of animals when pasture growth rates are less than potential intake rates. For example, in early spring on New Zealand dairy farms, potential intake rate is typically still much greater than pasture growth rate (Bryant 1990b). However, as time progresses, pasture growth rates overtake intake capacity. While conservation of pasture *in situ* is still important for ensuring future animal intake, excess pasture cover on the farm in mid spring must be avoided as this can lead to a more rapid seasonal decline in pasture quality (Butler et al 1985). Therefore, intake rates may be increased.

In late spring and summer the major role of grazing management is in the control of pasture quality (Bryant and L'Huillier 1986, Bryant 1990b). Spring rotational grazing is used on dairy farms in New Zealand to give stocking densities high enough to control spring flush growth, preventing herbage becoming tall and rank and reducing reproductive stem growth (Bryant 1990b). Paddocks not able to be maintained below a pre-grazing mass which limits reproductive growth (eg. Butler et al 1985) can be readily identified and retired for conservation as hay or silage.

Many of the potential benefits of rotational grazing outlined above have been hypothesised from component studies. However, most *systems* experiments have been unable to demonstrate that rotational grazing gives greater animal production than continuous grazing in either rangeland or sown pasture systems (Gammon 1978, Wheeler 1962, Heady 1961, Morley 1981). Pasture system productivity appears far more sensitive to stocking rate, animal genetics, and nutrient and water availability than to grazing management (McMeekan 1956, Bryant 1990a, McCall and Sheath (in press)).

Nevertheless, rotational grazing has become an integral part of farming practice, and even slight benefits in production due to grazing management should be utilised because the cost of adopting alternative grazing managements may be small.

A problem with system experiments is that only a limited number of opportunities can be explored. Choices have to be made regarding the best way to operate a rotational system. For example, there has been debate concerning the optimal amount of subdivision of pasture (Morley 1968, Morley et al 1969, Booysen et al 1974). Similarly, there is the question of optimal rest periods for individual paddocks to maximise pasture growth rate (Parsons et al 1988, Parsons and Penning 1988, and Morley 1968).

Results from grazing studies depend on the right combination of variables being studied in order to observe advantages from rotational grazing, as was shown by McMeekan and Walshe (1963). These issues motivate the present study.

A second problem with some studies is that they have had to assume that all paddocks will be treated identically and that animals will be shifted at regular intervals. This has allowed the results from intermittent grazing on a single paddock to be extrapolated to a rotational system context. However, such a restriction may prevent the full potential of multi-paddock systems from being realised.

This study focuses on one aspect of rotational grazing, that is, its ability to maximise intake of animals over the period of time when pasture growth rates are less than potential intake rates. This issue is important to the productivity of New Zealand dairy farms in the early spring from the commencement of lactation until spring growth rates outstrip animal intake capacity (Bryant 1990b).

In chapters 2 and 3 we considered a limited rotational grazing system and predicted intake gains in the order of 6% over continuous grazing. The present study takes a very general view of multi-paddock grazing by allowing the farmer to place his or her animals in any of the paddocks in the system each day. On such a system we compare herbage intake under four grazing strategies. In this way we hope to gain insight into how a multi-paddock system may be most effectively grazed to maximise herbage intake by grazing animals.

4.3 Method

Consider a late winter rotation of dairy cows from 15 July (the start of calving) through the New Zealand early spring until 15 September, when pasture growth rate begins to exceed animal requirements. There are a large number of possible grazing management options which the farmer may employ. These include the choice of stocking rate, rate of rotation, and conceivably, even the number of paddocks. The initial conditions of pasture mass may also vary.

Consider a number of different scenarios: suppose the farmer has $H = 100$ hectares of pasture. The farm may be subdivided into $m = 1$, 5, 10 or 20 paddocks. The stocking rate may be 300, 350, 370 or 400 cows on 100 hectares.

15 July to 15 September is a total of $T = 60$ days. Suppose this is divided into $P = 1$, 15, 30, or 60 grazing "periods" of length $\tau = 60$, 4, 2, or 1 days, respectively. For the duration of each period the animals are grazed in a single paddock as one mob.

Suppose also that the average pasture cover on 15 July is either 1700 or 2100 kgDM/ha (kilograms dry matter per hectare). If the average initial pasture is 1700 kgDM/ha, this may either be "1700–1700" (uniform cover) or "2500–900" (ie. a "wedge" with the best paddock having 2500 kgDM/ha and subsequent paddocks having successively less herbage in equal steps down to 900 kgDM/ha in the worst paddock). Similarly, if the average initial herbage cover is 2100 kgDM/ha, this may be either "2100–2100" (uniform) or "3300–900" (wedge). Thus there are four possible scenarios of initial herbage.

The farmer must also choose a strategy for rotating the animals through the paddocks. A mathematical simulation model of pasture growth and herbage intake allows us to predict the effects of particular grazing strategies on herbage intake, production and conservation. The *Discrete-Time Multi-Paddock Grazing Problem* is to find the sequence of grazing the paddocks that maximises production; in this case, intake of dry matter by the herd over T days.

4.3.1 Assumptions

For simplicity, assume that the pasture growth rate is constant throughout the period of interest and that the paddocks are of equal size and fertility. Clearly this is not ideal, as pasture growth rate increases steadily from July to October (Brougham 1959), but qualitative results should not be greatly affected. The pasture growth curves of Wright and Baars (1976) assume that daily net production (NP) is dependent on the herbage mass (HM) according to a logistic growth function. Thus, they give the pasture growth rate for mid-August as:

$$\mathrm{NP} = 0.0419\ \mathrm{HM}(1 - \mathrm{HM}/4000) \quad \mathrm{kgDM/ha/day} \tag{4.1}$$

This implies a ceiling yield of $1/b = 4000$ kgDM/ha and a maximum pasture net growth rate of $g = 41.9$ kgDM/ha/day achieved at a herbage mass of 2000 kgDM/ha. These are reasonable average values in the winter/early spring season in the Waikato region of New Zealand for ryegrass dominant pastures.

Secondly, assume that the rate of herbage removal by each animal is proportional to the herbage mass of the field being grazed, with proportion r per day. Hodgson (1985a) indicates that this is approximately true for grazing ruminants, and this is borne out by the results of Laca et al (1992) for cattle. Naturally, for high pasture mass there is an upper limit to daily intake rate due to animals' nutritional capacity (Poppi et al 1987), but in winter pastures with typically low pasture mass this limit will seldom be reached. Therefore a linear relationship between herbage mass and intake rate seems adequate for our purposes.

From calculations based on data from Bryant (1980) we assume that each cow per hectare eats $r = 0.47\%$ of the available herbage each day. For instance, a cow grazing a field with a herbage mass of 3000 kgDM/ha will ingest 14.1 kgDM green herbage per day. Under grazing, a herbage removal term is appended to equation 4.1 to give daily net herbage accumulation (NHA) as

$$\mathrm{NHA} = 0.0419\ \mathrm{HM}(1 - \mathrm{HM}/4000) - 0.0047s\mathrm{HM} \quad \mathrm{kgDM/ha/day} \tag{4.2}$$

where s animals/ha is the stocking density during grazing. In this case, the total daily herbage intake (I′) of the mob of n animals is

$$\mathrm{I}' = 0.0047n\mathrm{HM} \quad \mathrm{kgDM/ha/day} \tag{4.3}$$

This assumes that the instantaneous rate of removal of dry matter herbage by the animals is dependent only on the quantity of herbage available and is proportional to the number of animals, following Noy-Meir (1975). Although sward height is known to be a better predictor of sward response than herbage mass (Hodgson 1985b, Sibbald and Maxwell 1990), at present, most studies have measured herbage mass, so we have chosen this as our sward state variable. Equation 4.3 also disregards herbage quality considerations. However, in winter rotations on ryegrass dominant pastures in New Zealand herbage quality is generally not a significant factor in animal nutrition.

4.3.2 Grazing Strategies

The intake of the herd depends on both the herbage initially in the paddocks and the "strategy" for the 60 days, that is, the choice of paddock in each time period. Theoretically the farmer could choose any one of the m paddocks each day. Questions which arise are: should the paddocks be grazed cyclically, should the paddock with the most grass be chosen each day, or is it sometimes advantageous to graze a lower paddock to allow extra growth on higher mass paddocks which may then be utilised later?

A strategy for grazing the m paddocks for P periods is a sequence of fields, X, which we write as $X = (x(1), x(2), \ldots, x(P))$. Each $x(p)$ is a number between 1 and m and the periods p are numbered $1, 2, 3, \ldots, P$. If $x(p) = i$, this means that the animals graze field i during period p. The aim of the Discrete-Time Multi-Paddock Grazing Problem posed here is to find the sequence of $x(p)$'s that results in the maximum intake for the animals.

From this ideological position we compare four grazing managements, two of which are in common use throughout the world and two of which are untested variations of intermittent grazing.

The first grazing management considered is continuous grazing (denoted CG) in which the entire 100 ha is pooled into just one large paddock which is then grazed continuously for the 60 days. This management can be compared to the rotational managements when the initial herbage mass is uniform across all of the fields, as might occur in Northern Hemisphere grazing systems in early spring.

For the three rotational grazing managements the 60 days is subdivided into P time "periods" of length τ days. For example, $P = 30$ implies that there are thirty 2-day periods. τ is the minimum stay of the herd in one paddock. The actual grazing duration in a paddock is effectively constrained to be a multiple of this minimum stay. So for τ=2-day periods, animals can only be shifted on even numbered days.

The first rotational grazing management is strict cyclic rotational grazing (CR). In this strategy the animals are introduced into successive paddocks in strict rotational sequence, beginning with the paddock with the most initial herbage and working along to the paddock with the least initial herbage. Animals are shifted each time period regardless of post- or pre- grazing mass and visit the paddocks in the same order in each rotation.

Secondly, greedy rotational grazing (GR) is similar to CR except that at the start of each time period the animals are moved directly into the paddock with the most herbage at that point in time. This could mean an extended grazing duration in the current paddock or ignoring those paddocks in early stages of regrowth.

Lastly, optimal rotational grazing (OR) is a refinement of GR in which the sequence of paddocks grazed is that which maximises the total herbage intake of the animals over the entire 60 days. This optimal sequence is determined by computer search of the herbage intakes achieved for every possible sequence of grazing the paddocks. The search method is described in detail in section 4.3.4. While GR is optimal in a local sense, in that in each period the paddock with most herbage is grazed, OR is *globally* optimal, so that any long term advantages of *not* immediately grazing the paddock with most herbage will be realised.

Finding the OR strategy is a computationally expensive task so for all but the smallest problems it is impractical to do so. Therefore, we are interested in how well the CR and GR strategies perform relative to OR for small problems, since the CR and GR strategies are easy to determine even for very large grazing systems and are more practical to implement on the farm.

Because of the structure of the rotational strategies, the herbage intake from OR is never worse than that from GR, which in turn is never worse than that from CR. This is because GR and OR provide successive additional flexibility on top of the CR strategy, and this flexibility is not utilised unless the total herbage intake is thereby increased. Therefore,

$$\text{intake from CR} \leq \text{intake from GR} \leq \text{intake from OR}$$

4.3.3 Model

Equations 4.1, 4.2 and 4.3 give the rates of net herbage accumulation and herbage intake in a paddock. Equations 4.2 and 4.3, respectively, can be rewritten as

$$\frac{dw}{dt} = 4gbw(1-bw) - srw \quad \text{kgDM/ha/day} \tag{4.4}$$

$$\frac{dI}{dt} = nrw \quad \text{kgDM/day} \tag{4.5}$$

where w now replaces HM as representing the paddock herbage mass in kgDM/ha, g is the maximum pasture growth rate in kgDM/ha/d, $1/b$ is the ceiling yield in kgDM/ha, s is the stocking density in animals/ha, r is the relative per animal intake rate in ha/an/day, I is the total intake of the herd, and n is the number of animals.

These equations (4.4 and 4.5) can be integrated over τ days to give the post-grazing pasture mass, $w(\tau)$, and the herd intake, $I(\tau)$, for a paddock after one period of grazing:

$$w(\tau) = \frac{(1-rs/4gb)w(0)}{(1-rs/4gb-bw(0))\exp\left(-(4gb-rs)\tau\right)+bw(0)} \quad \text{kgDM/ha} \tag{4.6}$$

$$I(\tau) = \frac{nr}{4gb^2}\ln\left[1+\left(\exp\left((4gb-rs)\tau\right)-1\right)\frac{bw(0)}{1-rs/4gb}\right] \quad \text{kgDM} \tag{4.7}$$

where $w(0)$ kgDM/ha is the pre-grazing mass. Formally, we write the initial herbage masses in the paddocks as $w_1(0), w_2(0), \ldots, w_m(0)$ kgDM/ha, where the subscripts indicate the paddock and the argument "0" indicates the time period (here $p = 0$ since these are the initial conditions).

These equations form the basis for a simulation model of a grazing system, whereby given a particular sequence, X, of paddocks to be grazed, the resulting herd intake and final herbage cover may be calculated.

The total herbage intake of the animals over P periods, denoted $C(P)$, is the sum of the intakes in all fields on all days, ie.

$$C(P) = \sum_{p=1}^{P} \sum_{i=1}^{m} I(w_i(p-1), s_i(p)) \quad \text{kgDM} \tag{4.8}$$

where the function I is the herbage intake in period p in a field i with pre-grazing mass $w_i(p-1)$ kgDM/ha and stocking density $s_i(p)$ animals/ha. The stocking density in paddock i during period p is $s = n/(H/m)$ if $x(p) = i$ (ie. paddock i is being grazed during this period), and 0 otherwise. Recall that H is the total farm area in hectares, and m is the number of paddocks (which are of equal size).

C is also a function of strategy, X. So the problem of maximising total herbage intake can be thought of as choosing X to maximise $C(X)$. This X is the OR strategy and finding it is a non-linear integer programming problem. A method for finding the OR strategy is described below in section 4.3.4.

This simple system has many of the features of actual grazing systems. More complex models which consider pasture quality, treading damage, seasonal changes in growth rate, and pasture fouling are all possible extensions.

4.3.4 Finding the Optimal Strategy

Although an optimal strategy exists in this problem, it is not straightforward to find. The problem resists the normal means of mathematical optimisation and we are reduced to comparing all of the possible strategies, X, in order to find the one which maximises the herbage intake, $C(X)$. C will sometimes be obtainable as an analytic function of X as in the system described in section 4.3.3—otherwise, numerical calculation of C will be required.

Simulating all of the possible strategies is a daunting task. In each period there are m different paddocks that the farmer could choose to graze. Therefore, each of the $x(p)$ can take any one of m possible values and the strategy up to the end of period P has m^P possibilities, which may be a very large number, especially if P is large.

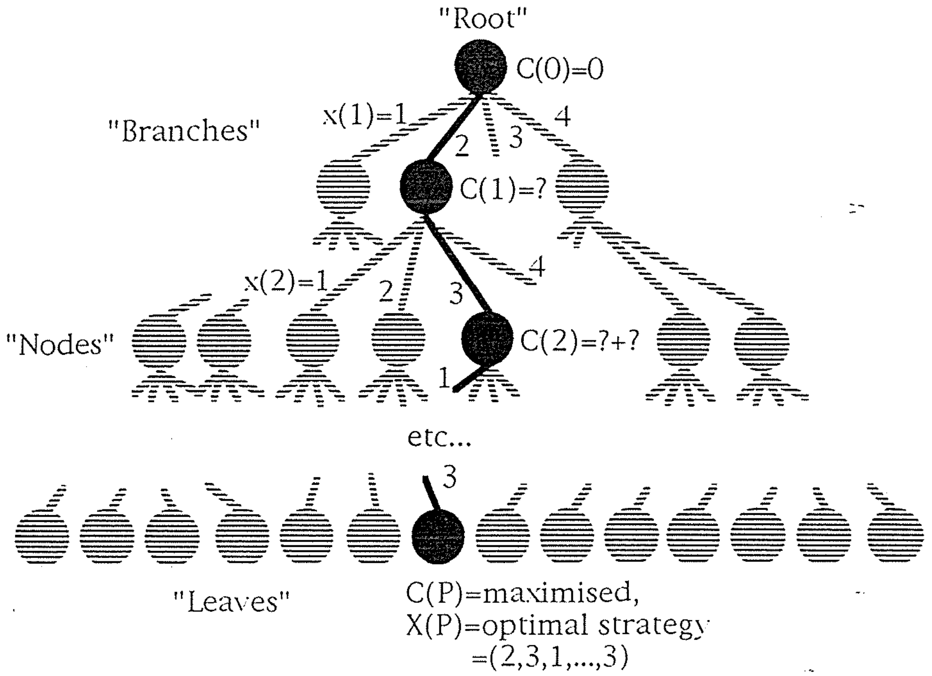

Figure 4.1: Tree layout of grazing strategies, $X(p)$, when there are $m = 4$ paddocks and P time periods. The optimal strategy is highlighted.

Actually, things are not quite as bad as this, because during the last k periods of grazing only the k paddocks with the most herbage need be considered; grazing any of the other paddocks can only give a lower total intake. Also, paddocks may have identical herbage mass (to within some acceptable tolerance) either initially or at some time during the experiment. In this case only one of the duplicate paddocks need be considered for grazing. In using our algorithm, therefore, we did not distinguish between paddocks with herbage masses different by less than 20 kgDM/ha. Taking advantage of these features of the problem reduces the number of strategies that need to be considered by several orders of magnitude. Nevertheless, this still leaves an astronomical number of strategies when P is large.

A further method of reducing the number of strategies to be searched may be employed if we organise the strategies into a "tree" as illustrated in Figure 4.1. The root node of the tree represents the initial conditions. The bottom nodes of the tree, the "leaves", represent the strategies for P periods,

$$X(P) = (x(1), x(2), \ldots, x(P))$$

and the intermediate nodes represent the "partial strategies" for p periods ($p < P$),

$$X(p) = (x(1), x(2), \ldots, x(p))$$

We can then use a *branch-and-bound algorithm* to search for the leaf, $X(P)$, that gives the greatest $C(X)$. As mentioned, certain branches of the tree may be disregarded, or "pruned", if there are duplicate fields at any time or during the last k days when only the top k fields need be considered.

If there are any constraints on the system, these also assist in pruning the tree. If at any node a constraint has been broken, then all of the branches below that node will be infeasible and may be pruned. In a grazing problem the farmer may wish to impose constraints on the minimum and/or maximum herbage masses that paddocks may reach. Here we require that pasture mass always be above 900 kgDM/ha to ensure an adequate minimum level of daily feeding and to maintain sward structure.

If the constraints are too strict, there may be no strategies which are feasible. In this case all of the $X(P)$ are pruned. Often, however, we would expect the constraints to allow a high degree of latitude in the strategies chosen. Therefore there may still be a large number of leaves to search despite the pruning due to constraint violations.

The "bound" is an additional method for pruning the tree. At each node $X(p)$ searched we calculate an upper bound for the values of $C(X(P))$ at all the leaves $X(P)$ descending from $X(p)$. If this upper bound is less than the current best value of $C(X)$ found during the search, then we know that none of $X(p)$'s descendants can possibly be optimal. Therefore all of $X(p)$'s descendant nodes can be pruned. In order to maximise the amount of pruning the upper bound should be as accurate as possible.

A simple bound to the values of $C(X)$ at $X(p)$'s descendent nodes can be calculated as follows: after a partial strategy $X(p)$ has been applied the herbage masses in the m paddocks are $w_1(p), w_2(p), \ldots, w_m(p)$. Suppose $w_{max}(p)$ is the paddock with the most herbage at this time. Now since all paddocks grow according to the same logistic growth relationship (equation 4.1), then if paddock w_{max} were allowed to grow for the remainder of the periods no other paddock could ever overtake it. Then w_{max} would be an upper bound to the herbage masses of the paddocks at every subsequent point in time.

Now the animals' intake rate increases monotonically with the pre-grazing mass of the paddock being grazed. So if we assume that at each period we can introduce the animals into a paddock with pre-grazing mass w_{max} (plus subsequent growth), this gives an upper bound for the intake in each period. Adding these hypothetical intakes to the intake calculated so far at $X(p)$ gives a total, $B(P)$. $B(P)$ is an upper bound to the intakes $C(X)$ at all the descendent leaves $X(P)$ of node $X(p)$, as required.

$B(P)$ is straightforward to calculate and provides a reasonable bound to $C(P)$ when $P - p$ is less than or equal to m, that is, when at most m time periods remain.

Beyond this its usefulness decreases. The bound is achieved (ie. $C(P) = B(P)$) when the top $P - p$ paddocks at time p have equal herbage mass and $P - p \leq m$.

The branch-and-bound tree search algorithm was implemented in the C programming language on a SUN computer, using the growth and grazing functions described in section 4.3.1. A listing of the program is given in appendix B.

4.4 Results

The farm system described above was simulated for the different combinations of initial herbage, stocking rate, grazing management, number of paddocks, and number of periods. Results of total herd intake and average residual herbage were recorded. Not all permutations of initial pasture, number of periods, and number of paddocks were carried out. In particular, CG was only simulated for those permutations where the initial pasture mass was uniform (ie. the "1700–1700" and "2100–2100" treatments). The number of paddocks m and periods P for CG were $(m, P) = (1, 1)$, because other permutations were meaningless. CR and GR were simulated for $(m, P) = (5, 15)$, $(5, 30)$, $(10, 30)$, $(5, 60)$, $(10, 60)$, and $(20, 60)$. The $(1, 1)$ combination is trivial for rotational grazing. OR was simulated only for $(m, P) = (5, 15)$ because of time constraints—the algorithm for finding the optimal strategy took up to 20 hours per simulation to run even at these low levels of subdivision. This gave a total of 216 simulation runs.

