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# **The Implications of Climate Change on Forage — Based Livestock Systems in Scotland**

by

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**SAC Auchincruive**

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## **ABSTRACT**

The thesis examined the effects of climatic change on livestock production within Scotland. In order to achieve this, a systems model of the dairy, beef and sheep enterprises was developed. The forage component describes the processes of photosynthesis, respiration and partitioning in grass and grass – white clover based systems, and the effect of temperature and CO<sub>2</sub> concentrations on these processes. The effects of water and nutrient stress on crop development are also incorporated into the sub-model. In the grass – white clover sward, the sub-model permits the sward to have different proportions of grass and white clover at each layer through the sward. The description of grazing by the livestock links the forage production sub-model to the sub-models describing the allocation of energy obtained from the grazed swards and concentrate feeding within the dairy cow, beef steer, and ewe and lambs.

The assessment of the effect of climate change on livestock production within Scotland requires an understanding of the linkages between climate and livestock production. Therefore, in order to predict the effect of changing the climate on animal production requires the development of a systems model, which describes the linkages between climate, forage and livestock production. In addition, the development of a systems model permits the effects to be assessed across a wide range of sites and a number of possible changes in climate. Consequently, the effects of climate change on livestock production were assessed by running the

model at five locations across Scotland, namely; Auchincruive, Blyth Bridge, Craibstone, Drummond Castle and Wick. The changes in climate that were assessed were increases in temperature of +1°C, +2°C and +3°C, changes in rainfall pattern and elevation of the ambient concentration of CO<sub>2</sub> from 350 ppmv to 520 ppmv.

Climatic change primarily affects livestock production through its effects on forage production. Under climatic change, the model predicted that the length of the growing and grazing season will increase with the extensions occurring at both ends of the season. Relative to current climatic conditions elevated CO<sub>2</sub> concentrations coupled with the associated changes in climate resulted in an enhancement in harvestable dry-matter yield that ranged from 20% to nearly 60% and increases in the percentage of white clover in the harvestable material by up to 126%. Equally, the model has shown that livestock production is also enhanced under climate change. Accordingly, milk production, and the daily gain in liveweight of beef steers and lambs was simulated to increase by 3—13%, 1—12% and 4—28% respectively. The larger increases tended to occur on grass – white clover swards. On the other hand, the harvestable dry-matter yield from grass swards was reduced with elevated temperatures, while the yield obtained from grass – white clover swards tended to increase marginally with temperature at elevated ambient CO<sub>2</sub> concentrations.

In general, global warming is predicted to increase forage and livestock production within Scotland. However, the location of the site is also important in determining the effect of climate change as the magnitude and, in some cases, the directions of the changes varied between sites. The effects of climate change were also

dependent on the actual level of changes in temperature. In addition, there were interactions between CO<sub>2</sub> concentration and both temperature and rainfall, as well as interactions between temperature and rainfall. Although the three enterprises showed similar trends in their response to climate change, there were differences in the magnitude of the response as well as differences in the factors that resulted in significant changes. There were also differences in the response of the grazed and the ungrazed swards. This underlines the complexity of the interactions and the difficulty of extrapolating the results to other locations and to other levels of climatic conditions. The advantage of developing a model is that all these complex interactions can be captured and potentially the site – specific consequences of climate change on forage and livestock production predicted.

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# CHAPTER 1

## INTRODUCTION

### **1.1 Introduction**

This chapter specifically examines the background, the aims and objectives of the thesis under the following sections:

1. climate forcing;
2. predicted climate change;
3. effects of carbon dioxide and climate change on crop productivity;
4. the impact of climate change on agriculture;
5. the implications of climate change for forage and livestock production;
6. the role of modelling; and finally
7. the aims of the study.

### **1.2 Climate Forcing**

Modification of the radiation balance of the earth, referred to as 'climate forcing', can be due either to natural or anthropogenic factors. Cloud, water vapour, ice and snow cover, as well as climate forcing, affect the meteorological system and determine how the climate changes. Natural climate forcing is the result of changes in solar radiation due to changes in the orbit of the earth, and natural aerosols in the atmosphere. These include particles of sea salt, smoke, minerals and volcanic dust. The anthropogenic factors that are influencing climate change are man-made tropospheric aerosols and increasing concentrations of the greenhouse gases. These gases include carbon dioxide (CO<sub>2</sub>), methane (CH<sub>4</sub>), nitrous oxide (N<sub>2</sub>O), ozone (O<sub>3</sub>) and

chlorofluorocarbons (CFCs), and they absorb the infra-red radiation. Industrialisation and urban pollution have increased both the anthropogenic factors. Mechanised agriculture has also increased the aerosols in the atmosphere.

The changes in the solar radiation received by the earth vary on a time-scale ranging from ten years to hundreds of thousands of years. Three orbital effects have been identified. First, there is the shape of the earth's orbit that has a cyclical period of 95000 years and influences the total radiation intercepted by the earth. The second, which modifies the summer – winter contrast is the axial tilt, and this has a cycle of 41000 years. The final orbital effect is due to the axial path wobble which results in a shift in the timing when the earth is closest to the sun. This has a 2100-year cycle, and it determines the relative warmth of the summer and winter in the respective hemispheres. Sunspots result in an increased emission of solar radiation, especially if they are located near the equator of the sun. The maximum number of sunspots occurs on an eleven-year cycle.

The aerosols that occur in the stratosphere are mainly due to volcanic eruptions (Hansen and Lacis, 1990), and these particles can exist in the atmosphere for periods of one to three years. These particles in the stratosphere obstruct the sunlight from reaching the surface of the earth. The effect of a large volcanic eruption such as El Chichón in March 1982 could, during the following decade, result in a forcing effect on global temperature of approximately one third of that exerted by the greenhouse gases (Barry and Chorley, 1992). However, these particles in the atmosphere backscatter the short-wave radiation and thus increase the surface albedo and cause cooling, whereas the greenhouse gases would increase global temperature. The

other natural aerosols and the man-made aerosols are in the troposphere. These aerosols are likely to be washed out of the atmosphere by precipitation or fall out by dry deposition within a few weeks (Gates, 1993). In contrast, urban pollutants tend to absorb infra-red radiation warming the atmosphere and reduce the solar radiation reaching the surface of the earth (Barry and Chorley, 1992). In most circumstances the aerosols have a cooling effect on the climate (Hansen and Lacis, 1990).

The greenhouse gases are transparent to incoming radiation, but they affect the atmosphere by absorbing the outgoing infra-red radiation. The overall result is to increase the temperature of the atmosphere. Without the greenhouse effect the earth would be approximately 33°C colder than it is at present and life as we know it would not exist (Schneider, 1990). Prior to the industrial revolution, the concentration of carbon dioxide in the earth's atmosphere was  $275 \pm 10$  parts per million by volume (ppmv) (Neftel, Moor, Oescheger, and Stuafter, 1985). This had increased to 353 ppmv by 1990 (Intergovernmental Panel on Climate Change (IPCC), 1990) and 358 ppmv by 1994 (IPCC, 1996). Thus, in recent years the rate of increase is 1.5 ppmv per year (IPCC, 1996). Table 1-1 shows the pre-industrial and the present concentrations of some of the greenhouse gases as well their annual rates of increase. During the period 1850 to 1989, anthropogenic greenhouse forcing has been equivalent to a 1% increase in solar radiation received by the earth, with approximately 57% of the increase occurring since 1958 (Hansen and Lacis, 1990). They calculated the greenhouse forcing for the periods 1850 to 1957 and 1958 to 1989 as  $0.87 \text{ Wm}^{-2}$  and  $1.17 \text{ Wm}^{-2}$ , and the contribution that each gas has made is shown in Figure 1-1. The Global Warming Potential (GWP) is an index of the relative

contribution of the emissions of the different greenhouse gases to the radiative forcing of the atmosphere over a given time period (Hammitt, Jain, Adams and Wuebbles, 1996). This is typically expressed as the radiative forcing due to the instantaneous release of 1 kg of a trace gas in a constant atmosphere relative to the effects of releasing 1 kg of CO<sub>2</sub>. The net GWP is composed of the direct warming effects and the indirect cooling effects. The GWP and the lifetime of some of the greenhouse gases is shown in Table 1-2 (IPCC, 1996). Evidently the GWP of the hydrofluorocarbons and the fluorocarbons (see IPCC 1996) is substantial.

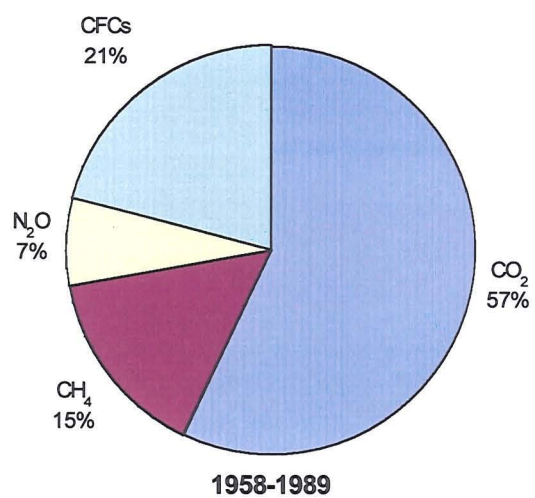
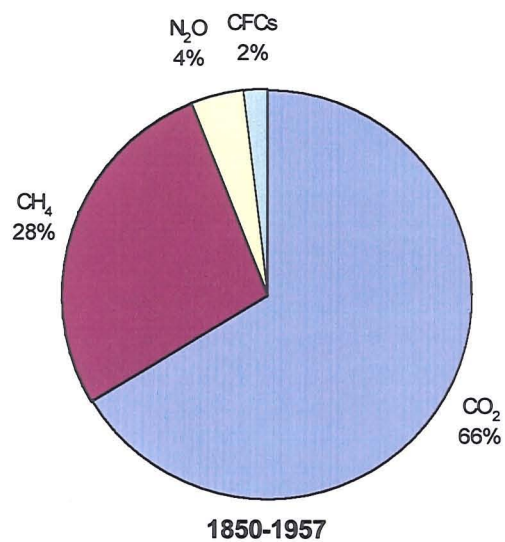
*Table 1-1 The concentration of the greenhouse gases and their contribution to global warming in 1994*

Gas	Pre-Industrial Concentration (ppmv)	Current Concentration (ppmv)	Increase per year (%)
CO <sub>2</sub>	~280	358	0.4
CH <sub>4</sub>	~0.70	1.72	0.6
N <sub>2</sub> O <sup>1</sup>	~275*10 <sup>-3</sup>	312*10 <sup>-3</sup>	0.2
CFC—11 <sup>1</sup>	0	0.268*10 <sup>-3</sup>	0
HCFC—22 <sup>2</sup>	0	0.110*10 <sup>-3</sup>	5

Note 1 Estimated from 1992—1993 data

2 A CFC substitute

Source IPCC (1996)



*Figure 1-1 The contributions that greenhouse gases have made to radiative forcing for the periods 1850—1957 and 1958—1989.*

**Table 1-2**    *The Global Warming Potential and the lifetime of some of the greenhouse gases*

Gas	Lifetime	GWP Direct Effects Index for Time Horizons of		
	years	20 years	100 years	500 years
CO <sub>2</sub>	variable	1	1	1
CH <sub>4</sub>	12±3	56	21	6.5
N <sub>2</sub> O	120	280	310	170
HFC—23	264	9,100	11,700	9,800
HFC—32	5.6	2,100	650	200
HFC—41	3.7	490	150	45
HFC—125	32.6	4,600	2,800	920
HFC—134	10.6	2,900	1,000	310
Sulphur hexafluoride	3,200	16,300	23,900	34,900
Perfluoromethane	50,000	4,400	6,500	10,000
Perfluoroethane	10,000	6,200	9,200	14,000
Perfluoropropane	2,600	4,800	7,000	10,100
Perfluorobutane	2,600	4,800	7,000	10,100

Source IPCC (1996)

### **1.3 Predicted Climate Change**

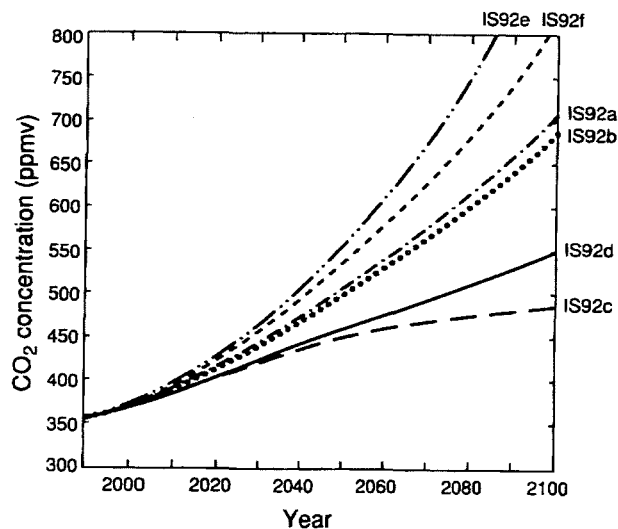
The IPCC (1992) reported that over the last 100 to 130 years the mean global air temperature had increased by  $0.45 \pm 0.15^{\circ}\text{C}$ . However, during the last 40 years the mean global temperature has increased by about  $0.2^{\circ}\text{C}$  to  $0.3^{\circ}\text{C}$  (IPCC, 1996). With the increases in the anthropogenic greenhouse gases there will be a concomitant change in climate. During the 1980s three General Circulation Models (GCMs), namely GISS (Goddard Institute for Space Studies), GFDL (Geophysical Fluid Dynamics Laboratory) and UKMO (United Kingdom Meteorological Office), were developed which predicted the climatic conditions under an instantaneous doubling of the atmospheric  $\text{CO}_2$  concentration (see Table 1-3). These equilibrium GCMs contain no information about when the future climate will be realised. Transient GCMs have now been developed which model the atmospheric  $\text{CO}_2$  as increasing gradually over time.

*Table 1-3 The climate change scenarios predicted by the GCMs under doubled concentrations of atmospheric  $\text{CO}_2$*

GCM	Year <sup>1</sup>	CO <sub>2</sub> (ppmv)	Change in average global	
			Temperature (°C)	Precipitation (%)
GISS	1982	630	4.2	11
GFDL	1988	600	4.0	8
UKMO	1986	640	5.2	15

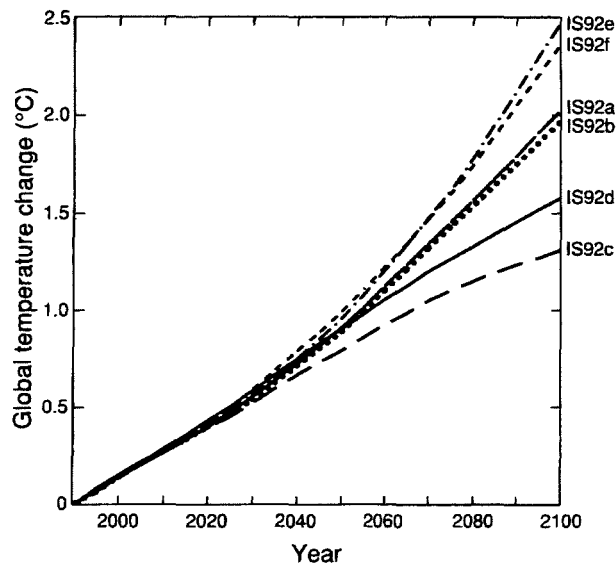
Note <sup>1</sup> Year when calculated

The IPCC (1992) developed six scenarios (IS92a to IS92f) for the predicted emissions of the greenhouse gases to the year 2100. The scenarios differ in terms of population growth, economic growth, energy supplies, CFC emissions and other factors that may affect the emissions of the greenhouse gases. The CO<sub>2</sub> concentrations for the IPCC scenarios and the associated best guess changes in the global mean temperatures for 2050 and 2100 are shown in Figure 1-2 and Figure 1-3 respectively. The upwelling-diffusion energy-balance model was used to calculate the future temperatures (Wigley and Raper, 1990). However, depending on the sensitivity of the climate to enhanced CO<sub>2</sub> levels, the change in global mean temperature by the year 2100 for the full set of IS92 scenarios range from 0.9°C to 3.5°C (IPCC, 1996).



Source IPCC (1996)

*Figure 1-2 The atmospheric CO<sub>2</sub> concentrations for the IS92 scenarios*



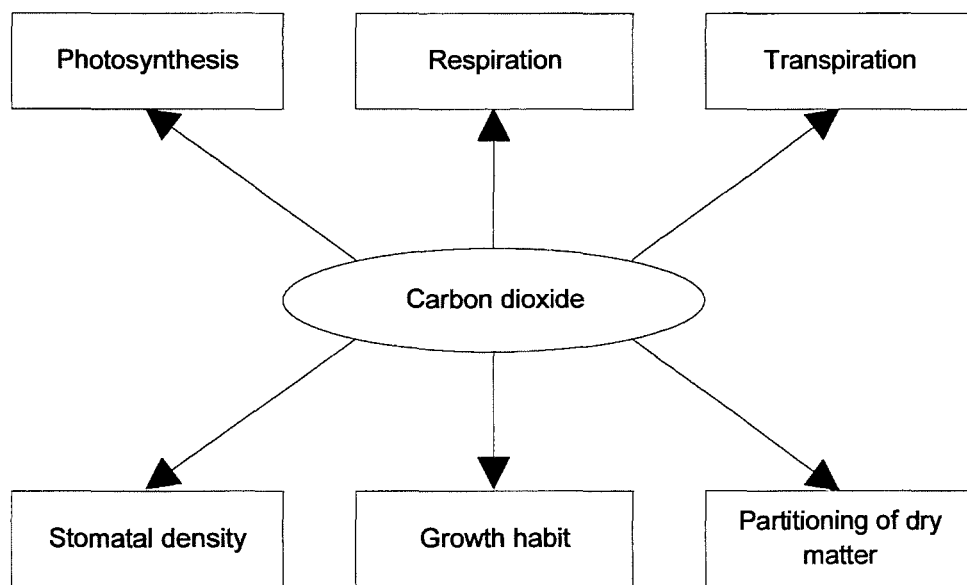
Source IPCC (1996)

*Figure 1-3 The projected global mean surface temperature changes for the IS92 scenarios*

These scenarios are not predictions of future emission levels but are illustrative of a wide range of feasible assumptions, and thus the IPCC Working Group I does not favour any one particular scenario. However, the IPCC (1996) is uncertain regarding its predictions for the timing, magnitude and regional pattern of climate change. The temperature increase in the northern hemisphere predicted by the GCMs will be greater than in the southern (Viner, Hulme and Raper, 1995). Accordingly, there is considerable uncertainty regarding the effects that climate change will have on agriculture at a regional level (Parry and Carter, 1988; Parry, Carter, and Porter 1989; Parry, 1990).

## **1.4 The Effect of CO<sub>2</sub> and Climate Change on Crop Production**

The ambient concentration of CO<sub>2</sub> directly affects the physiology of plants, as shown in Figure 1-4. These effects result in plant yield being influenced by the ambient concentration of CO<sub>2</sub>. It is therefore critical that the effects of increasing the CO<sub>2</sub> concentrations on plant growth and development can be determined when assessing the consequences of climate change on crop production. This section examines the effects of CO<sub>2</sub> on plant growth and concludes by discussing the effect of changes in ambient CO<sub>2</sub> concentration on plant yield.



*Figure 1-4 The aspects of plant growth that are affected by the ambient concentration of CO<sub>2</sub>.*

### **1.4.1 Effects of Enhanced CO<sub>2</sub> on the Photosynthesis Process**

The process of photosynthesis is partly dependent on the availability of CO<sub>2</sub>. The CO<sub>2</sub> enters the plant cells through the stomata by diffusion, it is then combined with water

and converted into carbohydrates by photosynthetic enzymes. The response of the plants to increased  $\text{CO}_2$  concentration is affected by whether the early products of the photosynthetic pathway are based on compounds with three ( $\text{C}_3$  plants) or four ( $\text{C}_4$  plants) carbon atoms. Under current ambient conditions of  $\text{CO}_2$  the rate of photosynthesis of  $\text{C}_4$  plants is higher than that for  $\text{C}_3$  plants. However, as  $\text{CO}_2$  concentration increased to 700 ppmv the rate of photosynthesis for  $\text{C}_3$  plants has been observed to increase by 66%, whereas it increased by only 4% for  $\text{C}_4$  plants (Kimball, Mauney, Nakayama and Idso, 1993a). In  $\text{C}_4$  plants the rates of photosynthesis are independent of the concentration of oxygen ( $\text{O}_2$ ) within the plant, but with  $\text{C}_3$  plants light stimulates the process known as photorespiration. In this process the carbohydrates are combined with  $\text{O}_2$  to release  $\text{CO}_2$  and water into the atmosphere. This occurs because the  $\text{O}_2$  and the  $\text{CO}_2$  compete for the receptor sites on the enzyme Rubisco. At current concentrations of  $\text{CO}_2$  Tolbert and Zelitch (1983) reported that the net gain in carbon in  $\text{C}_3$  species from photosynthesis can be reduced by as much as 50% by photorespiration. Thus, the increased rate of photosynthesis as a result of an enhanced  $\text{CO}_2$  environment is due in part to two factors. First, there is a reduction in the loss of carbohydrates through the photorespiration process. Second, the supply of the substrate ( $\text{CO}_2$ ) is increased.

Jolliffe and Tregunna (1968), and Berry and Björkman (1980) reported that as temperature rises to the optimum the stimulation of photosynthesis increases. As the solubility of the  $\text{CO}_2$  compared to  $\text{O}_2$  is reduced with increasing temperature and the specificity of the enzyme Rubisco for  $\text{CO}_2$  is also reduced, increasing the concentration of the  $\text{CO}_2$  within the plant will have more of an inhibitory effect on

photorespiration at higher rather than lower temperatures. Long (1991) predicts that as the concentration of CO<sub>2</sub> increases to 500 ppmv and then to 650 ppmv, the optimum temperature for photosynthesis of C<sub>3</sub> crops will increase by 3°C and 5°C respectively.

The concentration of nitrogen has been recognised as a limiting factor in the photosynthesis process (Field and Mooney, 1986; Gastal and Saugier, 1989). Nevertheless, Nijs, Behaeghe and Impens (1995) observed that the relative effect of leaf nitrogen concentration at elevated CO<sub>2</sub> concentrations only marginally affects the stimulation of photosynthesis. In experiments with perennial ryegrass (*Lolium perenne*) they noted that the maximum carboxylation rate was reduced in leaves with the same concentration of nitrogen when the concentration of CO<sub>2</sub> was increased. The efficiency of nitrogen is therefore reduced at increased concentrations of CO<sub>2</sub>.

#### **1.4.2 Effects of Enhanced CO<sub>2</sub> Concentrations on Respiration**

The effect of an enriched CO<sub>2</sub> atmosphere on respiration differs between plants and organs within plants. The results of Poorter, Gifford, Kriedemann and Wong (1992) who surveyed published reports as well as conducting their own experiments revealed that enhancing atmospheric CO<sub>2</sub> levels on leaf respiration expressed per unit of leaf area ranged from 50% inhibition to a 200% stimulation. However, when the respiration rate is expressed on a dry weight basis, the rates are decreased. This is as a result of starch accumulation which may occur under increased CO<sub>2</sub> concentrations (Farrar and Williams, 1991), but does not require a high input of metabolic energy (Poorter, 1993). The accumulation of starch can result in the specific leaf area declining when plants are grown at elevated CO<sub>2</sub> levels (Poorter,

1993). The effect on root respiration ranged from inhibiting the rate by 45% to a 30% stimulation (Poorter *et al.*, 1992). Nevertheless, in many of the experiments the respiration rates were only measured once.

#### **1.4.3 Effects of Enhanced CO<sub>2</sub> Concentrations on Transpiration**

With the increase in CO<sub>2</sub> concentrations the rates of transpiration per unit leaf area are expected to decrease. This is because the enriched CO<sub>2</sub> atmosphere will cause partial closure of the stomata, which will restrict the rate of transpiration more than it restricts the process of photosynthesis. Doubling the current levels of CO<sub>2</sub> is predicted to decrease the rates of transpiration by between 25% and 50% (Cure and Acock, 1986), and stomatal conductance by 40% (Morrison, 1987). For some species, Pearcy and Björkman (1983) reported a doubling of the water use efficiency with a doubling of the concentration of CO<sub>2</sub> in the atmosphere, where the water use efficiency is defined as the ratio of photosynthesis to transpiration. Nevertheless, as the size of the plants may increase with increasing CO<sub>2</sub>, the total water requirements of the crop may not necessarily be reduced.

The water that is lost through transpiration cools the leaf surface. Thus, as a result of enriching the atmosphere with CO<sub>2</sub> and the partial closure of the stomata the temperature of the leaf is likely to rise. Idso, Kimball and Mauney (1987a) and Jones, Allen and Jones (1985) have shown that the temperature of the leaf can rise by between 1°C and 3°C. Initially as less water is transpired, the water vapour pressure within the leaves will increase and the humidity of the surrounding air will drop (Wolfe and Erickson, 1993). Both these factors will contribute to increasing the rates of transpiration per unit of leaf area.

#### **1.4.4 Effects of Enhanced CO<sub>2</sub> Concentrations on the Stomata**

The stomatal density has been observed to decrease in plants grown at concentrations of CO<sub>2</sub> below 350 ppmv (Woodward 1986, 1987; Woodward and Bazzaz, 1988). However, according to Woodward (1988), Woodward and Bazzaz (1988) and Jarvis (1989) enhancing the CO<sub>2</sub> levels has not resulted in an increased stomatal density. In contrast Ferris, Nijs, Behaeghe and Impens (1996a) observed that the stomatal density of perennial ryegrass leaves was increased by enhanced CO<sub>2</sub> concentrations during the summer, but decreased during the spring. Nevertheless the stomatal density has been observed by Oberbauer, Strain and Fletcher (1985) to decrease in a species of tropical tree (*Pentaclethra macroloba*).

#### **1.4.5 Effects of Enhanced CO<sub>2</sub> Concentrations on Growth Habits**

The increased rate in photosynthesis may not result in as large an increase in either growth or yield. Allen (1991a) reported that a 50% increase in photosynthesis in soybean resulted in a 40% increase in biomass and only a 30% increase in marketable seed yield. The leaf area index of the crop which intercepts the light has an important effect on the productivity of the crop. However, an increased leaf area may exacerbate any water or nutrient deficiency experienced by the crop. Depending on the water and nutrient status of the crop and how it partitions the biomass between the root, shoot, leaves, stems, fruits and seed, enhanced atmospheric CO<sub>2</sub> levels may have a beneficial or detrimental effect on marketable yield.

The different growth habits of plants may be affecting their response to augmented CO<sub>2</sub> concentrations. Five factors that may explain some of the differences have been identified by Poorter (1993). First, species with strong sinks or the ability to increase

the sink size may be more responsive. Second, nitrogen fixing plants may be more responsive as the nodules represent a large sink (Arnone and Gordon, 1990), but under many experimental conditions the plants are grown under nutrient rich conditions and thus nitrogen fixation would not be occurring (Poorter, 1993). Third, crops which have been selected for vigour, as opposed to wild species, seem to be more responsive. Fourth, there appears to be a significant correlation between plant growth rate and its response to CO<sub>2</sub> enhancement. Fifth, the review of Cure and Acock (1986) indicated that dicotyledonous species were more responsive than monocotyledons.

#### **1.4.6 Effects of Enhanced CO<sub>2</sub> Concentrations on the Partitioning of Dry Matter**

Dry matter partitioning in the plant is influenced by other environmental factors as well as the atmospheric concentration of CO<sub>2</sub>. It is revealed from a survey of experiments which included perennial ryegrass and white clover (*Trifolium repens*) compiled by Stulen and den Hertog (1993) that, where water and nutrient are non-limiting, enhanced CO<sub>2</sub> tends not to affect the root:shoot ratio and the leaf weight ratio. However, when the plants were subjected to either water or nutrient stress the root:shoot ratio tended to increase. An increase in the root:shoot ratio has also been observed in some field grown crops (Lawlor and Mitchell, 1991). An enriched CO<sub>2</sub> atmosphere affects the branching of the roots as opposed to the rate of elongation of the individual root axes (Stulen and den Hertog, 1993). Flowering, seed set and senescence were affected unpredictably (Woodward, Thompson and McKee, 1991). In cotton, senescence was reported to increase with augmented CO<sub>2</sub> concentrations

(Chang, 1975), remain the same for wheat (*Triticum aestivum*) (Gifford, 1977) and decrease for a C<sub>3</sub> grass (Carter and Peterson, 1983).

There is a lack of understanding of resource allocation in plants grown under an enhanced CO<sub>2</sub> environment (Woodward *et al.*, 1991). This problem may be partly explained by experimental conditions as plants usually have been grown in small pots, and thus the response is a measure of the effect of CO<sub>2</sub> and the limited soil resources. However, two further problems affect the ability to predict how individual species are going to respond to CO<sub>2</sub>. First, the size and strength of the assimilate sink that may influence the rate of photosynthesis (Jarvis, 1989), cannot be predicted. Second, the chemical composition of the exported assimilates may change with CO<sub>2</sub> (Madore and Grodzinski, 1985) which in turn may influence the conversion of the assimilates to plant material (Woodward *et al.*, 1991).

#### **1.4.7 Effects of Enhanced CO<sub>2</sub> Levels on Plant Yield**

The effects of enhanced CO<sub>2</sub> on the plant growth characteristics outlined in Figure 1-4 influence plant yield. However the responses of plant yield to increased ambient concentration of CO<sub>2</sub> are modified by:

- the levels of water and nutrient stress;
- long-term exposure to enhanced concentrations of CO<sub>2</sub>; and
- growth under field conditions.

The net effect of enhanced CO<sub>2</sub> levels on plant yield are described in this section.

#### **1.4.7.1 Plant Yield**

During the past four decades tree ring data from high-altitude conifers has indicated an increase in the growth rates which corresponds to the increase in atmospheric concentration of CO<sub>2</sub> (La Marche, Graybill, Fritts and Rose, 1984). Nevertheless, Johnson, Polley and Mayeux (1993) reported that the sensitivity of photosynthesis to CO<sub>2</sub> concentration is higher at levels below, as opposed to above, current concentrations (350 ppmv). The enrichment of the CO<sub>2</sub> levels in 50%—75% of the commercial greenhouses world-wide has yielded increases of between 30% and 40% for some crops when the CO<sub>2</sub> concentration approaches 1000 ppmv (Wittwer, 1986). This indicates that CO<sub>2</sub> has beneficial effects for crops grown under greenhouse conditions. Nevertheless, the CO<sub>2</sub> concentrations in greenhouses without CO<sub>2</sub> supplementation is depleted to a level of 200—250 ppmv (Goldsberry, 1986), and thus the yield increases reported are larger than would occur if the control environment had been maintained at current ambient levels. Kimball (1983) predicted that increasing CO<sub>2</sub> concentrations from 330 ppmv to 660 ppmv would increase yields by 33% with a 95% confidence limit of  $\pm 6\%$ . When CO<sub>2</sub> concentrations were increased to 1000 ppmv yield increases are predicted to be as much as  $67\% \pm 10\%$ . However, Wittwer and Robb (1964) recognised that the quantity of water and fertilisers applied to the crop has to be increased in order to maximise the benefit of the CO<sub>2</sub> enriched atmosphere. The ideal controlled growing conditions experienced in a greenhouse may be partly responsible for the large increase in yield.