4.4.1 Initial Herbage and Stocking Rate

The intake and herbage data are analysed using standard data analysis techniques. There is no random variation in the data—all variation is due to interactions between the different treatments. The aim is to locate the most significant factors that influence animal intake and residual herbage in a multi paddock grazing system.

Figure 4.2 shows the variation in total herd intake due to stocking rate and initial pasture. The variation in each column (which is due to the effects of strategy and subdivision and is indicated by black blocks in the graph) is small relative to the effect of stocking rate and average initial pasture. It is of note that this variation is greater in those treatments where the initial pasture is distributed as a wedge.

Figure 4.3 shows the average change in both per hectare and per cow intake as stocking rate increased. Over this range of stocking rates, per hectare intake increased and per cow intake decreased with stocking rate.

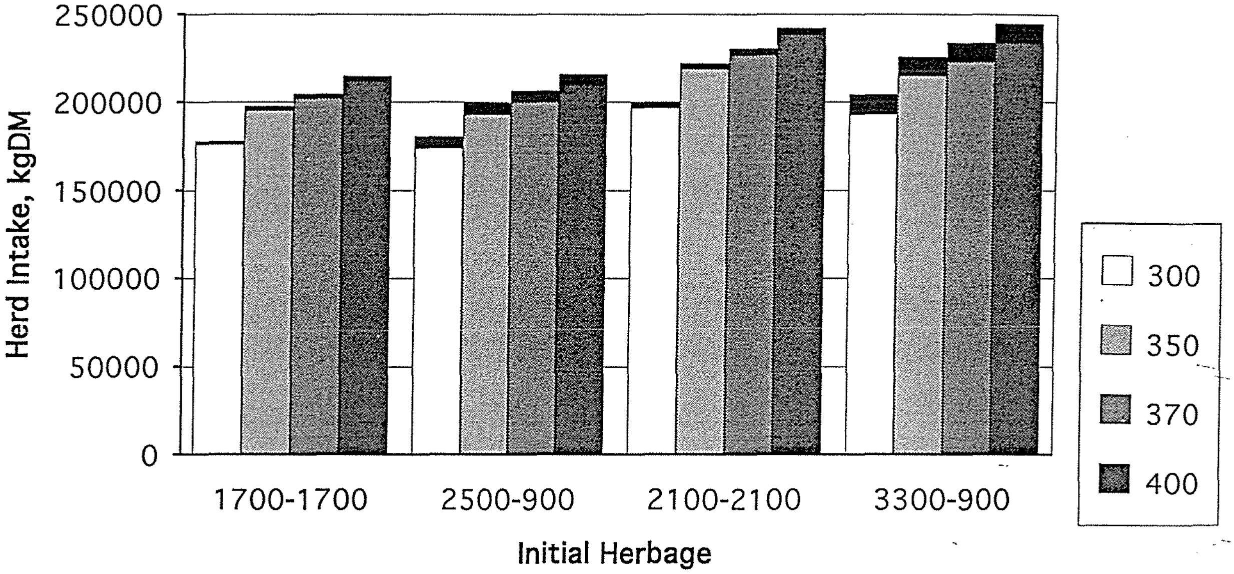

Figure 4.2: Herd intake (kgDM/60days) for the four initial pasture scenarios and the four stocking rates (300, 350, 370, and 400 animals). The black blocks atop each column indicate the range of intakes calculated. This variation is due to interactions with strategy and subdivision.

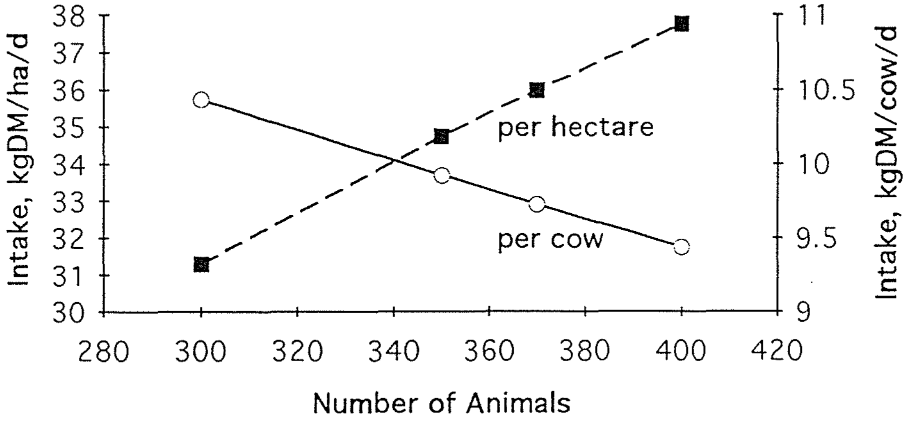

Figure 4.3: Average per hectare (– – – –) and per cow (————) intakes against stocking rate.

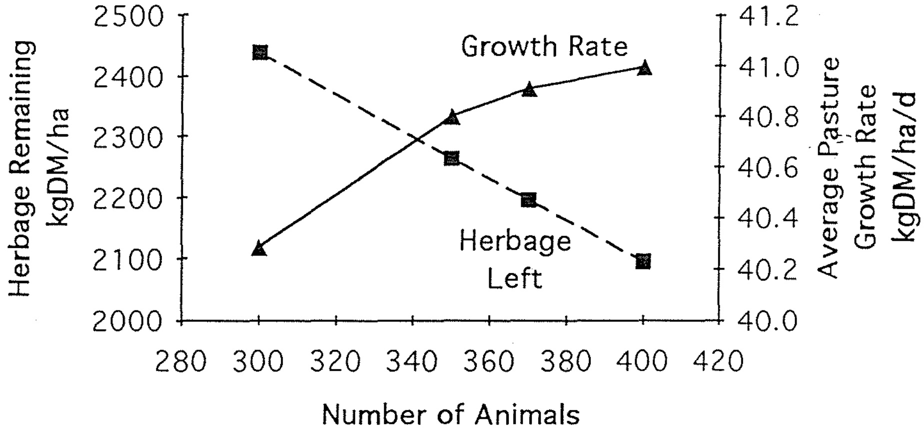

Figure 4.4: Average pasture growth rate (————) and herbage cover remaining (– – – –) against stocking rate.

Average pasture grown per day, PG, was calculated as

$$PG = [(\bar{w}(P) - \bar{w}(0)) + C(P)/H]/T \quad \text{kgDM/ha/d}$$

where $\bar{w}(0)$ and $\bar{w}(P)$ are respectively the average initial and final herbage cover per hectare, $C(P)/H$ is the total intake per hectare, and T is the total time in days. By comparison, the maximum possible pasture growth rate is $g = 41.9$ kgDM/ha/d.

Figure 4.4 shows the effect of stocking rate on herbage cover remaining on September 15 and on pasture grown. Both values are averaged over all paddocks. Final herbage cover decreased with stocking rate and average pasture growth rate increased with stocking rate. This trend was the same under all grazing strategies.

Apart from stocking rate, the only other factor that greatly influenced the animals' intake was the average herbage cover on July 15, and the effect of this was modest. This is clearly seen in Figure 4.2, where greater initial average herbage results in a greater intake. Those treatments with average initial pasture mass of 2100 kgDM/ha gave an overall average of 24380 kgDM (around 12%) more feed to the herd than those treatments with average initial pasture mass of 1700 kgDM/ha. Initially the "2100" treatments had 24% more grass, but the average difference by September 15 was only 5.4% (an average of 2307 kgDM/ha from the "2100" treatments above 2189 kgDM/ha from the "1700" treatments).

The average pasture growth rate was 41.1 kgDM/ha/d from the "1700" treatments and 40.4 kgDM/ha/d from the "2100" treatments, so pasture grown decreased slightly as initial herbage increased.

Stocking rate and average initial pasture were by far the most important determinants of intake. Using linear regression, these effects accounted for $R^2 = 98\%$

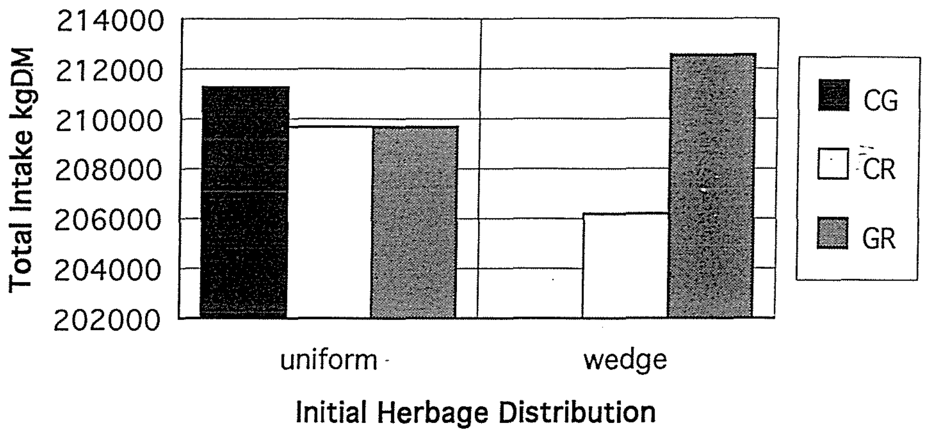

Figure 4.5: Effect of pasture distribution (uniform/wedge) and strategy on herd intake (note: wedge/CG is not meaningful and OR=GR so no data are given).

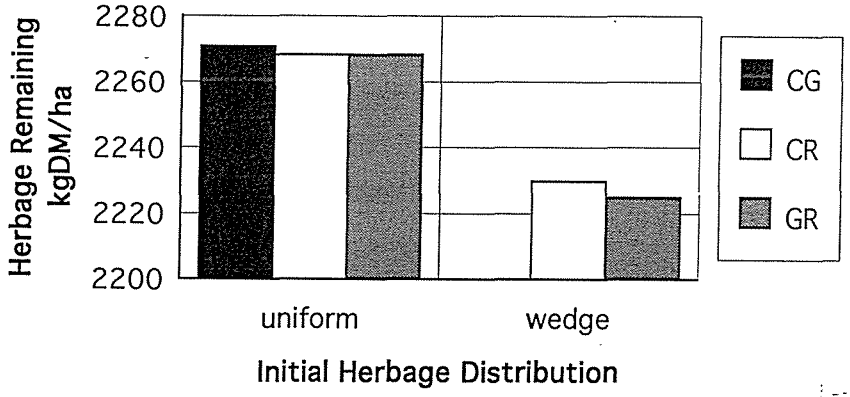

Figure 4.6: Effect of pasture distribution and strategy on quantity of herbage left on September 15 (note: wedge/CG is not meaningful and OR=CR so no data are given).

of the variation in herbage intake. Therefore the effects of initial pasture mass distribution, grazing strategy, and number of paddocks and grazing periods were relatively unimportant in determining intake. Nevertheless, we proceed to examine these small effects.

It is not clear from Figure 4.2 that it is important whether herbage was uniformly distributed or in a "wedge". However, Figures 4.5, 4.6 and 4.7 show that there is some interaction between the grazing management and the initial pasture distribution.

In particular, we see that in uniform pastures, CG gave greater intake, herbage conservation, and pasture growth than any of the rotational strategies.

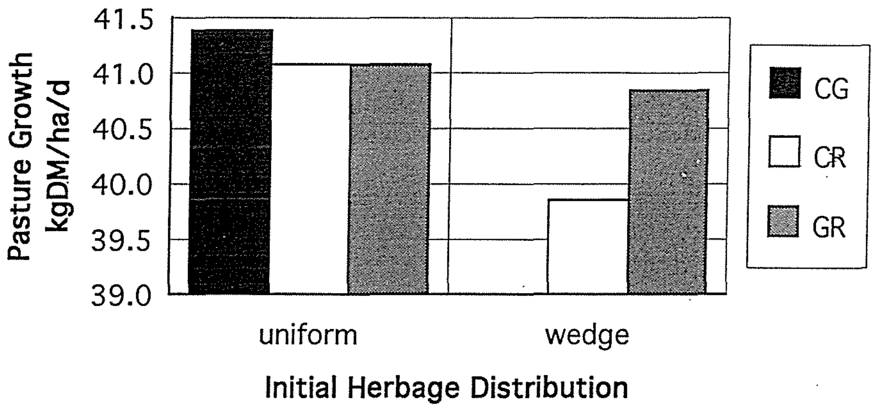

Figure 4.7: Effect of pasture distribution and strategy on herbage grown (note: wedge/CG is not meaningful and OR=CR so no data are given).

However, GR gave better intake (but worse herbage conservation and pasture growth) on wedge-distributed pastures than in situations of uniform initial pasture. The CR strategy performed worse on wedge distributions than on uniform pastures in terms of intake, conservation, and growth rate.

4.4.2 Grazing Strategy

In all simulations the cyclic, greedy, and optimal sequences of paddocks grazed were recorded. For instance, for the scenario where the initial herbage was a 2500–900 kgDM/ha wedge in 5 paddocks grazed by 370 animals for 15 four-day periods, the GR strategy was graze the paddocks in the sequence: $1 - 2 - 1 - 3 - 2 - 4 - 1 - 3 - 5 - 2 - 4 - 1 - 3 - 5 - 2$ (where paddock 1 is that with greatest initial herbage and paddock 5 is that with the least).

In all of the simulations on uniformly distributed pastures, the GR and OR sequences are identical to the cyclic sequence of grazing the paddocks, CR. This means that CR was optimal in those scenarios where OR was trialed .

Further, in all of the simulations on wedge distributed pastures, the sequence of paddocks for GR was not strictly cyclic, and in all cases yielded higher herd intake. In these treatments GR gave an average of 6382 kgDM (about 3%) more intake than CR (see Figure 4.5). For those cases where OR was trialed on wedge pastures it was found to be identical to GR (ie. GR was optimal). In wedge systems the greedy strategy was first to graze the paddocks down to a more even range of pasture masses and to graze them cyclically thereafter, as illustrated by the example above. After only 4 time periods this example was already cyclic. This was a typical result.

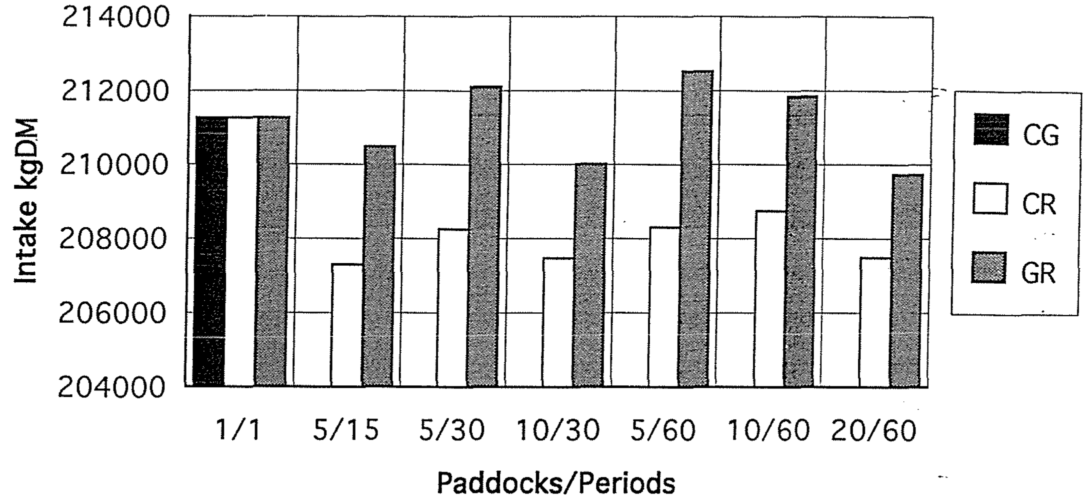

Figure 4.8: The effect of strategy, number of periods, and number of paddocks on intake.

4.4.3 Subdivision

Increasing subdivision of the total area into paddocks was detrimental to herbage intake, although this effect was fairly small. Figure 4.8 shows the effect of management and subdivision of area and time on intake. While intake was increased by increasing the number of time periods (ie. decreasing the time in each paddock and increasing the frequency of decisions about where to move the animals), increasing the number of paddocks reduced intake.

4.5 Discussion

4.5.1 Stocking Rate and Initial Average Pasture

It is clear that stocking rate is the most powerful predictor of herd intake and amount of pasture remaining at the end of the 60 days of grazing (Figures 4.2, 4.3, and 4.4).

Intake per hectare increases with stocking rate, as has been stated by McMeekan (1956) and observed by Jagusch et al (1978) and others in experiment. This suggests that each additional stock unit increments the utilisation of available pasture, since the pasture grown was similar under all stocking rates. As expected, the intake per cow decreased with stocking rate. At 400 animals on 100 hectares the average over the 60 days considered was around 9.5 kgDM/animal/d, which is a minimal intake rate. Workman and Fowler (1986) and Wright and Pringle (1983) show that the economic optimum stocking rate is lower than the point where per hectare production no longer increases with additional stock units. Therefore stocking rates this high would not be economical in practice, and this low per animal intake will be avoided. This would also prevent damage to the sward associated with high stocking rates (Gammon 1978).

The amount of herbage remaining on the farm on 15 September decreased as stocking rate increased (Figure 4.4), reflecting greater pasture utilisation with stocking rate. Consequently, stocking rate also has a major effect on the timing and amount of conservation possible as hay or silage. The rate of decrease was not as rapid as one might have intuitively expected and the remaining pasture cover even at the higher stocking rates was not particularly low, being above 2000 kgDM/ha, the herbage mass at which pasture growth rate was maximal. The reason for pasture mass being retained was because of pasture mass constraints on cow intake. These meant that even under CG at 4 cows/hectare, intake per hectare was only 37.6 kgDM/ha/d at 2000 kgDM/ha. This compares with the environmentally determined maximum pasture growth rate at 2000 kgDM/ha of 41.9 kgDM/ha/d.

Because of this, it is possible that our simulation did not examine the situation where pasture growth is limiting to production. It is this situation where rotational grazing is thought to offer advantages over continuous grazing (Clark et al 1986, McMeekan 1960, and see chapter 3). Another possible reason for these high pasture masses is that we neglected additional losses of herbage due to secondary effects such as treading, fouling, and removal by other pasture organisms. Also, in practice, pasture growth rates fluctuate daily due to climate effects. These effects could compound with the effects of grazing and cause greater fluctuations in pasture level in real pastures than we observed in simulation.

The second most important factor determining intake and herbage conservation was the average pasture in the paddocks at the start of grazing (July 15). This supports evidence from Bryant (1984) showing that the amount of feed on the farm in July has a relatively small effect (compared to stocking rate and cow quality) on production and on herbage on the farm in spring. This is reasonable since much of the herbage eaten during 15 July to 15 September was grown during this period and initial cover did not significantly influence average growth rate. Much of the initial cover advantage could not be utilised by the grazing strategies if high pasture growth rates were to be maintained. Consequently, it was carried through until the end of the period. The advantage of additional initial pasture cover is only likely to be manifested through its effect on pasture growth.

4.5.2 Grazing Method

Our results concur with Bryant and L'Huillier (1986) and McMeekan (1956) that the effects of "management" (ie. grazing strategy, number of paddocks, and number of grazing periods) on production are relatively minor. However, we were able to examine these minor effects. The remainder of the discussion summarises our findings.

Because CG performed as well as or better than the rotational strategies in most scenarios, this calls into question the proposal that rotational management can increase animal intake. Nevertheless, rotational grazing may be profitably used for other purposes such as control of excess reproductive growth or conservation of herbage. However, herbage conservation is achieved because rotational grazing restricts herbage intake, not because it stimulates herbage growth—increased production should not be expected.

In CG when intake is in excess to pasture growth, intake decreases approximately exponentially with time (McCall et al 1986, Sheath and Rattray 1985). Therefore the animals might have restricted intake rate for several days near the end of the grazing time. This would be detrimental to animal productivity. In rotational grazing this effect would be brief since animals are regularly moved into paddocks with more grass. In our trials, pasture cover at 15 September was similar under CG and the rotational strategies, so in fact this problem was not encountered. Even at the highest stocking rate, final pasture cover under CG was above 2000 kgDM/ha, the mass at which pasture growth rate was maximum. Since pasture growth was neither depressed under CG nor stimulated under rotational grazing, this explains why the rotational managements did not outdo CG in terms of productivity.

The only time that rotational grazing outstripped CG was when initial pasture was in a wedge. In systems where cows are turned out onto pasture in the spring (eg. Buckmaster and Parker (in press)) pasture would be uniform and CG preferable. In these situations there was no difference between the rotational grazing strategies—the GR and OR strategies were always identical to CR and they always limited intake. In New Zealand systems a wedge of pasture exists at the start of lactation because rotational grazing is used to conserve herbage *in situ* over winter (Bryant and Cook 1980). Under these conditions, intake was greatest with greedy rotation (GR) because this strategy was able to take advantage of differences in pasture mass between paddocks.

Since in a rotational grazing system only one paddock may be grazed at any one time, the sequence of paddocks chosen to be grazed must ensure that the rest period of each paddock is as close as possible to the length of time which maximises the average regrowth rate in that paddock (see Parsons and Penning 1988). The greedy strategy (GR) seems to go some way towards achieving this by ignoring paddocks with less herbage, ie. those in regrowth.

In addition, by evening up the pastures, GR grazed systems are less susceptible than CR systems to being grazed below the minimum pasture constraint. This robustness makes GR an attractive strategy for practical use although the additional effort in measuring paddocks and moving the animals over possibly long distances might discourage the use of GR without some modifications. It would also be important to find a grazing duration that allowed sufficient pasture growth in ungrazed paddocks between grazings in order to prevent the animals grazing the whole farm down too low.

The low production observed from CR in systems with uneven paddocks (Figure 4.5) reflects the failure of the CR strategy to properly utilise herbage grown in a wedge system where the rate of rotation is not synchronised to the pasture growth rate. In our simulations, the rate of rotation for CR was predetermined, and may have been either too fast or too slow for the optimal recovery and utilisation of paddocks (cf. Morley 1968, Parsons et al 1988, Parsons and Penning 1988, Bryant and Cook 1980). As this is the usual strategy used in rotational grazing experiments, it is clear that some experiments comparing continuous and rotational grazing have been invalid because researchers have not chosen the appropriate rate of rotation.

In every trial for which the optimal strategy was found, OR and GR were found to be identical. This indicates that GR is often optimal. Although there may be instances where GR is sub-optimal (chapter 2 suggests this will be so), these did not occur for any of the scenarios examined in this study and so might be unlikely to occur in practice. This is fortunate since the GR strategy is straightforward to implement in practice, whereas the general OR strategy requires a complicated and time consuming computer search to determine the optimal grazing sequence.

One reason why differences between GR and OR might have been masked was the use of a "tolerance" in the search procedure for the optimal strategy (see section 4.3.4). When at any time two fields had pasture masses different by less than 20 kgDM/ha they were considered to be identical and only one was considered for grazing. This is reasonable from a practical point of view since measurements of pasture mass have relatively large errors. However, from the point of view of an exact mathematical simulation, this approximation may have masked small differences between the GR and OR strategies. Another reason is that OR strategies may have had limited flexibility to exhibit superiority because of the need for only 15 time periods.

Finally, GR is less likely to be optimal when there is a big change in pasture growth through the period as GR initially reduces pasture cover and hence pasture growth rate early in the period.

4.5.3 Subdivision of Land and of Time

Increasing the number of paddocks and the number of time periods in a rotational grazing system gives increased flexibility of management options. However, our results show that while increasing the number of time periods allows some increase in herbage intake, increasing the number of paddocks reduces herbage intake. Morley et al (1969) and Booysen et al (1974) proposed that a small number of paddocks is sufficient in order to maximise intake, and our results support this conclusion. This is because subdivision restricts intake and allows increased herbage conservation *in situ.* At some point, increasing subdivision restricts animals intake to a greater extent than it increases additional pasture growth from rested paddocks. Once a wedge has been eliminated and pasture mass in all paddocks brought to near optimal growth rates, subdivision is no longer required to maximise intake. This suggests that rotational grazing management is best used to take advantage of inhomogeneous distribution of pasture within a grazing system. This brings to mind the comment of Bryant and Sheath (1987) that subdivision is most useful to separate areas of different productivity. Our results support this hypothesis.

4.5.4 Conclusions

The results from this extensive set of simulated grazing experiments reveal results supporting several well established and less well established ideas regarding grazing management and productivity. Use of this relatively simple model of pasture growth and removal has provided a theoretical basis for some of these statements, showing that even a crude representation of pasture dynamics can sometimes be used to explain features of grazing systems. Detailed considerations of sward structure and biology and complex plant-animal interactions are not necessary to explain them.

This inspires confidence in the use of this kind of simple mathematical modelling as a theoretical tool in agriculture, whereby hypotheses may first be formed and defended on these terms before field experimentation is attempted.

The effort required to perform in the field experiments equivalent to these simulations would be enormous. This highlights two of the advantages of modelling: it is cheaper than field experimentation, and noise can be eliminated. In addition, all input parameters are known precisely. However the weakness of modelling is that one must construct a model that appropriately describes the physical situation one is interested in. This may not be straightforward, especially if the physical situation is not well understood.

This study re-emphasises several points that have often been made before: (1) that continuous grazing maximises intake when pasture growth is in surplus to animal requirements, (2) that animals' herbage intake under rotational grazing is likely to be poor unless the rate of rotation is carefully synchronised to the pasture growth rate, (3) that grazing management makes little difference in maximising intake in comparison to stocking rate and average initial pasture, and (4) that subdivision of land can decrease productivity where maximum intakes are required.

The most interesting suggestion arising from this particular study is that a greedy strategy of grazing can increase growth and utilisation on multi-paddock systems with an inhomogeneous distribution of pasture.

Part II

Modelling Senescence in Grazed Pasture

Chapter 5

A Differential-Delay Model of Pasture Accumulation and Loss in Controlled Grazing Systems

5.1 Abstract

A grazing population dynamics model is proposed where organisms in a grazed population have a fixed lifespan. The motivating context is that of ruminants grazing grass-dominant pasture. The model takes the form of a differential-delay equation in which the rate of loss of pasture due to senescence at some time depends on the rate at which leaves are reaching maturity at that time. Comparisons are made with data from a continuous grazing experiment due to Bircham and Hodgson (*Grass and Forage Science*, 1983, 38:323–331), leading to a prediction of 21.9 days for herbage lifespan. Predictions of herbage utilisation are consistent with measured data. The model predicts lower senescence in swards in regrowth than in grazed swards at the same herbage mass. Solutions and equilibria are obtained for the linear form of the model with continuous grazing pressure. Solutions and bounds are obtained for the linear model with intermittent grazing pressure, and its usefulness in modelling grazed pastures is discussed.

A delay model is a simple but powerful means of including the concept of fixed herbage lifespan in grazing modelling. Questions of herbage lifespan and percentage utilisation are naturally contained in the mechanism of a differential-delay model. These are not so well handled by models that treat senescence of herbage empirically.

5.2 Introduction

The ability to model harvested (eg. grazed) populations accurately allows the dual goals of sustainability and optimised production to be pursued, since the effects of different harvesting schemes on the growth of the grazed population can be predicted. In addition, a good model describing the population mechanisms both identifies those factors that most influence the system's behaviour and focuses experimental effort on areas that are insufficiently well understood.

One context in which predicting grazed population dynamics is of economic interest is that of grazing domestic ruminants on grass-dominant pasture. The dynamics of grazed pasture depend on the balances between new tissue growth, aging, removal by grazing animals, senescence, and decay. A successful model must incorporate the known biological factors affecting the flow of leaf and other tissue through the sward. One such factor affecting pasture accumulation is leaf loss due to senescence, death, and disappearance. The "senescence syndrome" is a programmed internal degenerative process leading to the death of organisms (or parts of organisms) as a natural part of their life cycle, even in the absence of outside influences (Noodén 1988). In grasses, both the senescence of individual leaves, beginning at the tip and proceeding towards the base, and the post-reproductive senescence of whole tillers are observed. The latter is not addressed in this paper.

Senescent tissue is not immediately lost to the grazeable pool. For this reason, the term "loss" is more precise in this context, meaning leaf that has senesced to such an extent that it is lost to the grazed pool. Loss in this sense involves no physiological change and is a simply a pragmatic description. In Chapman et al (1984), for instance, leaves are considered to be "dead" when less than 10% of the lamina remains green. Subsequent decomposition and disappearance of litter and dead leaves on the plant are due to the action of micro-organisms in the base of the sward rather than to grazing.

By removing leaf prior to maturity, grazing reduces the rate of tissue loss due to senescence. It is claimed that one of the advantages of rotational over continuous grazing methods is that the (unproductive) loss of herbage due to senescence can be reduced by careful management, implying that a greater proportion of leaf is removed by the animals (Parsons 1988).

Grazing models have treated senescence in a variety of ways. Noy-Meir (1975, 1976, 1978) modelled grazed pasture dynamics as a predator-prey system, assuming that the rate of senescent tissue loss from the grazeable pool was dependent only on the current herbage biomass and that the relationship was linear (Noy-Meir 1978, models G_1–G_3). This assumption was supported by a subsequent field study showing that the rate of senescence in grass-dominant pasture continuously grazed by sheep at a constant herbage mass is linearly dependent on herbage mass (Bircham and Hodgson 1983). However, Johnson and Parsons (1985) challenged the assumption that a linear relationship adequately describes senescence in pasture systems not at equilibrium, in particular pastures under regrowth. By mimicking the delay between new growth and leaf death, their model predicts different rates of senescence between grazed and ungrazed pastures at the same herbage mass (leaf area index).

Our aim is to test a simple model of pasture growth under grazing that incorporates leaf death explicitly as a function of the age of leaves, and to compare the predictions from the model to experimental data. The use of a differential-delay equation arises naturally from the consideration of aging and death in the grazed population and has the advantage of incorporating a simple, biologically meaningful mechanism for senescence rather than an empirical relationship between senescence and herbage mass. We will not examine the question of diet selection.

Despite neglecting interactions that some would consider important, simple models are often of as much or greater use than complicated models, because cause and effect are more readily analysed. And yet even simple models often mimic subtle phenomena observed in the real world. It is shown that the differential-delay model both agrees with data from a grazing experiment (Bircham and Hodgson 1983) and corroborates Johnson and Parsons' (1985) hypothesis regarding senescence in pastures under regrowth.

Therefore, the differential-delay model appears to be a simple yet powerful means for modelling grazed populations with fixed lifespan that displays many of the features of much more complex models and yet is more directly biologically meaningful. For this reason it is an appropriate tool for synthesising biological knowledge of grazing processes.

5.3 Differential-Delay Model

The formulation of a model describing the dynamics of herbage in a grazed pasture is implied by Bircham and Hodgson (1983):

$$\frac{dw}{dt} = G - R - S, \tag{5.1}$$

where $w(t)$ is the herbage mass in some appropriate units and G, R, and S are respectively the rate of new growth, the rate of removal by grazing, and the rate of herbage loss due to senescence.

A fourth term, E say, should be appended to represent additional losses of pasture due to other factors such as treading, fouling, and ingestion by other organisms.

However, we neglect explicit treatment of these effects.

The functions G, R, and S may depend on a number of variables; in particular, S has usually been assumed to be a linear function of w,

$$S = mw(t) \tag{5.2}$$

where m is a constant. This has been used by modellers (eg. Noy-Meir 1978) and observed by experimenters in continuously grazed pastures (eg. Bircham and Hodgson 1983). However, this relation is empirical and is not founded on the detailed sward biology.

5.3.1 Delayed Senescence

Suppose a particle of pasture entering the grazeable pool (ie. "born") at some time t will die a fixed time τ later provided it hasn't been removed by grazing in the interim. Define pasture mass $w(t)$ as the mass of grazeable and photosynthesising herbage, which could equally well be expressed in terms of lamina mass or leaf area. Here $w(t)$ will be expressed as kilograms of dry matter per hectare (kgDM/ha). Let the rate of new leaf growth and the rate of pasture removal by the animals at time t be G and R kgDM/ha/day, respectively.

Assuming that animals graze indiscriminately (ie. that pasture is of a uniform high quality and all forage components are equally accessible to grazing), they remove equal proportions of all age classes of pasture leaf. This proportion is R/w per day. The proportion of leaf tissue "born" at time $t - \tau$ remaining ungrazed at time t is then,

$$\exp\left[-\int_{t-\tau}^{t} \frac{R(s)}{w(s)} ds\right] \tag{5.3}$$

This expression is the "non-utilisation", that is, the proportion of herbage that is lost to senescence instead of being used by the animals, the opposite of the "utilisation" calculated in some grazing studies.

If the "birth rate" at time $t - \tau$ was $G(t - \tau)$, the rate of death at time t is then

$$G(t-\tau)\exp\left[-\int_{t-\tau}^{t} \frac{R(s)}{w(s)} ds\right] \quad \text{kg/ha/day}$$

Thus the rate of pasture loss due to senescence at time t is explicitly dependent on the age of leaf tissue in the sward.

The net pasture mass dynamics at time t are therefore, from equation 5.1 (accumulation = growth – grazing – death),

$$\frac{dw}{dt} = G - R - G(t-\tau)\exp\left[-\int_{t-\tau}^{t} \frac{R(s)}{w(s)} ds\right] \tag{5.4}$$

Rates of loss are difficult to measure in general and must be obtained indirectly. Bircham and Hodgson (1983) admit that "the rate at which live tissue becomes dead tissue ... is difficult to measure". They estimated the rate of loss due to senescence by measuring the leaves on individual tillers. It seems likely that there could be considerable error in estimates of rates of loss due to senescence obtained in this way. On the other hand, leaf lifespan is much easier to ascertain, as in Chapman et al (1984), which presents survival tables for three pasture species throughout the year.

The differential-delay model presented here removes the need to estimate the coefficient of senescence m in equation 5.2. Instead, the constant τ must be known. However, τ has the advantage of being a biologically meaningful quantity whereas the relative rate of senescence, m, is not. Therefore, provided the delay model gives reasonable agreement with what experimental evidence exists, its use is favoured because it relies on biological parameters that are much better understood.

The curves of leaf lifespan measurements presented by Chapman et al (1984) show that the lifespan of individual leaves is distributed approximately normally with a relatively small standard deviation. Our delay model assumes that all leaves have exactly equal lifespans. This is likely to accentuate the effects of delayed senescence, in contrast to multi-compartment or matrix age models, which tend to spread out the effect of aging. For this reason the delay model is preferred, but also because alternative age models sometimes require a large number of model parameters that have no specific biological meaning and so are difficult to estimate.

5.3.2 Linear Delay Model

In general, the rates G and R depend on a large number of factors, such as season, plant species, and fertiliser application. In the simplest case the rate of new growth is proportional to the current amount of leaf and the animals graze a constant proportion of the existing pasture. In this case G and R are linear functions and the dynamics equation becomes

$$\frac{dw}{dt} = gw(t) - r(t)w(t) - gw(t-\tau)\exp\left[-\int_{t-\tau}^{t} r(s)ds\right] \qquad (5.5)$$

where g, and t are positive constants (ie. constant growing conditions) and $r(t)$ varies with time only and is proportional to the stocking density, which is controlled by the farmer.

The assumptions inherent in equation 5.5 involve some gross simplifications that require some defence. First, at low pasture mass (eg. 500–1300 kgDM/ha), maintenance respiration and leaf shading are low, and the assumption that growth is proportional to photosynthesis, which in turn is proportional to herbage mass, is both biologically and pragmatically reasonable, particularly in a period of vegetative growth such as winter and early spring. The resulting exponential growth (which arises from linear differential equations and so is sometimes called "linear" growth) has been used at low pasture mass by grazing researchers in several instances because of its mathematical simplicity and ubiquity in biological processes (eg. Noy-Meir 1978, Robson et al 1988, Brougham 1955, McCall et al 1986, and see chapter 2).

Similarly, studies in herbage intake suggest that daily intake is approximately proportional to herbage allowance at low herbage when nutritional limitations to intake are not significant (Poppi et al 1987). Sheep intake data from Bircham (1981) show this linear dependence over herbage masses in the range 500–1500 kgDM/ha.

Even if the linear model, equation 5.5, ultimately proves unacceptable, the general model, equation 5.4, can be easily upgraded with improved non-linear growth and intake response functions, although these may reduce the usefulness of analytical methods. For instance, a logistic function might be appropriate for pasture growth G, and a Michaelis-Menten expression for herbage intake R (cf. Noy-Meir 1978). In section 5.4 the hyperbolic growth function of Bircham and Hodgson (1983) will be adopted in order to make comparisons with data from their grazing experiment.

The assumption that the climate remains constant is the least acceptable. However, in modelling it is important to be able to separate climate effects from the effects of grazing management. Simple mathematical models offer a great advantage over complex computer simulations in this regard in that one can work backwards from observed effects to their causes within the model much more easily. This makes it possible to test hypotheses regarding the effects of particular grazing management schemes while avoiding the problems in field experiments associated with the weather. So ignoring climate and seasonal effects is a pragmatic choice.

5.4 Results

We now proceed with analysis of the general and linear forms of the delay equation (equations 5.4 and 5.5) and comparison of predictions from the delay model with published experimental data.

5.4.1 Equilibria of the General Equation

In a grazed pasture maintained at a constant pasture mass, $w'(t) = 0$ and $w(t) = w(t-\tau)$ =herbage mass, HM, a constant. From equation 5.4, therefore,

$$0 = G - R - G\exp\left[-\int_{t-\tau}^{t} \frac{R}{\mathrm{HM}} ds\right] \tag{5.6}$$

Assuming that G and R depend only on HM (ie. the equation is autonomous), this becomes

$$0 = G - R - G\exp\left[-\frac{\tau R}{\mathrm{HM}}\right]$$

which implies that

$$\tau = -\frac{\mathrm{HM}}{\mathrm{R}}\ln\left[1 - \frac{R}{G}\right] \text{ days} \tag{5.7}$$

We expect τ to be a constant for all values of HM, since Chapman et al (1984) found that leaf lifespan was independent of grazing management.

Comparison to Experimental Data

This relation between the functions G and R and the constants τ and HM allows a comparison with the observations of Bircham and Hodgson's experiment (1983) in which mixed perennial ryegrass, *Poa annua*, and white clover swards were maintained at constant herbage mass (500, 700, 1000, or 1700 kgDM/ha) by continuous but variable stocking with sheep during the northern spring and summer (May to July). Measurements were made during two periods, 11–21 June (period 1) and 2–16 July (period 2).

From their measurements of new growth and senescence, Bircham and Hodgson fitted curves for new growth G, senescence S, and net production NP as functions of the herbage mass HM. Since herbage was being maintained at a constant level, the rate of pasture removal by grazing, R (called "C" in Bircham and Hodgson 1983), was the same as the net production, giving zero net accumulation. These relations were (omitting the error analysis)

$$\begin{aligned} G &= 118 - 2.18 \times 10^7/\mathrm{HM}^2 \\ S &= 0.5 + 0.23\mathrm{HM} \\ \mathrm{NP} = R &= 113 - 0.02\mathrm{HM} - 2.14 \times 10^7/\mathrm{HM}^2 \end{aligned} \tag{5.8}$$

all expressed in kgDM/ha/d, where HM is in kgDM/ha.

Bircham's (1981) curves show that the intake rate of a single grazing animal unit (ie. a ewe, a lamb, or a ewe and a lamb) in the range 500–1500 kgOM/ha (organic matter per hectare) is approximately linearly related to the herbage mass.

However, due to the non-linearity of G with respect to herbage mass, the stocking density required to maintain a steady herbage level of HM was not constant. Since total intake is the product of stocking density and per animal intake rate, R was therefore non-linear. (Note: in Bircham 1981, DM and OM measurements of herbage mass are assumed to be equivalent).

Figure 5.1 shows the fitted values of G and R at each of the herbage levels in Bircham and Hodgson's experiment as well as the predicted τ at each value of HM, given by equation 5.7. A quadratic function of HM was regressed against τ. This was not significantly different from a constant (95% confidence). Thus τ predicted by the delay model from Bircham and Hodgson's rate data was approximately constant and had a mean of 21.9 days (3 weeks).

This result indicates that the delay model properly describes pasture dynamics in pastures maintained at a constant mass by grazing.

The predicted value of the average leaf lifespan (21.9 days) was lower than expected. Chapman et al (1984) measured the median leaf lifespan of leaves in mixed perennial ryegrass, browntop, and white clover swards under set stocking and rotational grazing in the southern December and January (which correspond to the northern June and July) at 5 weeks in all three plant species. They also found that leaf death rates and longevity were largely unaffected by grazing management.

However, a value of 3 weeks is not unreasonable. Ryegrass tillers have an average of 3 live leaves at any one time, and the leaf appearance rate is sometimes around 7 days in June and July, so this figure is quite acceptable (Robson et al 1988).

Chapman et al (1984) measured leaf lifespan between the day of leaf appearance and the time at which only 10% of the leaf laminae remained green. It is possible that leaves do not properly enter the pool of photosynthesising and grazed tissue as early as this or that they are lost from the grazed pool earlier than this. Other biases may arise from our assumption that all leaf ages are grazed with equal probability. This suggests that τ represents some "effective leaf lifespan" that is a corrected version of the actual leaf lifespan as defined and measured by Chapman et al.

It is intriguing that we were able to obtain this estimate simply by mathematical analysis of the pasture growth and net production rates. This suggests our quite simple model, equation 5.4, is appropriate.

Predictions Of Utilisation

Bircham and Hodgson found that the utilisation of ryegrass in their continuously grazed pastures was 65%. This is the average of utilisations calculated at each treatment herbage mass using the formula R/G (see equations 5.8). Utilisation is

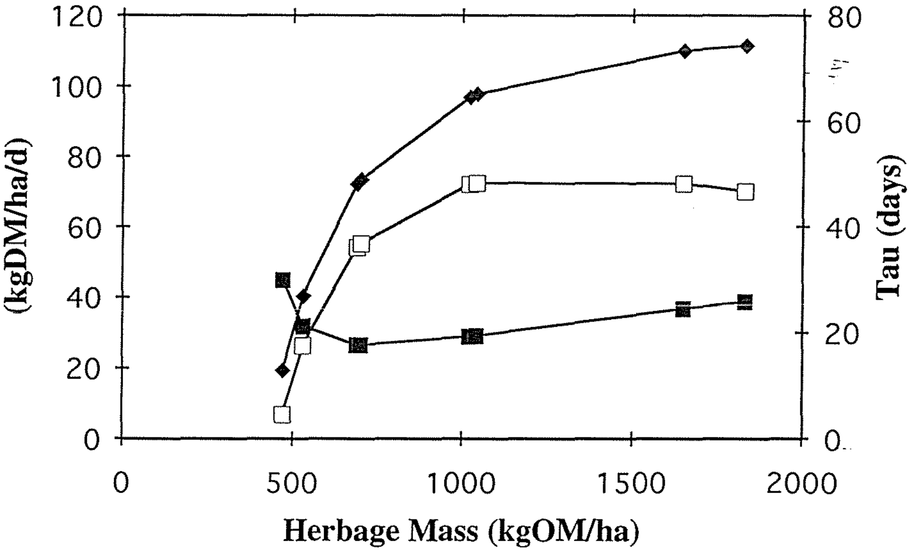

Figure 5.1: Fitted curves of growth rate G (black diamonds) and intake rate R (white squares) from Bircham and Hodgson (1983), and the associated τ predicted by the delay model (black squares).