Nevertheless, Poorter (1993) having surveyed 156 species from 89 reports stated that the response between and within species to augmented CO<sub>2</sub> concentrations was

highly variable. In some cases, plants described as being highly responsive in one report are unaffected in another. This may be due to interactions between the environment and CO<sub>2</sub> levels which are affecting growth (Wong, 1993; Potvin and Strain, 1985; Tolley and Strain, 1984) and intraspecific variation (Potvin and Strain, 1985). It has been observed that the response of plants grown in competition under elevated CO<sub>2</sub> was influenced by whether they were grown in open-top or growth chambers (Stewart and Potvin, 1996). The chambers differ in the rooting area and the environmental conditions experienced by the plants. Another possible explanation is that there is variation in plant weight within the experiment that may be affecting the weight ratio of the plants grown at enhanced CO<sub>2</sub> levels to the control plants (Poorter, 1993).

#### **1.4.7.2 Water and Nutrient Stressed Crops**

Under water stressed conditions, the predicted effect of an enriched CO<sub>2</sub> atmosphere could be as large as, if not larger than, the yield response predicted for non-stressed conditions (Kimball, 1986a). A similar response has been observed for field grown cotton (*Gossypium* species) (Kimball, 1986b) and rice (*Oryza sativa*) (Allen, 1991b) which were grown under nitrogen stressed conditions. When cotton was grown under nitrogen stress that was severe enough to depress yields of cotton (Kimball, Mauney, Nakayama and Idso, 1993b), under a doubling of CO<sub>2</sub> concentration the yields increased regardless of whether the crops experienced water stress. In these experiments the relative response of plants at low nitrogen levels was higher than those at high nitrogen levels. However, the results of maize (*Zea mays*) and cotton grown in a greenhouse indicate that the response was proportionally smaller for low

nitrogen treatments (Wong, 1979). Nevertheless the maximum yield with CO<sub>2</sub> enrichment occurs when the nitrogen available to the crop is at its optimum level. When phosphorus is limiting, enhancing the atmospheric CO<sub>2</sub> concentrations has been reported as having no effect on yield (Gourdriaan and de Ruiter, 1983). On the other hand, Conroy, Barlow, and Bevege (1986) found that growth was still stimulated when *Pinus radiata* was supplied with varying quantities of water and phosphorus.

#### **1.4.7.3 Long-Term Exposure to Enhanced CO<sub>2</sub>**

Once the plants have become acclimatised to the higher concentration of CO<sub>2</sub> the beneficial effect of yield tends to decline (Kramer, 1981; Bazzaz, 1990). From Cure and Acock's (1986) literature review and experiments conducted by Yelle, Beeson, Trudel and Gosselin (1989), Wolfe and Erickson (1993) calculated that the short-term response of photosynthesis to doubling the CO<sub>2</sub> concentration was approximately double the long-term response for C<sub>3</sub> and C<sub>4</sub> crops, as shown in Table 1-4. Sage, Sharkey and Sieman (1989) examined the effect of increased CO<sub>2</sub> concentration on five dicotyledon species. The activity of the enzyme Rubisco, after prolonged exposure to CO<sub>2</sub> levels of 950 ppmv, was reduced by between 30% and 60%. However, no two species showed the same quantitative response to CO<sub>2</sub> enrichment. According to Besford, Ludwig, and Withers (1990) the loss in extractable Rubisco activity may account for the decrease in the maximum rate of photosynthesis. Another explanation for the acclimatisation of the plants to increased CO<sub>2</sub> is that more carbohydrate is being supplied than can be utilised. Delucia, Sasek, and Strain(1985), and Nafziger and Keller (1976) suggest that for some species the over supply of carbohydrates results in the enlargement of starch grains within the cells of the leaves,

which causes damage to the organelles that are important in the photosynthesis process. The effect may be less significant in indeterminate crops as they have a continuous demand for carbohydrates.

*Table 1-4 The net photosynthetic response of C<sub>3</sub> and C<sub>4</sub> crops to increasing the CO<sub>2</sub> concentration from 300—350 ppmv to 680 ppmv*

Photosynthetic pathway	Crop		Change in net photosynthesis from doubling the CO <sub>2</sub> concentration (%)	
	Common name	Latin name	Short term	Long term
C <sub>3</sub>	Barley	<i>Hordeum vulgare</i>	+50	+14
	Cotton	<i>Gossypium</i> species	+60	+13
	Rice	<i>Oryza sativa</i>	+42	+46
	Soybeans	<i>Glycine max</i>	+78	+42
	Wheat	<i>Triticum aestivum</i>	+41	+27
	Tomato	<i>Lycopersicon esculentum</i>	+30	+9
	Average C <sub>3</sub> crop		+50	+25
C <sub>4</sub>	Maize	<i>Zea mays</i>	+26	+4
	Sorghum	<i>Sorghum</i> species	-3	+6
	Average C <sub>4</sub> crop		+25	+5

Sasek, DeLucia and Strain (1985) observed that the inhibition of photosynthesis was reversed when there was a parallel reduction in leaf starch. Down regulation, reduction in photosynthetic capacity, may be more pronounced in plants that have a reduced sink strength (Van Oosten and Besford, 1996). Because glasshouse crops have been selected for high yield and growth, and thus sink strength, the effect of down regulation may not have been observed in these crops. A diminished response over time might also occur because of the experimental conditions under which the plants are grown. This may occur if the plants are grown too close to one another or are grown in small pots that may result in self shading or in the plants becoming pot bound and thus subjecting the plants to water and nutrient stress (Poorter, 1993). According to Poorter (1993), it is also possible that after a period of time the stimulation in growth rate will be offset by the increased size of the plants and the accompanying lower relative growth rate. The relative growth rate tends to decline over time in fast growing plants. Luo, Field and Mooney (1994) suggest that the maximum rate of photosynthesis is down regulated through nitrogen dilution and feedback inhibition by the end products. However, the down regulation may be partially or completely compensated for by the increased leaf mass per unit area.

At low temperatures, the rate of photosynthesis of plants that have become acclimatised to increasing concentrations of CO<sub>2</sub> may be lower than under current levels of CO<sub>2</sub>. Oechel and Reichers (1987) observed that CO<sub>2</sub> enrichment had little effect on the natural vegetation of the tundra, whereas there was a significant increase in the productivity of a warm wetland vegetation at a low latitude site (Drake and Leadley, 1991). However, other environmental factors may have contributed to these

results. Nevertheless, Idso, Kimball, Anderson and Mauney (1987b) predicted the growth rates from a regression analysis from an experiment conducted in open top canopy chamber as -60%, 0%, 30% and 100% at 12°C, 18°C, 22°C and 30°C respectively. The species studied were carrot (*Daucus carota*), radish (*Raphanus sativa*), water hyacinth (*Eichhornia crassipes*), water fern (*Azolla pinnata*) and cotton. However, the growth of the aquatic species appeared to be more inhibited at elevated CO<sub>2</sub> concentrations and at temperatures below 18°C than the terrestrial species. In a similar experiment on carrot and radish, Idso and Kimball (1989) observed that a temperature increase of above 12°C resulted in a positive growth response.

#### **1.4.7.4 Plants Grown in the Field**

Under field conditions the yield is determined by the interactions that occur between light, temperature, water and nutrients as well as the ambient concentration of CO<sub>2</sub>. The competition for water, nutrients and light may be intensified by elevated atmospheric CO<sub>2</sub> concentrations and this will have implications for intraspecific competition (Schenk, Manderscheid, Hugen and Weigel, 1995). Körner (1995) reported that species, that were found to be responsive to elevated CO<sub>2</sub> in container experiments inside greenhouses, were completely unaffected under field conditions. Nevertheless, yield increases of between 20% and 80% for C<sub>3</sub> crops have been obtained from experiments performed in open top chambers when the plants were supplied with water and nutrients (Wolfe and Erickson, 1993). In experiments with open top chambers, the light levels and variations in humidity and temperature are more realistic than under greenhouse conditions. Nevertheless, the air temperature will be a few degrees higher and the movement of air around the crop will be reduced

compared to the natural environment (Lawlor and Mitchell, 1991). Both these factors will have effects on the rates of transpiration of the crop. The use of open top chambers under current CO<sub>2</sub> concentrations also tends to increase the growth of crops. This has been demonstrated by Rogers, Bingham, Cure, Smith and Surano (1983) and Rogers, Cure and Smith (1986) for maize and soybean (*Glycine max*) respectively.

In experiments involving complex ecosystems, the species mix used was often dictated by the investigator rather than natural selection (Körner, 1995). According to Körner (1995) this may have resulted in the system changing from the starting balance of species as soon as the experiments have started. The results that were assumed to be due to the enhanced atmospheric conditions may simply reflect the momentary status of the successional process. However, it is very difficult from field studies to unravel the complex interactions of the processes involved.

### ***1.5 The Impact of Climate Change on Agriculture***

The impact of climate change on agriculture will be twofold, namely the direct effect of increased CO<sub>2</sub> on plant growth and the indirect effects of increased annual average temperatures and changes in rainfall patterns. Two broad approaches have been used to assess the effects of climate change on agriculture. The first has estimated the shifts in climatic resources, and the consequent shifts in land use and farming types, and the second has considered the possible changes in yield at specific sites.

### **1.5.1 Effect on Cereal Crop Yields**

Assuming there is no direct physiological effect of CO<sub>2</sub>, Rosenzweig and Parry (1994) predicted that the yield of wheat, rice, coarse grains and protein crops would decline everywhere under the GISS, GFDL and UKMO GCMs. Nevertheless, the reductions in the mid to high latitudes were less than those experienced in the lower latitudes. When the direct effects of CO<sub>2</sub> are included, the GISS and GFDL GCMs predict that there will be a positive effect on agricultural production at the middle and high latitudes, while there will be a negative effect in the low latitudes. However, with the exception of Australia and parts of Europe, the UKMO scenario forecasts yield reductions. Leemans and Solomon (1993) investigated the effects of the GFDL scenario on the change in distribution and yield of ten crops on a world-wide scale, and the results are shown in Table 1-5. Nevertheless, yields in areas where the crops are currently grown are predicted to decline by approximately 15% for all crops except tropical maize, rice, sugar cane and cassava. The yields of these crops are expected to increase by between 0.4% and 3.5%. On the other hand, the area grown of all these crops is predicted to increase by between 10% and 32% of the current area, which is sufficient to result in an overall increase in yield.

Table 1-5 Future potential yields of major crops

Crop		Area of land with a		Increase in total
Common name	Genera	decrease in yield (10 <sup>3</sup> km <sup>2</sup> )	increase in yield (10 <sup>3</sup> km <sup>2</sup> )	yield (%)
Temperate maize	<i>Zea</i>	12,026	19,667	27.7
Tropical maize	<i>Zea</i>	29,372	15,502	12.7
Spring wheat	<i>Triticum</i>	14,963	13,824	28.1
Winter wheat	<i>Triticum</i>	17,062	12,035	30.2
Rice	<i>Oryza</i>	32,824	15,771	13.4
Millet <sup>1</sup>		29,014	22,605	20.7
Soybeans	<i>Glycine</i>	19,179	14,870	17.4
Beans	<i>Phaseolus</i>	34,515	14,154	12.2
Sugar cane	<i>Saccharum</i>	22,637	10,413	16.2
Cassava	<i>Manihot</i>	33,353	5,951	14.8

Note <sup>1</sup> Millet is a very heterogeneous crop. The genera of millet included in this study were *Elusine*, *Panicum*, *Setaria*, *Echinochloa*, *Pennisetum* and *Sorghum*.

Increasing the average annual temperature by 2°C would result in increasing the land area suitable for growing grain maize by 2,400,000 km<sup>2</sup>, approximately 25% (Kenny and Harrison, 1992). A northward shift of approximately 200—350 km °C<sup>-1</sup> in western Europe and 250—400 km °C<sup>-1</sup> in eastern Europe is predicted for grain maize

production under global warming (Carter, Porter and Parry, 1992). In contrast, Saarikko and Carter (1996) predict a shift northwards of 160—180 km °C<sup>-1</sup> for spring wheat. Harrison and Butterfield (1996) predict, using the transient UKMO scenario, that by the middle of the next century the land area suitable for growing winter wheat will have expanded into mid-Scandinavia and most of Russia, while the area suitable for growing sunflowers will have expanded into northern Germany, central England, northern Poland, southern Finland and southern Sweden.

With regards to considering the consequence of climate change on agricultural production a significant proportion of work has concentrated on the four major cereals, namely wheat, maize, soybean and rice. The effects of global warming on wheat, maize, soybean and rice production has been assessed in several countries and continents, and is shown in Table 1-6—Table 1-9 respectively. The predictions from wheat models have been compared against actual yields of wheat grown under enhanced CO<sub>2</sub> (Mitchell, Lawlor, Mitchell, Gibbard, White, and Porter, 1995; Moot, Henderson, Porter and Semenov, 1996).

### **1.5.2 Effect on Arable Crop Yields**

The effects of climate change on agricultural production have also been assessed for grapevines (*Vitis vinifera*) in Italy (Bindi, Fibbi, Gozzini, Orlandini and Miglietta, 1996), cauliflower (*Brassica oleracea*) and pea (*Pisum sativum*) in Europe (Kenny, Harrison and Parry, 1993), potatoes (*Solanum tuberosum*) in England and Wales (Davies, Jenkins, Pike, Shao, Carson, Pollock and Parry, 1996), faba bean (*Vicia faba*) in Scotland (Peiris *et al.*, 1996) and groundnuts (*Arachis hypogaea*) in USA (Peart *et al.*, 1995).

*Table 1-6 The countries and continents where the effect of global warming on wheat production has been assessed.*

Country/Continent	Citation
Argentina	Rodriguez and Fernandez (1995)
Australia	Wang, Handoko and Rimmington (1992)
Bangladesh	Karim, Hussain and Ahmed (1996)
Britain	Favis-Mortlock, Evans, Boardman and Harris (1991) Mitchell (1996) Peiris, Crawford, Grashoff, Jefferies, Porter and Marshall (1996) Semenov, Wolf, Evans, Eckersten and Iglesias (1996)
Brazil	Siqueira, Farias and Sans (1994)
Canada	Touré, Major and Lindwall (1994) Brklacich and Stewart (1995)
Europe	Nonhebel (1996)
Finland	Laurila (1995)
France	Delecolle, Ruget, Ripoche and Gosse (1995)
Japan	Seino (1995)
Russia and the former Soviet States	Menzhulin, Koval and Badenko (1995)
Spain	Semenov <i>et al.</i> (1996)
US	Stockle, Dyke, Williams, Jones, and Rosenberg (1992) Adams, Fleming, Chang, McCarl and Rosenzweig (1995) Mearns, Rosenzweig, Goldenberg (1996) Riha, Wilks and Simoens (1996) Rosenzweig and Tubiello (1996)

*Table 1-7 The countries and continents where the effect of global warming on maize production has been assessed.*

Country/Continent	Citation
Brazil	Siqueira <i>et al.</i> (1994)
China	Wang and Lin (1996)
European Community	Wolf and Van Diepen (1994)
France	Delecolle <i>et al.</i> (1995)
Japan	Seino (1995)
Philippines	Buan, Maglinao, Evangelista and Pajuelas (1996)
Spain	Iglesias and Minguez (1995)
US	Cooter (1990)
	Stockle <i>et al.</i> (1992)
	Adams <i>et al.</i> (1995)
	Peart, Curry, Rosenzweig, Jones, Boote, Allen (1995)
	Phillips, Lee and Dobson (1996)
	Riha <i>et al.</i> (1996)
	Xevi, Gilley and Feyen (1996)
Venezuela	Maytin, Acevedo, Jaimez, Andressen, Harwell, Robock and Azocar (1995)
Zimbabwe	Makadho (1996)

**Table 1-8** *The countries and continents where the effect of global warming on soybean production has been assessed.*

Country/Continent	Citation
Brazil	Siqueira <i>et al.</i> (1994)
China	Jin, Ge, Chen and Zheng (1994)
US	Stockle <i>et al.</i> (1992)
	Adams <i>et al.</i> (1995)
	Curry, Jones, Boote, Peart, Allen and Pickering (1995)
	Phillips <i>et al.</i> (1996)
	Riha <i>et al.</i> (1996)

**Table 1-9** *The countries and continents where the effect of global warming on rice production has been assessed.*

Country/Continent	Citation
Asia	Matthews, Kropff, Bachelet and Laar (1995)
	Neue, Ziska, Matthews and Dai (1995)
Bangladesh	Karim <i>et al.</i> (1996)
China	Jin, Ge, Chen and Zheng (1995)
Japan	Horie, Kropff, Centeno, Nakagawa, Nakano, Kim and Ohnishi (1995)
	Seino (1995)
Philippines	Buan <i>et al.</i> (1996)

### 1.5.3 Effect on Forage Crop Yields

With respect to grassland systems, Bergthorsson, Björnsson, Dyrmondsson, Gudmundsson, Helgadóttir and Jonmundsson (1988) assessed the effects of climate change on the production of hay in Iceland using a regression model based on temperature and nitrogen fertiliser application rates. Hunt, Trilica, Redente, Moore, Detling, Kittel, Walter, Fowler, Klein, and Elliot (1991) have developed a model which has the specific objectives of predicting the seasonal and year-to-year dynamics of primary producers, microbes, and soil fauna and nitrogen availability in grasslands. The effects of CO<sub>2</sub> level and climate change on these dynamics were also described. The model has been developed for monocultures of crested wheatgrass (*Agropyron cristatum*) and blue grama (*Bouteloua gracilis*) which are native to the US. The SPUR model (Simulation of Production and Utilization of Rangelands) can simultaneously simulate the growth of 15 plant species typically found in the US (Hanson, Skiles and Parton, 1988). It has been used to assess the effects on grassland and livestock production in the US (Baker, Hanson Bourdon and Eckert, 1993; Hanson, Baker and Bourdon, 1993) and Mongolia (Bolorsetseg and Tuvannsuren, 1996). Coffin and Lauenroth (1996) used an individual-plant based gap dynamics simulation model (STEPPE-GP), which was developed for shortgrass steppe communities, coupled with a multi-layer soil-water layer model (SOILWAT) to assess the effects of climate change on C<sub>3</sub> and C<sub>4</sub> grasses across the eastern states of the US. Thornley, Fowler and Cannell (1991), and Sheehy, Gastal, Mitchell, Durand, Lemaire and Woodward (1996) have developed models of temperate grasslands typically found in Western Europe which are capable of being used to assess the effects of climate change on the vegetative stage of growth. The model of Thornley *et al.* (1991) has been used to

assess how temperature and the concentration of CO<sub>2</sub> effect the total above- and below-ground carbon sequestered in a simulated sward.

Bergthorsson *et al.* (1988) predicted that increasing the annual average temperature in Iceland by 4°C and the precipitation by 15% would result in the yield of hay increasing by 66%. The model described by Hunt *et al.* (1991) for US temperate grasslands predicted that increasing the annual average temperature by 3°C would have little effect on annual primary production, whereas enhancing the CO<sub>2</sub> concentration would increase the yield. In contrast Hanson *et al.* (1993) predicted that increasing the atmospheric concentration of CO<sub>2</sub> would not significantly increase plant production in north-eastern Colorado. Nevertheless, when enhanced CO<sub>2</sub> concentrations were coupled with increased temperature and precipitation, the yield of forage was increased although it was of poorer quality, which ultimately led to reduced animal production. Global warming is predicted to enhance the yield of rangeland forage crops in the US (Baker *et al.*, 1993). However, in California this is not predicted to result in increased animal intake and in the Southern Great Plains the animal intake was actually decreased. Coffin and Lauenroth (1996) predicted that there will be a change in the balance of species in the grassland communities of eastern US with C<sub>4</sub> grasses becoming more dominant with global warming. In Mongolia the effect of climate change is likely to be negative for forage and livestock production in the Gobi desert area and favourable in the colder regions (Bolorsetseg and Tuvannsuren, 1996). Increasing the annual average temperature by 2°C reduces carbon sequestered by approximately 15% (Thornley *et al.*, 1991). In contrast, increasing carbon sequestration was enhanced by 34% and 64%, when the CO<sub>2</sub> concentration

was increased from 280 ppmv to 350 ppmv, and from 350 ppmv to 600 ppmv respectively.

## **1.6 Importance of Forage and Livestock Production**

Climate change and the associated increased concentration of atmospheric CO<sub>2</sub> have an effect on grassland and animal production. Nevertheless, the direction of the effect is partly dependent on the actual change in temperature and rainfall as well as the species of grasses grown. However, to date the majority of the work studying the effects on forage and livestock production under climate change and incorporating the effects of enhanced atmospheric CO<sub>2</sub> concentrations has largely been based on grasslands typically found in the US (Hunt *et al.*, 1991; Baker *et al.*, 1993; Hanson *et al.*, 1993; Coffin and Lauenroth, 1996). Although there are indications that increased levels of CO<sub>2</sub> will result in increased production of perennial ryegrass (Casella, Soussana and Loiseau, 1996; Jones, Jongen and Doyle, 1996a; Jones, Jongen, Garvey and Baxter, 1996b), there is no indication of how changes in the temperature and precipitation during the growing season will impact on forage and livestock production in the UK or Scotland.

In Scotland, livestock production, excluding pigs and poultry, account for approximately 60% of total outputs from agriculture which in 1994 was valued at £1799.5 million (Scottish Office Agriculture, Environment and Fisheries Department (SOAEFD), 1995). Of the land area used for crops and grassland in Scotland, 63.6% of the area is under grass which is mainly utilised for livestock production. Thus, the dairy, beef and sheep enterprises are significant in Scotland both in terms of the land area which they utilise and the contribution these livestock enterprises make to

agricultural output. In terms of the nutritional value of herbage, British ruminant livestock gain 71% of their metabolisable energy (ME) and 67% of their crude protein requirements from conserved grass and grazing (Holmes, 1989). On an enterprise basis, in Britain the dairy cows derived 60%, beef cattle 79%, and sheep 97% of their daily feed energy from grass (Jollans, 1981).

In Britain, forage production in lowland areas is commonly based on perennial ryegrass (Robson, Parsons and Williams, 1989). Although, perennial ryegrass and white clover are important forage species in British livestock production only 20% of the grassland in the United Kingdom contains more than 5% of white clover (Robson *et al.*, 1989). This species has an important environmental role as it can fix its own nitrogen. It also has a higher nutritive value than grass and it tends to stimulate intake (Thomson, 1984). The importance of white clover to livestock systems may be altered under a global warming scenario.

Livestock production is dependent on the production of herbage, and thus any impact of climate change and of increased concentration of greenhouse gases on forage and hence livestock production will be of prime importance to Scottish agriculture. Consequently, it is necessary to gain an understanding of how forage and hence livestock production will be influenced in the UK under enhanced CO<sub>2</sub> and the associated changes in climate.

### **1.7 Role of Plant Growth Modelling**

In a changing climate, the success of agriculture is dependent on its ability to adapt. However, the crop–climate interactions are complex and the climatic variables are

changing throughout the life of the plant (Kimball *et al.*, 1993a). For this reason plant models that incorporate the effects of enhanced atmospheric CO<sub>2</sub> concentrations and the interactions of the crops with all the climatic variables are required for predicting the effect of climate change on crop growth (Kimball *et al.*, 1993a). However, according to Reynolds and Acock (1985) only the essential parts of the system should be described, and Pachepsky, Haskett and Acock (1996) listed the following criteria for a good model:

1. the minimum number of parameters with reasonable error;
2. the simplest form with minimum error;
3. based on physical, chemical and biological laws where possible;
4. the minimum deviation between predicted and empirical values; and
5. the minimum variance of output.

## **1.8 The Aims and Hypotheses**

The aims of this study have been:

1. to develop a simulation model of grass and grass – white clover swards, which is capable of quantifying the effect that climate change could have on the productivity of grassland in Scotland,
2. to develop models capable of simulating the effect of the projected changes in forage production under global warming and enhanced CO<sub>2</sub> levels on dairy, beef and sheep production within Scotland,

3. to assess the separate as well as the joint effects of changes in temperature and rainfall on forage production and the livestock enterprises, and
4. to assess how important including the yield - enhancing effects of elevated CO<sub>2</sub>, as distinct from the temperature effects of global warming, are on forage production and the livestock enterprises.

The hypotheses that will be tested are:

1. The growing season will be lengthened by increases in the annual average temperature.
2. Production from grass and grass – white clover swards will be enhanced by:
  - a) elevated ambient CO<sub>2</sub> levels;
  - b) increases of 1°C, 2°C and 3°C in the annual average temperature;
  - c) changes in the rainfall pattern; and
  - d) elevated CO<sub>2</sub> coupled with increases in the annual average temperature and changes in rainfall.
3. The effect of increases in the annual average temperature will not result in linear increases in the yield from the grass sward or in the components of yield from grass – white clover sward.
4. The proportion of white clover harvested from mixed swards will be increased by:
  - a) elevated ambient CO<sub>2</sub> levels;

- b) increases of 1°C, 2°C and 3°C in the annual average temperature;
- c) changes in the rainfall pattern; and
- d) elevated CO<sub>2</sub> coupled with increases in the annual average temperature and changes in rainfall.

5. The grazing season for dairy cows, beef cattle and sheep will be increased by:

- a) elevated ambient CO<sub>2</sub> levels;
- b) increases of 1°C, 2°C and 3°C in the annual average temperature;
- c) changes in the rainfall pattern; and
- d) elevated CO<sub>2</sub> coupled with increases in the annual average temperature and changes in rainfall.

6. The production from dairy cows, beef cattle and sheep will be enhanced by:

- a) elevated ambient CO<sub>2</sub> levels;
- b) increases of 1°C, 2°C and 3°C in the annual average temperature;
- c) changes in the rainfall pattern; and
- d) elevated CO<sub>2</sub> coupled with increases in the annual average temperature and changes in rainfall.

7. The production from dairy cows, beef cattle and sheep grazing grass – white clover swards will show a greater percentage increase in the production levels than those grazing pure grass swards.

8. The trends in production will not be affected by site.

## ***1.9 Chapter Structure of Thesis***

Chapter 2 describes the current knowledge of the effect of increases in ambient temperature and global warming on grass and white clover production grown in both monocultures and in a mixture. This chapter also reviews the current state of models of forage and livestock production systems. The development of the model describing grass and grass – white clover production from cut and grazed swards is outlined in Chapter 3. The models of dairy cow, beef steer and sheep production are described in Chapter 4, while the forage production and livestock models are validated against experimental data in Chapter 5. In Chapter 6 the effects of climate change on forage and livestock production in Scotland are explored, while Chapter 7 discusses the effects of climate change in relation to the hypotheses outlined in Section 1.8, Chapter 1. Chapter 7 also outlines possible future developments of the models.

## **CHAPTER 2**

### ***THE CURRENT KNOWLEDGE REGARDING GLOBAL WARMING AND MODELLING OF GRASSLAND SYSTEMS – AN APPRAISAL***

#### ***2.1 Introduction***

Chapter 1 has illustrated the effects of climate change on crop and agricultural production. This chapter specifically describes the effects of changes in CO<sub>2</sub> and the associated changes in climate on forage crops, notably on grass and white clover growth. The approach adopted, as outlined in Chapter 1, to assess the impacts of climate change on forage and livestock production is the development of a mechanistic model. Consequently, this chapter concludes with a review of the current state of models of forage and livestock production systems.

#### ***2.2 The Effects of Climate Change on Forage Production***

The plant processes of photosynthesis, respiration, transpiration and partitioning for perennial ryegrass and white clover plants under a global warming scenario will be affected by both the changes in CO<sub>2</sub> concentrations and the associated increases in temperature. This may lead to changes in growth habit and ultimately plant yield. This section therefore describes the effects of:

1. elevated temperature on plant growth; and
2. global warming on:
  - 2.1. shoot biomass;
  - 2.2. root biomass;
  - 2.3. rate of photosynthesis;
  - 2.4. rate of dark respiration;

- 2.5. rate of transpiration;
- 2.6. leaf growth characteristics and habit; and
- 2.7. nitrogen concentration

for both monocultures of perennial ryegrass and white clover. The effects of global warming on the mixed sward are also discussed for the following:

1. yield composition of the sward;
2. water stress; and
3. leaf growth characteristics.

## **2.2.1 Perennial Ryegrass Production**

### **2.2.1.1 *Effect of Elevated Temperature***

Some aspects of plant growth are enhanced by increases in ambient temperature, while others are reduced. These effects are outlined in this section. Rising temperature increases the rates of leaf appearance, leaf extension and growth, while the rates of leaf death, senescence and weight per unit leaf length decline (Clark, Newton, Bell and Glasgow, 1995). However, according to Davies (1977) and Robson *et al.* (1989), there is a considerable degree of synchronisation between the appearance of new leaves and the death of existing leaves. The final size and shape of the leaf, and the rate and duration of leaf expansion are also influenced by temperature, with the optimum temperature for most aspects of leaf growth of northern temperate grasses being in the region 20—25°C (Robson, Ryle and Woledge, 1988). Davidson and Robson (1986) reported that the specific leaf area increased with temperature. In contrast, increased ambient temperatures during the summer result in decreasing the specific leaf area (Ferris, Nijs, Behaeghe and Impens, 1996b).

The affect of temperature on the rate of photosynthesis is variable. On one hand, Woledge and Dennis (1982) reported an increase in the rate of photosynthesis with elevated temperature, while on the other, Nijs and Impens (1996) reported a decrease. Increasing the ambient air temperature can result in the vapour pressure deficit also increasing, which will reduce the rates of stomatal conductance and photosynthesis (Woledge, Bunce, and Tewson, 1989), and the density of the stomata is also increased (Ferris *et al.*, 1996a). The rate of respiration is also increased with elevated temperatures (Robson, 1981). Nijs and Impens (1997) reported that increasing the ambient temperature by 4°C reduced the final yield by 12% relative to the control over a 90-day growing period.

### **2.2.1.2 Effect of Global Warming**

#### **2.2.1.2.1 Effect of Global Warming on Shoot and Root Biomass**

With global warming, shoot production is enhanced, although the effects on root production are variable. Consequently, the impact of elevated ambient CO<sub>2</sub> concentrations on the root:shoot ratio is also variable. The evidence for these impacts is outlined below.

Enhancing the atmospheric CO<sub>2</sub> concentration by 300 ppmv increased the shoot biomass by 11—22% after 57 days of growth (Schenk *et al.*, 1995). A similar response was observed by Nijs, Impens and Behaeghe (1989a). On the other hand the yield enhancement reported by Schenk, Jäger, and Weigel (1997a) was between 5% and 9% when the atmospheric CO<sub>2</sub> concentration was increased from 380 ppmv to 670 ppmv. However, the response between years may differ as observed by Schapendonk, Dijkstra, Groenwold, Pot and Van de Geijn (1996), who reported an

increase of 19.9% in the accumulated carbon in the first year of the experiment and 25.1% in the second for a doubling of the atmospheric CO<sub>2</sub> levels. Jones *et al.* (1996b) observed that doubling the CO<sub>2</sub> concentration of field-grown swards resulted in an increase in yield of 20%, 28%, 21% and 8% in the first, second, third, and fourth years respectively. However, an increase of 43% in the harvestable yield of young spaced plants was detected (Jones *et al.*, 1996b). On the other hand, Schenk *et al.* (1995) observed that plant density did not affect the enhanced growth.

Over a growing season Casella *et al.* (1996) observed increases of 6% in the yield of the material harvested from the May, June and October cuts, whereas the yield was enhanced by 48% for the July and September cuts when the swards were subjected to a lack of moisture. In contrast Jones *et al.* (1996a) reported a greater increase in yield for May and August than for June and July. Although the dry-matter yield was enhanced by CO<sub>2</sub> concentration, the relative daily growth rate was unaffected by CO<sub>2</sub> level (Bunce and Caulfield, 1991). In contrast, Hardacre, Laing and Christeller (1986) reported an increased growth rate, although the effect of elevated CO<sub>2</sub> was reduced at high irradiance levels. Nevertheless, Nijs and Impens (1996) observed a reduction in yield of 29% for a perennial ryegrass sward grown under winter conditions experienced in Belgium. Coupling the elevated CO<sub>2</sub> with an increase in temperature of 4°C reduced the decrease to 13%. However, in another experiment, Nijs and Impens (1997) reported that elevating the ambient concentration of CO<sub>2</sub> increased the yield by 38%, while coupling the increased CO<sub>2</sub> levels with a temperature increase of 4°C reduced the increase to 19%. The level of nitrogen fertiliser application may also affect the enhancement of yield by increased CO<sub>2</sub> concentrations; with lower nitrogen application resulting in greater increases in harvestable material (Casella *et al.*, 1996).