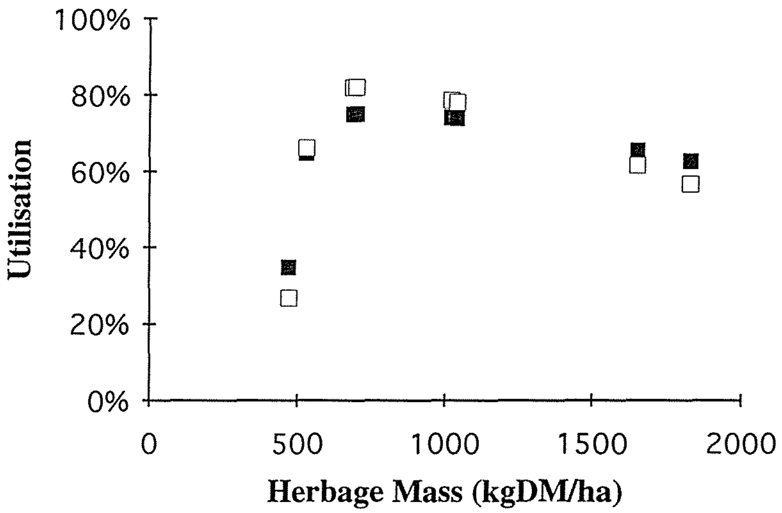

Figure 5.2: Utilisation predicted by the delay model (white squares) and Bircham and Hodgson's (1983) calculated values (black squares).

the proportion of tissue that is grazed rather than being lost to senescence and decay. Similarly, Chapman et al (1984) measured the utilisation of ryegrass, browntop, and white clover leaf tissue in the range 34–80%, which was independent of the grazing management.

The differential-delay model of grazing directly addresses the question of percentage utilisation. The proportion of leaf grown at time $t-\tau$ that is lost to senescence (at time t) is given by the coefficient in equation 5.3. For a constant grazing rate, R/w, such as in Bircham and Hodgson's experiment (1983), this simplifies to $\exp(-r\tau)$. The utilisation is then $1-exp(-r\tau)$. In the case of Bircham and Hodgson's experiment, r is the ratio of intake (which is equivalent to net production, NP) to herbage mass, that is,

$$\begin{aligned} r(\mathrm{HM}) &= \mathrm{NP}/\mathrm{HM} \\ &= 113/\mathrm{HM} - 0.02 - 2.14 \times 10^7/\mathrm{HM}^3 \quad \text{per day} \end{aligned}$$

from equation 5.8. We therefore expect the utilisation in a continuously grazed field to vary with the pasture level, and this relation is shown in Figure 5.2. A leaf lifespan of τ=21.9 days was used, consistent with the results above.

The predictions of utilisation from the delay model were not significantly different from those calculated from the field measurements (paired two-sample t-test, 95% confidence). These predictions also lie within the range observed by Chapman et al (1984), except for the prediction at the lowest pasture mass. This exception is probably due to inaccuracies in the predictions of net production from Bircham and Hodgson's fitted hyperbola at low pasture mass. That model (see equations 5.8) has a zero at 454 kgDM/ha and thus is unlikely to be valid at low pasture mass.

The close agreement between the predictions of utilisation from the delay model and those measured in the field show that the delay model is consistent and gives a convenient method to predict utilisation.

5.4.2 Linear Continuous Grazing

Equation 5.5 describes the change of pasture mass $w(t)$ over time under grazing pressure $r(t)$ in the case where the linearity assumptions hold. Analysis of equation 5.5 leads to a number of consequences that can be related back to the physical situation of animals grazing pasture and provide insight into the dynamics of any real-world system in which the assumptions hold.

We first consider the case where $r(t)$ is a constant, r_1 say, in $t > 0$. This is the situation in a continuous grazing system where the stocking density is constant.

Equation 5.5 then simplifies to

$$\frac{dw}{dt} = gw(t) - r_1 w(t) - gw(t-\tau)exp(-r_1\tau) \tag{5.9}$$

with initial conditions $w_1(t)$ defined in $0 \leq t \leq \tau$.

When $g = 0$ or $\tau = 0$, or when τ is large, this reduces to a non-delay equation with an exponential solution, so we restrict our attention to the region where $g, \tau > 0$. Setting $r(t) \equiv 0$ (ie. no grazing) provides no such simplification; we still have a differential-delay equation to solve as net growth still depends on the imbalance of new growth and senescence.

Equation 5.9 is a constant coefficient, linear, differential-delay equation as discussed in Bellman and Cooke (1963). Bellman and Cooke provide methods for solving such equations and determining the stability of equilibrium solutions, which we shall briefly discuss.

Stability of $w = 0$

Steady states of equation 5.9 are situations where $w(t)$ remains constant over time. One such steady state occurs when $w = 0$, in which case there is no pasture. It is the stability of this steady state that is of the most interest, as this indicates whether the pasture will be grazed to extinction or not.

In chapter 4 of their book, Bellman and Cooke (1963) show that the zero steady state ($w = 0$) of a differential-difference equation such as equation 5.9 is stable if all roots of its "characteristic equation" have negative real part. The characteristic equation for equation 5.9 is

$$h(s) = s - (g - r_1) + g\exp(-r_1\tau - s\tau) = 0 \tag{5.10}$$

Multiplying this by $-\tau\exp(s\tau)$ and using Hayes' result, which is given in chapter 13 of Bellman and Cooke, all the roots of the exponential polynomial $h(s)$ have negative real part if and only if

(a) $(g - r_1)\tau < 1$,

(b) $(g - r_1)\tau < g\tau exp(-r_1\tau)$, and

(c) $(g\tau exp(-r_1\tau))^2 < a_1^2 + (g - r_1)^2\tau^2$,

where a_1 is the root of $a = (g - r_1)\tau\tan(a)$ in $(0;\pi)$. In the case of our problem these simplify to a single condition:

(d) $g - r_1 - g\exp(-r_1\tau) < 0$

This watershed is shown in Figure 5.3 for the case where τ=30 days. This then is the condition for stability of the zero steady state of equation 5.9. As we would expect, this condition will be met if r_1 is sufficiently large, that is, if the grazing pressure is sufficiently high. In particular, it will always be stable if $r_1 \geq g$.

Neutral Stability Condition

In addition to the zero solution, when

$$0 = g - r_1 - g \exp(-r_1 \tau) \tag{5.11}$$

there is the possibility of other positive steady states. As this occurs only for a vanishingly small range of values of the parameters, it is not of much practical interest. The stability of these steady states is not obvious. However, when equation 5.11 is satisfied, the characteristic function $h(s)$ has its rightmost root at $s = 0$. Later we will show that the real part of the rightmost root of $h(s)$ is the exponent of the dominant term of the solution, so in this case $w(t)$ approaches a constant (whose value depends on the initial conditions). However, this cannot be said to be a stable steady state—rather, its stability is neutral.

Figure 5.4 shows three numerical solutions to equation 5.9 for different values of r_1. These show how the herbage mass increases to infinity, settles at a neutral steady state, or tends to a stable zero steady state as the right-hand side of equation 5.11 is positive ($r_1 = 0.04$), zero ($r_1 = 0.05$), or negative ($r_1 = 0.06$), respectively, even though the initial conditions are identical in $(0; \tau)$.

These findings suggest that the linear model, equation 5.5, does not lend itself naturally to modelling steady continuous grazing, as there are no attracting stable states (besides zero) like those expected in Noy-Meir (1975) and Johnson and Parsons (1985), where for a sufficiently low set stocking density the pasture will tend to a positive equilibrium. In the linear model, maintaining a constant grazing pressure r_1 leads to the pasture either declining to zero or increasing without bound. McCall et al (1986) used this property of linear models to study pasture being grazed down. Situations of high pasture mass where a second steady state is likely to occur are not covered by the linear model, as it does not address the drop-off in pasture growth rate at high pasture mass. Therefore, the assumptions of linearity are reasonable only at low pasture mass. However, this may make the linear model appropriate for studying short-duration rotational grazing systems where pasture masses are not allowed to rise near ceiling yield. In section 5.4.3 we examine intermittent grazing using the linear model.

Series Solution

The solution of equation 5.9 is (using Laplace transform techniques):

$$w(t) = \frac{1}{2\pi i} \int_{c-i\infty}^{c+i\infty} \exp(st)(h(s))^{-1} p(s) ds \tag{5.12}$$

where

$$p(s) = w_1(\tau)\exp(-s\tau) - g\exp(-r_1\tau)\int_0^\tau w_1(x)\exp(-sx)dx$$

which depends on the initial conditions, and c is a constant, sufficiently large as to be greater than the real part of all of the roots of $h(s)$ (Bellman and Cooke 1963, chapter 4). The singularities of the integrand of equation 5.12 lie at the roots s_n of $h(s)$ and are all simple poles (except when $g\tau = 1$, in which case there is a double pole at $s = -r_1$). Assuming $g\tau \neq 1$, the solution is the sum of the residues at these singularities; that is,

$$w(t) = \sum_n \frac{p(s_n)\exp(s_n t)}{h'(s_n)} \tag{5.13}$$

Bellman and Cooke (chapter 4) show that the roots of $h(s)$ for an equation of this type are infinitely many and lie asymptotically along the curve

$$\text{Re}(s) + (1/\tau)\log|s| = (1/\tau)(\log g - r_1\tau)$$

which is symmetric to the real axis, lies entirely to the left of the imaginary axis, and approaches an exponential curve as $s \to -\infty$.

Asymptotic Solution to the Continuous Case

The complete series solution for a differential-delay equation such as ours is an infinite sum of exponential terms, expression 5.13. Those terms whose exponents have negative real part will vanish as time increases. Bellman and Cooke's Theorem 4.3 indicates that if c is any negative number such that no zeros of $h(s)$ lie on the line $\text{Re}(s) = c$, then the sum of the residues of those zeros to the right of this line forms an asymptotic solution of equation 5.9. We can use this theorem to form an asymptotic solution from the residues due to the real roots of $h(s)$, as follows.

Result 5.1 *For equation 5.9, $h(s)$ has at most two real roots, and all the complex roots (which occur in conjugate pairs) lie to the left of the real roots and have negative real parts.*

Proof We show this by making a substitution of variable, $z = (s - g + r_1)\tau$. Then

$$\begin{aligned} \tau h(s) &= z + g\tau\exp(-g\tau)\exp(-z) \\ &= z + G\exp(-z), \end{aligned} \tag{5.14}$$

where G is a constant, $0 < G \leq \exp(-1)$. This amounts to a scaling of the complex s plane. Substituting $z = x + iy$, we split the equation into real and imaginary parts, respectively,

$$G\exp(-x)\cos(y) = -x \tag{5.15}$$

$$G\exp(-x)\sin(y) = y \tag{5.16}$$

When $y = 0$ there are two negative real solutions, one of which is at $z = -g\tau$ (ie. $s = -r_1$). We denote these two solutions as z_0 and z_{00}, respectively, where $z_0 \leq -1 \leq z_{00} \leq 0$. Therefore, $s_0 \leq (g - r_1) - 1/\tau \leq s_{00} \leq (g - r_1)$. s_0 and s_{00} can easily be found numerically.

As $G \to 0$, $z_{00} \to 0$ and $z_0 \to -\infty$. At the other extreme, when $G \to \exp(-1)$, both z_0 and z_{00} converge at -1 ($s_0 = s_{00} = (g - r_1) - 1/\tau$).

There are no non-real singularities for $x \geq x_0$. First, for $\ln(G) \leq x$ (note that $\ln(G) \leq -1$) there are no non-zero solutions to equation 5.16 since $G\exp(-x) \leq 1$. Next, in $x_0 < x < x_{00}$ there are no solutions to equation 5.15, since $G\exp(-x) < -x$ in this region. At $x = x_0$, equation 5.15 becomes $\cos(y) = 1 \Rightarrow y = 2n\pi$. Substituting into equation 5.16 gives $G\exp(-x)\sin(2n\pi) = 2n\pi \Rightarrow 0 = 2n\pi \Rightarrow n = 0$. So again there are no non-real solutions at this point. Therefore, no non-real singularities exist when $x \geq x_0$ (or equally, $\mathrm{Re}(s) \geq s_0$).

It is clear from equation 5.16 that y and $-y$ will both satisfy the equations for a given x. So the complex singularities occur in conjugates, all of which lie to the left of s_0. Furthermore, $z_0 \leq -g\tau \Rightarrow z_0/\tau + g - r_1 \leq 0 \Rightarrow s_0 \leq 0$.

Corollary Since we have shown that all of the complex roots of $h(s)$ lie to the left of the real roots and have negative real parts in our case, we are able to take the residues due to the real singularities as an asymptotic solution:

$$w(t) \sim \frac{p(s_0)\exp(s_0 t)}{h'(s_0)} + \frac{p(s_{00})\exp(s_{00} t)}{h'(s_{00})} \tag{5.17}$$

Because the contribution of the neglected terms is greatest at small t, the accuracy of this approximation will be worst at $t = \tau$. In the knife-edge case where $g\tau = 1$, there is a double pole at $s_0 = s_{00} = -r_1$, and a different form must be used.

5.4.3 Linear Rotational Grazing

Now consider the effect of changing the stocking density. This is the rotational grazing case in which animals are either introduced into or removed from the field at various times. Assume that the known grazing pressure $r(t)$ is stepwise constant

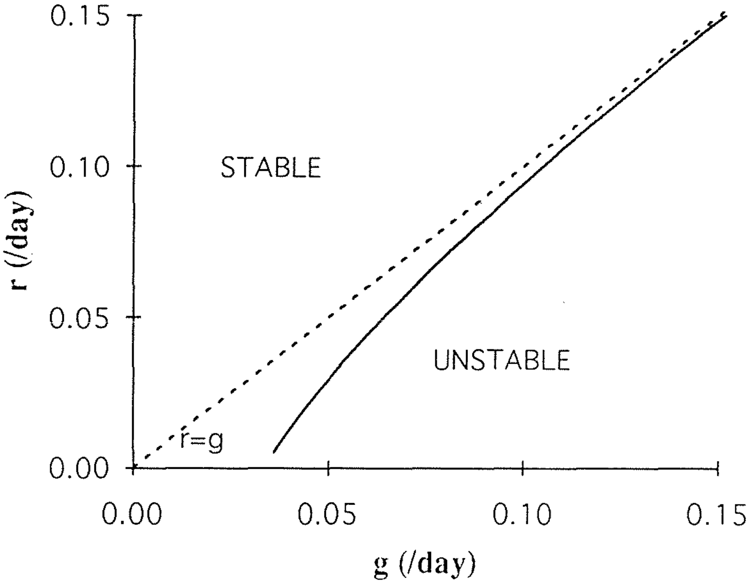

Figure 5.3: Grazing rate r required for stability of the steady state at $w = 0$ (ie. grazing to extinction) when $\tau = 30$ days. $w = 0$ is a stable steady state above the curve, unstable below.

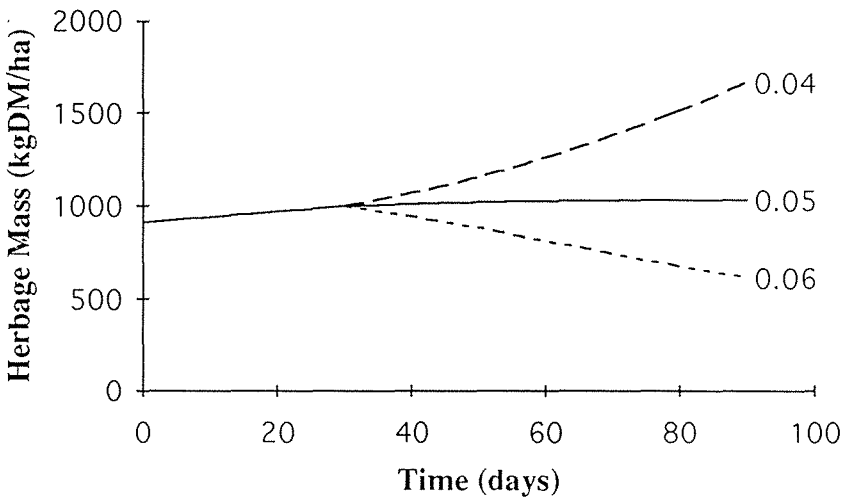

Figure 5.4: Numerical solutions of equation 5.9 with the same initial conditions and $r_1 = 0.04, 0.05, 0.06$, respectively. $r_1 = 0.05$ satisfies equation 5.11.

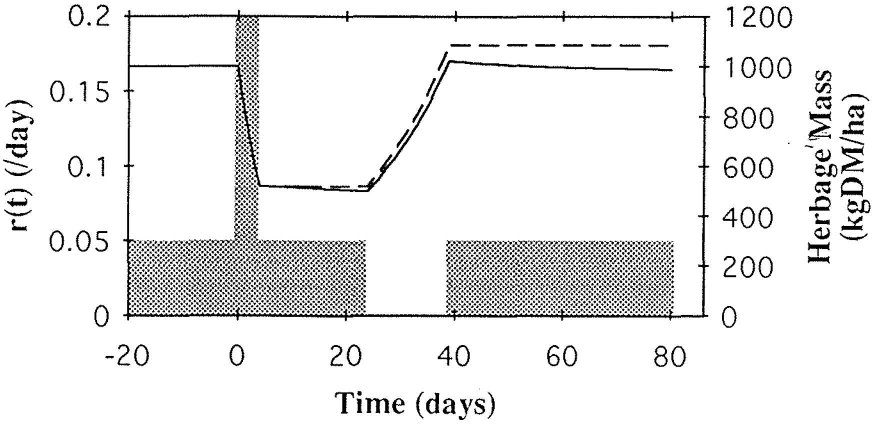

Figure 5.5: Simulated solution of the rotational grazing case. The shaded bars show the grazing pressure $r(t)$, the solid line the changes in $w(t)$ predicted by the linear delay model, and the dashed line the predictions from a non-delay model.

with time, so that over short periods stocking density is constant, and animals are introduced and removed in discrete numbers. This is obviously reasonable in a real grazing system.

Define a time interval $(0;t_1)$ such that

$$t_1 = \max\{t^* : 0 < t^* \le \tau, r(t) = r_1 \text{ and } r(t-\tau) = r_0 \text{ in } t \in (0;t^*)\}$$

Equation 5.5 is then, in $(0;t_1)$,

$$\frac{dw}{dt} = gw(t) - r_1 w(t) - gw_0(t-\tau) I \exp(-r_1 t)\exp(-r_0(t_1 - t)) \tag{5.18}$$

where $w_0(t)$ is the initial condition known in $(-\tau;0)$ and the constant I is

$$I = \exp\left[-\int_{t_1-\tau}^{0} r(s)ds\right]$$

the mortality from time $t_1 - \tau$ to time 0. The solution $w(t)$ in $(0;t_1)$ is now obtained by the integrating factor method as follows:

$$\begin{aligned}
\frac{dw}{dt} - (g - r_1)w(t) &= -gw_0(t-\tau)I\exp(-r_1 t)\exp(-r_0(t_1-t)) \\
\frac{d}{dt}[\exp(-(g-r_1)t)w(t)] &= -gw_0(t-\tau)I\exp(-r_1 t)\exp(-r_0(t_1-t))\exp(-(g-r_1)t) \\
&= -gw_0(t-\tau)I\exp(-r_0 t_1)\exp((r_0-g)t)
\end{aligned}$$

Integrating gives

$$\exp(-(g-r_1)t)w(t) = k - gI\exp(-r_0 t_1)\int_0^t w_0(s-\tau)\exp((r_0-g)s)ds$$

where k is a constant. Now let $w(0) = w_0(0)$ at time $t = 0$, so $k = w_0(0)$. Therefore,

$$w(t) = \exp((g-r_1)t)w_0(0) - gI\exp((g-r_1)t)\exp(-r_0t_1)\int_0^t w_0(s-\tau)\exp((r_0-g)s)ds \tag{5.19}$$

defined in $(0; t_1)$. By stepping forward in time interval by interval, this provides the solution to equation 5.5 for all $t > 0$ in the case where $r(t)$ is stepwise constant.

Figure 5.5 shows a simulation of intermittent grazing on a paddock with variable stocking density (shown by the shaded bars). The solid curve shows the predicted herbage mass from the delay model, and the dashed line that from a model with linear, non-delayed senescence (equation 5.2). The two curves diverge exponentially. This divergence arises from the necessity to estimate the parameter τ in the delay model and the parameter m in the non-delay model. As mentioned before, τ is likely to be a much easier value to estimate in practice than m. In addition, the senescence term S in the non-linear non-delay model, equation 5.1, may depend on several unknown parameters. For instance, if S is quadratic, two parameters would be needed. The senescence term in the delay model (equation 5.4) requires only one parameter, τ, no matter how non-linear the functional relations are.