Nevertheless, there was no significant interaction between nitrogen and CO<sub>2</sub> on the yield. The response of different cultivars of perennial ryegrass to enhanced CO<sub>2</sub> differs (Campbell, Laing, Greer, Crush, Clark, Williamson and Given, 1995).

The effect of increasing the temperature coupled with elevated CO<sub>2</sub> concentrations on yield appears to be partly dependent on the initial temperature. Casella *et al.* (1996) observed that increasing the temperature up to 18.5°C had a positive affect, whereas increasing the temperature above this level had a negative affect. Nijs and Impens (1996) and Nijs and Impens (1997) observed decreases in yield of between 12% and 14% when the ambient temperature was elevated by 4°C. On the other hand, increasing the temperature in France during the summer had no significant effect (Casella *et al.*, 1996). However, as the leaf emergence and extension rates are dependent on temperature, the enhancement of shoot growth by increased CO<sub>2</sub> concentrations will be influenced by the ambient temperature.

The effect of increasing the CO<sub>2</sub> concentration from 390 ppmv to 690 ppmv on root biomass ranged from -4% at four plants per pot to +107% at 36 plants per pot (Schenk *et al.*, 1995). In contrast to the weight of shoot material, which increased exponentially over the growing period, Nijs and Impens (1997) reported that the weight of roots did not increase after 55 days of growth. Increasing the level of nitrogen fertiliser at enhanced CO<sub>2</sub> concentrations also augmented the root biomass (Soussana, Casella and Loiseau, 1996).

Ryle, Powell and Tewson (1992a) observed a reduction in the root:shoot ratio with elevated CO<sub>2</sub> concentrations. In contrast Nijs, Impens and Behaeghe (1989a) reported an increase of 22% in the root:shoot ratio, while Schapendonk *et al.* (1996)

observed an increase in the ratio of 18% in the first year of the experiment and 58% in the second. Jongen, Jones, Hebeisen and Blum (1995) also observed that the root:shoot ratio increased with elevated CO<sub>2</sub> although the magnitude of the response was affected by the time of year the measurements were made and the rate of nitrogen application. This was confirmed by Soussana *et al.* (1996), although at low nitrogen application rates enhancing the CO<sub>2</sub> levels had no effect on the root:shoot biomass.

The optimal distribution of resources and biomass between the root and the shoot is often assumed to balance the nitrogen uptake of roots and the carbon uptake of the shoots (Nijs and Impens, 1997). However, Nijs and Impens (1997) observed that this functional equilibrium does not hold for enhanced ambient CO<sub>2</sub> conditions as the uptake of carbon was excessive relative to the nitrogen uptake. Nevertheless, increasing the temperature for ambient and elevated CO<sub>2</sub> conditions did maintain the balanced activity of the root and the shoots (Nijs and Impens, 1997), although the availability of moisture can affect the below ground respiration rate and hence the below ground biomass (Casella and Soussana, 1997).

#### **2.2.1.2.2 Effect of Global Warming on the Rate of Photosynthesis**

Enhancing the concentration of CO<sub>2</sub> in the atmosphere from 340 ppmv to 680 ppmv increased the rate of net photosynthesis of young expanded leaves by 35—46%, and this increased to 60—75% when expressed on a whole plant basis (Ryle *et al.*, 1992a). Comparable with this, Nijs *et al.* (1989a) reported an increase of 45% in the rate of gross leaf photosynthesis at light saturation when CO<sub>2</sub> was enhanced from 350 ppmv to 600 ppmv. However, in perennial ryegrass the plants become acclimatised to

the CO<sub>2</sub> conditions as the rate of net photosynthesis declines over time (Ryle *et al.*, 1992a, Casella and Soussana, 1997). Notwithstanding, the down regulation of photosynthesis may not negate the gains made by the substantial increase in the rate of photosynthesis under elevated CO<sub>2</sub> (Casella and Soussana, 1997). Jones *et al.* (1996b) observed that acclimatisation occurred towards the end of the regrowth period, and thus the interval between cuts may affect whether acclimatisation was observed for agricultural grasses. The photochemical efficiency was also enhanced with elevated CO<sub>2</sub> concentrations (Nijs *et al.*, 1989a). In contrast, the extinction coefficient was not affected by enhanced CO<sub>2</sub> (Casella and Soussana, 1997). Nijs and Impens (1993) observed that 91% of the stimulation of the rate of CO<sub>2</sub> uptake was the result of increases in the rate of photosynthesis and the photochemical efficiency. Nevertheless, in the longer-term the stimulation effect of enhanced CO<sub>2</sub> concentration was reduced (Greer, Laing and Campbell, 1995) or in some cases resulted in a reduction in the rate compared to ambient conditions (Nijs and Impens, 1996). Combining the increased CO<sub>2</sub> levels with increased ambient air temperature resulted in the rate of photosynthesis being increased compared to the rate under enhanced CO<sub>2</sub> only (Nijs and Impens, 1996). Nevertheless, Greer *et al.* (1995) observed that the maximum stimulation occurred at 18°C.

#### **2.2.1.2.3 Effect of Global Warming on the Rate of Dark Respiration**

The canopy dark respiration rates were observed to increase by a factor of thirteen when CO<sub>2</sub> was increased from 350 ppmv to 600 ppmv (Nijs *et al.*, 1989a), and was affected by the drought status of the sward (Casella and Soussana, 1997). Nevertheless, CO<sub>2</sub> concentration did not significantly affect the rates of respiration expressed per kilogram of material of either leaves or the whole plant (Ryle *et al.*,

1992a). In contrast, Bunce and Caulfield (1991) and Schapendonk and Goudriaan (1995) reported that enhancing the CO<sub>2</sub> concentration decreased the rate of respiration per kilogram of herbage. Thus, the plants either had a lower maintenance respiration requirement or an increased growth conversion rate.

#### **2.2.1.2.4 Effect of Global Warming on the Rate of Transpiration**

The stomatal conductance and transpiration rates were also reduced at elevated CO<sub>2</sub> levels resulting in an increased water use efficiency (Ryle *et al.*, 1992a). Nevertheless, the effect of augmented CO<sub>2</sub> concentrations on the water use efficiency was affected by the available soil moisture and the level of nitrogen application (Casella *et al.*, 1996).

#### **2.2.1.2.5 Effect of Global Warming on the Leaf Growth Characteristics**

The effect of enhanced CO<sub>2</sub> concentrations on leaf growth is dependent on the individual characteristic. The ambient concentration of CO<sub>2</sub> does not appear to affect the growth, senescence per tiller or lamina weight per unit length of the perennial ryegrass (Clark *et al.*, 1995). However, according to Clark *et al.* (1995), the rate of senescence was a function of the efficiency of the harvesting procedure, and may not reflect the effect of enhanced CO<sub>2</sub> on senescence. Ryle *et al.* (1992a) observed that augmenting the atmospheric CO<sub>2</sub> levels resulted in a significant reduction in the specific leaf area. The reduction in specific leaf area is exacerbated during the summer compared to the spring when the CO<sub>2</sub> levels are enhanced (Ferris *et al.*, 1996b). Differences have also been observed between spring and summer on the effect of CO<sub>2</sub> and temperature on leaf growth characteristics (Ferris *et al.*, 1996b). Roumet and Roy (1996) observed that wild species of *L. perenne* had a lower specific

leaf area than cultivated varieties and were less responsive than the cultivated varieties to enhanced CO<sub>2</sub>. The lower specific leaf areas were associated with higher concentrations per unit of leaf area of nitrogen, lignin and cellulose, and by a higher proportion of dense tissues. Although the effect of CO<sub>2</sub> on the thickness of leaves was insignificant, enhancing the CO<sub>2</sub> concentration and the temperature increased the thickness of leaves in summer and decreased it in spring relative to the controls (Ferris *et al.*, 1996a).

#### **2.2.1.2.6 Effect of Global Warming on Tillering**

The tiller number of perennial ryegrass has been reported to increase with elevated CO<sub>2</sub> (Schapendonk *et al.*, 1996). However, in contrast, no effect on tiller numbers was observed in perennial ryegrass swards either grown in monoculture (Ryle *et al.*, 1992a; Schenk *et al.*, 1995) or grown in a mixed sward (Clark, *et al.*, 1995).

#### **2.2.1.2.7 Effect of Global Warming on Nitrogen Concentration**

The nitrogen concentration within the above-ground plant is decreased under global warming, although the impact on the total nitrogen yield is dependent on the effect of global warming on both the nitrogen concentration and the plant biomass. The effect of growing perennial ryegrass under enhanced CO<sub>2</sub> conditions resulted in a significant reduction in the nitrogen concentration within the leaf (Ryle *et al.*, 1992a; Soussana and Hartwig, 1996). This resulted in the nitrogen concentration in the total shoot weight and the whole plant also being significantly lower (Ryle *et al.*, 1992a). Similarly, Schenk *et al.* (1995) observed a reduction in the nitrogen concentration of the shoot, although the concentration in the root biomass was unchanged by elevated CO<sub>2</sub>. Nevertheless, the total nitrogen yield obtained from the shoots was unchanged,

while the total nitrogen yield harvested in the root material was increased (Schenk *et al.*, 1995). Soussana *et al.* (1996) observed that enhancing the CO<sub>2</sub> concentration resulted in a decrease in the nitrogen yield, whereas increasing the temperature alleviated the decline resulting from increasing the CO<sub>2</sub> concentration. On the other hand, Nijs and Impens (1996) observed that enhanced CO<sub>2</sub> and temperature during the winter had no significant effect on the leaf nitrogen levels. However, the effect on the nitrogen concentration of the leaf laminae varied throughout the growing season with the spring and the autumn cuts having enhanced nitrogen concentrations, while the nitrogen concentration for the summer cuts was not affected (Soussana *et al.*, 1996). Nevertheless, the influence of global warming on the nitrogen levels within the plant is affected by the level of nitrogen fertiliser applied (Soussana *et al.*, 1996).

#### **2.2.1.3 Conclusions Regarding the Effect of Climate Change on Perennial Ryegrass**

Increasing the ambient temperature:

- increases the rates of leaf appearance, leaf extension and plant growth; and
- increases the rate of respiration.

Nevertheless, increasing the temperature has been observed to both increase and decrease:

- leaf senescence;
- specific leaf area; and
- the rate of photosynthesis.

Elevating the ambient concentration of CO<sub>2</sub>:

- increases in shoot biomass production, although the magnitude varies inter- and intra-seasonally and acclimatisation may occur, while the level of response also varies with nitrogen fertilisation rate and ambient temperature;
- is inconclusive as far as root biomass production is concerned;
- has an inconclusive effect on the root:shoot ratio;
- enhances the rate of photosynthesis, although acclimatisation may occur;
- either has no effect or decreases the rate of respiration;
- decreases in the rate of transpiration and stomatal conductance;
- reduces the specific leaf area;
- has no affect on leaf growth and senescence;
- either has no effect or increases the number of tillers;
- decreases the nitrogen concentration of the above-ground plant, while in the root the concentration is unchanged; and
- has a variable effect on the total nitrogen yield.

## **2.2.2 White Clover Production**

### **2.2.2.1 Effect of Elevated Temperature**

As with the perennial ryegrass crop, temperature affects the rate of crop development, and the direction of the change is again dependent on the actual process. Elevating the ambient temperature increases the rate of leaf appearance, leaf weight, leaf area, the length of the petiole and the growth per growing point (Clark, *et al.*, 1995; Davies

and Jones, 1992), but decreases the branching of apical meristems and the lifespan of the leaves (Hart, 1987). In contrast, leaf size is apparently not affected by temperature (Junttila, Svenning and Solheim, 1990). However, the rate of development also differs between cultivars (Davies and Jones, 1992; Junttila *et al.*, 1990). As regards the components of yield, increasing the temperature resulted in the growth rate of the shoot being enhanced, whereas the growth rate of the root was unaffected, and thus resulted in a decrease in the root:shoot ratio (Hatch and MacDuff, 1991). In contrast, Ryle and Powell (1992) observed that the root growth rate was reduced by increasing temperature. As the rate of development increases with higher temperatures, the leaf:stem ratio tends to decline and thus reduces the digestibility of the crop (Buxton, 1996).

The rates of photosynthesis (Campbell *et al.*, 1995; Ryle, Woledge, Tewson and Powell, 1992b; Woledge and Dennis, 1982) and respiration (Woledge and Dennis, 1982) are enhanced by raising the ambient temperature, whereas the rates of transpiration and stomatal conductance decline (Ryle *et al.*, 1992b). Nevertheless, if the vapour pressure deficit increases with the temperature, the rates of stomatal conductance and photosynthesis are reduced, although white clover is less sensitive to increases in the vapour pressure deficit than perennial ryegrass (Woledge *et al.*, 1989). The relative growth rates and the leaf protein content are also enhanced by increasing temperature (Campbell *et al.*, 1995). As the temperature increases, the net uptake of nitrogen increases, but the proportional contribution of the nitrogen uptake supplied by biologically 'fixed' nitrogen declines (Hatch and MacDuff, 1991).

### **2.2.2.2 Effect of Global Warming**

#### **2.2.2.2.1 Effect of Global Warming on Shoot and Root Biomass**

Global warming enhances the rates of shoot and biomass production, although the effects on the root:shoot ratio are variable. The evidence for these effects is outlined in this section. The effect of increasing atmospheric CO<sub>2</sub> levels by 300 ppmv was an increase of 29% and 66% respectively in shoot and root biomass after 57 days of growth (Schenk *et al.*, 1995). Nevertheless, the increase in the shoot biomass harvested over a four-month period was between 16% and 38% when the atmospheric CO<sub>2</sub> concentration was increased from 380 ppmv to 670 ppmv (Schenk *et al.*, 1997a). Similarly, during an experiment, where the plants were continually defoliated, increasing the concentration of CO<sub>2</sub> resulted in an increased shoot and root biomass throughout the 81 days (Ryle and Powell, 1992). Nevertheless Ryle, Powell and Davidson (1992c) observed that, after an initial period, the relative growth rate of plants grown at current ambient conditions was similar to those grown at enhanced CO<sub>2</sub> levels. However, the effect of elevated CO<sub>2</sub> on the growth rate is affected by the irradiance levels experienced by the crop with high light levels resulting in a greater increase than low light levels (Hardacre *et al.*, 1986). On the other hand, planting density did not influence the effect of climate change on the yield of white clover (Schenk *et al.*, 1995).

As regards the root:shoot ratio, Ryle and Powell (1992) reported that it was decreased by both increased concentrations of CO<sub>2</sub> and elevated temperatures. Nijs, Impens and Behaeghe (1989b), and Ryle *et al.* (1992c) also observed the same effect with increasing CO<sub>2</sub> concentrations. In contrast, Scheidegger and Nösberger (1984) reported an increase in the root:shoot ratio with increasing CO<sub>2</sub> levels in the first

growth period, whereas, after defoliation, CO<sub>2</sub> had no effect. Significantly, in a field experiment the effect of increased concentrations of CO<sub>2</sub> on the root:shoot ratio was influenced by the application rate of nitrogen (Jongen *et al.*, 1995). This suggests that the reduction in the root:shoot ratio may be partly due to some physical restriction of root growth.

#### **2.2.2.2.2 Effect of Global Warming on the Rate of Photosynthesis**

The rate of gross leaf photosynthesis at light saturation was stimulated by 90% when CO<sub>2</sub> was enhanced from 350 ppmv to 600 ppmv (Nijs *et al.*, 1989b). According to Ryle *et al.* (1992b), the rate of whole plant photosynthesis was elevated by 57—75% when CO<sub>2</sub> levels were augmented from 340 ppmv to 680 ppmv and the temperature was increased by 3°C. Nevertheless, they only observed a 17—29% increase in the rate of net leaf photosynthesis measured at constant irradiance levels and enhanced CO<sub>2</sub> levels. As the irradiance increased the stimulation of the rate of net photosynthesis with elevated CO<sub>2</sub> levels also increased (Ryle *et al.*, 1992b). As with perennial ryegrass, the stimulation of the rate of CO<sub>2</sub> uptake was the result of increases in the rate of photosynthesis and the photochemical efficiency (Nijs and Impens, 1993; Nijs *et al.*, 1989b). Ryle *et al.* (1992b) and Nijs *et al.* (1989b) observed no reduction in the rate of net photosynthesis with acclimatisation.

#### **2.2.2.2.3 Effect of Global Warming on the Rate of Dark Respiration**

The eleven-fold increase in rates of dark respiration observed by Nijs *et al.* (1989b) when CO<sub>2</sub> levels were enhanced from 350 ppmv to 600 ppmv may be partly connected to the increased plant size. However, the rate of leaf respiration may also

have been elevated. In contrast, Ryle *et al.* (1992b) observed no significant effect on leaf or plant rates of respiration expressed per kilogram of material.

#### **2.2.2.2.4 Effect of Global Warming on the Rate of Transpiration**

Augmenting the ambient levels of CO<sub>2</sub> increases the resistance of the stomata and decreased transpiration rates which results in increasing the water use efficiency (Ryle *et al.*, 1992b; Nijs *et al.*, 1989b). This effect was observed to be enhanced under increasing irradiance levels (Ryle *et al.*, 1992b).

#### **2.2.2.2.5 Effect of Global Warming on the Leaf and Stolon Growth Characteristics**

Augmenting the CO<sub>2</sub> concentration results in significantly increased lamina weight per unit area (Clark *et al.*, 1995) and weight of a fully expanded trifoliate leaf. (Clark *et al.*, 1995; Ryle *et al.*, 1992c). After a six-week experiment, white clover plants grown at 680 ppmv had twice the total expanded leaf surface than those grown at 340 ppmv (Ryle, *et al.*, 1992c). Increasing leaf number contributed 70% of the increase, with the remaining 30% due to the expansion of the individual leaf area. The leaf appearance rate and the lamina area per petiole were unaffected by enhanced CO<sub>2</sub> concentrations, although there was a tendency for the leaf area to increase under elevated CO<sub>2</sub> and increasing temperature (Clark *et al.*, 1995). Enhanced CO<sub>2</sub> increases the number of stolons rather than the number of leaves per plant (Ryle and Powell, 1992). The specific leaf area can be reduced by elevated CO<sub>2</sub> (Ryle and Powell, 1992; Overdieck and Reining, 1986). Ryle *et al.* (1992c) observed a similar trend for the first half of a six-week experiment. However, in the second three-week period the specific leaf areas for both CO<sub>2</sub> treatment levels were similar. On the other

hand, Manderscheid, Bender, Schenk and Weigel (1997) observed that the specific leaf area was not affected by elevated CO<sub>2</sub> concentrations.

#### **2.2.2.2.6 Effect of Global Warming on Nitrogen Concentration and the Biologically Fixed Nitrogen**

Increased CO<sub>2</sub> levels tends to decrease the nitrogen concentration of the root (Schenk *et al.*, 1995) and shoot (Zanetti, Hartwig, Lüscher, Hebeisen, Frehner, Fischer, Hendrey, Blum and Nösberger, 1996), although the total nitrogen in the shoot and root is increased (Zanetti *et al.*, 1996; Schenk *et al.*, 1995). Similarly, Soussana and Hartwig (1996) reported that the yield of nitrogen harvested in the plant material was augmented with elevated CO<sub>2</sub> concentrations. Nevertheless, Ryle and Powell (1992) reported that, in plants grown under enhanced CO<sub>2</sub> levels, the nitrogen concentration within the leaves fell and that of the stolons increased, although the nitrogen concentration of the root, nodules and total biomass was unaffected.

The nitrogen fixed by white clover was increased by the equivalent of 74 kg nitrogen ha<sup>-1</sup> when atmospheric CO<sub>2</sub> concentration was raised from 390 ppmv to 690 ppmv (Schenk *et al.*, 1995). Similarly, Zanetti *et al.* (1996) also reported increases in the symbiotically fixed nitrogen in swards containing white clover as either a monoculture or in a mixture. However, a greater enhancement in the fixed nitrogen was observed for mixtures. This increase in nitrogen fixation as a result of enhanced CO<sub>2</sub> could be due to an increase in the number of nodules per plant and the mean weight per nodule (Ryle and Powell, 1992). On the other hand, the increase could be due to reduced soil nitrogen availability resulting from increased nitrogen demand by the system (Zanetti *et al.*, 1996). In contrast, Crush (1993) predicted that the effect of CO<sub>2</sub> concentration on the ability of white clover to fix nitrogen would have limited effect.

### **2.2.2.3 Conclusions Regarding the Effect of Climate Change on White Clover**

The impacts of elevated ambient temperature on white clover production are that:

- leaf weight, leaf area, length of the petiole, senescence and leaf growth are enhanced;
- the growth rate of the shoot is increased;
- the rates of photosynthesis and respiration are increased;
- the rate of stolon branching declines;
- the rate of transpiration and stomatal conductance are reduced; and
- the growth rate of the root is either decreased or is not affected.

Increasing the ambient CO<sub>2</sub> concentration:

- increases shoot and root biomass production;
- has no conclusive effect on root:shoot ratio, but the effect can be influenced by the application rate of fertiliser;
- enhances the rate of photosynthesis, but no acclimatisation was observed;
- has no conclusive effect on the rate of respiration;
- decreases the rate of transpiration;
- increases the lamina weight;
- has either no effect or increases the rate of leaf appearance and lamina area;
- either reduces or has no effect on the specific leaf area;
- decreases the nitrogen concentration of the leaves, although the effect on the stolons and root is variable;

- either has no effect or increases the total nitrogen yield; and
- increases the rate of biologically fixed nitrogen by the white clover.

### **2.2.3 Effect of Global Warming on Production of Mixed Perennial Ryegrass and White Clover Swards**

#### **2.2.3.1 Effect of Global Warming on the Sward Yield and Composition**

Global warming tends to increase the yield harvested from mixed swards as Overdieck and Reining (1986) reported a 60% increase in production at ambient temperatures. Similarly, Newton, Clark, Bell, Glasgow and Campbell (1994) reported that augmented CO<sub>2</sub> levels resulted in an increase of 7.2% in herbage accumulation and 50.6% in root material. However, this increase in above-ground pasture growth with elevated CO<sub>2</sub> concentrations was only significant when the temperature was maintained at the highest level used in the experiment.

According to Schenk *et al.* (1997a), the enhancement in yield for the mixed sward was lower than that observed for pure white clover swards. Increasing the CO<sub>2</sub> concentration from 330 to 900 ppmv for simulated grass – white clover swards resulted in an increase in growth rate of 32%, whereas the growth rate was increased by 39% and 52% respectively for grass and white clover grown in monoculture (Hardacre *et al.*, 1986). However, the actual yield of white clover harvested decreased when the ambient concentration of CO<sub>2</sub> was elevated from 525 ppmv to 700 ppmv, although both yields were significantly higher than for ambient conditions (Clark, Newton, Bell and Glasgow, 1997). On the other hand, the growth rates of the perennial ryegrass were suppressed for CO<sub>2</sub> concentrations of 525 ppmv compared to

either the control (325 ppmv) or CO<sub>2</sub> concentrations of 700 ppmv. The response of mixed swards to elevated CO<sub>2</sub> also varied during the season (Clark *et al.*, 1997). They observed that the growth rates of the white clover increased throughout the season with the biggest increase occurring in the late autumn. Nevertheless, acclimatisation was not observed in turf taken from a mixed sward (Newton, Clark, Bell and Glasgow, 1996), although it is recognised that the CO<sub>2</sub> fertilisation effects are not necessarily independent of the duration of the experiment (Clark *et al.*, 1997). Nonetheless, according to Clark *et al.* (1997) increasing the experimental period from 1 year to 14 months actually increased the yield response.

In grass – white clover pasture turf, doubling the current ambient concentrations of atmospheric CO<sub>2</sub> (350 ppmv) is reported to have increased in the proportion of white clover from 22% to 38%, while decreasing perennial ryegrass from 34% to 22% (Newton *et al.*, 1994). Schenk *et al.* (1997a) and Zanetti *et al.* (1996) have also observed that enhancement of white clover in the sward was greater than that experienced by the perennial ryegrass component. A similar effect of white clover becoming more dominant at elevated CO<sub>2</sub> concentrations is described for a mixed white clover – *Poa pratensis* sward (Stewart and Potvin, 1996), and in mixtures containing several species (Clark *et al.*, 1997; Campbell *et al.*, 1995; Newton, Clark, Bell, Glasgow, Tate, Ross, Yeates and Sagger, 1995). Nevertheless, Overdieck and Reining (1986) observed that the growth of the shoots and the roots of perennial ryegrass continued to be enhanced at elevated CO<sub>2</sub> levels, whereas the growth of white clover was unaffected after the first cut. It has also been observed that increased ambient daily temperature at current concentrations of CO<sub>2</sub> increased the

proportions of white clover biomass and leaf area in the mixed sward (Faurie, Soussana and Sinoquet, 1996).

The yield response of the components to enhanced levels of CO<sub>2</sub> varied with the application of nitrogen fertiliser. In mixed swards, when no nitrogen was applied, elevating the CO<sub>2</sub> concentration to 670 ppmv increased the white clover yield by between 20 and 42%, while the effect on the yield of perennial ryegrass ranged from a decrease of -33% to an increase of 5% (Schenk, Jäger and Weigel, 1997b). In contrast, when the nitrogen fertiliser was increased to 200 kg ha<sup>-1</sup>, Schenk *et al.* (1997b) observed that the enhancement in the yield of white clover (16—38%) tended to be reduced, whereas the enhancement in the yield of perennial ryegrass tended to be increased (-1—9%) relative to the situation where no nitrogen was applied. Similarly, the proportion of white clover biomass and leaf area in the mixed sward was decreased by nitrogen fertiliser applications (Faurie *et al.*, 1996).

According to Zanetti *et al.* (1996), the change in the sward composition with elevated CO<sub>2</sub> will have implications for the enhancement in the nitrogen fixed symbiotically by the white clover. As the proportion of white clover in the sward increases the demand for nitrogen by the sward will decrease and therefore the decrease in the available soil nitrogen is reduced. Consequently, as the nitrogen fixed by the white clover is a function of the nitrogen demands of the system, the increase in nitrogen fixation with elevated CO<sub>2</sub> will decline as the proportion of white clover in the sward increases.

However, Hardacre *et al.* (1986) observed that the growth responses of perennial ryegrass, white clover and the mixed sward were influenced by the light levels under which they were grown. In the cases of white clover and mixed swards, there was

also a significant interaction between the light levels and the CO<sub>2</sub> concentration. At high light levels this resulted in the response of the mixed sward to increased CO<sub>2</sub> levels being of the same magnitude as the ryegrass sward, whereas at low light levels and low rates of fertiliser applications the response was similar to that of a white clover sward.

#### **2.2.3.2 Effect of Global Warming on Mixed Swards under Water Stress**

Under water-stressed conditions, the rate of photosynthesis of a mixed sward was enhanced under elevated CO<sub>2</sub> (Newton *et al.*, 1996). The root length density was also significantly increased by CO<sub>2</sub>, but was not significantly affected by soil moisture deficit. However, at elevated CO<sub>2</sub> levels the root length density was unaffected by drought, whereas it was reduced under ambient concentrations of CO<sub>2</sub>. Nevertheless, this was not observed for the above ground growth rate. After rewatering, the growth of the turf under ambient conditions was enhanced. Thus, the relative enhancement of increased CO<sub>2</sub> concentrations on the above-ground growth was reduced. The effect of water stress at elevated CO<sub>2</sub> on the composition of the turf was to reduce the proportion of white clover and increase the proportion of C<sub>3</sub> grasses (Newton *et al.*, 1996).

#### **2.2.3.3 Effect of Global Warming on the Leaf Growth Characteristics**

In a 1:1 mixture of perennial ryegrass and white clover, the number of leaves per plant does not appear to be affected, but the area of each leaf is apparently increased under elevated CO<sub>2</sub> conditions (Overdieck and Reining, 1986). The specific leaf area is also observed to decline for both the perennial ryegrass and white clover components. However, it was only significant for the white clover (Overdieck and

Reining, 1986). Similarly, Clark *et al.* (1997) observed that the specific leaf area of the white clover declines with elevated CO<sub>2</sub> levels, although the specific leaf area of the perennial ryegrass is not affected.

The growth response per growing point to enhanced CO<sub>2</sub> levels is increased at higher temperatures (Clark *et al.*, 1995). Similarly, elevating the ambient concentration of CO<sub>2</sub> also tends to increase the growth per growing point, although this is not significant (Clark *et al.*, 1997). Nevertheless, the number of white clover growing points increases with elevated CO<sub>2</sub> concentrations and this effect is the major determinant of the increased yield (Clark *et al.*, 1997). On the other hand, Clark *et al.* (1997) observed that for CO<sub>2</sub> concentrations of 525 ppmv the number of grass tillers at the start of the second year is approximately half of those found at the 325 ppmv and 700 ppmv CO<sub>2</sub> levels.

As white clover tends to have a higher growth rate than perennial ryegrass in the spring and summer (Woledge, Reyner, Tewson and Parsons, 1992) the enhanced CO<sub>2</sub> concentrations may result in a greater stimulus to white clover than perennial ryegrass. This will result in the proportion of white clover in the sward being increased. Elevating the ambient concentration of CO<sub>2</sub> increases the height of the clover component, whereas the height of the perennial ryegrass component declines (Schenk *et al.*, 1997b).