The behaviour of the non-delay model in Figure 5.5 (dashed line) follows the grazing rate. By contrast, when $r(t) = 0.05$ in the delay model (solid line), satisfying condition 5.11 for steady herbage mass, $w(t)$ is not steady. There is still movement due to changes in the rate of senescence, which in turn are due to past changes in stocking density.

Bounds To The Solutions

We now derive upper and lower bounds to the solutions of equation 5.5.

Result 5.2 *If $w(t)$ is the solution of equation 5.5 in an interval containing $t = 0$, then the function $\bar{w}(t)$ defined by*

$$\frac{d\bar{w}}{dt} = g\bar{w}(t) - r(t)\bar{w}(t), \quad \bar{w}(0) = w(0) \tag{5.20}$$

is a bound for $w(t)$ such that $\bar{w}(t) \geq w(t)$ in $t > 0$ and $\bar{w}(t) \leq w(t)$ in $t < 0$.

Solving equation 5.20 gives

$$\bar{w}(t) = w(0)\exp\left[\int_0^t g - r(s)ds\right], \tag{5.21}$$

which is everywhere positive.

Proof If at some time $\bar{w}(t) = w(t)$, then $\bar{w}'(t) \geq w'(t)$ since the last term of equation 5.5 is always negative or zero. Therefore $\bar{w}(t)$ can cross $w(t)$ at most once, at $t = 0$ say, and thereafter will always lie above $w(t)$. Therefore, if $\bar{w}(0) = w(0)$, then $\bar{w}(t)$ is a lower bound for $w(t)$ in $t < 0$ and an upper bound in $t > 0$.

Result 5.3 *If in* $(-\tau; 0)$ *the condition*

$$\frac{dw}{dt} \geq -r(t)w(t) \tag{5.22}$$

is satisfied, then

$$\frac{dw}{dt} \geq -r_1 w(t) \tag{5.23}$$

is satisfied in $(0; t_1)$*, where* t_1 *is defined as for equation 5.18.*

Proof Assume that condition 5.22 is true. Now substituting the solution 5.19 into the first term of equation 5.18 gives, in $(0; t_1)$,

$$\begin{aligned}\frac{dw}{dt} &= g\exp((g-r_1)t)w_0(0) \\ &\quad -g^2 I\exp((g-r_1)t)\exp(-r_0 t_1)\int_0^t w_0(s-\tau)\exp((r_0-g)s)ds \\ &\quad -r_1 w(t) - g w_0(t-\tau) I\exp(-r_1 t)\exp(-r_0(t_1-t))\end{aligned} \tag{5.24}$$

Define a function $\underline{w}_0(t)$ in $(-\tau; 0)$ such that

$$\frac{d\underline{w}_0(t)}{dt} = -r(t)\underline{w}_0(t), \quad \underline{w}_0(t_1-\tau) = w_0(t_1-\tau)$$

Solving gives

$$\underline{w}_0(t) = w_0(t_1-\tau)\exp\left[\int_{t_1-\tau}^{t} r(s)ds\right]$$

Reasoning as in the proof of Result 5.2, whenever $\underline{w}_0(t) = w_0(t)$, $\underline{w}_0'(t) \leq w_0'(t)$. Therefore, $\underline{w}_0(t)$ can cross $w_0(t)$ at most only once, at $t = t_1 - \tau$, and thereafter $\underline{w}_0(t) \leq w_0(t)$. Therefore, $\underline{w}_0(t) \geq w_0(t)$ in $t < t_1 - \tau$, and $\underline{w}_0(t) \leq w_0(t)$ in $t > t_1 - \tau$. From this it follows that

$$w_0(t-\tau) \leq \underline{w}_0(t-\tau) = w_0(t_1-\tau)\exp[-r_0(t-t_1)] \text{ in } t \in (0; t_1) \tag{5.25}$$

and

$$w_0(0) \geq \underline{w}_0(0) = w_0(t_1-\tau)\exp\left[-\int_{t_1-\tau}^{0} r(s)ds\right] = w_0(t_1-\tau)I \tag{5.26}$$

Substituting equation 5.25 into the second and fourth terms of equation 5.24 gives

$$\begin{aligned}
\frac{dw}{dt} &\geq g\exp((g-r_1)t)w_0(0) \\
&\quad -g^2 I\exp((g-r_1)t)\exp(-r_0 t_1)\int_0^t w_0(t_1-\tau)\exp(-r_0(s-t_1))\exp((r_0-g)s)ds \\
&\quad -r_1 w(t) - g w_0(t_1-\tau) I\exp(-r_1 t) \\
&= -r_1 w(t) + g\exp((g-r_1)t)[w_0(0) - I w_0(t_1-\tau)]
\end{aligned}$$

after some rearranging, and since the last term is positive from equation 5.26, $w'(t) \geq -r_1 w(t)$ in $(0; t_1)$ as required.

Assumption 5.4 *Assume that there exists a time t^* such that*

$$\frac{dw}{dt} \geq -r(t)w(t) \tag{5.27}$$

is satisfied in $(t^*; t^*+\tau)$.

Condition 5.27 is easily satisfied over a period of τ days at some time in the past. If condition 5.27 were not satisfied in any past interval this would imply that the rate of loss due to senescence was often greater than the rate of new growth. From a biological point of view this is pathological.

Result 5.5 *If Assumption 5.4 is satisfied, then*

$$\frac{dw}{dt} \geq -r(t)w(t)$$

for all $t > t^*$.

The proof follows immediately from Result 5.3 by induction.

Result 5.6 *If $w(t)$ is the solution of equation 5.5 in an interval containing $t = 0$, then the function $\underline{w}(t)$ defined by*

$$\frac{d\underline{w}}{dt} = -r(t)\underline{w}(t), \quad \underline{w}(0) = w(0) \tag{5.28}$$

is a bound for $w(t)$ such that $\underline{w}(t) \leq w(t)$ in $t > 0$ and $\underline{w}(t) \geq w(t)$ in $t < 0$.

Solving equation 5.28 gives

$$\underline{w}(t) = w(0)\exp\left[-\int_0^t r(s)ds\right] \tag{5.29}$$

which is everywhere positive.

Proof As before, if at some time $\underline{w}(t) = w(t)$, then $\underline{w}'(t) \leq w'(t)$ by Result 5.5. Therefore, $\underline{w}(t)$ can cross $w(t)$ at most once, at $t = 0$, and thereafter $\underline{w}(t) \leq w(t)$. Therefore, $\underline{w}(t) \leq w(t)$ in $t > 0$, and $\underline{w}(t) \geq w(t)$ in $t < 0$.

Initial Conditions

For a delay equation such as equation 5.5, the initial conditions consist of a function $w_0(t)$ that is known over a time period of length τ. If the formulation, equation 5.5, is to be valid over all time, then $w_0(t)$ must itself be a solution of equation 5.5. We have in Results 5.2 and 5.6 upper and lower bounds for the solution $w(t)$ of equation 5.5 in the region $t > 0$, which also give lower and upper bounds, respectively, for the initial condition function $w_0(t)$ in $t < 0$. However, stronger constraints on the initial conditions can be obtained from the above process.

Result 5.7 *If $w_0(t)$ is a solution to equation 5.5 in $[-\tau; 0]$, then $w_0(t)$ is a valid initial condition for equation 5.5 in $[0; \tau]$ and*

$$w_0(t) \in \{w : w \in \mathrm{C}[-\tau; 0], w(0) > 0, -r(t)w \leq dw/dt \leq (g - r(t))w\} \qquad (5.30)$$

(omitting the trivial case $w(t) \equiv 0$).

Proof Since the last term of equation 5.5 is non-positive, as previously noted, we have the upper bound on the derivative of $w_0(t)$ in equation 5.30. The lower bound on the derivative of $w_0(t)$ in equation 5.30 is obtained from Result 5.5.

5.4.4 Senescence Rates under Regrowth and Grazing

Another method of comparing how the delay model estimates loss due to senescence differently from the non-delay model is to examine how the rate of senescence changes with respect to the pasture mass and grazing management. Most previous models have used a linear relation between senescence and herbage mass or a component of herbage mass. This has been justified by results such as those of Bircham and Hodgson (1983) on continuously grazed paddocks at constant pasture mass, where decay was found to be highly correlated and linear with pasture mass. However, Johnson and Parsons (1985) predicted by means of a multi-age-compartment model that although a linear relation may be appropriate in a grazed pasture, it would not be appropriate in an intermittently grazed sward in a situation of regrowth following grazing down. This is because a non-delay model ignores the lag between leaf birth and death, which is important in intermittently grazed swards (Robson et al 1988).

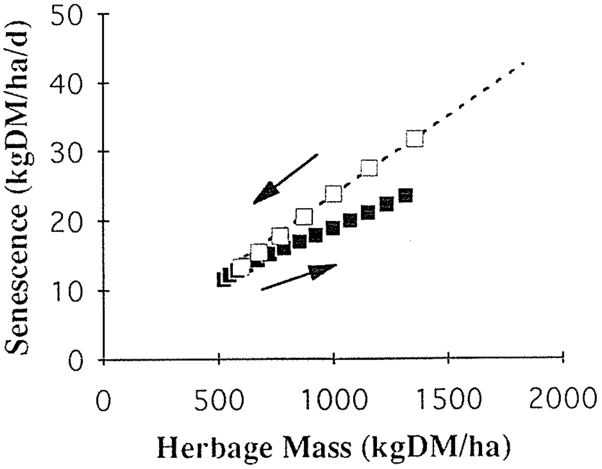

Figure 5.6: Modelled rates of senescence under grazing down (white squares) and under regrowth (black squares). The dashed line shows senescence predicted by Bircham and Hodgson (1983) for continuous grazing at the same herbage mass.

Although the Johnson and Parsons model is not a strict delay model, it mimics a delay effect by considering tissue flows between different age classes of leaf.

Figure 5.6 shows the relationship between herbage mass and senescence produced by simulating grazing down and regrowth of pasture with the delay model. The form used was:

$$\frac{dw}{dt} = G(w(t)) - r(t)w(t) - G(w(t-\tau))\exp\left[-\int_{t-\tau}^{t} r(s)ds\right] \qquad (5.31)$$

where $G(w) = 118 - 2.18 \times 10^7/w^2$ kgDM/ha/d (from equation 5.8) and $\tau = 22$ days. The pasture growth function was that of Bircham and Hodgson (1983), and grazing down was done with a fixed stocking density ($r(t)$=constant) where the rate of removal by a single animal was linearly related to instantaneous herbage mass, as was true of the sheep originally used by Bircham and Hodgson (see Bircham 1981).

Prior to grazing down, the pasture was maintained at a constant mass of 1354 kgDM/ha with a daily grazing rate of 74.5 kgDM/ha/d. This initial scenario was chosen because it fitted both Bircham and Hodgson's experiment and the condition (equation 5.6) for continuous grazing at a steady herbage mass in the delay model. The pasture was then grazed down to 520 kgDM/ha using a grazing pressure of $r(t)$=0.2 per day. After this the grazing pressure was removed ($r(t) = 0$) and the herbage was allowed to regrow.

During grazing down, the rate of senescence at a given herbage mass was the same as that observed by Bircham and Hodgson (1983) in continuously grazed pastures (shown in Figure 5.6 by a dashed line). The equation of this line is given in equations 5.8.

However, during regrowth, senescence was depressed due to the relative scarcity of mature leaf in the sward. This agrees qualitatively with the results from Johnson and Parsons' model (Johnson and Parsons 1985) over the range of Bircham and Hodgson's measurements: 470–1830 kgDM/ha (leaf area index 0.8–4.9). It is interesting that this single non-linear delay equation, equation 5.31, is able to produce the same conclusions as the far more complex model of Johnson and Parsons.

5.5 Discussion

The differential-delay formulation presented here can conceptually be applied to any grazing-type plant-herbivore system where the herbivore numbers are controlled (but not necessarily constant) and the plant units have a fixed lifespan. Other applications are in the controlled harvesting of fixed populations of fixed lifespan organisms, such as fisheries, by humans. By altering the functions G and R in equation 5.4, more realistic response functions can be introduced (logistic growth, seasonal variation in growth rate, etc.), although analytical solutions are then unlikely to be obtainable. Nevertheless, these formulations may still be straightforward to solve numerically.

It has been shown that the linear form of the delay model allows calculation of bounds on the future predicted herbage mass. However, a linear model is probably insufficiently subtle to adequately model continuous grazing. This suggests that the stability of grazing systems is highly dependent on the response functions, particularly the rate of new growth, as suggested by Noy-Meir's analysis of different response functions (Noy-Meir 1978). Nevertheless, analysis of the steady states provided a condition (equation 5.11) to predict whether a particular grazing pressure would drive the herbage mass to extinction or not, and this condition will be approximately correct for real grazing systems, thus giving a critical stocking density (Figure 5.3). Explicit solutions for herbage mass were also obtained for the linear delay model for systems of both continuous and rotational grazing.

A few field studies have examined the rate of loss due to senescence relative to the standing pasture mass (eg. Bircham and Hodgson 1983). Although it is known that pasture loss is dependent on leaf age, most models have looked for simpler relationships between the rate of pasture death and the current herbage mass, assuming, for instance, that the rate of pasture loss is linear on w(t) (eg. Noy-Meir 1978). Johnson and Parsons' model (Johnson and Parsons 1985) was more tentative about this assumption and as a result predicted that the rate of senescence differs between grazed and ungrazed swards. Our non-linear delay model (equation 5.31) predicts with Johnson and Parsons (1985) that senescence in a regrowing pasture is less than that in a grazed pasture at the same herbage mass, in the range 470–1830 kgDM/ha (leaf area index 0.8–4.9).

Several points of agreement were found between the predictions from the delay model and the experimental results of Bircham and Hodgson (Bircham 1981, Bircham and Hodgson 1983). The delay model predicted a leaf lifespan constant of 21.9 days from their growth and senescence data. This estimate is reasonable for this time of year (June/July).

Predictions of percentage utilisation of herbage were also not significantly different from those measured by Bircham and Hodgson, providing a second point of validation for the model.

In this study we have considered a single variable model of pasture accumulation that explicitly treats senescence as the consequence of leaf aging. This model is simple enough to allow analysis of the dynamical relationships within the grazed sward, such as steady states, utilisation, and leaf lifespan, and yet displays many of the subtle features of pasture systems such as the difference in senescence between grazed and ungrazed swards. The model is also easily modified to accommodate non-linear pasture growth and grazing response functions.

For some applications, alternative models may be either too simplistic to adequately describe pasture dynamics, such as Noy-Meir's (Noy-Meir 1975), which neglects the delay between tissue birth and death, or too complex to allow ready analysis, as with Johnson and Parsons' 13-equation system with five age compartments (1985). Johnson and Parsons' model also has the disadvantage of introducing a large number of unknown coefficients. The model presented here, on the other hand, provides an economical method of introducing a mechanism of senescence while avoiding the introduction of excess parameters. Even in non-linear forms of the differential-delay model, only one parameter is needed to handle the rate of senescence: τ, the leaf lifespan. This parameter is both biologically meaningful and subject to easy measurement in the field; neither of these qualities can be ascribed to many of the parameters introduced in Johnson and Parsons' model, for instance.

These are compelling reasons for adopting this differential-delay model in the study of grazed pastures.

Chapter 6

Simulation of Rotational Grazing with Delayed Senescence

6.1 Introduction

Having formulated the delayed senescence model in chapter 5 it is of interest to examine whether fluctuations of senescence caused by intermittent grazing result in a higher or lower intake for the animals.

Field evidence suggests that rotational grazing should be able to support higher stocking rates than continuous grazing when used in the winter to conserve herbage (McMeekan 1960). However, few studies support the hypothesis that herbage intake or animal production are increased under rotational grazing (Wheeler 1962, Morley 1981), except possibly through the ability to carry more stock (McMeekan and Walshe 1963).

There are, however, suggestions that senescence is depressed under intermittent grazing, due to the delay between leaf formation and death, and that this may be able to be manipulated by grazing management to allow increased utilisation of pasture grown. However, due to higher stocking densities in rotational grazing and the resulting additional losses due to treading and fouling, these gains are unlikely to be observed in practice (Parsons 1988). A theoretical approach offers a means to test this hypothesis (Johnson and Parsons 1985a).

Other studies of pasture regrowth following defoliation stress that utilisation is optimised when the duration of regrowth is such that the average rate of production between successive grazings is maximised (Morley 1968, Parsons and Penning 1988). That is, the efficiency of a system of rotational grazing depends on the timing and severity of defoliation.

Because of this current interest in understanding the dynamics of grazed pastures under intermittent grazing and because the delayed senescence model of chapter 5 was designed with this problem in mind, the next logical step is to make a comparison between continuous and rotational grazing using the delay model, in order to establish whether animal intake is increased under rotational grazing management.

6.2 Method

A simple simulation is proposed to test this hypothesis. The control treatment is continuous grazing of $H = 5$ hectares of pasture at a constant herbage mass of $w = 1000$ kgDM/ha for a total of $T = 60$ days by a group of animals whose intake rate (when spread over 5 hectares) is $r = 5\%$ of the available pasture per day. We are interested in the total herd intake, the average percentage daily intake (constant in this study), the total loss of pasture due to senescence, and the average daily percentage loss due to senescence.

Grazing may be modelled using a delayed senescence model or an equivalent non-delay model. In both cases linear forms are chosen for simplicity. The effect of non-linear response functions would be simply to depress both growth rate and grazing rate at high herbage mass. This is discussed in section 6.4, below.

The linear delay model is equation 5.5, that is,

$$\frac{dw}{dt} = gw(t) - r(t)w(t) - gw(t-\tau)\exp\left[-\int_{t-\tau}^{t} r(s)ds\right] \tag{6.1}$$

Leaf lifespan was chosen arbitrarily at $\tau = 30$ days. In this case we require the specific pasture growth rate to be $g = 6.436\%$ per day, from equation 5.11, because $r = 5.000\%$ per day must be the critical value for steady state grazing.

The equivalent non-delay model is

$$\frac{dw(t)}{dt} = gw(t) - rw(t) - lw(t) \tag{6.2}$$

where $l = g\exp(-r\tau) = 1.436\%$ per day is the specific rate of pasture loss due to senescence. This figure was chosen to make the delay and non-delay simulations comparable.

Rotational grazing of 5 one-hectare paddocks was simulated with a range of rotation lengths, T_r. These were: $T_r = \tau/2 = 15$ days, $T_r = \tau = 30$ days, and $T_r = 3\tau/2 = 45$ days. We might expect the advantage of intermittent grazing to be greatest when the rotation length is less than the leaf lifespan, because leaf death is depressed most immediately following defoliation (Parsons 1988).

	Constant Senescence				
	Continuous Grazing	**15 day Rotation**	**30 day Rotation**	**45 day Rotation**	
Total Intake	15000	14790	16625	17628	**kgDM**
Average Intake Rate	0.05	0.05	0.05	0.05	**/day**
Total Senescence	4308	3838	4365	5150	**kgDM**
Average Senescence Rate	0.01436	0.01436	0.01436	0.01436	**/day**

	Delayed Senescence				
	Continuous Grazing	**15 day Rotation**	**30 day Rotation**	**45 day Rotation**	
Total Intake	15000	14074	15873	17141	**kgDM**
Average Intake Rate	0.05	0.05	0.05	0.05	**/day**
Total Senescence	4308	4295	4845	6217	**kgDM**
Average Senescence Rate	0.01436	0.01733	0.01780	0.02263	**/day**

Table 6.1: Effect of delayed senescence and rotation length on total intake, average rate of intake, total senescence, and average rate of senescence. These values are obtained by using simulation of the linear delay and non-delay models over $T = 60$ days.

6.3 Results

The results of total intake, average rate of intake, total senescence, and average rate of senescence are tabulated in Table 6.1. Figure 6.1 shows time courses of herbage simulated by the delay model for continuous and rotational grazing with the three rotational lengths. Results simulated with the non-delay model were similar.

Continuous grazing gives a total herd intake of $rwHT = 15000$ kgDM. The average rate of daily intake is simply r per day. The total loss of leaf due to senescence in this time is $lwHT = gw\exp(-r\tau)HT = 4308$ kgDM, which is an average loss of $l = g\exp(-r\tau) = 1.436\%$ per day. These results are the control against which the results from the rotational simulations may be compared.