#### **2.2.3.4 Conclusions Regarding the Effect of Climate Change on Mixed Perennial Ryegrass and White Clover Swards**

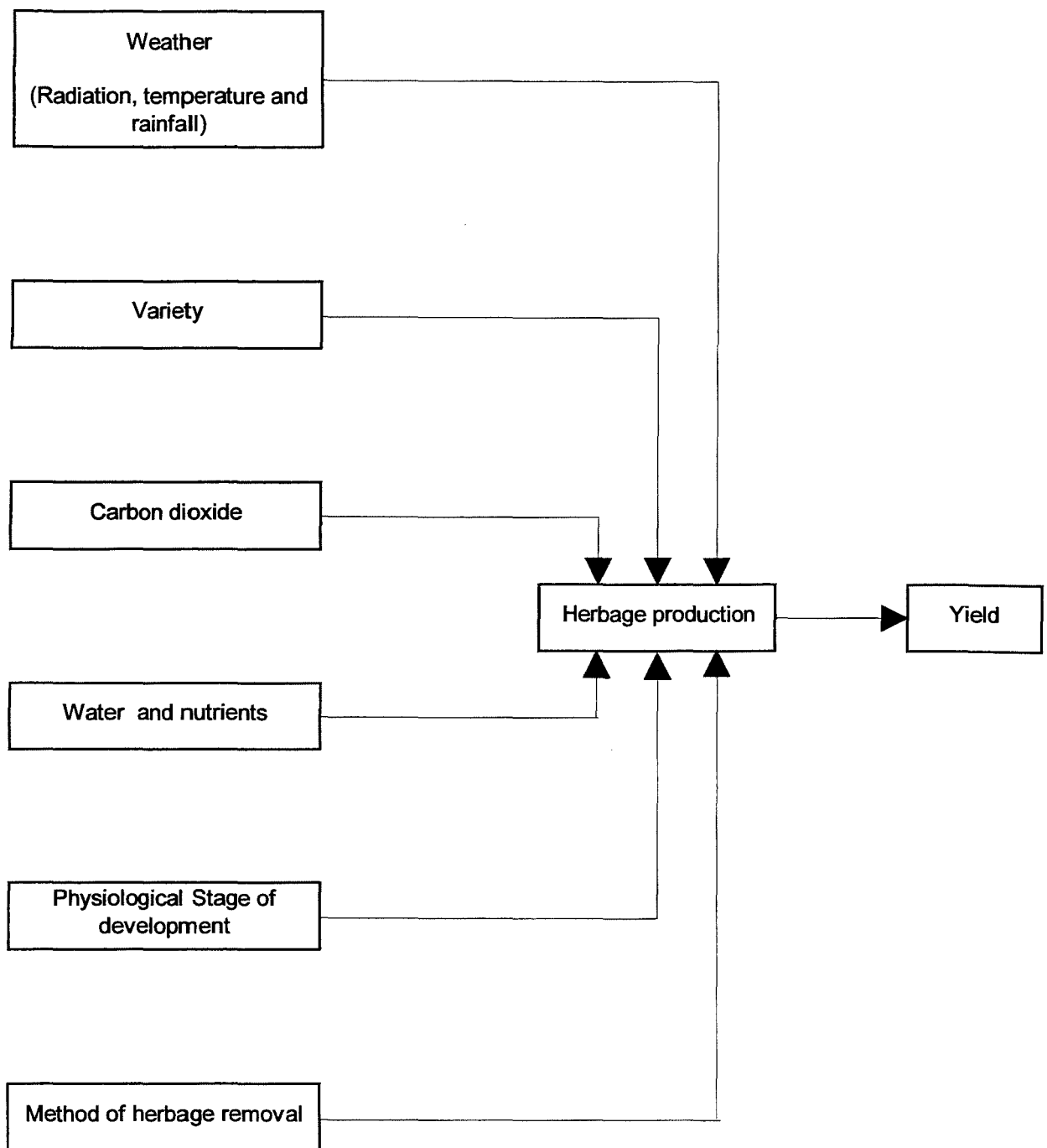
Augmenting the ambient concentration of CO<sub>2</sub> modifies the growth of mixed swards in the following ways:

- the yield increases;
- the percentage of white clover in the sward is also increased;
- the change in yield for each component is dependent on the rate of nitrogen fertiliser applications and the level of water stress experienced by the crop;
- leaf area increases;
- the specific leaf area of white clover declines while the reduction the specific leaf area for the perennial ryegrass component is either non-existent or is smaller than exhibited by the white clover component; and
- the number of growing points for the white clover component tends to increase, whereas the number of perennial ryegrass tillers declines.

### **2.3 Modelling Forage Production**

The objective of modelling forage production systems is to simulate interactions of all the important factors influencing the growth of forage. This requires an understanding of a complex system, which can be broken down into several discrete elements. This review summarises the developments and evolution of forage production models. The elements that require to be modelled include environmental and physiological factors and are summarised in Figure 2-1. In grasslands and moorlands that contain more than one species, recognition is needed that there is competition between herbage species for the limited resources. This can therefore result in different responses between species to enhanced CO<sub>2</sub> and temperature, and thus it is inappropriate to model pastures as a “green box” (Campbell *et al.*, 1995) or predict the effect on mixtures by studying monocultures (Díaz, 1995).

There are two broad approaches to modelling, namely empirical and mechanistic. The first is based on statistically derived relationships. This requires a large bank of data from which the relationships are estimated. Empirical models tend to be specific to the localities from where the data were originally derived. The second approach, mechanistic modelling, requires that the mechanisms of plant growth are described within the model. These mechanisms include photosynthesis, respiration and partitioning. The relationships describing the individual processes are empirically derived. The representation of the photosynthesis process in mechanistic crop growth models varies from empirically based relationships through semi-empirical descriptions to complex biochemical models.



*Figure 2-1 Environmental and Physiological Factors that affect Herbage Yield.*

An inherent part of the modelling process is the validation phase. This consists of two stages, namely;

1. validation at the level of the assumptions; and

2. validation of the simulations based on the combination of individual equations.

However, the validation process is essentially a subjective procedure. This is because models may be partly dependent upon non-quantitative, subjective knowledge and the available data may be of doubtful validity (Dillon and Anderson, 1990).

The review of modelling will be divided into the following sections:

1. empirical grassland models;
2. models of the photosynthesis process;
3. mechanistic grassland models;
4. models of the grazing situation; and
5. systems models.

### **2.3.1 Empirical Grassland Models**

Sinclair and Corrall (1978), from trials on irrigated and non-irrigated swards, proposed a model to predict the observed differences in yield. Subsequently Corrall (1984) developed the model by dividing the growing season into three stages in order that the effect of the changes in physiological development of the grasses could be incorporated. Herbage growth rate has also been described by Brereton and Ryan (1984) as a function of the daily temperature from May-September, radiation and the soil moisture deficit.

A number of empirical models describing grass growth have been derived from grassland manuring (GM20) trials (Morrison, Jackson and Sparrow, 1980). Doyle, Corrall, Thomas, Le Du and Morrison (1983) used this data to determine site

classifications, which were an indication of the potential of the sites. In this model, they predicted grass growth from available water capacity, mean summer rainfall and fertiliser nitrogen as well as the site classification. Doyle and Lazenby (1984) further developed the model in order that it could predict growth at a range of sites. The effect of the cut number, assuming the herbage was cut every four weeks, and soil nitrogen was incorporated into an empirical model of grass growth by Doyle, Ridout, Morrison and Edwards (1986). The model was further extended to describe the partitioning of the grass area between cutting and grazing for the dairy herd, and the effects of altitude on grass growth were also incorporated (Doyle and Edwards, 1986). Dowle, Doyle, Spedding and Pollot (1988) incorporated latitude, altitude and drainage into a similar model.

Empirical models have also been developed to predict the yield of grass – clover swards. In the model developed by Doyle and Morrison (1983) the quantity of nitrogen available for grass growth is dependent on the applied nitrogen, the level of soil nitrogen, the nitrogen ‘fixed’ by the clover and the nitrogen excreted by the grazing stock. Soil moisture has an effect on the uptake of the various forms of nitrogen. Grass growth is dependent on the available nitrogen, whereas clover growth is dependent on the seasonal growth profiles, water and a competition effect that is based on the quantity of nitrogen fertiliser applied. Doyle, Morrison and Peel (1987) refined the model to incorporate the effects of temperature, radiation and soil moisture deficit on clover growth. In the model by Cacho, Finlayson and Bywater (1995), forage production is predicted by a sigmoid curve with leaf mass as the input variable. The effects of botanical composition, soil temperature, water and nutrient availability modifies the herbage production.

There are even fewer multi-species models of forage production. Armstrong, Gordon, Hutchings, Illius, Milne and Sibbald (1997a) have developed an empirical model of forage growth for seven dwarf-shrub dominated and five grass-dominated vegetation types which are commonly found in hill areas of the UK. The empirical description of grass growth is based on models of Doyle and Lazenby (1984), and Doyle and Edwards (1986). Blackburn and Kothmann (1989) have developed a model that predicts the standing biomass, crude protein and digestibility of live and dead parts of a sward, which can be composed of several different species of grasses and forbes. The model was designed to be integrated with a diet selection model. However, it does not simulate growth.

The effect of climate change on the distribution of agricultural grassland in England and Wales was predicted by the model developed by Rounsevell, Brignall and Siddons (1996), which is based on a range of yield and trafficability/poaching classes. Incorporated in the model is a simple water balance model based on potential evapotranspiration and rainfall. However, the model is based on empirical evidence under current climatic conditions and does not predict dry-matter yield. As such, this model is only appropriate for assessing the long-term effects of changes in climate rather than year-to-year variability.

### **2.3.2 Models of the Photosynthesis Process**

#### **2.3.2.1 Empirical Models**

Most empirical models describe net photosynthesis in terms of the relative growth rate (Torssell and Kornher, 1983). Thus, Bootsma and Boisvert (1991) and Bootsma, Boisvert and Dumanski (1994) described net biomass production as a function of the

maximum rate of biomass production, which is modified by the fraction of the day that is overcast and the maximum leaf photosynthesis rate. Incorporated in Bootsma and Boisvert (1991) and Bootsma *et al.* (1994) models of grass and lucerne production are the effect of moisture stress on yield and the effects of temperature and daylength on the cutting schedule. Armstrong and Castle (1995) have described a model of grass growth where the maximum growth rate is modified by radiation, crop weight, nitrogen supply, temperature and the soil water balance. Models have also been developed where the rate of net photosynthesis is dependent on the radiation received by the crop and the efficiency of conversion of radiation to herbage (e.g. Broad and Hough, 1993; Brereton and Hope-Cawdery, 1988). These models have often been refined to include Beer's law and thus the effect of light attenuation through the canopy (e.g. Maas, 1993; Amir and Sinclair, 1991a). The effect of increased atmospheric CO<sub>2</sub> can be incorporated into these models by predicting the increase in the efficiency of conversion with increased CO<sub>2</sub> from experimental data (Easterling, Crosson, Rosenberg, McKenney and Frederick, 1992).

According to Johnson and Thornley (1984), the rectangular hyperbola is the most widely used empirical model for describing leaf gross photosynthesis. In their model, the function was integrated through the canopy to calculate canopy gross photosynthesis. The light intercepted by the canopy is described by Beer's law, and the photosynthetic activity of each leaf is a function of the irradiance received by that leaf. The effect of shading of leaves from direct sunlight on the rate of photosynthesis can be included in the model. However, this model results in a poor fit to experimental data (Marshall and Biscoe, 1980).

### **2.3.2.2 Semi-Empirical Models**

The non-rectangular hyperbola is a semi-empirical model, which results in an extremely good fit to the experimental data (Marshall and Biscoe, 1980). As with the rectangular hyperbola, the radiation intercepted by the leaf is described by Beer's law, and canopy gross photosynthesis is calculated by integration. With the non-rectangular model, the maximum rate of photosynthesis and the initial slope of the curve (photochemical efficiency) reflect the underlying physiological process; however, this is not the case with the rectangular hyperbola (Marshall and Biscoe, 1980). Johnson, Parsons and Ludlow (1989) have extended the model of photosynthesis, outlined by Marshall and Biscoe (1980), to mixed canopies. Thornley *et al.* (1991) even incorporated the effect of increasing atmospheric CO<sub>2</sub> concentrations by defining the maximum rate of leaf photosynthesis and the photochemical efficiency as functions of the atmospheric CO<sub>2</sub> levels. The photochemical efficiency is also dependent on the CO<sub>2</sub> conductance and the photorespiration constant, but independent of temperature (Thornley *et al.*, 1991). A positive correlation between the maximum rate of leaf photosynthesis and the leaf nitrogen concentration has been observed in perennial ryegrass (Woledge and Pearse, 1985) as well as a number of other species (DeJong, 1982; Sands, Cromer, and Kirschbaum, 1992, Sheriff, 1992; Connor, Hall and Sadras, 1993). However, the function describing the relationship between leaf CO<sub>2</sub> assimilation and leaf nitrogen may differ between species (Sinclair and Horie, 1989). This has been incorporated into the model by either modifying the rate by the nitrogen concentration of the plant (Thornley, *et al.* 1991) or by a linear ramp function (Thornley, 1991).

Hikosaka and Terashima (1995) have developed a model of leaf photosynthesis where the dependence of the process on radiation is described by the non-rectangular hyperbola. The quantity of the enzymes per leaf and light harvesting complexes required for the photosynthesis process are determined by the model; from this the nitrogen content per leaf was calculated. However, the model calculated the allocation of nitrogen between the photosynthetic components for a given maximum rate of leaf photosynthesis.

#### **2.3.2.2.1 Incorporating the Daily Fluctuations of Temperature and Irradiance in the Model of Photosynthesis**

The rate of gross photosynthesis is dependent on temperature and irradiance that fluctuate throughout the day. Johnson and Thornley (1984) have incorporated the daily variations in temperature and irradiance into their model of gross photosynthesis, while still using the mean daily values for these variables. This has required the expansion of the equation for photosynthesis into a Taylor series. The coefficients of variation of temperature and radiation, the correlation coefficient between temperature and radiation, and the second derivatives of photosynthesis with temperature and radiation incorporate the effects of the daily fluctuations into the model.

Sands (1995a) has developed a simple model that calculates the daily canopy photosynthesis that incorporates the within-day variation in radiation. The model assumes that photosynthetically active radiation within the canopy follows Beer's law, and the effect of daily variation in radiation in the model has been simplified into formulae that require no integration. The variation in temperature has been incorporated into the model by calculating the function for the average morning and average afternoon temperature. The effects of nitrogen on canopy photosynthesis

have been built into the model by assuming that the maximum rate of leaf photosynthesis is linearly dependent on nitrogen concentration (Sands, 1995b). However, this assumes that the nitrogen concentration in the canopy declines with the solar radiation intercepted and that the nitrogen is optimally distributed for photosynthesis (Sands, 1995b). Nevertheless, within the model, the effects of soil and water status have been ignored. The daily model of canopy photosynthesis (Sands, 1995a) has been extended to calculate annual canopy photosynthesis, incorporating the daily and seasonal variations in radiation and temperature (Sands, 1996). The annual intercepted radiation is calculated from daily values, which incorporated details of the canopy structure and development. The acclimatisation of photosynthesis to seasonal variation in temperature has also been included in the model.

#### **2.3.2.3 Complex Biochemical Models**

Hunt *et al.* (1991) have described a model of net photosynthesis where the rate is dependent on the intracellular and ambient concentration of CO<sub>2</sub>, and the stomatal and the boundary layer resistance. This is modified by the effect of temperature on the rates of gross photosynthesis and respiration, and the effect of transpiration on the rate of gross photosynthesis. The effects of CO<sub>2</sub> and shoot nitrogen levels modified by light intensity on fixation rate are incorporated into the model. Long (1991) has also described a biochemical based mechanistic model of leaf photosynthesis that was developed by Farquhar, von Caemmerer and Berry (1980) and Farquhar and von Caemmerer (1982). The model describes the response of Rubisco, an enzyme that fixes the CO<sub>2</sub> in the plant, and photosynthesis to the concentration of CO<sub>2</sub> and O<sub>2</sub>. The rate of photosynthesis in the canopy is calculated separately for leaves in direct sunlight and in the shade. From the model, the effects of increased temperature and

enhanced CO<sub>2</sub> levels on the rate of photosynthesis can be predicted. In the model described by Long (1991), the intracellular concentration of the CO<sub>2</sub> is dependent on leaf temperature. However, the intracellular CO<sub>2</sub> concentration is defined as a function of the ambient concentration of CO<sub>2</sub>, the rate of net photosynthesis and the stomatal conductance to water vapour in the models described by Baldocchi (1994) and Nikolov, Massman and Schoettle (1995). In the equation described by Nikolov *et al.* (1995), the boundary layer conductance to water vapour is also included, whereas Leuning (1995) included the water vapour deficit. However, this results in a model where the rates of photosynthesis and the stomatal conductance are interdependent and affect each other through the intracellular concentration of CO<sub>2</sub> (Aphalo and Jarvis, 1993). Nikolov *et al.* (1995) solved the set of equations using an iterative method. However, in non-linear biological systems iterative solutions can become unstable, and thus Baldocchi (1994) developed an analytical solution.

Nevertheless, these models are describing net photosynthesis at the level of the leaf. Friend and Cox (1995) and Leuning, Kelliher, De Pury and Schulze (1995) have developed models that are solved simultaneously for net photosynthesis and stomatal conductance at the canopy level. In the model by Leuning *et al.* (1995) evapotranspiration was then determined using the Penman-Monteith (Monteith, 1965) equation that incorporates stomatal conductance. Nevertheless, the models do not incorporate the effects of water stress on stomatal conductance, and hence the effects of stress on net photosynthesis and transpiration are not included.

### **2.3.3 Mechanistic Models**

Mechanistic models of forage growth have followed three broad strategies. The first describes crop growth in terms of net photosynthesis with other factors modifying the quantity of assimilate that is converted into actual growth. The net photosynthesis has been described either in terms of the growth rate or the radiation use efficiency. The second approach describes all crop growth processes at the level of the individual tiller, whereas the level used for the third approach is at the total sward. The process of photosynthesis in the second approach has been calculated from either the rectangular or the non-rectangular hyperbola. In the models of the total sward, the process of photosynthesis has been described by the non-rectangular and rectangular hyperbolae as well as other empirical equations. The one exception is the model of forage production described by Hunt *et al.* (1991) in which a biochemical description of photosynthesis is employed.

#### **2.3.3.1 Models Describing the Process of Net Photosynthesis**

In the model of grass growth, described by Brereton and Hope-Cawdery (1988), the rate of dry-matter growth is dependent on the solar radiation received at the crop surface, the efficiency of conversion and whether the plant is vegetative or reproductive. The effect of hourly air temperatures is also incorporated into this model. Broad and Hough (1993) extended the model to include the effect of the leaf area index on the radiation intercepted.

Torssell and Kornher (1983) developed a model of grass growth where the herbage mass in any given time period is dependent on the existing biomass, the leaf area index and the weather. The influence of weather is based on indices for temperature,

radiation and plant available soil water. The model developed by Lemaire, Gosse and Chartier (1984) based the process of accumulating aerial dry matter on the global incident radiation, leaf area index, the efficiency of conversion of photosynthesis and a root:shoot partitioning coefficient. Within the model, temperature and nitrogen have an effect on the ratio of leaf expansion and leaf senescence. The relationship between dry-matter production, radiation and the effect of conversion of solar energy was modelled by Szász (1984). The physiological stage of development as well as factors relating to soil, water and climate affected the efficiency of conversion of radiation to dry matter. The influences of management factors are described in the model by empirical relationships or statistical variables.

Gustavsson, Angus and Torssell (1995) have developed a model that simulates the above-ground dry-matter growth, concentrations of crude protein and the metabolisable energy of stands of timothy, where the dry-matter growth is based on the model by Torssell and Kornher (1983). The crude protein concentration is estimated in relation to nitrogen uptake and the dry matter growth of the grass. The nitrogen uptake is dependent on the supply of available soil nitrogen, which is dependent on the fertiliser applied, mineralisation and the removal of the crop, and the capacity of the crop to absorb nitrogen. The factors used to determine the metabolisable energy content are the crude protein concentration, the phasic development, which is dependent on temperature and photoperiod, and the digestibility of the organic matter. The model is used to predict the dry matter, crude protein content and the metabolisable energy of timothy and meadow fescue swards in Sweden (Gustavsson *et al.*, 1995; Gustavsson, 1995). However, the first sampling date from the swards is used as calibration data for the model, and the forward

predictions are made for the subsequent harvests (Gustavsson *et al.*, 1995; Gustavsson, 1995).

### **2.3.3.2 Models at the Level of the Individual Tiller**

Johnson, Ameziane and Thornley (1983), Johnson and Thornley (1983 and 1985) and Thornley and Verberne (1989) have developed the Hurley model of grass growth that is only concerned with modelling the vegetative phase of growth. In this model the processes of photosynthesis, respiration, partitioning of the assimilate and senescence are described. The plant in the Hurley model is divided into structural and storage components. The models of Johnson and Thornley (1983 and 1985) have extended the model of Johnson *et al.* (1983) by describing the tiller in terms of four age categories of leaves. Each age category was divided into structural and storage components. As there are usually three live leaves per tiller, each age category contains one leaf per tiller, and the fourth category contains the senescencing leaves. The effect of temperature on photosynthesis is described by a  $Q_{10}^1$  relationship by Johnson *et al.* (1983), whereas Johnson and Thornley (1983 and 1985) assumed the effect could be described by a linear relationship. In the models by Johnson and Thornley (1983 and 1985), respiration is also affected by temperature. The models by Johnson *et al.* (1983) and Johnson and Thornley (1983) have assumed that crop growth is unconstrained by water and nutrients. The effect of available nitrogen (Johnson and Thornley, 1985) has also been incorporated into the model. In this model, temperature has an effect on the rate of nitrogen uptake, which then affects the partitioning of the assimilate between the root and shoot compartments. Thornley and

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<sup>1</sup>  $Q_{10}$  – the factor by which the rate increases for a temperature increment of 10° K

Verberne (1989) have extended the modelling of nitrogen in the model by describing the influence of animal excreta on the soil nitrogen and organic matter. Thornley *et al.* (1991) and Thornley (1996) have extended the Hurley model by including the effects of ambient concentration of CO<sub>2</sub> and water on grass growth. Parsons, Harvey, and Johnson (1991) have further developed the model of Johnson and Thornley (1983, 1984) in order to incorporate the growth of clover in grass – clover swards, where clover growth is described at the level of the stolon.

### **2.3.3.3 Models of the Total Sward**

McMurtrie and Wolf (1983) developed a model of grass and tree growth that described the processes of photosynthesis, respiration and assimilate partitioning. In the model, the intensity of the radiation reaching the grass is reduced by the radiation intercepted and reflected by the tree canopy. Competition for water and nutrients is incorporated into the model by modifying the rates of photosynthesis for the grass component and reducing the fraction of the assimilates partitioned to the leaves of the trees. Caloin (1994) modified this model in order to analyse dry-matter partitioning in *Dactylis glomerata*. The plant is assumed to be vegetative and is described in two compartments, namely the shoot and the root. Duru, Durcrocq and Tirilly (1995) have developed a model of the vegetative regrowth of cocksfoot and tall fescue swards, where photosynthesis is described as a function of the global radiation, the leaf area index and the radiation use efficiency. Incorporated in the model is the influence of nitrogen status on the leaf area index and the radiation use efficiency. The nitrogen status is defined as the ratio of the herbage nitrogen concentration to the optimum nitrogen concentration.

The model developed by Sheehy, Cobby and Ryle (1980) describes the sward canopy in terms of the vegetative development. However, grass growth is not constrained by water and nutrients. The processes of photosynthesis, respiration, partitioning of assimilate and senescence are outlined in the model. They assumed that the effect of the different stages of environmental factors would exert their influence on the partitioning assimilates through their affect on canopy photosynthesis, and thus fixed allocation rules are used to partition the photosynthate. The sward is described in terms of the leaf, root and stem compartments. Sheehy *et al.* (1996) extended the earlier model to include the effects of nitrogen and CO<sub>2</sub> on vegetative grass growth. The photosynthetic response to changes in ambient CO<sub>2</sub> concentrations is based on the work of Thornley *et al.* (1991). In order to include the effects of nitrogen on plant growth the sections in the earlier model describing the partitioning of assimilates and the transformation of assimilates into plant tissue are replaced. The rates of growth of the structural material were controlled by the concentration of nitrogen in the substrate pool. However, if there are insufficient carbohydrates to provide the skeleton of the new material and to support the respiratory cost of synthesis, the actual growth of the structural material are modified. Within the model, the translocation of substrates from one compartment to another is described using the concept of pressure driven flow that has been modelled by Sheehy, Mitchell, Durand, Gastal and Woodward (1995).

Saugier, Ripley, and Lueke (1974) incorporated the effect of water use on crop growth in their model of a matador grassland. They modelled the growth in terms of radiation, energy balance and micro climate, water flow, soil heat flow, photosynthesis and production. Doyle, Barrs, and Bywater (1989) described a model of the growth of a grass sward where the processes included were photosynthesis, effect of water and

nutrient availability, assimilate partitioning and senescence. In New Zealand, where the model was developed, the primary limiting nutrient is phosphate. The effects of water and phosphate stress are incorporated into the model by reducing the photosynthate in proportion to the stress experienced by the crop. The sward is divided into the leaf, stem and root. In this model, the only process affected by temperature is photosynthesis. In the Stockpol model developed by Marshall, McCall and Johns (1991), the pasture is divided into leaf, stem and dead material. Equations dependent on the pasture mass, time of year and the pasture cover govern the movement of pasture among the compartments.

The mechanistic models previously described are not capable of modelling a sward containing several plant communities. However, the SPUR (simulation of production and utilization of rangelands) model described by Hanson *et al.* (1988) can simultaneously simulate the growth and competition effects of a forage that consists of a homogenous mixture of up to fifteen plant species at a range of sites. In the model, the flow of carbon and nitrogen through the shoots, roots, propagules and standing dead are described for each species. In the SPUR model, actual soil evaporation is a function of the soil moisture status, and the potential transpiration is calculated as a function of the actual evaporation and the leaf area index (Hanson *et al.*, 1993). Within the model, the effects of enhanced CO<sub>2</sub> have been incorporated by assuming that it only affects the rate of net photosynthesis.

Laidlaw, Withers and Watson (1994) have developed a model of a grass – clover sward where photosynthesis is described by the rectangular hyperbola. The maximum rate of photosynthesis is adjusted by temperature and soil moisture deficit.

The model describes vegetative and reproductive growth by modifying the assimilate partitioning and senescence coefficients. Thornley, Bergelson and Parsons (1995) have developed a model of a grass – clover sward with the purpose of investigating the steady states, stability and species dynamics of a mixed community. The sward is a horizontally homogenous soup with no differentiation of the herbage mass into leaves or shoots. An empirical relationship based on the leaf area index is used to describe photosynthesis, and the effects of the response of the sward to radiation and CO<sub>2</sub> concentration are subsumed into the parameters. The assimilate is partitioned between the grass and clover component in relation to their effective leaf areas, and the partitioning between root and shoot is based on a teleonomic (goal – seeking) model (Thornley and Johnson, 1990). Included in the representation of the sward is a description of nitrogen uptake and a simple soil model.

#### **2.3.3.4 Models Based on a Biochemical Photosynthesis Model**

Hunt *et al.* (1991) developed a model of grass growth for a C<sub>3</sub> and a C<sub>4</sub> species grown as monocultures. Within the model, the effects of water stress, nitrogen uptake and the ambient concentration of CO<sub>2</sub> are represented. It is assumed that the rates of photosynthesis and transpiration are influenced by the water stress experienced by the crop. The translocation of the carbon and nitrogen in the plant are dependent on currently available photosynthate and the total nitrogen content of the root respectively, and the level of water stress experienced by the crop. The effects of mycorrhizal fungi, bacteria and above-ground herbivores on the crop are also incorporated in the model. The model developed by Chen and Coughenour (1994) also describes grass growth for C<sub>3</sub> and C<sub>4</sub> species. The plant growth sub-model describes leaf photosynthesis, stomatal conductance, biomass production and the

spatial distribution of the root system. The canopy microclimate, soil water dynamics and soil thermal dynamics are also described in this framework.

#### **2.3.4 Models of the Grazing Situation**

Forage production and quality can be greatly influenced by the grazing management of swards. Animal intake of forages can be described by empirical and mechanistic models. One approach adopted in mechanistic models is to describe the intake in terms of factors that impose limits to intake. Another approach was to describe intake in terms of the eating characteristics of the animal.

The empirical relationships between animal and feed characteristics and intake have been described by several empirical models (e.g. Agricultural Research Council, 1980; Christian, Freer, Donnelly, Davidson, and Armstrong, 1978; Graham, Black, and Faichney, 1976). In these models, the typical animal characteristics included are weight and/or age. The attributes of the feed usually included are either metabolisability or feed quality and/or availability. In modelling the intake of the grazing dairy cow, Meijs and Hoekstra (1984) incorporated green herbage availability and compound feeds.

Mechanistic models that have assumed that herbage availability is the only limiting factor have been outlined by Zemmeling (1980), Johnson and Parsons (1985), Parsons *et al.* (1991), Woodward and Wake (1993) and Woodward, Wake and McCall (1995). Woodward and Wake (1993) and Woodward *et al.* (1995) assumed that the intake rate of an animal depended only on the available herbage mass in the field. In relationships described by Zemmeling (1980), Johnson and Parsons (1985), and Parsons *et al.* (1991), intake was related to the maximum possible intake and either

the quantity of green herbage (Zemmelink, 1980) or the mass of leaves (Johnson and Parsons, 1985; Parsons *et al.*, 1991) per unit area. The model by Parsons *et al.* (1991) was capable of describing the intake of the grass and clover components for grass – white clover mixtures. Thornley and Verberne (1989) have extended the model of Johnson and Parsons (1985) to describe actual intake in terms of carbon and nitrogen.

In the MIAMH model (Genin and Quiroz, 1993), the potential physical capacity of the animal has an effect on intake. The model describes the composition of the diet for ruminants grazed on rangelands. As well as the physical limit to intake, the model incorporates four other indices. These indices relate to the probability of encountering the species, the composition of the bite in terms of leaf and stem, the quality of the species and the preference of the animal for the particular species.

In the models, described by Forbes (1977) and Finlayson, Cacho and Bywater (1995), both the physical and physiological limits to intake on a daily basis are considered. The physical limits are related to the size of the animal or the rumen and the digestibility of the feed, whereas the physiological limits are dependent on the energy requirements of the animal. Further developments to the model described by Forbes (1977) included decreasing the time-step to one minute and increasing the detail describing the limits to intake and the resulting rate at which the energy becomes available (Forbes, 1980). Doyle *et al.* (1989) presumed that daily intake was determined by the minimum of the physiological limits, the physical limits and the herbage availability. The herbage availability limits are described by the equation of Zemmelink (1980).

The models of Armstrong and Sibbald (1992), Baker, Bourdon and Hanson (1992), Forbes and Hodgson (1985), Parsons, Thornley, Newman and Penning (1994a) and Ginnett and Demment (1995) describe intake in terms of bite size, bite rate and time spent grazing. Armstrong and Sibbald (1992) describe the off-take of six grassland types and heather for a heather moorland where off-take is partitioned between each of the vegetation types. This model has been extended to describe the intake of ewes and lambs grazing seven dwarf-shrub-dominated and five-grass-dominated vegetation types, which are commonly found in the hill areas of the UK (Armstrong, Gordon, Hutchings, Illius, Milne and Sibbald, 1997b). In this model, the intake is limited by either the diet digestibility or grazing time. In the latter case, intake is predicted from the bite weight and the bite rate. Diet selection is affected by the crude protein content of each of the functional plant groups in the FORAGE model (Baker *et al.*, 1992). The model of Parsons *et al.* (1994a) describes the selection and intake of two species in a mixed sward where the vertical and horizontal distribution of the components differed within the field. The rate of intake in the model of Ginnett and Demment (1995) behaves as a Michaelis – Menten function. However, when the model was tested on giraffes, it was found that the average time required to crop a bite affected the mean bite size, and that prehension and mastication were not mutually exclusive activities. In contrast, in sheep it has been observed that prehension and mastication biting were mutually exclusive (Penning, Parsons, Orr and Treacher, 1991). Nevertheless, in the spring Penning *et al.* (1991) observed that the sward surface height affected grazing time, ruminating time, bite rate, mastication rate and bite mass for sheep. However, the total intake was unaffected.

Thornley, Parsons, Newman and Penning (1994) have developed a model of forage intake and selection in a two – species temperate sward that was based on cost – benefit analysis. Thus, the ruminant livestock attempts to select grass and clover from the sward so that marginal benefit equalled marginal cost. The results of this model suggest that the upper limit on uptake is not defined by the physiological or morphological constraints. The model developed by Newman, Parsons, Thornley, Penning and Krebs (1995) describes the intake of ruminant livestock from a two – species sward. In this model, an abbreviated model of the gut is combined with a terminal reward function that describes the probability that the animal would survive to reproduce. The livestock must choose between grazing species 1, grazing species 2, grazing whichever species it encounters, resting or ruminating.

#### ***2.3.4.1 Modelling the Effect of Climate on Forage Quality***

Forage quality can also be affected by the climate. Empirical models describing the effects of temperature, radiation, photoperiod and water stress on the metabolisable energy content (Fagerberg and Nyman, 1994) and crude protein content (Fagerberg and Nyman, 1995) of a timothy and meadow fescue mixture, red clover sward, and a grass – red clover mixture have been developed. However, the crude protein model requires that the initial value of the protein content has to be determined for each situation (Fagerberg and Nyman, 1995).