The essential features of the rotational results are as follows:

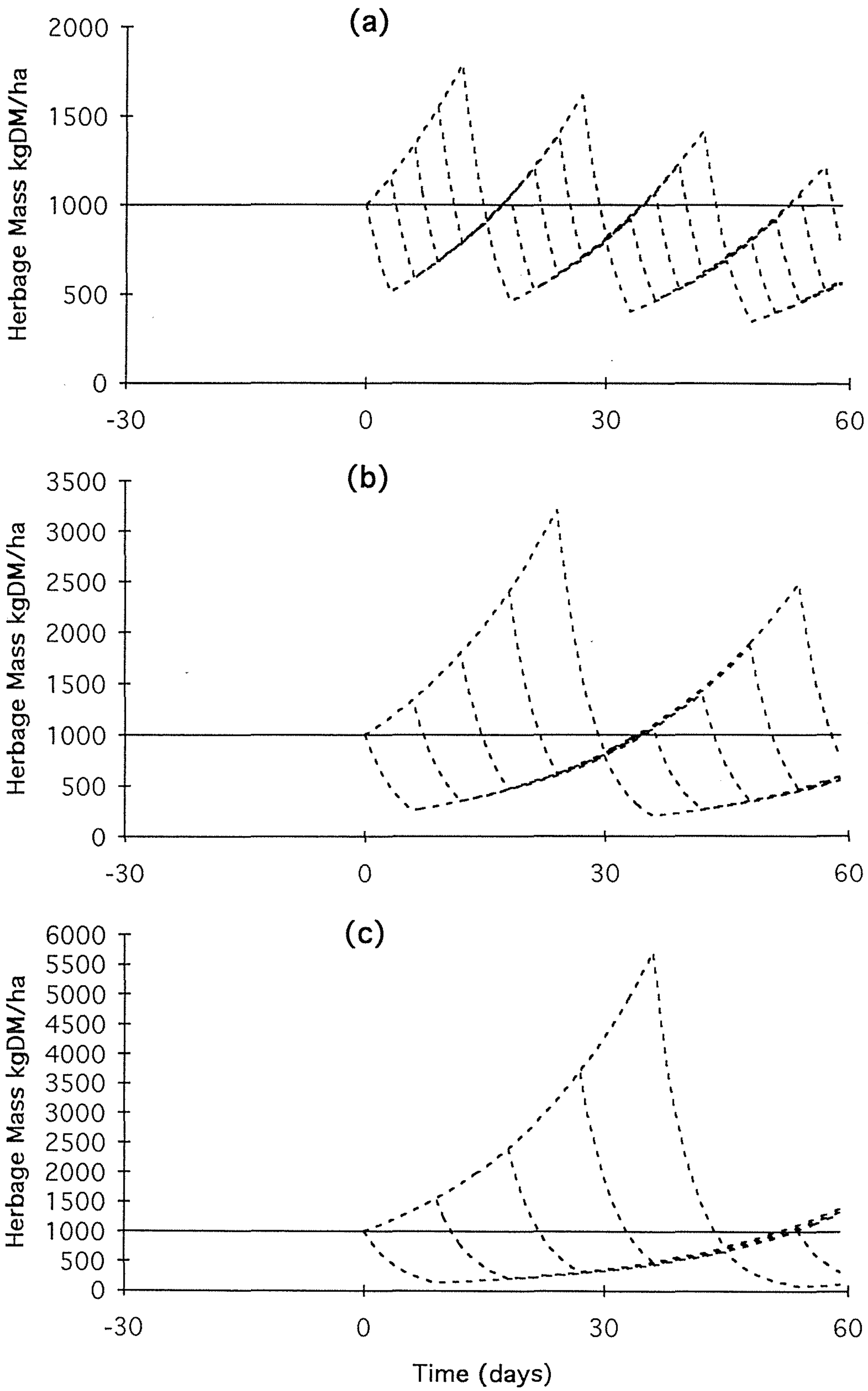

Figure 6.1: Simulated herbage masses for continuous grazing (————) and rotational grazing initiated at day 0 (·········). (a) rotation length $T_r = \tau/2 = 15$ days; (b) $T_r = \tau = 30$ days; (c) $T_r = 3\tau/2 = 45$ days. The five dotted lines correspond to the five paddocks in the rotational system.

- Total intake and senescence increased with rotation length.
- Fluctuations in herbage mass increased in amplitude as rotation length increased (see Figure 6.1).
- The percentage rate of senescence calculated by the delay model also increased with rotation length.
- Intake was greater under the non-delay model than under the delay model.
- Senescence and average specific senescence were both greater under the delay model.
- Average herbage mass decreased with time in all of the rotational treatments.

6.4 Discussion

These results suggest that the major influence affecting intake and senescence from grazed pasture is the average herbage mass. As rotational grazing causes fluctuations in herbage mass, this may have the effect of increasing the average herbage mass and thus intake and senescence (see Figure 6.1). However, in more realistic non-linear models the specific rate of growth declines at high herbage mass, as does the specific intake rate. Because of this, rotational grazing of real pastures is not likely to increase the average herbage mass across the pastures as much as the linear model used in the simulations was observed to do. Therefore, intake levels will be likely to be similar under continuous and rotational grazing (see chapters 2, 3, and 4).

The observed effect of rotation length increasing intake can likewise be ascribed to the increasingly high herbage masses being grazed as the period of rest increased under the linear model.

Under all of the rotational treatments the average herbage mass after each complete rotation declined gradually over time. This suggests that this stocking rate ($r = 0.05$) is too high to be maintained under rotational grazing. Since rotational grazing is generally thought to be able to carry greater stocking rates than continuous grazing (McMeekan 1960) this is surprising. This may be a consequence of the linear model, especially the linear approximation for intake rate, because intake rate should be bounded at high herbage mass.

The effects of using a delayed senescence model as opposed to a non-delay model can be deduced by comparing results between the two sets of treatments. The main feature of note is that as rotation length increased, the average rate of senescence increased in the delay simulations. That this also occurred in the non-delay model shows that some of the effect is due to the increased average herbage mass under rotational grazing. However, senescence in the delay model increased more rapidly. This is because the instantaneous rate of senescence,

$$gw(t-\tau)\exp\left[-\int_{t-\tau}^{t} r(s)ds\right]$$

(see equation 5.5) depends not only on the time averaged grazing rate, which was the same under continuous and rotational grazing at the same stocking rate, but also on the earlier herbage mass, $w(t-\tau)$. Under rotational grazing, herbage mass fluctuates, so the instantaneous senescence also varies. The results of this simulation suggest that the average rate of senescence under rotational grazing is greater than that under continuous grazing and also increases with rotation length.

Under the short (15 day) rotation, the intake from rotational grazing was lower than from continuous grazing. This is again due to the herbage mass. With the fast rotation, ungrazed paddocks had insufficient time to recover pasture cover. This is supported by field experiments showing that slow rotations allow superior production (Bryant and Cook 1980)

The linear model is clearly inadequate for appropriately modelling situations where the rest period is long. The effects of delayed senescence are also difficult to judge because the results are dominated by the effects of herbage mass. This would also make comparisons between senescence in continuously and rotationally grazed pastures difficult in practice.

The choice of whether a delay or non-delay model is more appropriate in modelling rotational grazing depends on the needs of the particular study. While delayed senescence is appealing from a biological viewpoint, this study shows that the results obtained are sometimes qualitatively indistinguishable from those obtained from its simpler non-delay counterpart. However, by comparison with the equivalent non-delay model, use of a delay model in this study has highlighted the increased senescence expected under rotational grazing.

Chapter 7

Conclusion

In this thesis we have presented dynamical systems methods for studying problems in agricultural grazing. In the past these problems have typically been studied experimentally. We have shown that many such problems may be approached theoretically with some success. This is relatively inexpensive and rapid compared to field trials. However, field validation is still ultimately necessary.

Rotational grazing is practised with a number of possible aims in mind, depending on the time of year. These range from conservation of herbage *in situ* to maximising intake for finishing beef animals.

Our conclusions are that rotational grazing may be effectively practised in order to meet the former objective. However, animal production is mainly dependent on stocking rate, initial herbage mass, and animal and pasture genetic characteristics which are independent of grazing management. In particular, rotational grazing usually restricts herbage intake and so increased intake can not be expected except in special circumstances and when an optimal strategy is used.

Senescence in grazed pasture is the result of leaf aging and thus the rate of senescence depends on the history of the sward. We have shown how this delay can be modelled and have illustrated some of the practical implications of delayed senescence in continuously and intermittently grazed pastures.

Several problems and extensions remain open for future modelling. One is the effect of treading and fouling on productivity, especially in rotational systems. A second concerns the differences in pasture quality and botany between continuously and rotationally grazed swards. Thirdly, a simple dynamic model of live-weight gain from herbage intake will be useful to future studies of grazing productivity. Fourthly, the effect of seasonal variation in pasture growth on the efficiency of rotational grazing systems also needs to be examined, since this obviously affects management choices throughout the year. And fifthly, methods for dealing with weather and other stochastic effects in a unified way will also be useful in the development of stochastic models of pasture growth. Monte Carlo methods are one approach to this problem.

Several data required for the theoretical study of agricultural grazing have not yet been adequately established. An important question is the proper form of the response functions determining pasture growth and animal intake. These need to be established with some urgency if work in this area is to proceed. In addition, detailed data concerning seasonal variation in pasture growth parameters are needed. Future experimentation should also provide dynamic information, showing the changes in the various quantities and fluxes measured as time proceeds, instead of averaging results over time. Because of the developing science of stochastic modelling, estimates of the variation in measured values will also be required to support future modelling efforts.

Final Word

In the past three years Professor Graeme Wake and I have attended a number of meetings and workshops at which we have had problems in agricultural biology and management described to us. The scientists who "own" these problems have been on the hunt for systematic and quantitative methods with which to study them. We have had the opportunity to suggest how mathematical thinking might contribute to the study of these problems. The collaborative nature of our research (my share of which is presented in this thesis[1]) has stimulated great interest.

Mathematics has previously been seen either as too esoteric for practical use or as simply beyond the expertise of most agriculturalists. Now, however, there seems to be a new optimism and openness among agriculturalists (in New Zealand at least) towards the mathematical techniques that have made such enormous contributions in the physical sciences over the last 300 years or so, particularly the use of differential equations. There is much more that can be done with differential equations in the field of modelling agricultural processes. For the success of such a venture however, mathematicians are needed who are willing to become students of agricultural science.

I personally have found these meetings to be of great interest. As mathematicians we are sometimes accused of irrelevance. Tackling these kinds of problems offers a means to gain credibility (and thus funding) in an increasingly market-driven world.

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[1] Two other published articles which have resulted from the collaboration between the Department of Mathematics at Massey and AgResearch Whatawhata are Hendy (1992) and Pleasants et al (in press a).

Also, the world is a fascinating and beautiful place—well worthy of study. There appear to be a great many fascinating and rich problems in agriculture which are waiting for a formulation and are of economic and environmental importance.

My supervisors Graeme Wake, Tony Pleasants, and David McCall are pioneers in bringing together mathematicians and agricultural biologists. I hope that such active consultancy will continue, as there are clear benefits for both parties. Ultimately these benefits extend to the wider community.

This thesis describes our first small steps into an area of mathematical modelling which is largely unexplored. Inevitably there have been false starts and ill chosen roads. It is hoped that better formulations and solutions to the problems we have studied will be forthcoming in the future as more mathematicians turn their attention to agricultural problems.

Appendix A

Optimal Swapover Times for f-Field Model

This appendix contains some results obtained by extending the two-field linear model of chapter 2 to consider a single rotation around f fields. This is a simplified version of the f-field rotational grazing problem described in chapter 1 (section 1.1).

The f fields are to be grazed in sequence beginning with field 1 and finishing with field f for a total of T days. Each field will be grazed once. The objective considered here is to maximise the animals' total intake over a single rotation.

Suppose that the fields have initial herbage masses $w_1(0), w_2(0) \dots w_f(0)$. The swapover times which are to be found are $t_1, t_2 \dots t_{f-1}$, respectively, such that

$$0 \le t_1 \le t_2 \dots t_{f-1} \le T \tag{A.1}$$

t_i is the time at which the animals finish grazing field i and are shifted into field $i+1$.

From equation 2.8, the intake in time period $i = 1, 2 \dots f$ is given by

$$c(t_i) - c(t_{i-1}) = \frac{kw_i(t_{i-1})}{a(1-m_i)}[\exp(a(1-m_i)(t_i - t_{i-1})) - 1] \tag{A.2}$$

Note that $t_0 = 0$, $c(0) = 0$ and $t_f = T$. Field i will begin to be grazed at time t_{i-1}. At this time its herbage cover will be $w_i(t_{i-1}) = w_i(0)\exp(at_{i-1})$. Substituting and summing gives the total intake at time T,

$$c(T) = \sum_{i=1}^{f} \frac{kw_i(0)\exp(at_{i-1})}{a(1-m_i)}[\exp(a(1-m_i)(t_i - t_{i-1})) - 1] \tag{A.3}$$

The total intake per animal, $c(T)$, is a function of the swapover times $t_1, t_2 \dots t_{f-1}$. A necessary condition to maximise $c(T)$ is that all of its partial derivatives (with respect to the swapover times) are simultaneously zero. The partial derivative of

$c(T)$ with respect to t_i involves only two terms of the sum in equation A.3, and is,

$$\begin{aligned}\frac{\partial c(T)}{\partial t_i} &= kw_i(0)\exp(at_{i-1})\exp(a(1-m_i)(t_i-t_{i-1})) \\ &+\frac{kw_{i+1}(0)\exp(at_i)}{1-m_{i+1}}[\exp(a(1-m_{i+1})(t_{i+1}-t_i))-1] \\ &-kw_{i+1}(0)\exp(at_i)\exp(a(1-m_{i+1})(t_{i+1}-t_i)) \qquad (\text{A.4})\end{aligned}$$

with $i = 1, 2 \dots f-1$.

Setting equation A.4 equal to zero and rearranging gives

$$t_{i+1} = t_i + \frac{1}{a(1-m_{i+1})}\ln\left(\frac{1}{m_{i+1}} - \frac{1-m_{i+1}}{m_{i+1}}\frac{w_i(0)}{w_{i+1}(0)}\exp(-am_i(t_i-t_{i-1}))\right) \quad (\text{A.5})$$

for $i = 1, 2 \dots f-1$.

This provides a recurrence relation for the optimal t_i. Suppose that we have an estimate for t_1. Recall that $t_0 = 0$. Provided that constraint A.1 is satisfied at every step, equation A.5 can be used to calculate the values of $t_2, t_3 \dots t_{f-1}$ and finally of t_f. Since T is specified for the problem, the discrepancy between the estimated value of t_f and the desired value of T can be used to improve the initial estimate of t_1. So the problem becomes to find t_1 in order to get $t_f = T$. This is now a single "equation" with one unknown, t_1, and may be solved numerically. The implication of obtaining such a relationship is that there is a unique critical point, since equation A.5 is a single valued function.

Satisfying the constraint A.1 requires that $t_{i+1} \geq t_i$. From equation A.5 this means that

$$\frac{1}{a(1-m_{i+1})}\ln\left(\frac{1}{m_{i+1}} - \frac{1-m_{i+1}}{m_{i+1}}\frac{w_i(0)}{w_{i+1}(0)}\exp(-am_i(t_i-t_{i-1}))\right) \geq 0$$

which simplifies to

$$\frac{w_i(0)}{w_{i+1}(0)} \leq \exp(am_i(t_i-t_{i-1})) \qquad (\text{A.6})$$

It is possible that this condition might be violated—in this case constraint A.1 must be applied so that $t_{i+1} = t_i$. This means that field i will not be grazed. We see from equation A.6 that if the sequence $w_1(0), w_2(0) \dots w_f(0)$ is decreasing then this never happens.

Rearranging equation A.5 we can see that the optimal times spent grazing each paddock, $t_i - t_{i-1}$, will be equally spaced and equal to δt when

$$\frac{w_i(0)}{w_{i+1}(0)} = \frac{\exp(am_i\delta t) - m_{i+1}\exp(a\delta t)}{1-m_{i+1}} \qquad (\text{A.7})$$

In particular, when the paddocks are equal in size (so that $m_1 = m_2 = \dots = m_f$), this implies that $w_i(0)/w_{i+1}(0)$ is constant for all i. Therefore we have the following result:

Result A.1 *If there are f fields of equal size, and if $w_1(0), w_2(0), \ldots, w_f(0)$ is a geometric sequence satisfying equation A.6, then the intake from a single grazing rotation is maximised when the grazing durations are all equal to the value of δt which satisfies equation A.7.*

This result is likely to be of academic interest only. If T is greater than a few days the linearity assumption will not hold. In practice T could be a month or more. Nevertheless, this illustrates the complexity added even in the linear case when we move from a two field to a multi-field rotation. If two or three rotations were considered this would further complicate matters. More sophisticated methods would be required to deal with further extensions.

Appendix B

The Multi-Paddock Grazing Problem Computer Program

Introduction

What follows is a complete listing of the C program used in simulating the Multi-Paddock Grazing Problem in chapter 4. This program simulates results for the CG, CR, GR and OR strategies. The bulk of the program is concerned with finding the optimal (OR) strategy.

The input file has a simple text format and is described in the program comments as follows:

```
/* INPUT FILE FORMAT:
     m              number of fields (int)
     H              total area of farm
     w1    wm       max & min initial masses
     p              total number of periods (int)
     T              total time
     n              number of animals (int)
     r              grazing rate per animal
     g              maximum pasture growth rate
     we             mass below which growth ceases
     1/b            ceiling yield
     wlow  whigh    min & max pasture constraints
     wtol           discernible diff between masses
*/
```

The left hand columns give the order of the parameters in the input file and the right hand columns are comments (these may not appear in the input file). Apart from those parameters marked "(int)" which are integers, all parameters are double precision floating point (ie. the "double" data type in C).

The parameters used in the simulations in chapter 4 were

```
/* INPUT FILE:
        m                fields (variable)
        100              hectares
        w1    wm         kgDM/ha (variable)
        P                periods (variable)
        60               days
        n                animals (variable)
        0.0047           per day
        41.9             kgDM/ha/day
        0                kgDM/ha
        4000             kgDM/ha
        900   4000       kgDM/ha
        20               kgDM/ha
*/
```

Again, the right hand column are comments which may not be included in the input file. Those parameters whose values varied from simulation to simulation are labelled "(variable)".