#### **2.3.5 Systems Models**

The systems models considered incorporate plant growth, the grazing animal and the output of the livestock. However, currently there are only four systems models of farmed livestock that are commonly grazed in Britain, with three describing beef

production (Hanson *et al.*, 1993; Doyle *et al.*, 1989; Doyle *et al.*, 1987) and one describing the sheep system (Cacho *et al.*, 1995).

Doyle *et al.* (1987) have described an empirical model of a beef production system from grass – white clover swards which describes herbage production, dry-matter intake and liveweight gain. A model of a rotationally grazed 18-month beef system, incorporating mechanistic models of grass growth, intake and animal growth, was described by Doyle *et al.* (1989). The animal growth component was based on the model by Oltjen, Bywater, Baldwin and Garrett (1986). The model developed by (Hanson *et al.*, 1993) also incorporates models of pasture growth (SPUR – Hanson *et al.* 1988), intake (FORAGE – Baker *et al.*, 1992) and the Colorado beef cattle production model (CBCPM). CBCPM is a modification of the Texan A&M beef model developed by Sanders and Cartwright (1979). It is a life-cycle simulation model that operates at the level of the individual animals.

The system model of sheep production developed by Cacho *et al.* (1995) incorporates a simplified pasture production model and mechanistic models of intake and sheep production (Finlayson *et al.*, 1995). The pasture production under grazing was estimated by a sigmoid equation.

## **2.4 Conclusion**

The forage models developed to date have been primarily concerned with predicting herbage production during the growing season (e.g. Sheehy *et al.*, 1996; Caloin, 1994; Broad and Hough, 1993; Johnson and Thornley 1985 and 1983; Johnson *et al.*, 1983; McMurtrie and Wolf, 1983) or have been used as a grassland management tool (Dowle *et al.*, 1988; Doyle *et al.*, 1986; Doyle and Lazenby, 1984; Doyle *et al.*, 1983).

The models developed as grassland management tools examine the effects of climate, and the decisions taken by the farmer with respect to nitrogen application rates and cutting dates on the production of herbage. Gustavsson *et al.* (1995) have predicted the forage metabolisable energy and crude protein content of the herbage, while Parsons *et al.* (1991) have incorporated off-take of the herbage by sheep.

The models that have incorporated the effects of enhanced CO<sub>2</sub> on the photosynthesis process and are thus capable of exploring the effects of climate change on the production of forage have been developed by Hunt *et al.* (1991), Thornley *et al.* (1991), Sheehy *et al.* (1996) and Hanson *et al.* (1988). However, Hunt *et al.* (1991), Thornley *et al.* (1991) and Sheehy *et al.* (1996) have described only the vegetative growth phase of a sward containing a single species. In contrast, the model of Hanson *et al.* (1988) can describe the growth of 15 plant species.

The effect of water stress on forage production has been incorporated into the models developed by Thornley (1996), Rounsevell *et al.* (1996), Cacho *et al.* (1995), Hanson *et al.* (1993), Hunt *et al.* (1991), Doyle *et al.* (1989), Doyle *et al.* (1987), Szász (1984), Doyle and Morrison (1983), McMurtrie and Wolf (1983), Torrsell and Kornher (1983) and Saugier *et al.* (1974). Nevertheless the models developed by Rounsevell *et al.* (1996), Cacho *et al.* (1995), Doyle *et al.* (1987), and Doyle and Morrison (1983) are empirical, and thus can only be successfully used under the conditions and sites for which they were developed. The inclusion of water stress in the mechanistic model permits the effects of climate on forage production to be studied. However, only the models of Thornley (1996), Hanson *et al.* (1993) and Hunt *et al.* (1991) describe the effects of water stress and the ambient concentration of CO<sub>2</sub> on crop development,

and thus are suitable for studying the effect of climate change on forage production. Nevertheless, the models by Hanson *et al.* (1993) and Hunt *et al.* (1991) have been developed for describing species more commonly found in the US, and the model of Hunt *et al.* (1991) is primarily concerned with predicting the effect of climate change on microbes, fungi and soil fauna. In contrast, the Hurley model incorporating the water sub-model developed by Thornley (1996) is primarily concerned with describing vegetative growth at the level of the individual tiller.

In conclusion, the aim of this study is to examine the effects of changes in climate and enhanced ambient CO<sub>2</sub> concentrations on the production of grass and grass – white clover swards throughout the growing season as well as the production of livestock grazing these swards. Consequently, a model of grass and grass – white clover growth has been constructed which describes vegetative and reproductive growth as well as the effect of water and nutrient stress on crop development. The removal of herbage by both cutting and grazing has been described within the model. This model is specified in Chapter 3 and the models describing livestock production are outlined in Chapter 4.

## CHAPTER 3

### *THE FORAGE MODEL*

#### **3.1 Introduction**

This chapter will describe the structure of the model of grass – white clover sward under cutting and its extension to include the removal of herbage through grazing.

#### **3.2 Grass – White Clover Model**

The model of the sward assumes that it is either pure grass or a grass – white clover mixture and that the sward is divided into paddocks. Forage production is calculated for each paddock on a daily basis and is presumed to be dependent on herbage mass, temperature, radiation, atmospheric CO<sub>2</sub> concentration, available nutrients and water. There are five state variables, leaf dry matter ( $D_L$ , kg DM ha<sup>-1</sup>), stem dry matter ( $D_S$ , kg DM ha<sup>-1</sup>), root dry matter ( $D_R$ , kg DM ha<sup>-1</sup>), dead material ( $D_D$ , kg DM ha<sup>-1</sup>) and the leaf area index of the crop ( $L$ , ha leaf ha<sup>-1</sup> (ground)). There are also five driving variables, namely the mean daily temperature ( $T$ , °C), the level of photosynthetically active radiation ( $PAR$ , MJ ha<sup>-1</sup> (ground) day<sup>-1</sup>), the atmospheric concentration of CO<sub>2</sub> (CO<sub>2</sub>, kg CO<sub>2</sub> m<sup>-3</sup>), the available moisture ( $W$ , mm) and the available nitrogen ( $N$ , kg ha<sup>-1</sup> day<sup>-1</sup>). Essentially temperature, photosynthetically active radiation and atmospheric CO<sub>2</sub> concentration are presumed to modify the rates of gross photosynthesis ( $P$ , kg CO<sub>2</sub> ha<sup>-1</sup> (ground) day<sup>-1</sup>). Net photosynthesis ( $P_n$ , kg CO<sub>2</sub> ha<sup>-1</sup> (ground) day<sup>-1</sup>) is then derived by deducting respiration losses ( $R$ , kg CO<sub>2</sub> ha<sup>-1</sup> (ground) day<sup>-1</sup>). Intuitively water and nutrient stress will modify the rate of gross

photosynthesis. However, the effect of stress on crop growth has been estimated from grass and grass – white clover harvestable yield data. The rate of respiration is not modelled as a constant proportion of gross photosynthate and consequently harvestable yield will be more closely related to net photosynthesis than gross photosynthesis. Hence, it has been assumed in the model that water and nutrient stress modify the rate of net photosynthesis. The net photosynthate, modified for stress, is then partitioned between leaf, stem and root. The resultant leaf, stem and root material are then either harvested or pass into the dead pool through decomposition. There is no evidence for acclimatisation occurring in either white clover (Ryle *et al.*, 1992b; Nijs *et al.*, 1989b) or grass – white clover swards (Newton *et al.*, 1996) under global warming and the evidence for acclimatisation for pure grass swards is inconclusive (Jones *et al.*, 1996a; Jones *et al.*, 1996b; Ryle *et al.*, 1992a). It is therefore assumed within the model that the effect of enhanced CO<sub>2</sub> and temperature is not diminished over time.

For convenience the model may be divided into seven sub-models concerned with:

1. calculation of photosynthetically active radiation;
2. effect of temperature;
3. photosynthesis;
4. respiration;
5. water and nutrient stress;
6. assimilate partitioning and senescence; and finally
7. herbage accumulation under cutting.

A schematic representation of the pasture growth is shown in Figure 3-1. The principal variables and parameters contained in the model are listed in Appendix I.

Within the model, time is measured in days from 1 January. The grass and white clover components within the model are distinguished separately and are divided into leaf, stem, root and dead material. In the case of grass, 'stem' comprises tillers and latent developing leaves as well as true stem. For white clover the stolons and petioles are included in the 'stem' component.

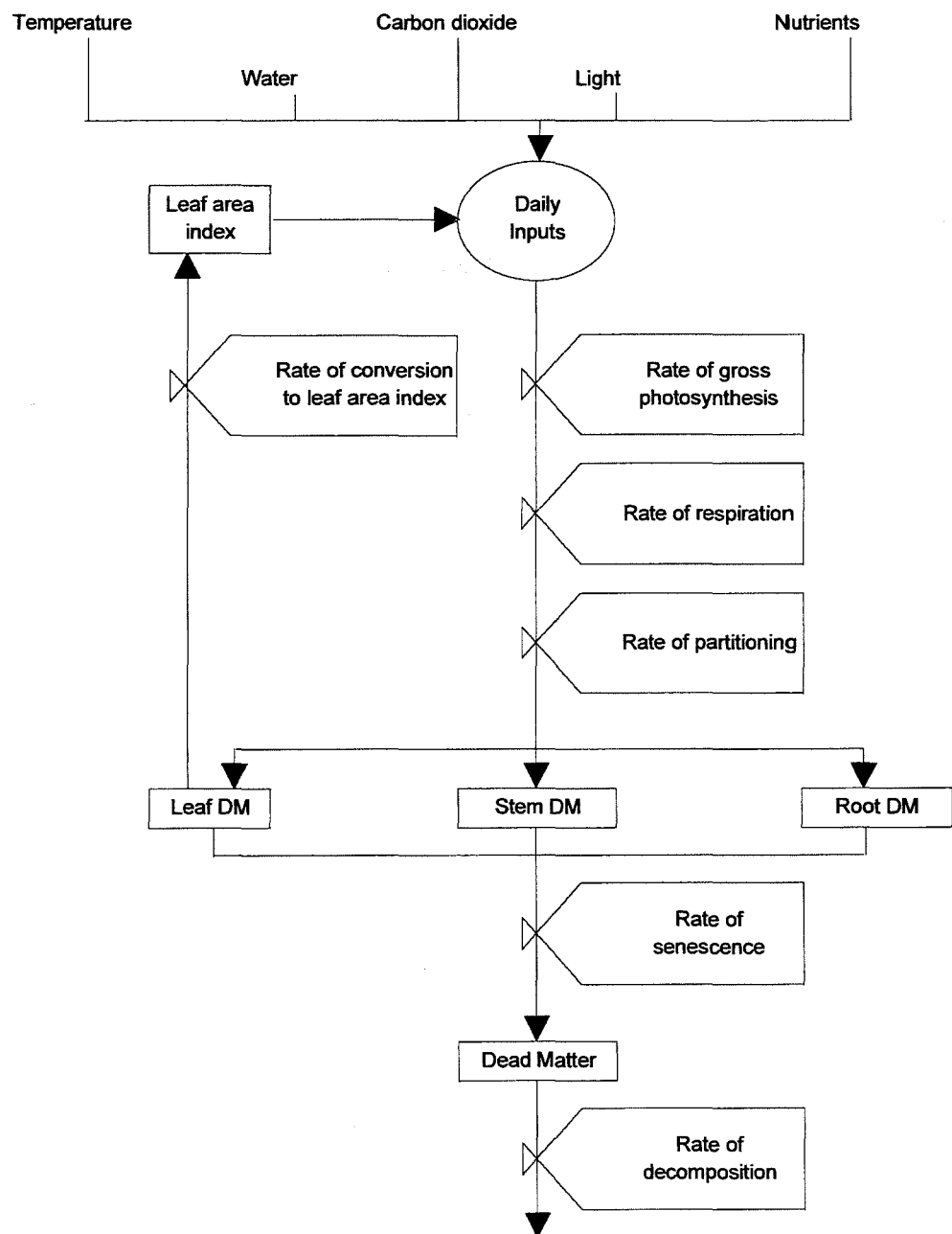


Figure 3-1 A schematic representation of the pasture growth model.

### 3.2.1 Sub-model 1 – Calculation of Photosynthetically Active Radiation

The solar radiation which is photosynthetically active is within the 400 to 700 nm waveband, which constitutes approximately 50% of the total radiation (Jones, 1985). The photosynthetically active radiation (PAR, MJ ha<sup>-1</sup> (ground) day<sup>-1</sup>) is therefore half the actual daily radiation ( $I_o$ , MJ ha<sup>-1</sup> (ground) day<sup>-1</sup>) which is related to the duration of bright sunshine hours and can be calculated from the 'Angstrom' formula (van Wijk and Scholte Ubing, 1963):

$$I_o = RX * (\alpha + \beta * \text{Sun}/\text{DayLen}) \quad (3.1)$$

where Sun is the number of sunshine hours per day and RX (MJ ha<sup>-1</sup> (ground) day<sup>-1</sup>) is the daily clear sky radiation. Following McGechan and Glasbey (1988), the following formulae are used to calculate the coefficients alpha and beta:

$$\alpha = A1 - A2 * \text{Lat} \quad (3.2)$$

$$\beta = B1 + B2 * \text{Lat} \quad (3.3)$$

where Lat is the latitude of the site in degrees, and A1, A2, B1 and B2 are selected for each month of the year from 'Angstrom' tables shown in Table 3-1 (McGechan and Glasbey, 1988). The calculation of RX, the daily clear sky radiation in MJ ha<sup>-1</sup> (ground) day<sup>-1</sup>, and of DayLen, the effective day length in hours are described in Appendix II.

*Table 3-1 'Angstrom' coefficients for estimating the daily radiation from sunshine hours.*

<b>Month</b>	<b>A1</b>	<b>A2</b>	<b>B1</b>	<b>B2</b>
January	0.34507	0.00301	0.34572	0.00495
February	0.33459	0.00255	0.35533	0.00457
March	0.36690	0.00303	0.36377	0.00466
April	0.38557	0.00334	0.35802	0.00456
May	0.35057	0.00245	0.33550	0.00485
June	0.39890	0.00327	0.27292	0.00578
July	0.41234	0.00369	0.27004	0.00568
August	0.36243	0.00269	0.33162	0.00412
September	0.39467	0.00338	0.27125	0.00564
October	0.36213	0.00317	0.31790	0.00504
November	0.36680	0.00350	0.31467	0.00523
December	0.36262	0.00350	0.30675	0.00559

### **3.2.2 Sub-model 2 – Effect of Temperature**

Temperature is primarily seen in the model as modifying the rates of gross photosynthesis and maintenance respiration. It is assumed in the model that the average daily temperature, even under global warming conditions, is less than or equal to the optimum temperature for growth. Hence the rate of photosynthesis or respiration is modelled as increasing linearly with temperature to a maximum at 20°C.

Essentially the growing season is presumed to commence when the average daily air temperature exceeds 4.5°C ( $St_g$ , °C) for seven consecutive days for grass (Broad and Hough, 1993) and 6°C ( $St_c$ , °C) for white clover (Peel, 1988). Should daily air temperature in spring fall again below these thresholds, growth ceases and recommences when the temperature requirement has been re-attained. In the autumn, grass growth is assumed to cease when the average daily temperature falls below 8°C (Broad and Hough, 1993) ( $End$ , °C) for three consecutive days and does not restart before the spring. In the model, it has been presumed that white clover growth also ceases at 8°C.

### 3.2.3 Sub-model 3 – Photosynthesis

#### 3.2.3.1 Monoculture

The canopy gross photosynthesis ( $P$ , kg CO<sub>2</sub> ha<sup>-1</sup> (ground) day<sup>-1</sup>) for a monoculture is defined by Johnson and Thornley (1984) as:

$$P = \frac{1}{2 * \Theta} * \int_0^L \left( Ph + P_{max} - \sqrt{(Ph + P_{max})^2 - 4 * \Theta * P_{max} * Ph} \right) d\ell \quad (3.4)$$

where

$$Ph = \frac{\alpha * k * PAR}{(1 - m)} * e^{-k\ell} \quad (3.5)$$

and PAR is the photosynthetically active radiation in MJ ha<sup>-1</sup> (ground) day<sup>-1</sup>,  $P_{max}$  is the leaf photosynthetic rate in kg CO<sub>2</sub> ha<sup>-1</sup> (leaf) day<sup>-1</sup> at saturating light levels ( $PAR \rightarrow \infty$ ) and at ambient atmospheric CO<sub>2</sub> concentration,  $k$  is the light extinction coefficient,  $m$  is

the leaf transmission coefficient,  $L$  is the canopy leaf area index ( $\text{ha (leaf) ha}^{-1}$  (ground)),  $\ell$  is the cumulative leaf area index,  $\alpha$  is the photochemical efficiency of photosynthesis ( $\text{kg CO}_2 \text{ MJ}^{-1}$ ) and  $\Theta$  is a dimensionless single leaf photosynthesis parameter with values between 0 and 1.

However, although Long (1991) reported that the optimum temperature for photosynthesis increases with enhanced  $\text{CO}_2$ , this has not been included in the model. A complex biochemical model would be required to model changes in the optimum temperature under global warming, necessitating the definition of additional parameters. Nevertheless, the rate of leaf photosynthesis at saturating light levels ( $P_{\max}^T$ ,  $\text{kg CO}_2 \text{ (leaf) day}^{-1}$ ) is dependent on temperature (Woledge and Dennis, 1982) and following Johnson and Thornley (1983) the functional form is described as:

$$P_{\max}^T = P_{\max}^0 * \frac{T - T_0}{T_{\text{Ref}} - T_0} * \text{DayLen}; \quad \text{for } T > T_0 \quad (3.6)$$

where  $P_{\max}^0$  ( $\text{kg CO}_2 \text{ (leaf) h}^{-1}$ ) is the maximum hourly rate of leaf photosynthesis,  $T$  ( $^{\circ}\text{C}$ ) is the mean daily temperature,  $T_0$  ( $^{\circ}\text{C}$ ) is the temperature at which photosynthesis ceases and  $T_{\text{Ref}}$  ( $^{\circ}\text{C}$ ) is the temperature at which  $P_{\max}$  is unconstrained by temperature. The light saturated daily rate of photosynthesis can then be calculated by multiplying the maximum hourly rate of leaf photosynthesis ( $P_{\max}^0$ ,  $\text{kg CO}_2 \text{ ha}^{-1} \text{ (leaf) h}^{-1}$ ) by the effective day length (DayLen, h), where DayLen is based on civil twilight as defined by equation (II.4), Appendix II.

The maximum rate of leaf photosynthesis is also affected by the irradiance in which the leaves are grown (Woledge, 1971). However, two contrasting approaches have been used to model the effect of irradiance on the rate of leaf photosynthesis. The first approach developed by Ludlow and Charles-Edwards (1980) assumes that the relationship is a linear function which passes through the origin. It is assumed to be a function of the irradiance intercepted by the leaves and can therefore be described by the extinction coefficient and the leaf area index of the sward. The second approach proposed by Acock, Charles-Edwards, Fitter, Hand, Ludwig, Warren-Wilson and Withers (1978) assumes that the leaves maintain sufficient photosynthetic machinery in their growth environment. Consequently, the maximum rate of leaf photosynthesis is a constant and is defined by the leaves at the top of the canopy. However, Johnson *et al.* (1989) observed that the former approach tended to under-predict, whereas the latter approach tended to over-predict the rate of canopy photosynthesis. Hence, Johnson *et al.* (1989) developed an equation which seeks to describe the variation in the maximum rate of leaf photosynthesis with the intercepted irradiance. Accordingly,  $P_{\max}$  (kg CO<sub>2</sub> (leaf) day<sup>-1</sup>) is presumed to be described by:

$$P_{\max} = P_{\max}^T * \left[ 1 - \frac{\varepsilon}{2} * (1 - e^{-(k * L)}) \right] \quad (3.8)$$

where  $\varepsilon$  is the rate of decline of  $P_{\max}^T$  (kg CO<sub>2</sub> (leaf) day<sup>-1</sup>) with irradiance. Although there is no theoretical basis for equation (3.8), it is a physiological plausible approximation (Johnson *et al.*, 1989). It is assumed in equation (3.4) that photosynthetically active radiation and temperature do not vary throughout the day. The photochemical efficiency is stimulated for both grass (Nijs *et al.*, 1989a) and white

clover (Nijs and Impens, 1993; Nijs *et al.*, 1989b) under global warming. Consequently, following Thornley *et al.* (1991), the effect of atmospheric CO<sub>2</sub> on  $\alpha$  and  $P_{\max}^0$  can be described by:

$$\alpha = \alpha_{\max} * \frac{1 - w}{\tau * CO_2} \quad (3.9)$$

$$P_{\max}^0 = \frac{P_{\max}^{CO_2}}{\left(1 + \frac{KP_{\max}}{CO_2}\right)} \quad (3.10)$$

where  $\alpha_{\max}$  is the maximum value of the photochemical efficiency (kg CO<sub>2</sub> MJ<sup>-1</sup>), CO<sub>2</sub> is the atmospheric concentration of CO<sub>2</sub> (kg CO<sub>2</sub> m<sup>-3</sup>),  $\tau$  is the CO<sub>2</sub> conductance parameter (m s<sup>-1</sup>) and  $w$  represents the photorespiration coefficient constant (kg m<sup>-2</sup> s<sup>-1</sup>). The CO<sub>2</sub> saturated value of the maximum hourly rate of leaf photosynthesis is denoted by  $P_{\max}^{CO_2}$  (kg CO<sub>2</sub> ha<sup>-1</sup> (leaf) h<sup>-1</sup>) and  $KP_{\max}$  is the CO<sub>2</sub> concentration at which  $P_{\max}^{CO_2}$  is half its maximal value (kg CO<sub>2</sub> m<sup>-3</sup>). Following Thornley (1991), the ambient atmospheric CO<sub>2</sub> concentration measured in ppmv was converted to kg CO<sub>2</sub> m<sup>-3</sup> by:

$$CO_2 = CO_{2, \text{ppmv}} * 10^{-6} * \frac{K_0}{T + K_0} * \frac{Atm}{Atm_{\text{Sea}}} * \rho_{CO_2} \quad (3.11)$$

where  $CO_{2, \text{ppmv}}$  is the atmospheric concentration of CO<sub>2</sub> measured in ppmv,  $T$  is the ambient temperature measured in degrees Celsius,  $K_0$  is 0°C measured in degrees Kelvin and  $\rho_{CO_2}$  (kg CO<sub>2</sub> m<sup>-3</sup>) is the density of CO<sub>2</sub> at one atmosphere.  $Atm$  (Pa) and

$Atm_{Sea}$  (Pa) are the atmospheric pressure measured at the site and sea-level respectively.

Following Johnson *et al.* (1983), the leaf area index is assumed to be proportional to the leaf dry weight. It is therefore assumed that leaf area index ( $L$ , ha (leaf) ha<sup>-1</sup> (ground)) and leaf dry weight ( $D_L$ , kg DM ha<sup>-1</sup>) are related as follows:

$$L = A * D_L \quad (3.12)$$

where  $A$  is the specific leaf area (ha leaf (kg DM)<sup>-1</sup>). It is recognised that equation (3.12) represents a gross simplification in that it implies that the specific leaf area ( $A$ , ha leaf (kg DM)<sup>-1</sup>) is not temperature dependent. However, data to describe the effects of temperature on the specific leaf areas of grass and white clover over an entire growing season are not available, although there is evidence to suggest that increased temperature will increase the specific leaf area (Davidson and Robson, 1986). In addition, given the way that the effects of temperature on photosynthesis are modelled (equation (3.6)), arguably the effects on the specific leaf area may already have been incorporated indirectly. In contrast, enhanced atmospheric CO<sub>2</sub> concentrations tend to decrease the specific leaf area of both the grass (Ferris *et al.*, 1996b; Ryle *et al.*, 1992a; Overdieck and Reining, 1986) and white clover (Ryle and Powell, 1992; Overdieck and Reining, 1986). However, the differences for grass were not always significant (Overdieck and Reining, 1986), and for both components the magnitude of the differences between the specific leaf area under elevated and current concentrations of CO<sub>2</sub> varied throughout the season (Overdieck and Reining, 1986). As there is a lack of data that describe how specific leaf area changes with

CO<sub>2</sub>, it has had to be assumed in the model that CO<sub>2</sub> concentrations do not affect the specific leaf area of either of the components.

### 3.2.3.2 Mixture

The rate of canopy photosynthesis for a mixture can be derived by summing the rate for the individual components (Johnson *et al.*, 1989). In the case of a grass – white clover mixture, the irradiance incident on the leaves for either component depends upon the leaf area of both grass and white clover. The rate of canopy gross photosynthesis ( $P_j$ , kg CO<sub>2</sub> ha<sup>-1</sup> (ground) day<sup>-1</sup>) for either component ( $j$ ) is represented by:

$$P_j = \frac{1}{2 * \Theta} * \int_0^L \left( Ph_j + P_{\max, j} - \sqrt{(Ph_j + P_{\max, j})^2 - 4 * \Theta * P_{\max, j} * Ph_j} \right) \frac{d\ell_j}{d\ell} d\ell \quad (3.13)$$

where

$$Ph_j = \frac{\alpha_j * k_j * PAR}{(1 - m_j)} * e^{-(k_g * \ell_g + k_c * \ell_c)} \quad (3.14)$$

and  $d\ell_j/d\ell$  describes the vertical distribution of each component through the depth of the canopy ( $L$ , ha (leaf) ha<sup>-1</sup> (ground)). Subscript  $g$  refers to grass and  $c$  to white clover. The dependency of the maximum rate of leaf photosynthesis on the irradiance in which the leaves are grown is described by:

$$P_{\max} = P_{\max}^T * \left[ 1 - \frac{\varepsilon}{2} * \left( 1 - e^{-(k_g * \ell_g + k_c * \ell_c)} \right) \right] \quad (3.15)$$

where  $P_{\max}^T$  (kg CO<sub>2</sub> (leaf) day<sup>-1</sup>) is the rate of leaf photosynthesis at saturating light levels modified by the effect of temperature and  $\epsilon$  is the rate of decline of  $P_{\max}^T$  with irradiance. In order to solve equation (3.13), it is necessary to describe the vertical leaf distribution through the depth of the canopy. In grass – white clover swards, under continuous grazing, the vertical distribution of the grass and white clover leaves is approximately homogenous (Johnson *et al.*, 1989). However, in a cut sward, Woledge (1988) observes a predominance of white clover in the upper layers of the canopy. The effects of rotational grazing on a sward are similar to a cutting regime. It is therefore probable that white clover will predominate in the upper layers of a rotationally managed sward. The vertical distribution of white clover through the sward has been estimated from data obtained from Woledge *et al.* (1992) and can be described by:

$$\frac{d\ell_c}{d\ell} = a1 * \frac{\ell}{L} - a2 * \left[ \frac{\ell}{L} \right]^2 \quad (3.16)$$

where  $\ell$  (ha (leaf) ha<sup>-1</sup> (ground)) is the cumulative leaf area index which is leaf area index being used at the specified step in the integration process,  $L$  (ha leaf ha<sup>-1</sup> (ground)) is the leaf area index of the sward and  $a1$  and  $a2$  are constants. The proportion of grass leaf area at a given depth in the canopy can therefore also be determined. Simpson's rule has been used to integrate equation (3.13).

#### 3.2.4 Sub-model 4 – Respiration

The total respiration requirement of the sward can be divided into growth and maintenance components. The growth respiration is related to the gross

photosynthate, and the maintenance respiration is related to the mass of the plant and the growth conversion efficiency (Thornley, 1976). The maintenance respiration requirement increases linearly with temperature (Johnson and Thornley, 1983). The following equation describes the respiration requirements of each component ( $R_j$ , kg CO<sub>2</sub> ha<sup>-1</sup> day<sup>-1</sup>) of the sward:

$$R_j = (1 - Y_j) * P_j + r_j * Y_j * M_j * \frac{T - T_0}{T_{Ref} - T_0}; \quad \text{for } T > T_0 \quad (3.17)$$

where  $Y_j$  is the growth conversion coefficient (kg CO<sub>2</sub> (kg CO<sub>2</sub>)<sup>-1</sup>) measuring the conversion yield of the growth process,  $r_j$  (kg CO<sub>2</sub> (kg DM)<sup>-1</sup> day<sup>-1</sup>) is the maintenance respiration coefficient,  $P_j$  (kg CO<sub>2</sub> ha<sup>-1</sup> day<sup>-1</sup>) is the canopy gross rate of photosynthesis and  $M_j$  (kg DM ha<sup>-1</sup>) is the total dry-matter weight of the particular component  $j$  (Johnson and Thornley, 1983). As the effect of increased ambient CO<sub>2</sub> on the rate of respiration per kilogram is inconclusive for pure grass swards (Ryle *et al.*, 1992a; Schapendonk and Goudriaan, 1995; Bunce and Caulfield, 1991) and is reported as having no effect in white clover swards (Ryle *et al.*, 1992b), it has been assumed within the model that enhanced CO<sub>2</sub> has no effect on the rate of respiration.

### 3.2.5 Sub-model 5 – Water and Nutrient Stress

The effect of a reduction in the availability of water or plant nutrients will be to reduce the rate of net photosynthesis of each component, either by reducing the efficiency of photosynthesis or by reducing the length of the growing period. The effects of water and nutrient stress on photosynthesis have been modelled by reducing the net photosynthate in proportion to the stress experienced by the crop.

The principal limiting nutrient for pasture in Scotland is nitrogen. The daily available nitrogen ( $N$ ,  $\text{kg ha}^{-1} \text{ day}^{-1}$ ) is expressed as a proportion of the nitrogen at saturating level ( $N_{\text{max}}$ ,  $\text{kg ha}^{-1} \text{ day}^{-1}$ ). The available soil water ( $W$ ,  $\text{mm}$ ) is expressed as a proportion of the soil water required for maximum growth ( $W_{\text{max}}$ ,  $\text{mm}$ ). The empirically derived relationships expressing the effect of water and nutrient stress on the photosynthate for grass and white clover have been estimated from part of the GM23 data (J. Gilbey, *personal communication*). The proportionate reduction in photosynthesis due to stress for grass ( $\phi_g$ ) and white clover ( $\phi_c$ ) are presumed to be described by:

$$\phi_g = \left( \beta_1 * \sqrt{W/W_{\text{max}}} + \beta_2 * \sqrt{N/N_{\text{max}}} \right)^2 \quad (3.18)$$

$$\phi_c = \beta_3 + \beta_4 * W/W_{\text{max}} \quad (3.19)$$

where  $\beta_1$ — $\beta_4$  are constants. Where nitrogen is non-limiting, the empirical observations and the fitted equations imply that white clover is slightly less sensitive to water stress than grass.

### **3.2.5.1 Estimation of Nitrogen Availability**

The amount of nitrogen ( $N$ ,  $\text{kg ha}^{-1} \text{ day}^{-1}$ ) that is available to the sward is dependent on the available pool of nitrogen in the soil, the fertiliser nitrogen applied, and the quantity of nitrogen that is biologically ‘fixed’ by the white clover. It is assumed that the soil nitrogen is released over a period of 245 days commencing from the start of the growing season. Fertiliser nitrogen was applied between 1 March and 1 April. If growth starts before 1 April, the fertiliser nitrogen is assumed to be applied ten days

after the start of growth. If this had not occurred by 1 April then the fertiliser nitrogen is assumed to be applied on that date. In grass – white clover swards, the nitrogen available to the grass that is ‘fixed’ biologically by the white clover ( $N_c$ ,  $\text{kg ha}^{-1} \text{ day}^{-1}$ ) increases linearly with the proportion of white clover ground cover following the observation of Cowling (1982) and is described by the following relationship:

$$N_c = \kappa * \frac{L_c}{L} \quad (3.20)$$

where  $L$  ( $\text{ha (leaf) ha}^{-1} \text{ (ground)}$ ) is the total leaf area index of the sward,  $L_c$  ( $\text{ha (leaf) ha}^{-1} \text{ (ground)}$ ) is the leaf area index of the white clover component and  $\kappa$  is a constant. White clover can take up much of the available soil nitrogen (Vallis, Henzell, and Evans, 1977). However, according to Harris (1987), it may be assumed that in many situations no soil nitrogen is absorbed by the white clover. The application of fertiliser nitrogen to pot-grown grass – white clover mixtures has shown that ryegrass takes up approximately 95% of the available fertiliser nitrogen (Walker, Adams and Orchiston, 1956). Thus, it has been assumed that the white clover ‘fixes’ sufficient nitrogen for its own requirements and that the fertiliser and soil nitrogen are used solely by the grass component, although it is recognised that this is a simplification of what happens in reality.