The Program

A listing of the program follows:

```
/* "branch3.c" 15 June 1993  */
/*  Program for simulating multi-paddock grazing.  Includes */
/*  Branch and Bound search algorithm for finding optimal sequence */
/*  of fields to visit in a multi paddock grazing problem */

/* includes: */
#include     <stdio.h>    /* standard I/O library */
#include     <math.h>     /* mathematics library */
/* Compile Note: When compiling, use the -lm option at
the end of the option list, e.g. "cc branch3.c -o branch -lm" */

/* constants defines: */
#define      MAXPERIODS   200   /* max no of time periods */
#define      MAXFIELDS    100   /* max no of fields */
#define      DEBUG        0     /* print diagnostic messages ? */

/* type definitions and structures: */
typedef      int          strattype[MAXPERIODS]; /* max size of strats */
typedef      double       fieldset[MAXFIELDS];      /* max no of fields */

struct       INP   /* stores all the data needed to do a search */
{
      int          m ;          /* number of paddocks */
      double       H ;          /* total hectares */
      fieldset     w0 ;         /* initial field masses */
      int          p ;          /* number of time intervals */
      double       T ;          /* total time in days */
      int          n ;          /* no of animals */
      double       r ;          /* marginal removal rate per animal */
      double       g ;          /* maximum growth rate, kg/ha/d */
      double       we ;         /* mass at which growth is zero */
      double       b ;          /* 1/ceiling yield, ha/kg */
      double       wlow,whigh; /* pasture mass constraints */
      double       wtol;        /* tolerance for "identical" fields  */
} ;

struct       DIAG  /* stores diagnostic results of a search */
{
      double       nodes ;      /* total number of nodes in tree */
      double       visited ;    /* counter for no of tree nodes visted */
      double       trimmed;     /* counter for no of nodes trimmed */
} ;

struct       AUX   /* stores aux values used by growth fns */
{
      double       alpha ;      /* coeff of w^2 in growth eqn */
      double       beta0;       /* coeff of w when no grazing */
      double       beta1;       /* coeff of w under grazing */
      double       gamma;       /* constant term of growth eqn */
      double       delta0;      /* discriminant of growth eqn no graz*/
      double       edelta0;     /* exp(-delta0*tstep) */
      double       delta1;      /* discriminant of growth eqn graz */
      double       edelta1;     /* exp(-delta1*tstep) */
      int          negdiscr;    /* negative discriminant => use tans */
      double       lambda1;     /* alternative discriminant for grazing*/
      double       tlambda1;    /* tan of lambda1 */
      double       tstep ;      /* length of one interval in days */
      double       incoeff;     /* coefficient for calculating intake */
      double       wlow,whigh; /* pasture mass constraints */
```

```
        double          wtol;           /* tolerance for "identical" fields  */
        int             m ;             /* no of paddocks */
        int             p ;             /* no of periods */
        double          T ;             /* total time in days */
        double          n ;             /* number of animals */
} ;

struct          NODE    /* stores information about a node */
{
        double          in;             /* intake so far at that node */
        fieldset        w;              /* field masses at that node */
        strattype       s;              /* strategy so far at that node */
        int             pl;             /* periods left to bottom of tree */
        int             feas;           /* 0/1 whether node is a feasible strat */
} ;

/* declare global variables */
struct          AUX     aux ;           /* holds aux values used by fns */
struct          DIAG    diags ;         /* hold any diagnostic values */

/* function declarations follow: */
/*========================================*/
void setaux(x)
        struct INP *x;
/* takes input parameters and calculates auxiliary
        values used by the grow() graze() and intake() fns */
{
        double          temp ;          /* temporary value */

        aux.tstep=x->T/x->p;            /* time step */
        aux.whigh=x->whigh;
        aux.wlow=x->wlow;
        aux.wtol=x->wtol;
        aux.m=x->m;
        aux.p=x->p;
        aux.n=x->n;
        aux.T=x->T;

        temp=4*x->g/((1/x->b-x->we)*(1/x->b-x->we));
        aux.alpha=-temp;
        aux.incoeff=-x->n*x->r/(2*aux.alpha) ;
        aux.beta0=(1/x->b+x->we)*temp;
        aux.beta1=(1/x->b+x->we)*temp-x->n/(x->H/x->m)*x->r;
        /* note: 0 suffix => no grazing, 1 suffix => grazing */
        aux.gamma=(- x->we/x->b)*temp;

        aux.delta0=sqrt(aux.beta0*aux.beta0-4*aux.alpha*aux.gamma);
        aux.edelta0=exp(-aux.delta0*aux.tstep);

        temp=aux.beta1*aux.beta1-4*aux.alpha*aux.gamma;
        aux.negdiscr=(temp<0);          /* check for negative discriminant */
        if (aux.negdiscr)
                {
                if (DEBUG) printf("Grazing always outstrips growth\n");
                aux.lambda1=sqrt(-temp)/(2*aux.alpha);
                aux.tlambda1=tan(aux.alpha*aux.lambda1*aux.tstep) ;
                }
        else
                {
```

```
                if (DEBUG) printf("Growth sometimes outstrips grazing\n");
                aux.delta1=sqrt(temp);
                aux.edelta1=exp(-aux.delta1*aux.tstep);
                }
}
/* end of setaux() */
/*=========================================*/
int grow(wa, wb)
        double *wa, *wb ;
/*      Takes the field mass at wa and calcs the new field
        mass at wb after one time interval's growth.  Returns 1 if
        constraint violated, 0 otherwise.       */
{
        double          e0 ;            /* intermediate value */

        e0=aux.edelta0*(aux.delta0+aux.beta0+2*aux.alpha* *wa)/
                           (aux.delta0-aux.beta0-2*aux.alpha* *wa);
        *wb=(aux.delta0*(1-e0)/(1+e0)+aux.beta0)/(-2*aux.alpha);

        /* Check maximum mass constraint */
        if (*wb>aux.whigh) return 1; else return 0;
}
/* end grow() */
/*=========================================*/
int graze(wa, wb)
        double *wa, *wb ;
/*      Takes the field mass at wa and calcs the new field
        mass at wb after one time interval's grazing.  Returns 1 if
        constraint violated, 0 otherwise                                        */
{
        double          e1 ;            /* intermediate value */

        if (aux.negdiscr)
                {
                e1=(*wa+aux.beta1/(2*aux.alpha))/aux.lambda1;
                *wb=aux.lambda1*(aux.tlambda1+e1)/(1-aux.tlambda1*e1)
                        -aux.beta1/(2*aux.alpha);
                }
        else
                {
                e1=aux.edelta1*(aux.delta1+aux.beta1+2*aux.alpha* *wa)/
                                        (aux.delta1-aux.beta1-2*aux.alpha* *wa);
                *wb=(aux.delta1*(1-e1)/(1+e1)+aux.beta1)/(-2*aux.alpha);
                }

        /* Check minimum and maximum mass constraints */
        if ((*wb>aux.whigh)||(*wb<aux.wlow)) return 1; else return 0;
}
/* end graze() */
/*====================================================*/
double intake(w)
        double *w;
/*      Calculates the intake achieved by grazing a field
        with initial herbage at w for one time interval */
{
        double          d1 ;            /* useful constant */
        double          in ;            /* the intake */

        if (aux.negdiscr)
```

```
                {
                d1=(*w+aux.beta1/(2*aux.alpha))/aux.lambda1;
                in=aux.incoeff*(aux.beta1*aux.tstep
                                        +2*log(1-d1*aux.tlambda1)
                                        -log(1+aux.tlambda1*aux.tlambda1));
                }
        else
                {
                d1=(aux.delta1+aux.beta1+2*aux.alpha* *w)/
                        (aux.delta1-aux.beta1-2*aux.alpha* *w) ;
                in=aux.incoeff*((aux.delta1+aux.beta1)*aux.tstep
                                +2*log((1+d1*aux.edelta1)/(1+d1)));
                }
        return in ;
}
/* end intake() */
/*===================================================*/
double bound(x)
        struct NODE *x;
/*      bound() calculates an upper bound for the intake from all nodes
        below this one for the recursive search.
        This is done by assuming the top paddock keeps growing even
        though we keep grazing it. */
{
        register        int     i;      /* counter */
        double          maxin;          /* bound below current node */
        double          wmax ;          /* maximum herbage mass field */
        double          intake();       /* intake function */
        double          nextmax;        /* field for wmax for next m periods */

        for (wmax=x->w[0], i=1; i<aux.m; i++)
                if (x->w[i]>wmax) wmax=x->w[i];                 /* find max paddock */

        maxin=x->in;            /* init intake bound */
        i=0;
        while (i<x->pl)
                {
                i++;
                maxin+=intake(&wmax);           /* graze max field */

                /* calc maximum field bound at start of next period */
                if (wmax<aux.whigh)
                        {
                        if (grow(&wmax,&wmax))          /* pretend wmax grows */
                                wmax=aux.whigh;
                        }

                }

        return maxin;  /* bound on possible intake below current node */
}
/* end bound () */
/*===============================================*/
double          countnodes(pleft)
        int pleft;
/*      Counts the number of nodes that lie below a node at level
        pleft.  This only includes nodes that would be visited.  However
        duplicates are all counted. The node at node pleft is also
        included. */
```

```
{
      double        num=1;        /* counter for number of nodes */
      double        this=1;       /* number of nodes at current level */
      double        next;         /* multiplier of branches at this level*/
      register      int    i;     /* counter */

      for (i=aux.p-pleft; i<aux.p-1; i++)
      {
            /* multiplicity at next depth*/
            if (aux.m<aux.p-i) next=aux.m; else next=aux.p-i;
            this*=next;           /* no of nodes at next depth */
            num+=this;            /* add to current total */
      }
      return num;
}
/* end countnodes() */
/*===============================================*/
double        countleaves(pleft)
      int     pleft;
/*    Counts the number of leaves that lie below a node at level
      pleft.  This only includes leaves that would be visited.
      However duplicates are all counted. */
{
      double        this=1;       /* number of nodes at current level */
      double        next;         /* multiplier of branches at this level*/
      register      int    i;     /* counter */

      for (i=aux.p-pleft; i<aux.p-1; i++)
      {
            /* multiplicity at next depth*/
            if (aux.m<aux.p-i) next=aux.m; else next=aux.p-i;
            this*=next;           /* no of nodes at next depth */
      }
      return this;
}
/* end countleaves() */
/*=======================================================*/
void shellsort(v,w,size)
      double        *v ;    /* points to vector of values to be sorted */
      int           *w ;    /* points to list of indices returned */
      int           size ;/* number of items to sort */
/*    Sorts the input vector *v into descending order and puts
      the original positions of the terms of *v into *w.
      *v remains unchanged.  Thanks to Michael Charleston */
{
      register      int    i;
      int           j, k;
      int           gap, tempi ;
      double        tempf ;
      double        tempv[MAXFIELDS] ;

      for (i = 0; i < size; i++) tempv[i] = v[i];
      for (i = 0; i < size; i++) w[i] = i;

      for (gap = size/2; gap > 0; gap /= 2)
      for (i=gap; i < size; i++)
      for (j=i-gap; (j>=0)&&(tempv[j]<tempv[j+gap]); j-=gap)
            {
            k = j+gap;
```

```
            tempf = tempv[j];
            tempv[j] = tempv[k];
            tempv[k] = tempf;
            tempi = w[j];
            w[j] = w[k];
            w[k] = tempi;
            }
}
/* end shellsort() */
/*============================================*/
void evalnode(mother,best)
      struct NODE *mother, *best;
/*    evalnode() is used recursively in the branch and bound search.
      It searches the tree below the mother node, considering which
      daughter nodes to search - those who are good enough to be
      useful in the final k days, and are not duplicates.  The best
      node found so far is stored in best. */
{
      struct NODE daughter;     /* allocate space for node info  */
      register      int    i,j; /* counters */
      int           f,ff;       /* index of the next biggest field */
      int           k,kk;       /* number of branches to follow */
      int sortwi[MAXFIELDS];    /* sorted fields' indices */
      int           toohigh;    /* no of paddocks which grow too high*/
      int           toolow;     /* checks whether paddock may be grazed*/
      double        growf;      /* used to store mass after growth */
      double        wmax;       /* highest pasture mass */
      double        pc;         /* percentage of bestin reached by bound */
      int           pleft;      /* periods left to bottom of tree */
      int           p;          /* total depth of the tree */
      int           m;          /* number of fields */
      void          printnode();

      ++diags.visited;          /* increment count of nodes visited */
      if (mother->feas) return;
      daughter.feas=0;          /* must be feasible to get to here */

      pleft=mother->pl;         /* use this a lot so give it a name */
      p=aux.p;                  /* ditto */
      m=aux.m;                  /* ditto */

      if (DEBUG)
            {
            printf("\n");
            printnode(mother);
            printf("Nodes left = %e\n",
                  diags.nodes-diags.trimmed-diags.visited);
            }

      /* if at bottom of tree , check if it's the best so far */
      /* do this first because we spend a lot of time at the bottom */
      if (pleft==1)
            {
            /* choose top field */
            f=0;
            wmax=mother->w[0];
            for (i=1; i<m; i++)
                  if (wmax<mother->w[i])
                        {
```

```
            f=i;
            wmax=mother->w[i] ;
            }
    daughter.in=mother->in+intake(&wmax) ;
    if (daughter.in > best->in)
        {
        for (i=0; i<m; i++)       /* calc masses */
            if (i==f)
                {
                if (graze(mother->w+i,daughter.w+i))
                    return;
                }
            else
                {
                if ( grow(mother->w+i,daughter.w+i))
                    return;
                }
        /* update best node */
        if (DEBUG) printf("New best leaf node found\n");
        best->in=daughter.in;
        best->feas=0;       /* yes, feasible node found */
        best->pl=0;
        for (i=0; i<m;i++)              /* copy masses */
            best->w[i]=daughter.w[i];
        for (i=0; i<p-1; i++)     /* copy strategy */
            best->s[i]=mother->s[i];
        best->s[p-1]=f+1;
        }
    return ;
    }

/* check whether it is possible for a descendent to be better */
pc=100*bound(mother)/best->in;
if (DEBUG) printf("Bound = %f pc\n",pc);
if (pc<=100)
    {
    /* if (DEBUG) printf("Bound active\n"); */
    diags.trimmed+=countnodes(pleft)-1;
    return ;
    }

/* calc field growths - check for mass constraints */
for (toohigh=0, j=0; j<m; j++)
    {
    toohigh+=grow(mother->w+j,daughter.w+j);
    if (toohigh) ff=j;
    if (toohigh>1) /* of course, can't graze more than one */
        {
        if (DEBUG) printf("Too many get overgrown\n");
        diags.trimmed+=countnodes(pleft)-1;
        return ;
        }
    }

/* copy mother strategy to daughter */
for (i=0; i<p-pleft; i++)
        daughter.s[i]=mother->s[i];

if (toohigh==1) /* only option is to try grazing ff */
```

```
        {
        toolow=graze(mother->w+ff,daughter.w+ff);
        if (toolow)
                {
                if (DEBUG) printf(
                        "Can't graze field which would overgrow\n");
                diags.trimmed+=countnodes(pleft)-1;
                }
        else
                {
                if (DEBUG) printf("Spawn only daughter %d\n",ff+1);
                daughter.in=mother->in+intake(mother->w+ff);
                daughter.s[p-pleft]=ff+1;
                daughter.pl=pleft-1;
                evalnode(&daughter,best);
                }
        return;
        }

/*sort paddocks descending */
shellsort(mother->w,sortwi,m);
if (DEBUG)
        {
        printf("Sorted fields = ");
        for (i=0; i<m; i++) printf("%d ", sortwi[i]+1);
        printf("\n");
        }
/* calc k, max no of paddocks which need to consider */
if (pleft<m) k=pleft; else k=m;
/* remove duplicate paddocks from the list */
for (kk=0, j=1; j<k; j++)
        if (mother->w[sortwi[kk]] - mother->w[sortwi[j]]>aux.wtol)
                {
                kk++;
                sortwi[kk]=sortwi[j]; /* add j if signif different */
                }
        else
                {
                if (DEBUG) printf("Duplicate removed\n");
                diags.trimmed+=countnodes(pleft-1);
                }

/* now consider daughter nodes in order of decreasing intake */
/* nb: there are now no fields that violate growth constraint */
/* and no duplicates */
for (j=0; j<=kk; j++)
{
        f=sortwi[j];        /* take next field to graze*/

        /* check that grazing field f will be valid */
        growf=daughter.w[f];       /* store mass after growing f */
        toolow=graze(mother->w+f,daughter.w+f);

        if (toolow)
                {
                if (DEBUG) printf("Field %d too low to graze\n",f+1);
                diags.trimmed+=countnodes(pleft-1)*(kk-j+1);
                return;      /* none of the others will be feasible */
                }
```

```
                else
                        {
                        /* calc new intake at daughter node */
                        if (DEBUG) printf("Spawn daughter %d\n",f+1);
                        daughter.in=mother->in+intake(mother->w+f);
                        daughter.s[p-pleft]=f+1;
                        daughter.pl=pleft-1;
                        evalnode(&daughter,best);
                        }

                daughter.w[f]=growf; /* restore growth calculated */

        } /* end loop thru daughters */
}
/*end evalnode () */
/*========================================================*/
int     readint(infile)
        FILE *infile;
{
        int     i;

        fscanf(infile,"%d",&i);
        printf("%d\n",i);
        return i;
}
/* end of readint() */
/*========================================================*/
double          readdouble(infile)
        FILE *infile;
{
        double          d;

        fscanf(infile,"%lf",&d);
        printf("%f\n",d);
        return d;
}
/* end of readdouble() */
/*========================================================*/
void    loadparams(par)
        struct INP *par;
/*      This function reads the input values from the file (or keyboard)
into par, a pointer to a structure containing all the input params. */
{
        FILE            *infile;        /* file ptr to file with input params */
        FILE            *fopen();       /* function for opening files */
        int             readint() ;             /* reads an int from file */
        double          readdouble();           /* reads a double from file */
        char            infilename[50];         /* file name for input params */
        double          w1,wm  ;        /* max and min initial pasture masses */
        int             i;              /* counter */
        int             k;

        /*      INPUT FILE FORMAT:
                        m       H                               fields          total area
                        w1      wm                              max & min initial masses
                        p       T                               periods         total time
                        n       r                               animals         grazerate
                        g       we      1/b                     growth params
                        wlow    whigh   wtol                    constraints                     */
```

```
        printf("Enter filename, or 0 for keyboard input: " );
        scanf("%s",infilename);                  /* input infile name */
        infile=fopen(infilename,"r");
        if (!infile) infile=stdin;

        printf("Number of fields = ");
        par->m=readint(infile);

        printf("Total area (ha) = ");
        par->H=readdouble(infile);

        printf("Highest Initial Field Mass (kg/ha) = ");
        w1=readdouble(infile);

        printf("Lowest Initial Field Mass (kg/ha) = ");
        wm=readdouble(infile);

        k=par->m-1;          /* index of mth paddock */
        for (i=0; i<=k; i++)      /* wedge of initial masses */
              par->w0[i]=(w1*(k-i)+wm*i)/k;

        printf("Number of time periods = ");
        par->p=readint(infile);

        printf("Total time (days) = ");
        par->T=readdouble(infile);

        printf("Number of animals = ");
        par->n=readint(infile);

        printf("Marginal grazing rate per animal (ha/an/day) = ");
        par->r=readdouble(infile);

        printf("Maximum pasture growth rate (kg/ha/day) = ");
        par->g=readdouble(infile);

        printf("Pasture mass below which growth ceases (kg/ha) = ");
        par->we=readdouble(infile);

        printf("Ceiling yield (kg/ha) = ");
        par->b=1/readdouble(infile);

        printf("Minimum pasture mass constraint (kg/ha) = ");
        par->wlow=readdouble(infile);

        printf("Maximum pasture mass constraint (kg/ha) = ");
        par->whigh=readdouble(infile);

        printf("Minimum distinguishable difference in mass (kg/ha) = ");
        par->wtol=readdouble(infile);

        fclose(infile);
        printf("Finished reading parameters\n");
}
/* end of loadparams() */
/*=====================================================*/
void   printdiags()
{
```

```
	double		pc ;	/* used to calc percentages */

	printf("Total nodes = %e\n", diags.nodes);
	pc=100*diags.visited/diags.nodes;
	printf("Nodes visited = %e  (%f pc)\n", diags.visited, pc);
	printf("Nodes trimmed = %e\n", diags.trimmed);
}
/* end of printdiags() */
/*======================================================*/
void	printnode(x)
	struct NODE *x;
{
	int		i;
	double		herbage=0;	/* total up residual herbage */
	double		average;	/* avergae animal intake per day */

	if (x->pl=aux.p)
		average=0;
	else
		average=x->in/(aux.n*aux.tstep*(aux.p-x->pl));
	printf("Intake = %7.1f", x->in);
	printf(" (Average = %5.2f kg/an/day)\n",average);
	printf("Periods left = %d\n", x->pl);
	printf("Strategy = \n");
	for (i=0; i<aux.p; i++)
		{
		printf("%2d ", x->s[i]);
		if ((i%10==9)||(i==aux.p-1)) printf("\n");
		}
	if (x->feas) printf("*** INFEASIBLE ***\n");
	printf("Fields = \n");
	for (i=0; i<aux.m; i++)
		{
		printf("%7.1f ", x->w[i]);
		herbage+=x->w[i];
		if ((i%5==4)||(i==aux.m-1)) printf("\n");
		}
	herbage/=aux.m;
	printf("Average herbage = %7.1f kg/ha\n",herbage);
}
/* end of printnode() */
/*======================================================*/
void	createroot(params,root)
	struct INP   *params;
	struct NODE *root;
{
	int	i;

	root->in=0;
	root->pl=params->p;
	for (i=0; i<params->p; i++) root->s[i]=0;
	for (i=0; i<params->m; i++) root->w[i]=params->w0[i] ;
	root->feas=0;			/* no problems */
}
/* end of createroot() */
/*======================================================*/
void	findopt(root,optimal)
	struct NODE *root, *optimal;
{
```

```
        struct NODE temp;          /* temporary root for stepwise search */
        int          i,j;          /* counters */
        int          feasible;     /* is optimal feasible ? */

        /* initialise diags */
        diags.visited=0;
        diags.trimmed=0;
        diags.nodes=countnodes(root->pl);

        /* initialise optimal */
        optimal->in=0;
        optimal->pl=root->pl;
        feasible=0;                /* assume feasible opt exists */
        for (i=0; i<aux.m; i++) optimal->w[i]=root->w[i];
        for (i=0; i<aux.p; i++) optimal->s[i]=0;

        printf("Start search for optimal\n");
        system("date\n");                 /* write start time to screen */

        optimal->feas=1;                  /* assume no optimal in step */
        evalnode(root,optimal);           /* start recursive search */
        if (optimal->feas) printf("Infeasible\n");

        printf("Finish search for optimal\n");
        system("date\n");                 /* write stop time to screen */
        printdiags();                     /* print search diagnostics */

}
/* end of findopt() */
/*=========================================================*/
void    findgreedy(root,greedy)
        struct NODE *root, *greedy;
/*      Finds the strategy and intake from a root node if a greedy
        strategy is used where the top field is grazed each day.*/
{
        int          i ;           /* counter */
        int          f ;           /* field index */
        double       wmax ;        /* herbage in top field */

        /* initialise greedy node */
        greedy->in=0;
        greedy->pl=root->pl;
        greedy->feas=0;            /* assume it's okay */
        for (i=0; i<aux.m; i++) greedy->w[i]=root->w[i];
        for (i=0; i<aux.p; i++) greedy->s[i]=0;

        while ((greedy->pl>0)&&(greedy->feas==0))
               {
               /* choose top field */
               f=0;
               wmax=greedy->w[f];
               for (i=1; i<aux.m; i++)
                      if (wmax<greedy->w[i])
                             {
                             f=i;
                             wmax=greedy->w[f] ;
                             }

               greedy->s[aux.p-greedy->pl]=f+1;       /* store strat */
```

```
                greedy->in+=intake(&wmax) ;             /* increment intake */

                /* grow and graze fields */
                for (i=0; i<aux.m; i++)
                        {
                        if (i==f)
                                {
                                greedy->feas+=graze(greedy->w+i,greedy->w+i);
                                }
                        else
                                {
                                greedy->feas+=grow(greedy->w+i,greedy->w+i);
                                }
                        }

                /* decrement remaining periods */
                greedy->pl--;

                }
}
/* end of findgreedy() */
/*=====================================================*/
void    findcyclic(root,cyclic)
        struct NODE *root, *cyclic;
/*      Finds the strategy and intake from a root node if a cyclic
        strategy is used where the fields are grazed in strict
        rotation starting from the one with most herbage. */
{
        int             i ;             /* counter */
        int             f ;             /* field index */

        /* initialise cyclic node */
        cyclic->in=0;
        cyclic->pl=root->pl;
        cyclic->feas=0;                 /* assume it's okay */
        for (i=0; i<aux.m; i++) cyclic->w[i]=root->w[i];
        for (i=0; i<aux.p; i++) cyclic->s[i]=0;

        /* start at first field in the wedge.  The initial fields are */
        /* assumed to be in descending order to start with anyway */
        f=0;
        while ((cyclic->pl>0)&&(cyclic->feas==0))
                {
                cyclic->s[aux.p-cyclic->pl]=f+1;        /* store strat */
                cyclic->in+=intake(cyclic->w+f) ;

                /* grow and graze fields */
                for (i=0; i<aux.m; i++)
                        {
                        if (i==f)
                                {
                                cyclic->feas+=graze(cyclic->w+i,cyclic->w+i);
                                }
                        else
                                {
                                cyclic->feas+=grow(cyclic->w+i,cyclic->w+i);
                                }
                        }
```

```
             /* decrement remaining periods, choose next field */
             cyclic->pl--;
             f++;
             if (f>=aux.m) f=0;

             }
}
/* end of findcyclic() */
/*=======================================================*/
void  findcontinuous(params,cts)
      struct INP *params;
      struct NODE *cts;
{
      struct INP fake;    /* storage for bogus-psuedo-quasi-params */
      double      wsum;        /* sum of the herbage masses */
      double      wave;        /* avergae of herbage masses */
      double      wafter;      /* herbage after cts grazing */
      int         i;           /* counter */

      /* these parameters stay unchanged */
      fake.n=params->n;
      fake.wlow=params->wlow;
      fake.whigh=params->whigh;
      fake.wtol=params->wtol;
      fake.H=params->H;
      fake.T=params->T;
      fake.r=params->r;
      fake.g=params->g;
      fake.we=params->we;
      fake.b=params->b;

      /* these ones change */
      fake.p=1;                    /* 1 time period */
      fake.m=1;                    /* one paddock */
      for (wsum=0, i=0; i<params->m; i++) wsum+=params->w0[i];
      wave=wsum/params->m;         /* average pasture mass */
      for (i=0; i<params->m; i++) fake.w0[i]=wave;

      setaux(&fake);               /* set fake params */

      /* calc results of continuous grazing */
      cts->feas=graze(&wave,&wafter);
      cts->in=intake(&wave);
      cts->pl=0;
      for (i=0; i<params->p; i++) cts->s[i]=0;      /* zero strategy */
      for (i=0; i<params->m; i++) cts->w[i]=wafter;

      setaux(params);              /* reset real problem params */
}
/* end of findcontinuous() */
/*=======================================================*/
/* main program: */
main()
{
      struct INP   params ;        /* structure holding search params */
      struct NODE best ;           /* optimal leaf node */
      struct NODE root ;           /* root node - initial conditions */
      struct NODE greedy ;         /* greedy strategy leaf node */
      struct NODE cyclic ;         /* cyclic strategy leaf node */
```

```
        struct NODE continuous; /* intake from continuous grazing */

        loadparams(&params);        /* read params from file of kbd */
        setaux(&params);            /* calcs aux vars from params */

        printf("\nInitial conditions (root node) =\n");
        createroot(&params,&root);        /* init root node */
        printnode(&root);

        printf("\nContinuous grazing =\n");
        findcontinuous(&params, &continuous);
        printnode(&continuous);

        printf("\nCyclic strategy =\n");
        findcyclic(&root,&cyclic);        /* find cyclic RG strategy */
        printnode(&cyclic);

        printf("\nGreedy strategy =\n");
        findgreedy(&root,&greedy);        /* find greedy strategy */
        printnode(&greedy);

        printf("\nOptimal strategy =\n");
        findopt(&root,&best);       /* do search for optimal strat */
        printnode(&best);

}
/* end of main() */
/*===============================================*/
```