#### **3.2.5.2 Estimation of Moisture Availability**

Within the model it is assumed that the sward growth is unconstrained at an average soil moisture deficit of up to 12.5 mm (Garwood, Tyson, and Sinclair, 1979). Consequently,  $W_{\max}$  (mm) is defined as:

$$W_{\max} = AWC - 12.5 \quad (3.21)$$

where AWC (mm) is the available water capacity (AWC). With regard to the availability of water, the soil is assumed to be at field capacity on 1 January. The change in available water on subsequent days is assumed to equal the difference between rainfall and the actual evapotranspiration (AET, mm day<sup>-1</sup>). The potential evapotranspiration rates (PET, mm day<sup>-1</sup>) are calculated using a Penman equation (Penman, 1948) and can be described by the following equation:

$$PET = \frac{\Delta * \frac{R_0}{L_v} + S * V}{\Delta + S} \quad (3.22)$$

where  $\Delta$  is the slope of the saturation vapour pressure (mbars °C<sup>-1</sup>),  $R_0$  is the radiation corrected for the soil heat flux (J m<sup>-2</sup>),  $L_v$  is the latent heat of vaporisation of water (J kg<sup>-1</sup>) and  $S$  is the psychrometric constant (mbars °C<sup>-1</sup>). The evaporation component due to the wind and the vapour pressure deficit is denoted by the variable  $V$  (kg m<sup>-2</sup>). The equations describing the slope of the saturation vapour pressure ( $\Delta$ , mbars °C<sup>-1</sup>), net radiation ( $R_0$ , J m<sup>-2</sup>) and the evaporation component due to wind and vapour pressure ( $V$ , kg m<sup>-2</sup>) are described in Appendix III.

Following Amir and Sinclair (1991b) the calculation of actual evapotranspiration is calculated using a two-stage model. During the stage 1, the actual evapotranspiration (AET, mm) is presumed to be equal to the potential evaporation rate (PET, mm) until the proportion of available soil water ( $W$ , mm) falls to less than 0.5 (Amir and Sinclair, 1991b). In stage 2, the actual evapotranspiration rate (AET, mm) is defined as:

$$AET = PET * (\sqrt{S_2} - \sqrt{S_2 - 1}); \quad \text{for } W < 0.5 * AWC \quad (3.23)$$

where  $S_2$  is the number of days since the proportion of available soil water fell below 0.5 and AWC (mm) is the available water capacity . When the fraction of soil water has increased to 0.5, the calculation of the actual evaporation rate returns to stage 1. Waterlogging of the ground is presumed to occur if the soil water content is at the water holding capacity for seven consecutive days.

A doubling of the current concentration of  $CO_2$  is predicted to decrease the rates of transpiration per unit of leaf area by between 25% and 50% (Cure and Acock, 1986). However, due to increases in the leaf temperature and the water vapour pressure within the leaf as a result of the decrease in the rates of transpiration (Wolfe and Erickson, 1993), transpiration rates per unit of leaf area are likely to increase. The result of a more efficient use of water per unit of leaf area does not necessarily result in a reduction of the total water requirements as global warming can result in larger plants. As the process of transpiration and photosynthesis are linked (Farquhar and Sharkey, 1982; Wong, Rowan, and Farquhar, 1979), the successful modelling of transpiration would require a more complicated form of the photosynthesis and transpiration equations. These equations would also require to incorporate the effects of water stress. Both of the equations would require additional parameters to be defined, some of which are not available for grass and white clover. It is recognised that it is a simplification, but on balance it was decided to model potential evapotranspiration by equation (3.22).

### 3.2.6 Sub-model 6 – Assimilate partitioning and senescence

The net photosynthesis is expressed as  $\text{kg CO}_2 \text{ ha}^{-1} (\text{ground}) \text{ day}^{-1}$ , which is converted to dry matter by multiplying the net photosynthesis by the efficiency of converting  $\text{CO}_2$  to dry matter ( $\theta$ ,  $\text{kg CH}_2\text{O} (\text{kg CO}_2)^{-1}$ ). Following Doyle *et al.* (1989), pasture growth occurred when there was photosynthate surplus to the requirements for tissue maintenance and growth respiration. A fixed proportion ( $\rho$ ) of the photosynthate is assumed to be partitioned to the root (Johnson *et al.*, 1983). Although enhanced  $\text{CO}_2$  affects the root:shoot ratio of both grass and white clover, the proportion of the photosynthate allocated to the root is not presumed to be altered by the  $\text{CO}_2$  concentration. This is because both increases and decreases in the ratio have been reported for both grass (Schapendonk *et al.*, 1996; Sousanna *et al.*, 1996; Jongen *et al.*, 1995; Ryle *et al.*, 1992a; Nijs *et al.*, 1989a) and white clover (Jongen *et al.*, 1995; Ryle *et al.*, 1992c; Nijs *et al.*, 1989b; Scheidegger and Nösberger, 1984) plants. The remaining photosynthate is partitioned between the leaves and stem in the proportions of  $\lambda$  and  $(1 - \lambda)$ . Losses, through senescence, offset the production of new leaf and stem material. The rates of leaf ( $\gamma_L$ ) and stem ( $\gamma_S$ ) losses control the rate of senescence of the herbage. The senescent material passes into the pool of dead material, where it remains until it decomposes at a rate of  $\gamma_D$ . The photosynthate partitioned to the above-ground herbage ( $M_G$ ,  $\text{kg DM ha}^{-1}$ ), and the daily change in the quantity of leaf ( $\Delta_L$ ,  $\text{kg DM ha}^{-1}$ ), stem ( $\Delta_S$ ,  $\text{kg DM ha}^{-1}$ ) and dead material ( $\Delta_D$ ,  $\text{kg DM ha}^{-1}$ ) for each crop are described by the following equations:

$$M_G = (1 - \rho) * P_n * \theta \quad (3.24)$$

$$\text{delta}_L = \lambda * M_G - \gamma_L * D_L \quad (3.25)$$

$$\text{delta}_S = (1 - \lambda) * M_G - \gamma_S * D_S \quad (3.26)$$

$$\text{delta}_D = \gamma_L * D_L + \gamma_S * D_S - \gamma_D * D_D \quad (3.27)$$

where  $D_L$  (kg DM ha<sup>-1</sup>),  $D_S$  (kg DM ha<sup>-1</sup>) and  $D_D$  (kg DM ha<sup>-1</sup>) represent respectively the leaf dry matter, stem dry matter and dead material per hectare. After the growing season has ended, the processes of respiration and senescence are still assumed to occur. The respiration losses are partitioned between the leaf and stem components in the proportions of  $\lambda$  and  $(1 - \lambda)$ .

Sheehy *et al.* (1980) observed that, for grass, the physiological stage of development affected the proportion of photosynthate partitioned to the leaves ( $\lambda_g$ ) and the rate of leaf senescence ( $\gamma_{L,g}$ ). In spring, during the reproductive phase, less assimilate is partitioned to the leaves. The apparent life of the leaves is increased, implying a lower rate of leaf loss. The commencement of the reproductive phase of each species varies with temperature and light (Cooper, 1960). However, for simplicity, the changes in physiological states are assumed to occur on designated days. In white clover, there is less of a difference in growth between reproductive and vegetative phases (Spedding and Diekmahns, 1972). For white clover the proportion of photosynthate partitioned to the leaves ( $\lambda_c$ ) and stem, and the rate of leaf senescence ( $\gamma_{L,c}$ ) is therefore presumed to be independent of the physiological stage of the crop.

### 3.2.7 Sub-model 7 – Herbage Accumulation under Cutting

In the case of a grass sward, the actual quantity of herbage harvested under cutting is equated with the quantity of leaf and stem material in the sward less the predefined residual quantity of leaf ( $R_L$ , kg ha<sup>-1</sup>) and stem ( $R_S$ , kg ha<sup>-1</sup>) material that remains per hectare on the paddock. However, in a grass – white clover sward, the actual quantities of leaf and stem material for each component have to be determined. The preferential removal of white clover under cutting from the sward is determined from the selection coefficient  $v$  (Ridout and Robson, 1991) defined as:

$$v = \frac{w_d}{g_d} \bigg/ \frac{w_s}{g_s} \quad (3.28)$$

where  $w_d$  ( $g_d$ ) and  $w_s$  ( $g_s$ ) are the quantities in kg DM ha<sup>-1</sup> of white clover (grass) harvested and in the sward respectively. This is a generic equation where the variables can represent either leaf area or dry matter, where dry matter consists of leaf and stem weights. Woledge *et al.* (1992) determined the selection coefficient for white clover leaf area ( $v_L$ ) and dry matter ( $v_D$ ) in a cut sward. In the model, equation (3.28) has been re-arranged, as described in Appendix IV, in order that the quantities of white clover and grass leaf mass harvested can be calculated.

If the stem material of either the grass or white clover component calculated to be removed by equation (3.28) is greater than is present in the sward, then the amount of grass and clover stem material actually cut is in proportion to the amount of grass and white clover material in the sward. The white clover dead material removed from the sward is in the same proportion as the white clover stem material removed.

### **3.3 *Herbage Removal under Grazing***

A schematic representation of the extended model is provided in Figure 3-2. Within the model, the leaf area index of the crop is altered as the livestock graze. This affects the rate of photosynthesis and the growth rate of the crop, which in turn influences crop morphology in terms of the leaf-to-stem ratio in the sward. Changes in the leaf-to-stem ratio further regulate the digestibility of the herbage on offer and so influence the intake of the livestock. In a mixed sward, diet selection is also presumed to alter the composition of the sward, with the preferred species being disadvantaged. The botanical composition of the sward and the diet are thus changed by grazing in a dynamic way.

Basically, a spring-calving dairy herd, beef cattle or sheep rotationally grazed during the summer period on a pure grass or a grass – white clover sward is simulated. The pasture is divided into a maximum of twelve equal-sized paddocks. The sward is assumed to be composed of pure grass or a grass – white clover mixture. The extension of the model describing grazing includes a further six sub-models governing:

8. rules for conservation;
9. grazing rules;
10. calculation of actual herbage intake;
11. determination of the quantities of leaf, stem and dead material removed;
12. determination of the quantities of grass and white clover removed; and finally
13. determination of energy intake of grazing animals.

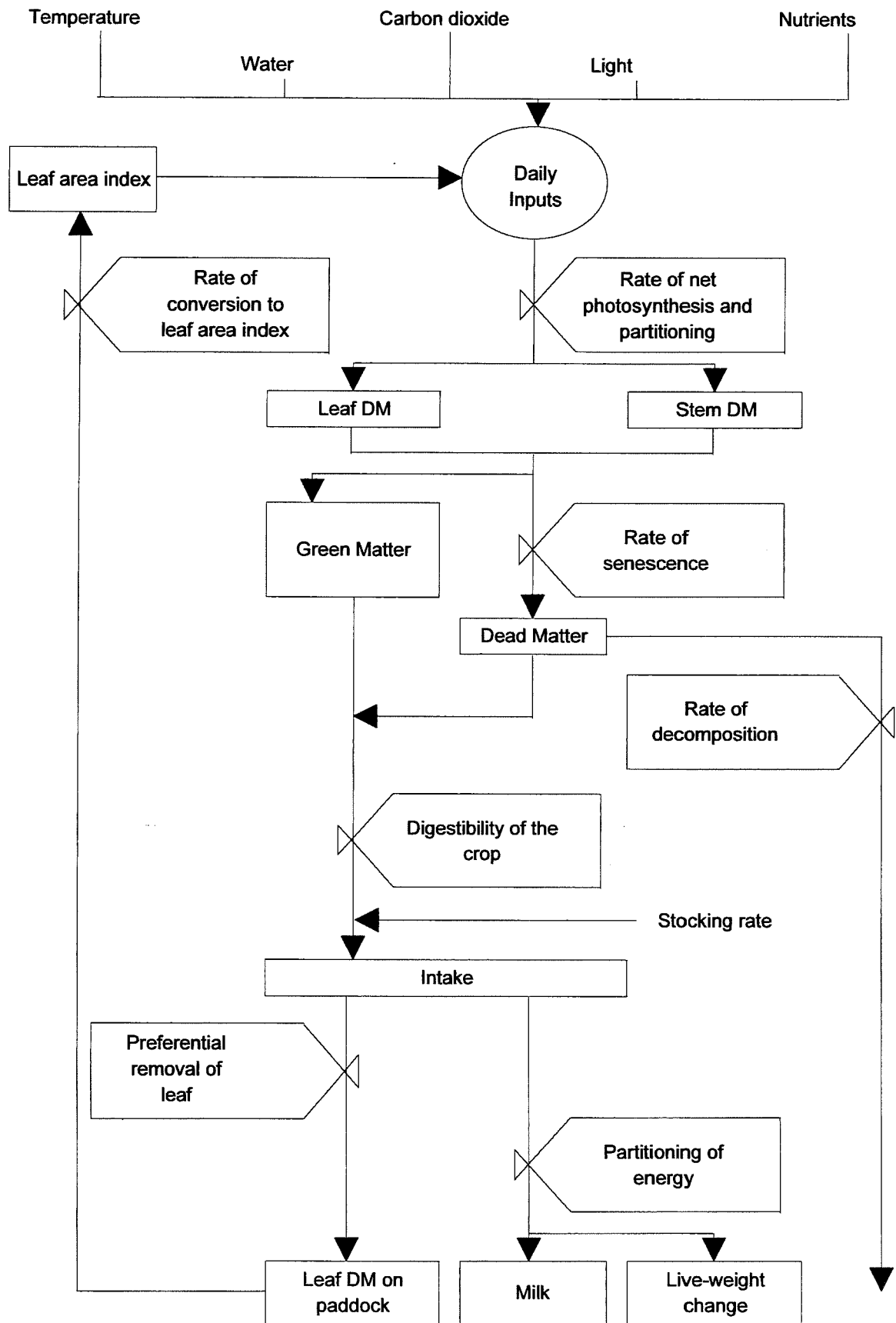


Figure 3-2 A schematic diagram of the grazing model.

### **3.3.1 Sub-model 8 – Rules for Conservation**

Within the model, it is assumed that half the area would be set aside for the first conservation cut and a third of the area for the second. However, if there is a shortage of pasture for grazing, the paddocks set aside for conservation are grazed. Any paddock that has not been grazed during the 30 days prior to the date of cutting is cut for conservation. The rules for determining the amount of conserved herbage from a mixed sward are described in section 3.2.7.

### **3.3.2 Sub-model 9 – Grazing Rules**

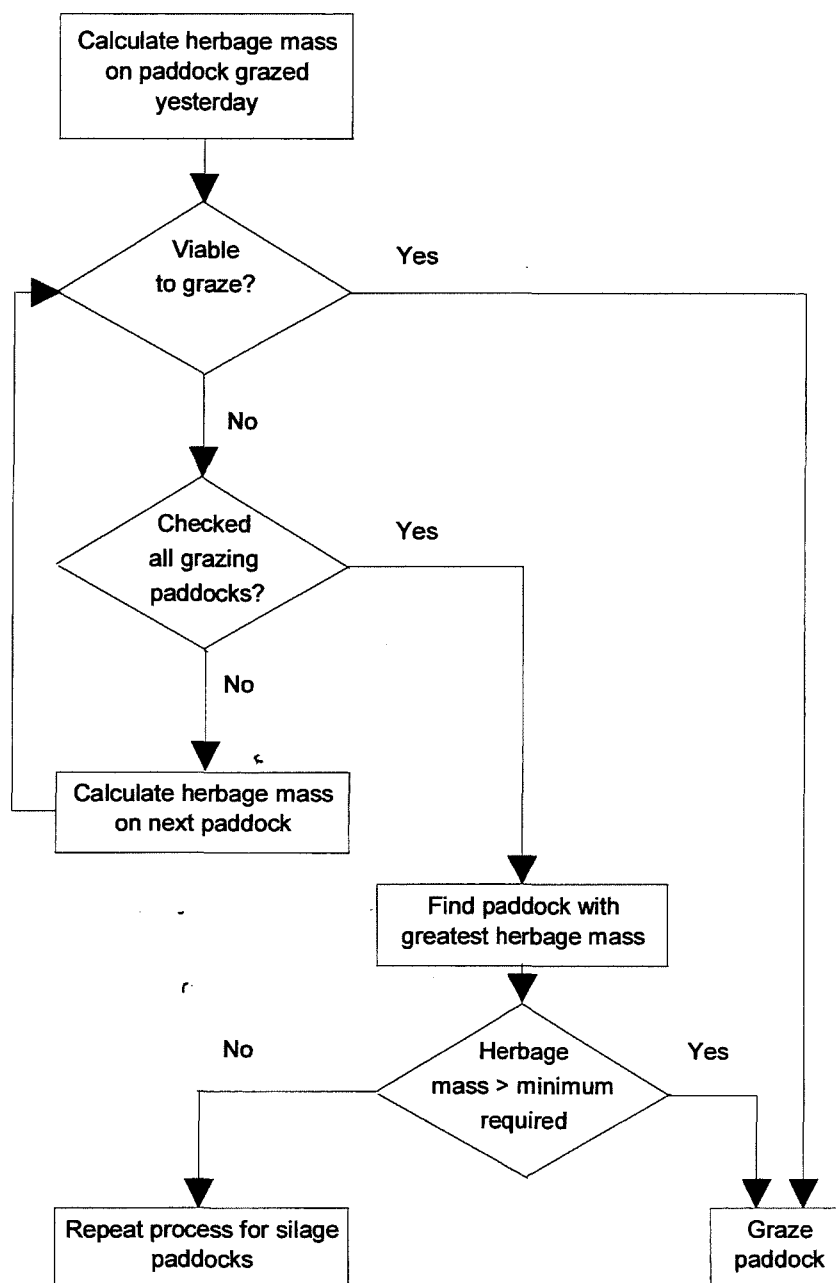
Combellas and Hodgson (1979) have observed that the intake of herbage by the dairy cow approaches an asymptotic value with increasing herbage allowance. At low herbage allowances, once the available herbage had been consumed the animals abandon any attempt to graze closer to the ground (Le Du, Combellas, Hodgson and Baker, 1979). Thus, in the model, it has been assumed that the livestock will not graze below a predefined herbage mass. This herbage mass has been defined for dairy cows, beef cattle and sheep. Under ideal conditions, the herbage mass available for grazing permits the livestock to consume the maximum daily intake of dry matter, and therefore their level of production is not constrained by the availability of the daily allowance of herbage.

In the model, the start of the grazing season is presumed to occur when the herbage mass on the paddock to be grazed has increased by 2.5% from the base level and there is also sufficient herbage mass on the paddock to allow grazing. For dairy cows and sheep, parturition is also assumed to have occurred before the grazing season commences. It is assumed that the livestock will remain on the paddocks until at least

15 September. The grazing season is considered to end when one of the following criteria is met:

1. the metabolisable energy available from dry-matter intake does not meet the metabolisable energy of maintenance and, in the case of dairy cows and sheep, the pregnancy requirements as well; or
2. the predicted dry-matter intake falls to less than 20% of the potential level; or
3. the available soil moisture has been greater than or equal to the available water capacity for seven consecutive days and thus poaching is likely to occur.

Grazing can still occur after the growing season has ended. The rotation of the livestock around the paddocks on a day-to-day basis is determined solely by quantity of herbage on each paddock (see Figure 3-3). The herbage biomass produced per hectare is converted to a per paddock basis by multiplying by the size of the paddock. When there is an ample supply of herbage, the livestock is moved if the available herbage mass on the grazed paddock is less than 95% of that required for maximum dry-matter intake. If there is a shortage of herbage, the paddock with greatest herbage mass is grazed, assuming that it has a greater herbage mass than the predefined minimum required for the specified grazing ruminant. However, if the herbage mass on that paddock is less than 75% of that required for maximum dry-matter intake, the paddocks set aside for silage production are used for grazing.

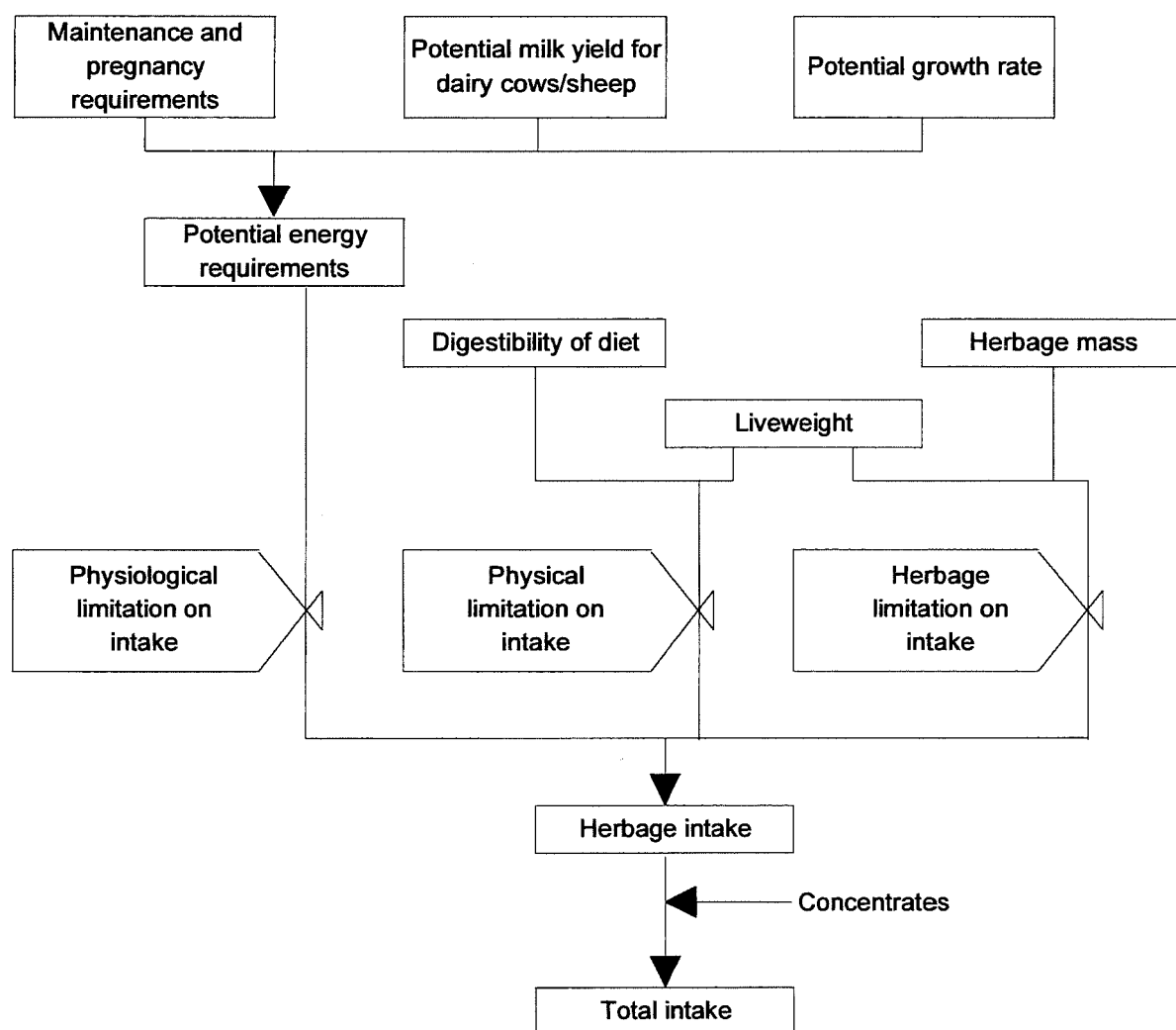


*Figure 3-3 A schematic representation the grazing regime*

### **3.3.3 Sub-model 10 – Calculation of Actual Herbage Intake**

The intake of dry matter by grazing ruminant animals is assumed to be regulated by three factors: (i) the feed availability; (ii) the physiological limit on intake; and (iii) the physical ability of the animal to consume feed (Loewer, Smith, Gay and Fehr, 1983).

The actual intake on any given day is determined by the most limiting factor as schematically represented in Figure 3-4. The calculations of the physiological limit to intake and the physical ability of the animal to consume feed, are described in the documentation for the individual livestock types, see Chapter 4.



*Figure 3-4 A schematic representation of the factors limiting intake*

### **3.3.3.1 Feed Availability**

When the quantity of herbage available for consumption is less than that required for 95% of maximum daily intake, the daily allowance of green herbage regulates intake.

The green herbage allowance is taken to be the green herbage mass above the minimum herbage mass required for grazing. Zemmeling (1980) described the relationship for tropical grasses between herbage intake ( $I_F$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) and the daily allowance of green herbage ( $H$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) as:

$$I_F = I_{\max} * \left(1 - \exp\left(-H/I_{\max}\right)^{b1}\right)^{1/b1} \quad (3.29)$$

where  $b1$  is a constant and  $I_{\max}$  is the maximum daily intake of herbage in kg DM head<sup>-1</sup> day<sup>-1</sup> and is described by the following relationship:

$$I_{\max} = LWT^{0.75} * F_{\max} - I_{\text{Conc}} * C_{\text{Replace}} \quad (3.30)$$

where  $LWT$  (kg head<sup>-1</sup>) is the liveweight of the specified ruminant,  $F_{\max}$  is the maximum dry-matter per kg of metabolic weight (kg DM (liveweight)<sup>-0.75</sup> head<sup>-1</sup> day<sup>-1</sup>) and  $I_{\text{Conc}}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) is the dry-matter intake of concentrates. Following Grainger and Mathews (1989), the rate of substitution of forage by concentrates ( $C_{\text{Replace}}$ , kg DM herbage (kg DM concentrates)<sup>-1</sup>) is defined as:

$$C_{\text{Replace}} = S_{R1} + S_{R2} * (I_F / LWT * 100) \quad (3.31)$$

Although this equation was derived for cows, it has been assumed in the model that it also applies to sheep. In the absence of any established relationships for temperate grasses, equation (3.29) has been adopted.

In order to determine the quantity of herbage required the variable  $H_{\text{Req}}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) is substituted for  $H$  in equation (3.29) and rearranged to give:

$$1 - \left[ \frac{I_F}{I_{\max}} \right]^{b1} = \exp(-H_{\text{Req}}/I_{\max})^{b1} \quad (3.32)$$

$$\Rightarrow -\ln \left[ 1 - \left[ \frac{I_F}{I_{\max}} \right]^{b1} \right] = b1 * \frac{H_{\text{Req}}}{I_{\max}} \quad (3.33)$$

$$\Rightarrow H_{\text{Req}} = \ln \left[ \frac{1}{1 - \left[ \frac{I_F}{I_{\max}} \right]^{b1}} \right] * \frac{I_{\max}}{b1} \quad (3.34)$$

It is assumed in the model that the specified livestock will be moved to the next paddock when the available herbage mass on the grazed paddock is less than 95% of that required for maximum dry-matter intake. Hence the ratio of  $I_F:I_{\max}$  is defined as 0.95. The quantity of herbage ( $H_{\text{Move}}$ , kg DM paddock<sup>-1</sup>) required for all the specified livestock to consume 95% of the maximum daily intake of dry matter, and therefore meet their potential level of production was defined as:

$$H_{\text{Move}} = \text{HPad}_{\text{Crit}} + H_{\text{Req}} * \text{SR} \quad (3.35)$$

where SR (stock ha<sup>-1</sup>) is the number of grazing livestock per forage hectare and  $\text{HPad}_{\text{Crit}}$  (kg DM paddock<sup>-1</sup>) is the minimum critical herbage mass per paddock required for grazing to occur. This is defined as the critical herbage mass per hectare ( $H_{\text{Crit}}$ , kg DM ha<sup>-1</sup>) multiplied by the area per paddock ( $P_{\text{ha}}$ , ha paddock<sup>-1</sup>).

### 3.3.4 Sub-model 11 – Determination of the Quantities of Leaf, Stem and Dead Material Removed

Observations by Jamieson and Hodgson (1979) have shown that grazing lambs and calves preferentially select green material. It has been assumed that grazing dairy cows, beef cattle and sheep also preferentially select green material. The proportions of leaf, stem and dead material in the sward also differ from the proportions in the diet (Ratnayake and Clark, 1984). Accordingly, following Doyle *et al.* (1989) the mean daily intakes of leaf ( $I_L$ , kg DM head<sup>-1</sup> day<sup>-1</sup>), stem ( $I_S$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) and dead material ( $I_D$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) have been assumed to be given by:

$$I_L = 1 - \exp\left(-b_2 * (\xi_L + \xi_S)\right) * \frac{\xi_L}{\xi_L + \xi_S} * I \quad (3.36)$$

$$I_S = 1 - \exp\left(-b_2 * (\xi_L + \xi_S)\right) * \frac{\xi_S}{\xi_L + \xi_S} * I \quad (3.37)$$

$$I_D = I - I_L - I_S \quad (3.38)$$

where  $\xi_L$  and  $\xi_S$  represent the proportions of green herbage accounted for by leaves and stem, respectively,  $I$  (kg DM day<sup>-1</sup>) is the total intake of herbage by the grazing livestock and  $b_2$  is a constant.

### 3.3.5 Sub-model 12 – Determination of the Quantities of Grass and White Clover Removed

In a grass – white clover sward, the quantities of leaf, stem and dead material of the individual components consumed are determined using the formulae described for

calculating the quantities of grass and white clover stem and leaf material that are cut for conservation (equations (3.28) and Appendix IV). However, evidence suggests that sheep selectively graze white clover from mixed swards. Ridout and Robson (1991) reported selection coefficients of 2.25 (1.55—3.29) and 2.52 (1.61—3.95) for white clover versus all other components in the sward and white clover versus grass respectively. Hence, the selection coefficient for grazing sheep is greater than the value for cutting.

Penning, Parsons, Orr, Harvey and Yarrow (1995) reported that cattle spent between 57% and 81% of their time grazing the white clover component of swards containing 25% and 75% white clover respectively. Similarly, Cosgrove, Anderson and Fletcher (1996) reported that during the grazing season cattle have been observed to spend between 45% and 65% of their time grazing white clover, although the lower value is not significantly different from 50%. As sheep and goats are able to attain a faster bite rate on legumes than on grass (Gong, Hodgson, Lambert and Gordon, 1996), it has been assumed that this also applies to cattle. Consequently, it is assumed that cattle also selectively graze white clover from a mixed sward. Accordingly, the value of the selection coefficient for grazing ( $v_{\text{cow}}$ ) is assumed to be greater than the value for cutting. Nevertheless, it is acknowledged that it is debatable as to whether cattle (A, Hameleers, *personal communication*) actively select white clover from mixed swards.

### **3.3.6 Sub-model 13 – Determination of Energy Intake of Grazing Animals**

Although there may be direct effects of climatic change on the nutritive value of the forage crop (Gustavsson *et al.*, 1995; Fagerberg and Nyman, 1994; Fagerberg and Nyman, 1995), these have been ignored, because they are likely to be dwarfed by

those due to changes in botanical composition. The proportionate digestibility, expressed as the digested organic matter in the dry matter consumed (D-value) of the grass ( $G_{dg}$ ) and white clover ( $C_{dg}$ ) components of the diet are thus given by:

$$G_{dg} = dg_{L,g} * I_{L,g} + dg_{D,g} * I_{S,g} + dg_{D,g} * I_{D,g} \quad (3.39)$$

$$C_{dg} = dg_{L,c} * I_{L,c} + dg_{D,c} * I_{S,c} + dg_{D,c} * I_{D,c} \quad (3.40)$$

where  $dg_{L,g}$ ,  $dg_{S,g}$ ,  $dg_{D,g}$ ,  $dg_{L,c}$ ,  $dg_{S,c}$  and  $dg_{D,c}$  are the respective proportionate digestibilities of the leaf, stem and dead components of the grass and white clover portions of the diet. The overall digestibility of the herbage consumed ( $dg$ ) is therefore represented by:

$$dg = \frac{G_{dg} + C_{dg}}{I} \quad (3.41)$$

In the model, the proportionate digestibilities of grass and white clover have been assumed to decrease as the season progresses (Osbourn, 1980). Thus, for six weeks at about the time the growth of grass changes from being reproductive to vegetative, the digestibilities of the leaf and stem fractions of both the grass and white clover components are reduced on a daily basis in the following manner.

$$dg_L = dg_L * Rdg_L \quad (3.42)$$

$$dg_S = dg_S * Rdg_S \quad (3.43)$$

where  $Rdg_L$  and  $Rdg_S$  are the percentages of the previous day's digestibility values. The digestibility of the grass stem is reduced in the same manner for a further four weeks. The seasonal observed and modelled D-values for the leaf and stem components for grass and white clover are shown in Figure 3-5 and Figure 3-6. The observed values for the grass components were obtained from Wilman, Ojuederie and Asare (1976) while observed values of the white clover component were assumed to decline at a rate of 0.8 units of D-value per week from early May to mid June (Osbourn, 1980). There is a tendency for the modelled value to be higher than the observed values. However, grazing animals tend to select herbage of higher D-value than the herbage on offer with difference ranging from 3 to 10 units of D-value on stripped grazed pastures (Osbourn, 1980).

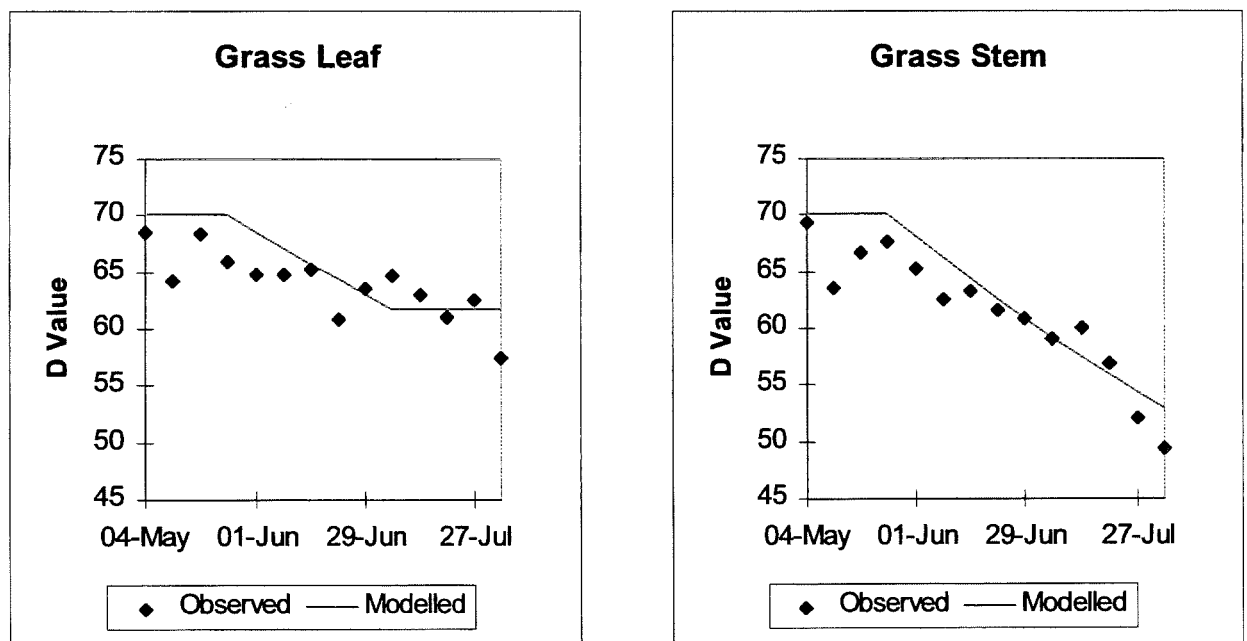


Figure 3-5 The observed and modelled D-values of the leaf and stem component for grass.

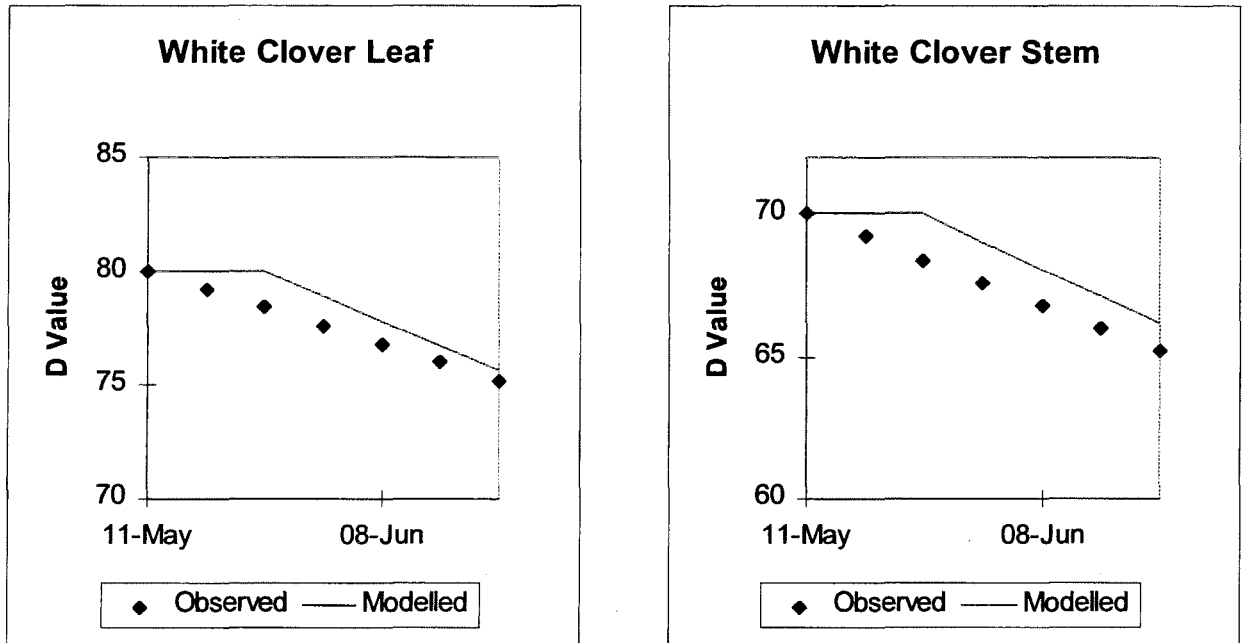


Figure 3-6 The observed and modelled D-values of the leaf and stem component for white clover.

The ME value of 1 kg of ingested herbage ( $M_{Fod}$ , MJ (kg DM)<sup>-1</sup>) is presumed to be given by (McDonald, Edwards and Greenhalgh, 1988):

$$M_{Fod} = 16 * dg \quad (3.44)$$

The ME value of the diet ( $ME_C$ , MJ head<sup>-1</sup> day<sup>-1</sup>) can therefore be described by:

$$ME_C = T_{Fod} + T_{Conc} \quad (3.45)$$

where

$$T_{Fod} = M_{Fod} * I \quad (3.46)$$

and

$$T_{\text{Conc}} = M_{\text{Conc}} * I_{\text{Conc}} \quad (3.47)$$

$M_{\text{Conc}}$  and  $I_{\text{Conc}}$  are the metabolisable energy of concentrates ( $\text{MJ (kg DM)}^{-1}$ ) and the intake ( $\text{kg head}^{-1} \text{ day}^{-1}$ ) of concentrate consumed.

### ***3.4 Initial Conditions, and the Values of the Parameters and Variables***

The solution of the model requires the specification of initial values of the state variables, and 83 variables and parameters. The derivation of the initial value and parameters are described in the following sections:

1. initial values of the state variables;
2. parameter value required to calculate the day length;
3. parameter values for the length of the growing season;
4. photosynthesis and respiration;
5. partitioning;
6. water and nutrient stress; and finally
7. herbage intake.

#### **3.4.1 Initial Values of the State Variables**

The initial conditions of the leaf dry matter ( $D_L$ ,  $\text{kg DM ha}^{-1}$ ), stem dry matter ( $D_S$ ,  $\text{kg DM ha}^{-1}$ ), dead material ( $D_D$ ,  $\text{kg DM ha}^{-1}$ ) and the leaf area index of the crop ( $L$ ,  $\text{ha leaf ha}^{-1}$  (ground)), as well as the proportion of white clover in a mixed sward on 1 January must be defined. In the model it was assumed that the total quantity of dry matter on a paddock at the beginning of a year is  $2700 \text{ kg ha}^{-1}$  (Carton, Brereton, O'Keeffe, and Keane, 1988) This has been divided between leaf, stem and dead fractions in the

same proportions as Doyle *et al.* (1989). Assuming that the proportion of white clover in a mixed sward is 0.1 (Orr, Parsons, Penning and Treacher, 1990), the initial conditions for pure grass and mixed grass – white clover swards are given in Table 3-2.

**Table 3-2 Initial Conditions for Grass and Grass – White Clover Swards**

<b>Sward</b>	<b>Parameter</b>	<b>Value</b>	<b>Source<sup>1</sup></b>
Grass	$D_D$	900.0	1
	$D_L$	1350.0	1
	$D_S$	450.0	1
	$L$	3.48	2
Grass – White Clover	$D_{D,c}$	90.0	1
	$D_{D,g}$	810.0	1
	$D_{L,c}$	135.0	1
	$D_{L,g}$	1215.0	1
	$D_{S,c}$	45.0	1
	$D_{S,g}$	405.0	1
	$L_c$	0.50	2
	$L_g$	3.13	2

Source<sup>1</sup> 1 See text; 2 Calculated from equation (3.12).

### **3.4.2 Parameter Value Required to Calculate the Day Length**

There are four possible definitions of day length which are defined in relation to the angle between the upper part of the sun's disc and the horizon, and are described by:

1. an angle of  $0^\circ$  between the upper part of the sun's disc and the horizon;
2. the sun being  $6^\circ$  below the horizon, defined as civil twilight;
3. the sun being  $12^\circ$  below the horizon, defined as nautical twilight; and
4. the sun being  $18^\circ$  below the horizon, defined as astronomical twilight.

According to France and Thornley (1984) it is uncertain as to which is the most appropriate biological definition of day length. Consequently, it has been assumed in the model that the day length is defined by civil twilight and thus the zenith angle ( $z$ , degrees) is defined as  $96^\circ$ .

### **3.4.3 Parameter Values for the Length of the Growing Season**

The parameter values for the start of grass ( $St_g$ ,  $^\circ\text{C}$ ) and white clover growth ( $St_c$ ,  $^\circ\text{C}$ ) and end of the growing season ( $End$ ,  $^\circ\text{C}$ ) are given in Table 3-3.

**Table 3-3** *The Values of the Variables Defining for the Length of the Growing for Grass and Grass – White Clover Swards*

Sward	Parameter	Value	Source <sup>1</sup>
Grass	St <sub>g</sub>	4.5	1
	End	8.0	1
White Clover	St <sub>c</sub>	6.0	2
	End	8.0	1

Source<sup>1</sup> 1 Broad and Hough, 1993; 2 Peel, 1988

#### **3.4.4 Values of the Parameters and Variables for the Photosynthesis and Respiration Processes**

The variables required for the equations describing photosynthesis and respiration are given in Table 3-4 for grass and white clover. The calculation of the rate of photosynthesis requires that the CO<sub>2</sub> saturated maximum rate of leaf photosynthesis be defined. In a mixed sward the vertical distribution of the grass and white clover components must also be described. In addition, the respiration coefficients for white clover have been defined. These values and the conversion of CO<sub>2</sub> to dry matter have been estimated in the text.

**Table 3-4 Variables Values for Photosynthesis and Respiration for the Grass and White Clover Components**

Parameter	Value	Source <sup>1</sup>	Parameter	Value	Source <sup>1</sup>
$\alpha_{\max, c}$	0.01	1	$k_g$	0.5	2
$\alpha_{\max, g}$	0.01	1	$KP_{\max}$	1.281e-3	8
$\varepsilon$	0.70	2	$m_c$	0.1	2
$\theta$	0.682	3	$m_g$	0.1	2
$\Theta$	0.95	4	$r_c$	0.05	3
$\rho\text{CO}_2$	1.9636	5	$r_g$	0.05	9
$\tau$	0.0015	1	$R_L$	675	10
$\varpi$	0.3e-6	1	$R_S$	325	10
$A_c$	0.00368	6	$P_{\max, c}^0$	43.2	3
$A_g$	0.00258	6	$P_{\max, g}^0$	43.2	3
Atm	101325	5	$T_0$	0.0	11
Atm <sub>Sea</sub>	101325	5	$T_{\text{Ref}}$	20.0	11
$k_0$	273.15	5	$Y_c$	0.63	3
$k_c$	0.8	7	$Y_g$	0.83	9

Source<sup>1</sup> 1 Thornley *et al.* (1991); 2 Johnson *et al.* (1989); 3 See text; 4 Johnson and Thornley (1985); 5 Thornley (1991); 6 Davidson and Robson (1986); 7 Brown and Blaser (1968); 8 Thornley and Cannell (1992); 9 Mogensen (1977); 10 Doyle *et al.* (1989); 11 Johnson *et al.* (1983).

#### **3.4.4.1 Maximum Rate of Leaf Photosynthesis at Ambient Concentrations of CO<sub>2</sub>**

The maximum value used in models for the rate of leaf photosynthesis for grass growth at ambient concentration of CO<sub>2</sub> varies between 0.75 mg CO<sub>2</sub> m<sup>-2</sup> (leaf) s<sup>-1</sup> (Johnson *et al.*, 1989) and 1.5 mg CO<sub>2</sub> m<sup>-2</sup> (leaf) s<sup>-1</sup> (Johnson *et al.*, 1983). Woledge and Dennis (1982) measured the maximum rate of net leaf photosynthesis for grass as approximately 1.1 mg CO<sub>2</sub> m<sup>-2</sup> (leaf) s<sup>-1</sup>. Consequently, in order to allow for the difference between net and gross photosynthesis, the value used in the model for the maximum rate of leaf photosynthesis at ambient concentrations of CO<sub>2</sub> ( $P_{\max, g}^0$ ) is 1.2 mg CO<sub>2</sub> m<sup>-2</sup> (leaf) s<sup>-1</sup>. This was converted to 43.2 kg CO<sub>2</sub> ha<sup>-1</sup> (leaf) h<sup>-1</sup>. This value was then substituted into equation (3.10) in order to calculate the CO<sub>2</sub> saturated value of the maximum rate of leaf photosynthesis ( $P_{\max, g}^{CO_2}$ , kg CO<sub>2</sub> ha<sup>-1</sup> (leaf) h<sup>-1</sup>) for the specified ambient concentration of CO<sub>2</sub>. The rate of leaf photosynthesis and the response to both irradiance and temperature is similar for both perennial ryegrass and white clover (Woledge and Dennis, 1982). Thus, the same value was used for the CO<sub>2</sub> saturated value of the maximum rate of white clover leaf photosynthesis ( $P_{\max, c}^0$ , kg CO<sub>2</sub> ha<sup>-1</sup> (leaf) h<sup>-1</sup>).

#### **3.4.4.2 White Clover Respiration Coefficients**

The respiration coefficients for grass were taken from published sources, while the values for the respiration coefficients for white clover ( $r_c$ , kg CO<sub>2</sub> (kg DM)<sup>-1</sup> day<sup>-1</sup> and  $Y_c$ , kg CO<sub>2</sub> (kg CO<sub>2</sub>)<sup>-1</sup>) were obtained by averaging the results of McCree (1970), McCree and Silsbury (1978) and McCree and Amthor (1982). These were all based on experiments on white clover in growth chambers.

#### **3.4.4.3 Vertical distribution of Clover through the Depth of the Canopy**

Woledge *et al.* (1992) have made observations on the vertical distribution of grass and white clover through the depth of the canopy throughout the growing season. These data were used to obtain a relationship for the vertical distribution of the proportion of white clover leaf area through the depth of the canopy to the total leaf area of the sward. Examination of the plots of the data suggested a relationship of the form of equation (3.16). However, the Durbin-Watson statistic for the ordinary least squared regression revealed that there was a positive correlation between the error terms, and thus the exact maximum likelihood method in Microfit (Pesaran and Pesaran, 1991) was used to obtain estimates of the coefficients. The estimated relationship is:

$$\frac{d\ell_c}{d\ell} = 1.594 * \frac{\ell}{L} - 0.581 * \left[ \frac{\ell}{L} \right]^2 \quad (3.48)$$

$\pm 0.124 \quad \pm 0.122$

where  $\ell$  (ha (leaf) ha<sup>-1</sup> (ground)) is the cumulative leaf area index which is leaf area index being used at the specified step in the integration process  $L$  is the leaf area index of the sward (ha (leaf) ha<sup>-1</sup> (ground)). The  $R^2$  for the equation was 0.99. The parameter values for  $a_1$  and  $a_2$  in equation (3.16) are therefore 1.594 and 0.581 respectively.

#### **3.4.4.4 Conversion of CO<sub>2</sub> to Dry Matter**

Dry matter is assumed to be in the form of carbohydrates (CH<sub>2</sub>O). The molecular weights are used to convert the CO<sub>2</sub> to dry matter assuming a conversion of one molecule of CO<sub>2</sub> to one molecule of CH<sub>2</sub>O. The molecular weight of CO<sub>2</sub> and CH<sub>2</sub>O are 44 g mol<sup>-1</sup> and 30 g mol<sup>-1</sup> respectively.

### 3.4.5 The Partitioning Coefficients

The partitioning coefficients for the grass and the white clover components are given in Table 3-5.

*Table 3-5 Partitioning Coefficients for the Grass and White Clover Components*

Sward	Parameter	Value	Source <sup>1</sup>	
Grass	$\gamma_{D, g}$	0.025	1	
	reproductive	$\gamma_{L, g}$	0.0146	2
	vegetative	$\gamma_{L, g}$	0.0311	2
		$\gamma_{S, g}$	0.0259	2
	reproductive	$\lambda_g$	0.60	2
	vegetative	$\lambda_g$	0.68	2
		$\rho$	0.1	3
White Clover	$\gamma_{D, c}$	0.025	1	
		$\gamma_{L, c}$	0.024	4
		$\gamma_{S, c}$	0.0259	2
		$\lambda_g$	0.33	5
		$\rho$	0.29	5

Source<sup>1</sup> 1 Doyle *et al.* (1989); 2 Sheehy *et al.* (1980); 3 Johnson *et al.* (1983); 4 Chapman, Clark, Land and Dymock (1984); 5 Chapman, Robson and Snaydon (1991)

### 3.4.6 Values of the Parameters and Variables for the Calculation of Water and Nutrient Stress

The effect of water and nutrient stress on sward growth has been modelled by reducing the photosynthate in proportion to the stress experienced by the crop. This requires that the potential rate of evapotranspiration and the nitrogen available to the crop are defined. The variables required to calculate the potential rate of evapotranspiration which is described in equation (3.22) and Appendix III) are defined in Table 3-6. The estimation of the parameters required for the equations which describe the nitrogen that is 'fixed' by the white clover and the proportionate reduction in the photosynthate, resulting from the water and nutrient stress, are described in the following section.

*Table 3-6 Values of the Variables Required for the Potential Evapotranspiration Equation*

Parameter	Value	Parameter	Value
be1	0.47	D8	0.5
be2	0.065	es1	6.1078
bs1	0.17	es2	17.269
bs2	0.83	ev1	0.2625
bt1	0.0048985	ev2	0.0062137
D0	0.95	L <sub>v</sub>	2465000.0
d1	4097.93	S	0.66

Source Agricultural and Food Research Council (1991)

#### **3.4.6.1 Water and Nutrient Stress on the Grass Component**

The estimation of the effect of water and nutrient stress is based on data from the grass – white clover grassland manuring trials (GM23) conducted by the Grassland Research Institute, Hurley. (J. Gilbey, *personal communication*). The effect of irrigation on yield of pure grass swards at varying levels of nitrogen use had been investigated at the Grassland, Research Institute, Hurley during the period 1978—1981. In order to obtain estimates for  $\beta_1$  and  $\beta_2$ , the parameters defined for equation (3.18), the yields are expressed as a proportion of the irrigated yield at an application rate of 600 kg of nitrogen fertiliser per hectare. At that level of application rate it is assumed that the sward is not stressed by the lack of nitrogen, and thus the yield is presumed to be maximised for a sward that is irrigated and receives 600 kg N ha<sup>-1</sup>. Hence the ratio of the non-irrigated to irrigated yield, where the irrigated sward receives 600 kg N ha<sup>-1</sup>, cannot be greater than one. The soil moisture deficit, obtained from the Biotechnology and Biological Science Research Council (BBSRC) ARCMET database for Hurley, was expressed as a proportion of the available water capacity. Similarly, the quantity of nitrogen applied is expressed as a proportion of the maximum rate of fertiliser nitrogen. On examination of the data, it was found that the distribution of all the variables was skewed. Thus, in order to obtain a normal distribution, the square roots of the variables were used in the regression analysis. The value obtained from the ordinary least squares regression analysis for  $\beta_1$  was 0.366 with a 95% confidence interval of 0.317—0.415, and  $\beta_2$  had a value of 0.664 with a 95% confidence interval 0.609—0.719. The  $R^2$  had a value of 0.70.

#### **3.4.6.2 White Clover Water Stress**

The effect of water stress on white clover growth was also investigated using data from GM23 (J. Gilbey, *personal communication*) which was conducted at Hurley. The data for the period 1979—1981 were used to obtain values for  $\beta_3$  and  $\beta_4$ . As for the grass stress equation, it was assumed that the non-irrigated:irrigated yield could not be greater than one. The analysis of the ordinary least squared regression revealed that there was a positive correlation between the error terms, and thus the exact maximum likelihood method in Microfit (Pesaran and Pesaran, 1991) was used to obtain estimates of the coefficient. The value of variable  $\beta_3$ , was found to be 0.216, with a 95% confidence of 0.098—0.335 and the value of  $\beta_4$  was 0.789 with a 95% confidence interval of 0.628—0.951. The  $R^2$  for the regression analysis was 0.75.

#### **3.4.6.3 Nitrogen Biologically 'fixed' by White Clover**

The quantity of nitrogen biologically fixed by white clover was estimated from observations by Frame and Boyd (1987) at SAC Auchincruive on the amount of nitrogen harvested in white clover and the proportion of white clover in the sward under varying levels of nitrogen application. The harvested yield was re-expressed in terms of the leaf area index. Increasing fertiliser nitrogen usage was expected to reduce the quantity of nitrogen biologically 'fixed' by white clover. However, the coefficient for the variable expressing the quantity of fertiliser nitrogen applied was found to be insignificant. The relationship between the nitrogen biologically 'fixed' ( $N_c$ ,  $\text{kg ha}^{-1}$ ) and the proportion of white clover leaf area in the sward ( $L_c/L$ ) was estimated using the exact maximum likelihood method in Microfit (Pesaran and Pesaran, 1991)

as there was a positive correlation between the error terms. The estimated equation is:

$$N_c = 1.085 * \frac{L_c}{L} \quad (3.49)$$

with a 95% confidence interval of 1.033—1.141 and an  $R^2$  of 0.99. The value of the coefficient  $\kappa$  is therefore 1.085. Nevertheless, the values quoted for the UK for the nitrogen 'fixed' by white clover are extremely variable as they range from 55 kg N ha<sup>-1</sup> (Munro and Hughes, 1966) to over 300 kg N ha<sup>-1</sup> (J. Gilbey, *personal communication*). However, the maximum 'fixation' resulting from equation (3.49), for a mixed sward containing 50 per cent white clover over a 245 day growing period, is only 133 kg N ha<sup>-1</sup>. Consequently, the nitrogen available to the grass component of the crop over the growing season was increased by 100 kg N ha<sup>-1</sup>.

### 3.4.7 Herbage Intake

The values ascribed to the parameters required for equations (3.29), (3.31), (3.36) and (3.37), and the values of the coefficients for the preferential removal of white clover by cutting and grazing livestock are given in Table 3-7. The digestibility coefficients for the leaf, stem and dead fractions of the grass component and the proportionate reduction in the digestibility for both the grass and white clover components are given in Table 3-8. The estimation of the digestibility coefficients for the white clover fractions of leaf, stem and dead material and the parameters for the preferential removal of white clover by the grazing livestock are described in the text. It is assumed that the metabolisable energy of the concentrates is 12.5 MJ (kg DM)<sup>-1</sup>

(Doyle *et al.*, 1987). The critical herbage mass required to permit grazing ( $H_{\text{crit}}$ , kg DM  $\text{ha}^{-1}$ ) and the maximum dry-matter intake ( $F_{\text{max}}$ , kg DM (liveweight) $^{-0.75}$   $\text{day}^{-1}$ ) are defined for each livestock category.

**Table 3-7** *Parameter values for the removal of herbage under cutting and grazing*

Parameter	Value	Source <sup>1</sup>
b1	1.23	1
b2	4.662	2
S <sub>R1</sub>	-0.445	3
S <sub>R2</sub>	0.315	3
v <sub>d, cut</sub>	1.22	4
v <sub>l, cur</sub>	0.98	4
v <sub>d, graze</sub>	1.46	5
v <sub>l, graze</sub>	1.15	5

Source<sup>1</sup> 1 Doyle *et al.* (1989); 2 Lantinga (1985); 3 Grainger and Mathews (1989); 4 Woledge *et al.* (1992); 5 See text

**Table 3-8 Presumed digestibilities of the different components of the grass and clover crops**

Feed	Variable	Proportionate Digestibilities	Source <sup>1</sup>
Grass	dg <sub>L, g</sub>	0.7	1
	dg <sub>S, g</sub>	0.7	1
	dg <sub>D, g</sub>	0.5	1
	Rdg <sub>L, g</sub>	0.997	1
	Rdg <sub>S, g</sub>	0.996	1
White Clover	dg <sub>L, c</sub>	0.8	2
	dg <sub>S, c</sub>	0.7	2
	dg <sub>D, c</sub>	0.5	3
	Rdg <sub>L, c</sub>	0.998	4
	Rdg <sub>S, c</sub>	0.998	4

Source<sup>1</sup>: 1 Wilman *et al.* (1976); 2 Wilman and Altimimi (1984); 3 See text; 4 Osbourn (1980)

#### **3.4.7.1 Selection Coefficient for the Preferential Removal of White Clover by Grazing Animals**

Woledge *et al.* (1992) have determined the selection coefficients for white clover leaf and dry matter from two experiments on grass – white clover swards. The selection coefficients for white clover leaf material for the two experiments have values of 1.8 and 1.22, and the corresponding values for dry matter are 1.56 and 0.94. As sheep are known to preferentially select white clover from a mixed diet (Edwards, Newman,

Parsons, Krebs, 1997; Parsons, Newman, Penning, Harvey, Orr, 1994b), it was assumed that the selection coefficients for the grazing livestock would be increased compared to a cut sward. The values used for the grazing ruminant were set at 1.46 and 1.15 for leaf and dry matter respectively while the corresponding values for the cut sward were 1.22 and 0.94. Nevertheless, the selection coefficients used for the grazing animal are within the range observed by Woledge *et al.* (1992), and they maintain the approximate ratio of the preferential removal of leaf to the removal of dry matter.

#### **3.4.7.2 Digestibility of the White Clover Components**

Wilman and Altimimi (1984) estimated the true digestibility, equivalent to the digestible organic matter in the dry matter (N. Offer, *personal communication*) of the leaf and stem components of white clover. These values were corrected for the ash component to give the digested organic matter expressed as a percentage of the dry matter consumed (D-value). It was assumed that the ash component of the white clover was 92.5 g kg<sup>-1</sup> (Givens and Moss, 1990). The white clover 'stem' material was assumed to consist of mainly of stolons and petioles, although it also includes some stalk material. The digestibility of the dead material in a grazed grass – white clover sward (Francis and Smethan, 1985) is of similar values to the digestibilities Wilman *et al.* (1976) quoted for Italian ryegrass. Thus, in the model, the digestibility of white clover dead material (dg<sub>Dc</sub>) was presumed to equal the value used for ryegrass.

### **3.5 Conclusion**

The theoretical basis of the forage model and the removal of herbage by cutting and grazing have been described in this chapter. Chapter 4 describes the livestock production models where the animals consume herbage produced by the forage model. The validation of the forage model is described in Chapter 5 which also describes the validation of the livestock models.

## **CHAPTER 4**

### ***THE RUMINANT LIVESTOCK MODELS***

#### ***4.1 Introduction***

The livestock enterprises that are modelled are (i) a spring-calving dairy herd; (ii) an eighteen-month beef finishing system; and (iii) a sheep flock which is lambed in the spring. During the summer period, the livestock are rotationally grazed on a pure grass or grass – white clover sward. The pasture is divided into twelve equally sized paddocks. Herbage production is calculated, for each paddock, on a daily basis and is dependent on the existing herbage mass, the availability of nutrients, temperature, radiation and ambient concentration of CO<sub>2</sub> (see Chapter 3). The principal variables and parameters are listed in Appendix V and the time-scale of the model is a day.

#### ***4.2 Dairy Cow Model***

The spring-calving herd is represented in the model by the 'average dairy cow', which is turned-out after calving and when there is sufficient herbage for grazing. Within the model, it is assumed that 25% of the herd are replaced annually. Therefore, in the model it is assumed that the 'average dairy cow' is composed of 25% first-year heifer, 25% second-year heifer and 50% cow in later lactation.

For convenience the model, which has a time interval of a day, is divided into three sub-models which are concerned with:

1. factors controlling herbage intake;

2. calculation of the herbage intake; and finally
3. the partitioning of the metabolisable energy (ME) between the requirements of the cow.

#### **4.2.1 Sub-model 1 – Factors Controlling Herbage Intake**

Herbage intake by grazing ruminant livestock is assumed in the model to be regulated by three factors (Loewer *et al.*, 1983):

1. the feed availability;
2. the physiological limit on intake; and
3. the physical ability of the animal to consume feed.

The actual intake of the grazing ruminant on any given day was determined by the most limiting factor (see Figure 3-4).

##### **4.2.1.1 Feed Availability**

The feed availability constraint on herbage intake has already been described in section 3.3.3.1.

##### **4.2.1.2 Physiological Limit to Intake**

The physiological limit to intake is considered to be regulated by the daily metabolisable energy (ME, MJ head<sup>-1</sup> day<sup>-1</sup>) requirements of the animal. Energy requirements of the dairy cow are divided into those for i) maintenance ( $E_M$ , MJ head<sup>-1</sup> day<sup>-1</sup>), ii) pregnancy ( $E_P$ , MJ head<sup>-1</sup> day<sup>-1</sup>), iii) milk production ( $E_L$ , MJ head<sup>-1</sup> day<sup>-1</sup>), and iv) growth and fattening ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>).