Bibliography

[1] Baars, J.A., Wright, A. and Wilson, D.A. (1976) Use of a simulation model for scheduling irrigations on pasture. In Proceedings of the Soil and Plant Water Symposium, Palmerston North, May 1976, 96–102. New Zealand Department of Scientific and Industrial Research, Wellington.

[2] Barlow, N.D. (1987) Pastures, pests, and productivity: simple grazing models with two herbivores. New Zealand Journal of Ecology, 10, 43–55.

[3] Bellman, R. and Cooke, K.L. (1963) Differential-difference equations. Academic, New York, pp462.

[4] Bircham, J.S. (1981) Herbage growth and utilisation under continuous stocking management. Ph.D. thesis, University of Edinburgh.

[5] Bircham, J.S. and Hodgson, J. (1983) The influence of sward condition on rates of herbage growth and senescence in mixed swards under continuous stocking management. Grass and Forage Science, 38, 323–331.

[6] Bircham, J.S. (1984) Pattern of herbage growth during lactation and level of herbage mass at lambing: their significance to animal production. Proceedings of the New Zealand Grassland Association, 45, 177–183.

[7] Blackburn, H.D. and Kothmann, M.M. (1989) A forage dynamics model for use in range or pasture environments. Grass and Forage Science, 44, 283–294.

[8] Booysen, P.deV., Klug, J.R. and York, B.S. (1974) Number of camps for rotational grazing of veld. Proceedings of the Grassland Society of South Africa, 9, 145–148.

[9] Brougham, R.W. (1955) A study in rate of pasture growth. Australian Journal of Agricultural Research, 6, 804–812.

[10] Brougham, R.W. (1956) Effect of intensity of defoliation on regrowth of pasture. Australian Journal of Agricultural Research, 7, 377–387.

[11] Brougham, R.W. (1959) The effects of season and weather on the growth rate of a ryegrass and clover pasture. New Zealand Journal of Agricultural Research, 2, 283–296.

[12] Bryant, A.M. (1980) Effect of herbage allowance on dairy cow performance. Proceedings of the New Zealand Society of Animal Production, 40, 50–58.

[13] Bryant, A.M. and Cook, M.A.S. (1980) A comparison of three systems of wintering dairy cattle. Proceedings of the Ruakura Farmers Conference, Hamilton, New Zealand, 32, 181–188.

[14] Bryant, A.M. (1982) Developments in dairy cow feeding and pasture management. Proceedings of the Ruakura Farmers Conference, Hamilton, New Zealand, 34, 75–81.

[15] Bryant, A.M. (1984) Feed and management strategies at Ruakura. Proceedings of the Ruakura Farmers Conference, Hamilton, New Zealand, 36, 20–24.

[16] Bryant, A.M. and L'Huillier, P.J. (1986) Better use of pastures. Proceedings of the Ruakura Farmers Conference, Hamilton, New Zealand, 38, 43–51.

[17] Bryant, A.M. and Sheath, G.W. (1987) The importance of grazing management to animal production in New Zealand. Proceedings of the 4th AAAP Animal Production Congress, Asian-Australian Association of Animal Production Societies, Hamilton, New Zealand, 13–17.

[18] Bryant, A.M. (1990a) Optimum stocking and feed management practices. Proceedings of the Ruakura Farmers Conference, Hamilton, New Zealand, 42, 55–59.

[19] Bryant, A.M. (1990b) Grazing management research at Ruakura. Unpublished paper presented to the Canterbury Farmers Conference, July 1990, Ashburton, New Zealand.

[20] Buckmaster, D.R. and Parker, W.J. (in press) A computer model for determining when to commence spring grazing. Proceedings of the XVII International Grassland Congress, Palmerston North, New Zealand, 8–21 February 1993.

[21] Butler, B.M., Chu, A.C.P., Matthews, P.N.P. and Korte, C.J. (1985) Effects of spring grazing management on herbage mass and sward characteristics in a ryegrass/white clover pasture. Proceedings of the XV International Grassland Congress, Kyoto, Japan, 1182–1184.

[22] Caughley, G. and Lawton, J.H. (1981) Plant-herbivore systems. In May, R.M. (ed) Theoretical Ecology: principles and applications. Blackwell, Oxford, England, Second edition, 132–166.

[23] Caughley, G. (1982) Vegetation complexity and the dynamics of modelled grazing systems. Oecologia, 54, 309–312.

[24] Chapman, D.F., Clark D.A., Land, C.A. and Dymock, N. (1984) Leaf and tiller or stolon death of Lolium Perenne, Agrostis spp. and Trifolium repens in set stocked and rotationally grazed hill pastures. New Zealand Journal of Agricultural Research, 27, 303–312.

[25] Chen, J.L. (1986) Optimal cutting frequency and intervals derived from Johnson and Thornley's model of grass growth. Agricultural Systems, 22, 305–314.

[26] Chen, J.L. and Wang, Q. (1988) A theoretical analysis of the potential productivity of ryegrass under grazing. Journal of Theoretical Biology, 133, 371–383.

[27] Christian, K.R. (1981) Simulation of grazing systems. In Morley, F.H.W. (ed) Grazing Animals. Elsevier, Amsterdam, New York, 361–377.

[28] Clark, D.A., Lambert, M.G. and Grant, D.A. (1986) Influence of fertiliser and grazing management on North Island moist hill country: 5. Animal production. New Zealand Journal of Agricultural Research, 29, 407–420.

[29] Davies, A. (1988) The regrowth of grass swards. In Jones, M.B. and Lazenby, A. (eds) The Grass Crop. Chapman and Hall, London, 85–127.

[30] Florez, A., Bryant, F.C. and Schlundt, A.F. (1986) Grazing strategies and sheep production in the Andes of Peru. Proceedings of the Second International Rangeland Congress, 236–237.

[31] Gammon, D.M. (1978) A review of experiments comparing systems of grazing management on natural pastures. Proceedings of the Grassland Society of South Africa, 13, 75–82.

[32] Gill, N.T. and Vear, K.C. (1958) Agricultural Botany. Duckworth, London, pp636.

[33] Goh, B.S., Leitmann, G. and Vincent, T.L. (1974) Optimal control of a prey-predator system. Mathematical Biosciences, 19, 263–286.

[34] Grant, S.A., Barthram, G.T., Torvell, L., King, J. and Elston D.A. (1988) Comparison of herbage production under continuous stocking and intermittent grazing. Grass and Forage Science, 43, 29–39.

[35] Gross, L.J. (1988) A stochastic model of grass growth under grazing. In Ricciardi, L.M. (ed) Biomathematics and Related Computational Problems. Kluwer Academic, Dordrecht, Netherlands, 177–185.

[36] Harris, W. (1983) Simulation by cutting of stocking rate and rotational and continuous management: 1. Herbage removal, standing herbage mass, and net herbage accumulation rate. New Zealand Journal of Agricultural Research, 26, 15–27.

[37] Heady, H.F. (1961) Continuous vs specialised grazing systems: a review and application to the California annual type. Journal of Range Management, 14, 182–193.

[38] Hendy, S.C. (1992) Strategies for optimising wool growth. Proceedings of the Operational Research Society of New Zealand, Christchurch, New Zealand, 28, 47–52.

[39] Hertzler, G. (1991) Dynamic decisions under risk: application of Ito stochastic control in agriculture. American Journal of Agricultural Economics, 73, 1126–1137.

[40] Hirata, M., Sugimoto, Y. and Ueno, M. (1991) Use of a mathematical model to evaluate the effects of dung from grazing animals on pasture production and utilization and animal production. Journal of the Japanese Society of Grassland Science, 37(3), 303–323.

[41] Hodgson, J. (1985a) The control of herbage intake in the grazing ruminant. Proceedings of the Nutrition Society, 44, 339–346.

[42] Hodgson, J. (1985b) The significance of sward characteristics in the management of temperate sown pastures. Proceedings of the XV International Grassland Congress, Kyoto, 63–67.

[43] Huffaker, R.G, Wilen, J.E. and Gardner, B.D. (1989) Multiple use benefits on public rangelands: an incentive based fee system. American Journal of Agricultural Economics, 71, 670–678.

[44] Jagusch, K.T., Rattray, P.V. and MacLean, K.S. (1978) The dynamics of pasture production under sheep. Proceedings of the New Zealand Society of Animal Production, 38, 129–138.

[45] Johnson, I.R. and Thornley, J.H.M. (1983) Vegetative crop growth model incorporating leaf area expansion and senescence, and applied to grass. Plant, Cell and Environment, 6, 721–729.

[46] Johnson, I.R. and Parsons, A.J. (1985a) A theoretical analysis of grass growth under grazing. Journal of Theoretical Biology, 112, 345–367.

[47] Johnson, I.R. and Parsons, A.J. (1985b) Use of a model to analyse the effects of continuous grazing managements on seasonal patterns of grass production. Grass and Forage Science, 40, 449–458.

[48] 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.

[49] Langer, R.H.M. (1990) Growth of grasses and clovers. In Langer, R.H.M. (ed) Pastures and Pasture Plants. A.H. & A.W. Reed, Wellington, New Zealand, 41–63.

[50] McCall, D.G., Townsley, R.J., Bircham, J.S. and Sheath, G.W. (1986) The interdependence of animal intake, pre- and post grazing pasture mass and stocking density. Proceedings of the New Zealand Grassland Association, 47, 255–261.

[51] McCall, D.G. and Sheath, G.W. (in press) Development of intensive grassland systems: from science to practice. Proceedings of the XVII International Grassland Congress, Palmerston North.

[52] McMeekan, C.P. (1956) Grazing management and animal production. Proceedings of the VII International Grassland Congress, Palmerston North, New Zealand,146–156.

[53] McMeekan, C.P. (1960) Grazing management. Proceedings of the Eighth International Grassland Congress (Reading), 21–26.

[54] McMeekan, C.P. and Walshe, M.J. (1963) The interrelationships of grazing method and stocking rate in the efficiency of pasture utilisation by dairy cattle. Journal of Agricultural Science, 61, 147–163.

[55] May, R.M. (1981 ed) Theoretical ecology: principles and practices. Blackwell, Oxford, England, Second edition, pp489.

[56] Milligan, K.E., Brookes, I.M, and Thompson, K.F. (1987) Feed planning on pasture. In Nicol, A.M (ed) Livestock Feeding on Pasture. Occasional Publication no. 10 of the New Zealand Society of Animal Production, Ruakura, Hamilton, New Zealand, 75–88.

[57] Morley, F.H.W. (1968) Pasture growth curves and grazing management. Australian Journal of Experimental Agriculture and Animal Husbandry, 8, 40–45.

[58] Morley, F.H.W., Bennett, D. and McKinney, G.T. (1969) The effect of intensity of rotational grazing with breeding ewes on phalaris-subterranean clover pastures. Australian Journal of Experimental Agriculture and Animal Husbandry, 9, 74–84.

[59] Morley, F.H.W. (1981 ed) Grazing Animals. Elsevier, Amsterdam, New York, pp411.

[60] Morley, F.H.W. (1981) Management of grazing systems. In Morley, F.H.W. (ed) Grazing Animals. Elsevier, Amsterdam, New York, 379–400.

[61] Noodén, L.D. (1988) The phenomena of senescence and aging. In Noodén, L.D. and Leopold, A.C. (eds) Senescence and Aging in Plants. Academic, San Diego, USA, 1–50.

[62] Noy-Meir, I. (1975) Stability of grazing systems: an application of predator-prey graphs. Journal of Ecology, 63, 459–481.

[63] Noy-Meir, I. (1976) Rotational grazing in a continuously growing pasture: a simple model. Agricultural Systems, 1, 87–112.

[64] Noy-Meir, I. (1978a) Stability in simple grazing models: effects of explicit functions. Journal of Theoretical Biology, 71, 347–380.

[65] Noy-Meir, I. (1978b) Grazing and production in seasonal pastures: analysis of a simple model. Journal of Applied Ecology, 15, 809–835.

[66] Parsons, A.J. and Johnson, I.R. (1986) The physiology of grass growth under grazing. In Frame, J. (ed) Grazing. British Grassland Society, Maidenhead, Berkshire, England, 3–13.

[67] Parsons, A.J. and Penning, P.D. (1988) The effect of the duration of regrowth on photosynthesis, leaf death and the average rate of growth in a rotationally grazed sward. Grass and Forage Science, 43, 15–27.

[68] Parsons, A.J., Johnson, I.R. and Harvey, A. (1988) Use of a model to optimise the interaction between frequency and severity of intermittent defoliation and to provide a fundamental comparison of the continuous and intermittent defoliation of grass. Grass and Forage Science, 43, 49–59.

[69] Parsons, A.J. (1988) The effects of season and management on the growth of grass swards. In Jones, M.B. and Lazenby, A. (eds) The Grass Crop. Chapman and Hall, London, 129–177.

[70] Pleasants, A.B., Wake, G.C. and Rae, A.L. (in press a) The allometric hypothesis when the size variable is random: issue of importance in the study of carcass composition. Submitted to Biometrics.

[71] Pleasants, A.B., McCall, D.G. and Sheath, G.W. (in press b) The management of pastoral grazing systems under biological and environmental variation. Submitted to Agricultural Systems.

[72] Poppi, D.P., Hughes, T.P. and L'Huillier, P.J. (1987) Intake of pasture by grazing ruminants. In Nicol, A.M. (ed) Livestock Feeding on Pasture. Occasional Publication no. 10 of the New Zealand Society of Animal Production, Ruakura, Hamilton, New Zealand, 55–63.

[73] Robson, M.J., Ryle, G.J.A. and Woledge, J. (1988) The grass plant—its form and function. In Jones, M.B. and Lazenby, A. (eds) The Grass Crop. Chapman and Hall, London, 25–83.

[74] Robson, M.J., Parsons, A.J. and Williams, T.E. (1989) Herbage production: grasses and legumes. In Holmes, W. (ed) Grass: its production and utilization. Blackwell, Oxford, England, Second edition, 7–88.

[75] Rook, A.J. and Penning, P.D. (1991) Stochastic models of grazing behaviour in sheep. Applied Animal Behaviour Science, 32, 167–177.

[76] Sharrow, S.H. (1983) Rotational vs continuous grazing affects animal performance on annual grass-subclover pasture. Journal of Range Management, 36(5), 593–595.

[77] Sheath, G.W. and Rattray, P.V. (1985) Influence of pasture quantity and quality on intake and production of sheep. Proceedings of the XV International Grassland Congress, Kyoto, 1131–1133.

[78] Sheath, G.W., Hay, R.J.M. and Giles, K.H. (1987) Managing Pastures for Grazed Animals. In Nicol, A.M. (ed) Livestock Feeding on Pasture. Occasional Publication no. 10 of the New Zealand Society of Animal Production, Ruakura, Hamilton, New Zealand, 65–74.

[79] Shiyomi, M., Takahashi, S., Akiyama, T. and Hakamata, T. (1983) A system model for short and long term prediction of grazing pasture productivity. Bulletin of the [Japanese] National Grassland Research Institute, 26, 17–29.

[80] Sibbald, A.R. and Maxwell, T.J. (1990) Contrasting approaches to systems research for sheep production in the hill and uplands of the United Kingdom. Proceedings of a Livestock Systems Symposium, Toulouse, France, 7 July 1990, Commission of the European Communities.

[81] Smeaton, D.C. and Rattray, P.V. (1984) Winter-spring nutrition and management effects on ewe and lamb performance. Proceedings of the New Zealand Grassland Association, 45, 190–198.

[82] Snaydon, R.W. (1981) The ecology of grazed pastures. In Morley, F.H.W. (ed) Grazing Animals. Elsevier, Amsterdam, New York, 13–31.

[83] Spedding, C.R.W. (1971) Grassland ecology. Clarendon, Oxford, pp221.

[84] Stocker, M. and Walters, C.J. (1984) Dynamics of a vegetation-ungulate system and its optimal exploitation. Ecological Modelling, 25, 151–165.

[85] Thornley, J.H.M. (1990) Formulation of the logistic growth equation and its application to leaf area growth. Annals of Botany, 66, 309–311.

[86] Waghorn, G.C. and Barry, T.N. (1987) Pasture as a nutrient source. In Nicol, A.M. (ed) Livestock Feeding on Pasture. Occasional Publication no. 10 of the New Zealand Society of Animal Production, Ruakura, Hamilton, New Zealand, 21–37.

[87] Walker, B.H., Ludwig, D., Holling, C.S. and Peterman, R.M. (1981) Stability of semi-arid savanna grazing systems. Journal of Ecology, 69, 473–498.

[88] Westoby, M., Walker, B. and Noy-Meir, I. (1989a) Opportunistic management for rangelands not at equilibrium. Journal of Range Management, 42(4), 266–274.

[89] Westoby, M., Walker, B. and Noy-Meir, I. (1989b) Range management on the basis of a model which does not seek to establish equilibrium. Journal of Arid Environments, 17, 235–239.

[90] Wheeler, J. (1962) Experimentation in grazing management. Herbage Abstracts, 32, 1–7.

[91] White, D.H., Bowman, P.J., Morley, F.H.W., McManus, W.R. and Filan, S.J. (1983) A simulation model of a breeding ewe flock. Agricultural Systems, 10, 149–89.

[92] Woodward, S.J.R., Wake, G.C., Pleasants, A.B. and McCall, D.G. (1993) A simple model for optimizing rotational grazing. Agricultural Systems, 41, 123–155.

[93] Woodward, S.J.R., Wake, G.C., McCall, D.G. and Pleasants, A.B. (in press a) Use of a simple model of continuous and rotational grazing to compare herbage consumption. Proceedings of the XVII International Grassland Congress, Palmerston North, New Zealand, 8–21 February 1993.

[94] Woodward, S.J.R., Wake, G.C. and McCall, D.G. (in press b) The discrete-time multi-paddock grazing problem. Submitted to Agricultural Systems.

[95] Woodward, S.J.R. and Wake, G.C. (in press) A differential-delay model of pasture accumulation and loss in controlled grazing systems. Mathematical Biosciences.

[96] Workman, J.P. and Fowler, J.M. (1986) Optimum stocking rate—biology vs economics. Proceedings of the Second International Rangeland Congress, 101–102.

[97] Wright, A. and Baars, J.A. (1976) A simulation of a grazing model with particular reference to soil-plant-climate relationships. Symposium on Meteorology and Food Production, New Zealand Meteorological Service, Wellington, 1975, 183–196.

[98] Wright, D.F. and Pringle, R.M. (1983) Stocking rate effects in dairying. Proceedings of the New Zealand Society of Animal Production, 43, 97–100.