#### 4.2.1.2.1 Requirements for Maintenance

Hulme, Kellaway and Booth (1986) described the maintenance requirements of the dairy cow by the following relationship:

$$E_M = \frac{1.4 * 0.28 * LWT^{0.75} * \exp(-0.03 * \text{Age})}{k_m} + 0.1 * E_{\text{Prod}} \quad (4.1)$$

where  $LWT^{0.75}$  (kg head<sup>-1</sup>) is the metabolic liveweight of the cow, Age is the age in years and  $E_{\text{Prod}}$  (MJ head<sup>-1</sup> day<sup>-1</sup>) is the energy required for production. In the model,  $E_{\text{Prod}}$  (MJ head<sup>-1</sup> day<sup>-1</sup>) is defined as the previous day's energy requirements for the actual production of milk and liveweight gain. In the model it is therefore assumed that  $E_{\text{Prod}}$  (MJ head<sup>-1</sup> day<sup>-1</sup>) on the previous day will be of the same order as the actual energy requirements on the present day. The net utilisation efficiency of ME for maintenance ( $k_m$ ) is related to the metabolisability of the feed, while the mean age of the 'average dairy cow' is assumed to be four years.

#### 4.2.1.2.2 Energy Requirements for Pregnancy

The daily energy requirements for pregnancy ( $E_p$ , MJ head<sup>-1</sup> day<sup>-1</sup>) have been derived using relationships for a 40 kg calf specified in Agricultural Research Council (1980) and are described as:

$$E_p = \frac{E_p * 0.0201 * \exp(-0.0000576 * \text{DayP})}{k_c} \quad (4.2)$$

where

$$\log (E_p) = 151.665 - 151.64 * \exp (-0.0000576 * \text{DayP}) \quad (4.3)$$

where DayP is the number of days since conception and  $k_c$  is the net utilisation efficiency of ME for pregnancy.

#### 4.2.1.2.3 Energy Requirements for Milk Production

The potential energy requirements for lactation ( $E_L$ , MJ head<sup>-1</sup> day<sup>-1</sup>) have been derived from estimates of the potential milk yield ( $Y$ , kg head<sup>-1</sup> day<sup>-1</sup>) based on a Wood's lactation curve (Wood, King and Youdan, 1980). The potential daily milk yield of the 'average dairy cow' is taken to be the weighted average of the potential daily milk yield of each age cohort. Following Wood *et al.* (1980), the milk yield of each age cohort (i) is described as:

$$Y = \text{Pot}_i * t^{Wb_i} * \exp (-Wc_i * t) \quad (4.4)$$

where  $Wb$  and  $Wc$  are constants describing the shape of the lactation curve, and  $t$  is the time in weeks since the beginning of lactation.  $\text{Pot}$  (kg head<sup>-1</sup> day<sup>-1</sup>) was defined by Wood *et al.* (1980) as the milk yield when:

$$t^{Wb_i} * \exp (t * Wc_i) = 1.0 \quad (4.5)$$

This occurs shortly after calving. The effect of seasonality and date of calving on yield noted by Wood (1969) were estimated by Mainland (1985). Following Mainland (1985), these were incorporated into the model by correcting for the percentage

deviation in the lactation curve per month due to seasonal variation ( $S_Y$ , % deviation) and the date of calving ( $C_Y$ , % deviation). The daily milk yield is therefore defined as:

$$Y = Y^* (1 + S_Y(Mn)) * (1 + C_Y(Mn)) \quad (4.6)$$

where  $Mn$  represents the month number since the start of the year and a month is assumed to be a period of five weeks. The energy requirements for milk yield ( $E_L$ , MJ head<sup>-1</sup> day<sup>-1</sup>) have then been derived as follows:

$$E_L = \frac{Y * L_E}{k_l} \quad (4.7)$$

where  $L_E$  (MJ kg<sup>-1</sup>) is the net energy value of 1 kg of milk containing 4% fat and  $k_l$  is the proportionate efficiency with which ME is assumed to be utilised for milk production and is related to the metabolisability of the feed.

#### 4.2.1.2.4 Energy Requirements for Fattening

Finally, the estimates of the daily energy requirements for growth and fattening ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>) assume that the potential growth ( $\Delta_w$ , kg head<sup>-1</sup> day<sup>-1</sup>) of an animal can be described by a Gompertz equation (Taylor, 1968):

$$\Delta_w = -N * LWT * \ln \left( \frac{LWT}{Wt_M} \right) \quad (4.8)$$

where

$$N = \frac{1}{36 * Wt_M^{0.27}} \quad (4.9)$$

where LWT (kg head<sup>-1</sup>) is the liveweight and  $Wt_M$  (kg head<sup>-1</sup>) is the weight of the animal at maturity. Thus  $E_F$  (MJ head<sup>-1</sup> day<sup>-1</sup>) can be described by:

$$E_F = \frac{\Delta_w * N_w}{k_{fl}} \quad (4.10)$$

where  $N_w$  (MJ kg<sup>-1</sup>) is the net energy requirement for 1 kg of liveweight gain. The proportionate efficiency of ME utilisation for growth and fattening for a lactating cow is denoted by  $k_{fl}$  and is considered to be a function of the metabolisability of the feed.

#### 4.2.1.2.5 Physiological Energy Requirements

The physiological energy requirements ( $E_{Ph}$ , MJ head<sup>-1</sup> day<sup>-1</sup>) of the 'average dairy cow' are then obtained by summing the four elements ( $E_M$ ,  $E_P$ ,  $E_L$  and  $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>). However, the energy retention of ruminant livestock is not linearly related to intake; it is estimated to decline by between 0.3% and 1.4% per unit increase in feeding level (van Es, 1976; Schiemann, Jentsch and Wittenburg, 1971). The physiological intake has consequently been corrected for feeding level, as recommended by the Agricultural Research Council (1980), in the following manner:

$$\text{Level} = \frac{E_{Ph}}{E_M} \quad (4.11)$$

$$C_{Ph} = E_{Ph} * (1 + 0.018 * (\text{Level} - 1)) \quad (4.12)$$

where  $C_{Ph}$  ( $\text{MJ head}^{-1} \text{ day}^{-1}$ ) is the ME, corrected for feeding level, required for the daily physiological production of milk and growth. The physiological limit to herbage intake ( $I_{Ph}$ ,  $\text{kg DM head}^{-1} \text{ day}^{-1}$ ) is given by:

$$I_{Ph} = \frac{C_{Ph} - M_{Conc}}{M_{Fod}} \quad (4.13)$$

where  $M_{Conc}$  ( $\text{MJ head}^{-1} \text{ day}^{-1}$ ) represents the daily metabolisable energy intake of concentrates and  $M_{Fod}$  is the metabolisable energy value of ingested herbage per kg dry matter as defined by equation (3.44).

#### **4.2.1.3 Physical Limit to Intake**

With feeds having a low digestibility, the actual intake may be lower than the physiological requirement. Feed intake is controlled by the rate of passage of undigested material through the digestive tract and the rate is positively related to the digestibility of the feed (Conrad, Pratt and Hibbs, 1964). Following Kahn and Spedding (1984) the physical limit ( $I_A$ ,  $\text{kg DM head}^{-1} \text{ day}^{-1}$ ) on daily intake is accordingly assumed to be given by:

$$I_A = \frac{d_{max} * LWT}{1 - dg_{Diet}} \quad (4.14)$$

where  $d_{max}$  ( $\text{kg DM (kg liveweight)}^{-1} \text{ day}^{-1}$ ) represents the ability of the digestive tract to process and void undigested feed residues and  $dg_{Diet}$  represents the average digestibility of the feed in terms of the proportion of digestible organic matter in the dry matter. The stage of lactation is considered to have an influence on the cow's

ability to process undigested feed residues. Following Kahn and Spedding (1984),  $d_{\max}$  is increased linearly up to a maximum value on day 150 of lactation and then decreased linearly back to the base level at the end of lactation. At the same time, following the recommendations of the Agricultural Research Council (1980), the physical limit to herbage intake is corrected for the effects of concentrate feeding. This is because, as the level of concentrates increases, the intake of herbage decreases, so that the net effect of supplementing the diet only results in a small increase in the dry-matter intake (Mayne, 1990). Thus, the physical limit to herbage intake was described as follows:

$$I_A = I_A - I_{\text{Conc}} * C_{\text{Replace}} \quad (4.15)$$

where  $I_{\text{Conc}}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) is the quantity of concentrates fed and  $C_{\text{Replace}}$  (kg DM herbage (kg DM concentrates)<sup>-1</sup>) is the substitution rate of concentrates for forage defined by equation (3.31).

#### 4.2.2 Sub-model 2 – Calculation of Herbage Intake and Metabolisable Energy

The actual daily intake ( $I$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) can be derived from equations (3.29), (4.13) and (4.15) on the basis of the most restrictive factor such that:

$$I = \text{minimum}(I_F, I_{Ph}, I_A) \quad (4.16)$$

However, this provides no information on the composition of the diet in terms of leaf, stem and dead material or grass and white clover which are described in sections 3.3.4 and 3.3.5 respectively. The actual intake of energy from the herbage and

concentrates consumed is specified in section 3.3.6. It has been assumed in the model that the quantity of concentrates ( $I_{\text{Conc}}$ , kg head<sup>-1</sup> day<sup>-1</sup>) fed to the 'average dairy cow' is determined by the milk yield and is thus described as:

$$I_{\text{Conc}} = Y * I_{\text{C, kg}} \quad (4.17)$$

where

$$I_{\text{C, kg}} = I_{\text{C, l}} * DM_{\text{C}} * kg_{\text{l}} \quad (4.18)$$

where  $I_{\text{C, kg}}$  (kg DM concentrates head<sup>-1</sup> kg<sup>-1</sup> milk) is the dry-matter quantity of concentrates fed per kilogram of milk whereas  $I_{\text{C, l}}$  (kg head<sup>-1</sup> l<sup>-1</sup> milk) is the fresh weight of concentrates fed per litre of milk. The variables  $DM_{\text{C}}$  (kg DM kg<sup>-1</sup> fresh weight) and  $kg_{\text{l}}$  (kg milk l<sup>-1</sup> milk) convert the concentrates from fresh weight to dry weight and the milk yield from litres to kilograms respectively.

However, the efficiencies of conversion of metabolisable energy are dependent on the metabolisability of the feed ( $M_{\text{E}}$ , MJ (kg DM)<sup>-1</sup>), which is defined by the following equation:

$$M_{\text{E}} = \frac{T_{\text{Conc}} + T_{\text{Fod}}}{(I_{\text{Conc}} + I) * GE} \quad (4.19)$$

where  $T_{\text{Conc}}$  (MJ head<sup>-1</sup> day<sup>-1</sup>) is the ME intake of the concentrates,  $T_{\text{Fod}}$  (MJ head<sup>-1</sup> day<sup>-1</sup>) is the ME intake of the forage,  $I$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) and  $I_{\text{Conc}}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) are the forage and concentrates consumed respectively and  $GE$  (MJ (kg DM)<sup>-1</sup>) is the gross energy of the feed. The net utilisation efficiency of ME for maintenance

( $k_m$ ), lactation ( $k_l$ ) and for growth and fattening for a lactating cow ( $k_{fl}$ ) have been defined by the Agricultural Research Council (1980) as:

$$k_m = 0.35 * M_E + 0.503 \quad (4.20)$$

$$k_l = 0.35 * M_E + 0.42 \quad (4.21)$$

$$k_{fl} = 0.95 * k_l \quad (4.22)$$

The actual intake ( $I$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) and the ME value ( $M_{Fod}$ , MJ head<sup>-1</sup> day<sup>-1</sup>) of the herbage affects the metabolisability ( $M_E$ , MJ (kg DM)<sup>-1</sup>) of the feed, which in turn affects the efficiencies of conversion ( $k_m$ ,  $k_l$  and  $k_{fl}$ ). These efficiency factors are important in determining the potential energy requirements for maintenance ( $E_M$ , MJ head<sup>-1</sup> day<sup>-1</sup>), milk production ( $E_L$ , MJ head<sup>-1</sup> day<sup>-1</sup>) and liveweight gain ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>) (see equations (4.1), (4.7) and (4.10)). In order to get the most accurate prediction of the physiological energy requirements, the efficiencies, and therefore the metabolisability, are based on the intake determined by herbage availability ( $I_F$ , kg DM head<sup>-1</sup> day<sup>-1</sup>). If  $I_{Ph}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) is less than  $I_F$  (kg DM head<sup>-1</sup> day<sup>-1</sup>), the components of intake, ME, and the efficiencies are recalculated for an intake of  $I_{Ph}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>). In the model  $I_A$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) is then determined, and if  $I_A$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) is the most limiting factor, the components of intake, ME and the efficiencies are re-determined. This meant that the efficiency of conversions used in calculating the energy partitioned to milk, and growth and fattening are based on the actual intake of the animal.

Once the components of actual herbage intake have been determined the quantities consumed are then deducted from their respective components on the paddock being grazed. The total intake of ME ( $ME_C$ , MJ head<sup>-1</sup> day<sup>-1</sup>), is composed of the forage and concentrate ME. Nevertheless, as the energy retained by ruminant livestock is not linearly related to intake, the ME consumed ( $ME_C$ , MJ head<sup>-1</sup> day<sup>-1</sup>) must be corrected for feeding level. The actual ME that is available for the maintenance, pregnancy, milk production, and growth and fattening ( $MEI$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is thus defined as:

$$MEI = \frac{ME_C}{1 + 0.018 * (Level - 1)} \quad (4.23)$$

where

$$Level = \frac{ME_C}{E_M} \quad (4.24)$$

#### 4.2.3 Sub-model 3 – Partitioning of the Metabolisable Energy

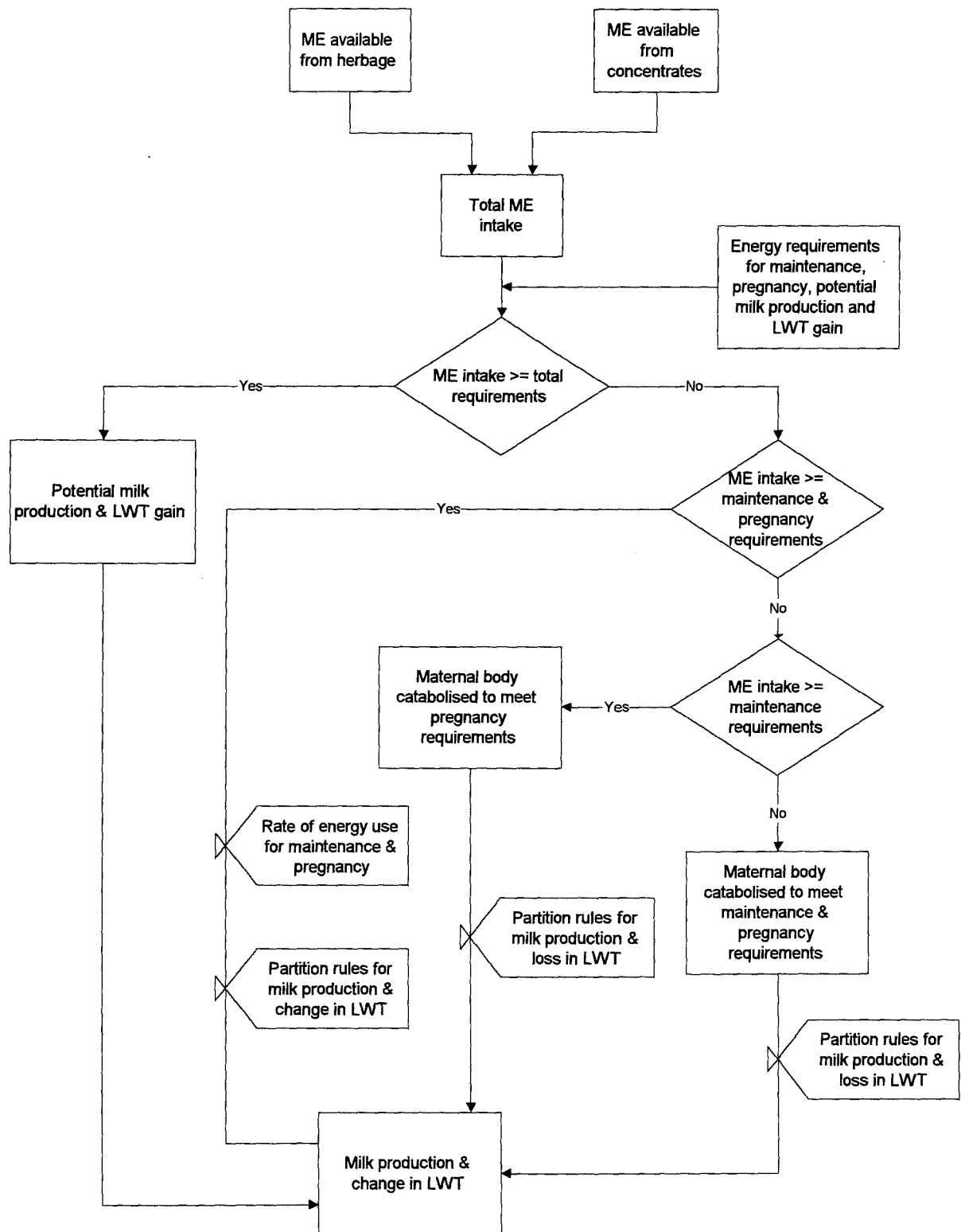
Within the model, the energy intake is partitioned between maintenance, pregnancy, growth and fattening and actual milk production as shown in Figure 4-1. The energy requirements for maintenance and pregnancy are considered to have priority. If there is insufficient energy available to meet the potential energy requirements of the animal, it is assumed that the potential energy requirements for milk ( $E_L$ , MJ head<sup>-1</sup> day<sup>-1</sup>) and growth ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>) are reduced by an equal amount (Bruce, Broadbent and Topps, 1984). Accordingly, the energy available for actual milk production ( $E_{AL}$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is described by:

$$E_L - E_{AL} = E_F - \Delta_E \quad (4.25)$$

where  $E_L$  ( $\text{MJ head}^{-1} \text{ day}^{-1}$ ) and  $E_F$  ( $\text{MJ head}^{-1} \text{ day}^{-1}$ ) represent the daily potential energy requirements for milk production, and growth and fattening. The actual energy available for growth is denoted by  $\Delta_E$  ( $\text{MJ head}^{-1} \text{ day}^{-1}$ ).

There are four different possible ME intake ( $\text{MEI}$ ,  $\text{MJ head}^{-1} \text{ day}^{-1}$ ) conditions which can occur and they are:

1. metabolisable energy intake meets the physiological requirements of the dairy cow;
2. metabolisable energy intake meets the maintenance and pregnancy requirements of the dairy cow but not the potential energy requirements for milk production and growth and fattening;
3. metabolisable energy intake meets the maintenance requirements of the dairy cow but the requirements for pregnancy and the potential energy requirements for milk production and growth and fattening are not fulfilled; and
4. metabolisable energy intake does not meet the requirements for maintenance and pregnancy.



**Figure 4-1** A schematic diagram of the partitioning of metabolisable energy in the dairy cow

The decision rules for these four possible situations are described in detail in Appendix VI and are outlined below.

- In the first case, the average dairy cow achieves potential milk and growth production.
- The second case occurs when the metabolic energy intake is insufficient to meet the energy requirements for potential milk and growth production, but the energy is sufficient to meet maintenance and pregnancy requirements. As a result of the energy deficit the potential energy requirements for milk and growth are reduced in equal amounts. If, as a consequence of the deficit in energy intake, the maternal body is catabolised the energy released from the maternal body production is used by the dairy cow for milk production.
- When the intake of metabolisable energy is insufficient to meet the requirements of pregnancy, case 3, there is catabolism of maternal body tissue to meet these requirements. The energy required for milk production by the dairy cow is also obtained from catabolising the maternal body. In these circumstances, the energy available for milk production may become less than zero. If this occurs, no milk is produced and the quantity of maternal body catabolised is restricted to the shortfall in energy requirements for pregnancy.
- In the final case, the metabolisable energy available is insufficient to meet the maintenance and pregnancy requirements. Consequently, the maternal body is catabolised to meet these energy requirements. Similarly

to case 3, the energy available from milk is also obtained from catabolising the maternal body. If there is no energy available for milk production, catabolism of the maternal body is restricted to the energy required for maintenance and pregnancy.

### **4.3 Beef Model**

The beef enterprise is assumed to be an eighteen-month beef finishing system, and thus the calves are presumed to be born in the autumn and finished out of yards after the second winter. The beef model is concerned with representing the grazing phase of production. The cattle are considered to be turned out at approximately six months of age, in the spring, and yarded at the end of the grazing season. In the model, the beef steer is represented in the model by the 'average beef steer'.

In the description, the model is divided into three sub-models concerned with:

1. factors controlling herbage intake;
2. calculation of the herbage intake; and finally
3. the partitioning of the metabolisable energy (ME) between the requirements of the 'average beef steer'

#### **4.3.1 Sub-model 1 – Factors Controlling Herbage Intake**

The intake of herbage intake by grazing ruminant livestock is influenced by feed availability, the physiological requirements of the animal and the physical limit to intake, in the same way as for dairy cows. However, the estimation of the physiological requirements of the animal differs from that of the dairy cow.

#### **4.3.1.1 Physiological Limit to Intake**

The physiological limit to intake for beef steers is determined by the daily metabolisable energy requirements arising from maintenance ( $E_M$ , MJ head<sup>-1</sup> day<sup>-1</sup>), and growth and fattening ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>). The maintenance requirements ( $E_M$ , MJ head<sup>-1</sup> day<sup>-1</sup>) are described by equation (4.1) and the age (Age, yrs) at turn-out is presumed to be 180 days or 0.493 years.

Within the model, the potential energy requirements for growth and fattening ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>) of the 'average beef steer' is presumed to be determined from the potential gain in the protein ( $\Delta_P$ , kg head<sup>-1</sup> day<sup>-1</sup>) and fat content ( $\Delta_F$ , kg head<sup>-1</sup> day<sup>-1</sup>) of the empty body weight and is described by:

$$E_F = \frac{\Delta_P * P_E + \Delta_F * F_E}{k_f} \quad (4.26)$$

where  $P_E$  (MJ kg<sup>-1</sup>) and  $F_E$  (MJ kg<sup>-1</sup>) are the energy values of protein and fat respectively and  $k_f$  is the proportionate efficiency of the ME utilisation for growth and fattening. The Agricultural Research Council (1980) defined  $k_f$  by:

$$k_f = 0.78 * M_E + 0.006 \quad (4.27)$$

where  $M_E$  is the metabolisability of the feed; defined by equation (4.19). The calculation of the energy requirements for the potential liveweight gain therefore requires that the potential change in protein ( $\Delta_P$ , kg head<sup>-1</sup> day<sup>-1</sup>) and fat ( $\Delta_F$ , kg head<sup>-1</sup> day<sup>-1</sup>) must be ascertained.

#### 4.3.1.1.1 Potential Gain in Protein

The net synthesis of protein is calculated from the rates of protein synthesis and the degradation. The rate of protein synthesis is a function of the level of DNA in the body and the level of nutrition (Oltjen *et al.*, 1986). It is assumed within the model that the DNA in the body is regulated by the current level of DNA (g head<sup>-1</sup>), the DNA content of the animal at maturity (DNA<sub>Max</sub>, g head<sup>-1</sup>) and the level of nutrition. The change in DNA content for a given day ( $\Delta_{DNA}$ , g head<sup>-1</sup> day<sup>-1</sup>) and the rate of protein synthesis ( $P_s$ , kg head<sup>-1</sup> day<sup>-1</sup>) are therefore defined as:

$$\Delta_{DNA} = K1 * (DNA_{Max} - DNA) * Nut1 \quad (4.28)$$

$$P_s = K2 * (T_{DNA})^{E2} * Nut2 \quad (4.29)$$

where K1, K2 and E2 are the constants, and Nut1 and Nut2 are the nutritional effects on DNA accumulation and protein synthesis respectively. The predicted DNA content of the body, if the animal attains the potential liveweight gain ( $T_{DNA}$ , g head<sup>-1</sup>) is therefore described as:

$$T_{DNA} = DNA + \Delta_{DNA} \quad (4.30)$$

The calculation of the energy required for the potential gain in protein assumes that the level of nutrition is optimal. According to Oltjen *et al.* (1986) the protein content of the empty body determines the rate of protein degradation. Oltjen *et al.* (1986) estimated the relationship describing the protein degradation ( $P_D$ , kg head<sup>-1</sup> day<sup>-1</sup>)

within the animal from work by Lobley, Milne, Lovie, Reeds and Pennie (1980) which is specified as:

$$P_D = K3 * P^{E2} \quad (4.31)$$

where K3 is the protein degradation constant and P (kg head<sup>-1</sup>) is the level of empty body protein. The net synthesis of protein per day ( $\Delta_P$ , kg head<sup>-1</sup> day<sup>-1</sup>) is therefore described by:

$$\Delta_P = P_S - P_D \quad (4.32)$$

The initial quantity of protein within the empty body (P, kg head<sup>-1</sup>) has been defined by the Agricultural Research Council (1980) as:

$$P = 10^{(LP1 * \text{Log}(EBW) - LP2)} \quad (4.33)$$

where LP1 and LP2 are constants.

#### **4.3.1.1.2 Potential Gain in Empty Body Weight**

The potential synthesis of fat is presumed to be a function of the potential gain in empty body weight and consequently the latter must be determined first. Following the Agricultural Research Council (1980) the empty body weight (EBW, kg head<sup>-1</sup>) can be converted to the liveweight (LWT, kg head<sup>-1</sup>) by:

$$EBW = \frac{LWT}{LEBW1} - LEBW2 \quad (4.34)$$

where LEBW1 is a constant and LEBW2 is the coefficient appropriate for cattle with an initial gut fill of 300 g kg<sup>-1</sup> empty body weight. Accordingly, the potential gain in empty body weight can be predicted from the potential gain in liveweight ( $\Delta_w$ , kg head<sup>-1</sup> day<sup>-1</sup>) which is defined by:

$$\Delta_w = -N * Wt_N * \ln\left(\frac{Wt_N}{Wt_M}\right) \quad (4.35)$$

where N is defined by equation (4.9),  $Wt_M$  (kg head<sup>-1</sup>) is the mature weight of the steer and  $Wt_N$  (kg head<sup>-1</sup>) is the liveweight if the animal had grown at the normative growth rate. When herbage intake is limited, the actual liveweight gain will be less than the normative liveweight gain. However, during periods of plenty, the animals will compensate for periods of limited intake and will consequently have a higher liveweight gain than predicted from the Gompertz equation. Following Kahn and Spedding (1984) the attainment of normative weight will take 26 days. Within the model, the potential liveweight gain is calculated on a daily basis, allowing for compensatory growth required for any previous time period. Nevertheless, the total daily weight gain is limited to 1.5 kg head<sup>-1</sup> day<sup>-1</sup> (Kahn and Spedding, 1984). Using equation (4.34) the gain in liveweight is converted to a change in the empty body weight. Hence the gain in empty body weight ( $\Delta_{EBW}$ , kg head<sup>-1</sup> day<sup>-1</sup>) is given by:

$$\Delta_{EBW} = EB - EBW \quad (4.36)$$

where EB (kg head<sup>-1</sup>) is the potential empty body weight on the present day and EBW (kg head<sup>-1</sup>) is the actual empty body weight on the previous day.

#### 4.3.1.1.3 Potential Gain in Fat

In the model the gain in empty body weight is a function of the net synthesis of protein and fat (Oltjen *et al.*, 1986). Because the predicted gain in empty body weight ( $\Delta_{EBW}$ , kg head<sup>-1</sup>) and the net protein synthesis ( $\Delta_P$ , kg head<sup>-1</sup> day<sup>-1</sup>) has been determined, the predicted gain in fat ( $\Delta_F$ , kg head<sup>-1</sup> day<sup>-1</sup>) can therefore be calculated as follows:

$$\Delta_F = \Delta_{EBW} - \frac{\Delta_P}{K4} \quad (4.37)$$

where K4 is a constant.

#### 4.3.1.1.4 Physiological Energy Requirements

The physiological energy requirements ( $E_{Ph}$ , MJ head<sup>-1</sup> day<sup>-1</sup>) of the 'average steer' are then defined as:

$$E_{Ph} = E_M + E_F \quad (4.38)$$

As for the dairy cow model, the physiological energy requirements of the 'average steer' are corrected for feeding level; described in equations (4.11) and (4.12). The physiological limit to intake are therefore described by equation (4.13).

#### 4.3.2 Sub-model 2 – Calculation of Herbage Intake and Metabolisable Energy

The actual herbage intake is determined by the minimum of  $I_F$  (kg DM head<sup>-1</sup> day<sup>-1</sup>),  $I_{Ph}$  (kg DM head<sup>-1</sup> day<sup>-1</sup>) and  $I_A$  (kg DM head<sup>-1</sup> day<sup>-1</sup>). The methodology for determining the minimum value and the metabolisability of the feed are described in

section 4.2.2. Once the actual herbage intake has been determined, the quantity of the components consumed are then deducted from their respective components on the paddock being grazed. The total intake of ME ( $ME_C$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is the combined ME from the intake of forage and concentrates which is corrected for feeding level according to the recommendations of the Agricultural Research Council (1980). Accordingly the actual ME ( $MEI$ , MJ head<sup>-1</sup> day<sup>-1</sup>) that is available to the animal is defined by equation (4.23).

### 4.3.3 Sub-model 3 – Partitioning of Metabolisable Energy

In the model the metabolisable intake of the 'average steer' is partitioned between maintenance and growth (see Figure 4-2). It is assumed that there is sufficient herbage available to meet the maintenance requirements of the steers. The remaining energy which is utilised for growth is partitioned between fat and protein synthesis. Equations (4.28)–(4.32) describe the potential net gain in protein. However, the change in DNA content and protein synthesis defined by equations (4.28) and (4.29) are effected by the level of nutrition ( $L_N$ ). Hence, following Oltjen *et al.* (1986), the effect of the nutrition level (Nut1) on DNA synthesis ( $\Delta_{DNA}$ , g head<sup>-1</sup> day<sup>-1</sup>) and protein synthesis ( $P_S$ , kg head<sup>-1</sup> day<sup>-1</sup>) are described by:

$$Nut1 = N1 + N2 * L_N \quad (4.39)$$

$$Nut2 = N3 + \frac{N4 * L_N}{N5 + L_N} \quad (4.40)$$

where N1, N2, N3, N4 and N5 are constants. Within the model, the level of nutrition ( $L_N$ ) is defined as:

$$L_N = \frac{MEI}{MEI_N} \quad (4.41)$$

where MEI ( $\text{MJ head}^{-1} \text{ day}^{-1}$ ) is the actual intake and  $MEI_N$  is the energy requirements for normal growth of a steer. According to Song and Dinkel (1978) there is a linear relationship between maximum ME intake per kilogram of metabolic body weight and the degree of maturity. The energy requirements for the normal growth of a British steer have been estimated by Oltjen *et al.* (1986) from National Research Council recommendations (1976) and is described as:

$$MEI_N = \left( Nm1 - \frac{Nm2 * EBW}{EBW_M} \right) * EBW^{E2} * cal \quad (4.42)$$

where  $EBW_M$  is the mature empty body weight, and Nm1, Nm2 and E2 are constants. The constant, cal ( $\text{MJ MCal}^{-1}$ ), converts megacalories to megajoules.

Once the net synthesis of protein ( $\Delta_P$ ,  $\text{kg head}^{-1} \text{ day}^{-1}$ ) has been determined the net fat synthesis ( $\Delta_F$ ,  $\text{kg head}^{-1} \text{ day}^{-1}$ ) is calculated from the following equation (Oltjen *et al.*, 1986):

$$\Delta_F = \frac{k_f * (MEI - E_M) - P_E * \Delta_P}{F_E} \quad (4.43)$$

The empty body weight of the steer is then determined by adding the gain in fat and protein to the existing fat and protein content of the body, while the liveweight the 'average steer' is determined from:

$$LWT = LEBW1 * (EBW - LEBW2) \quad (4.44)$$

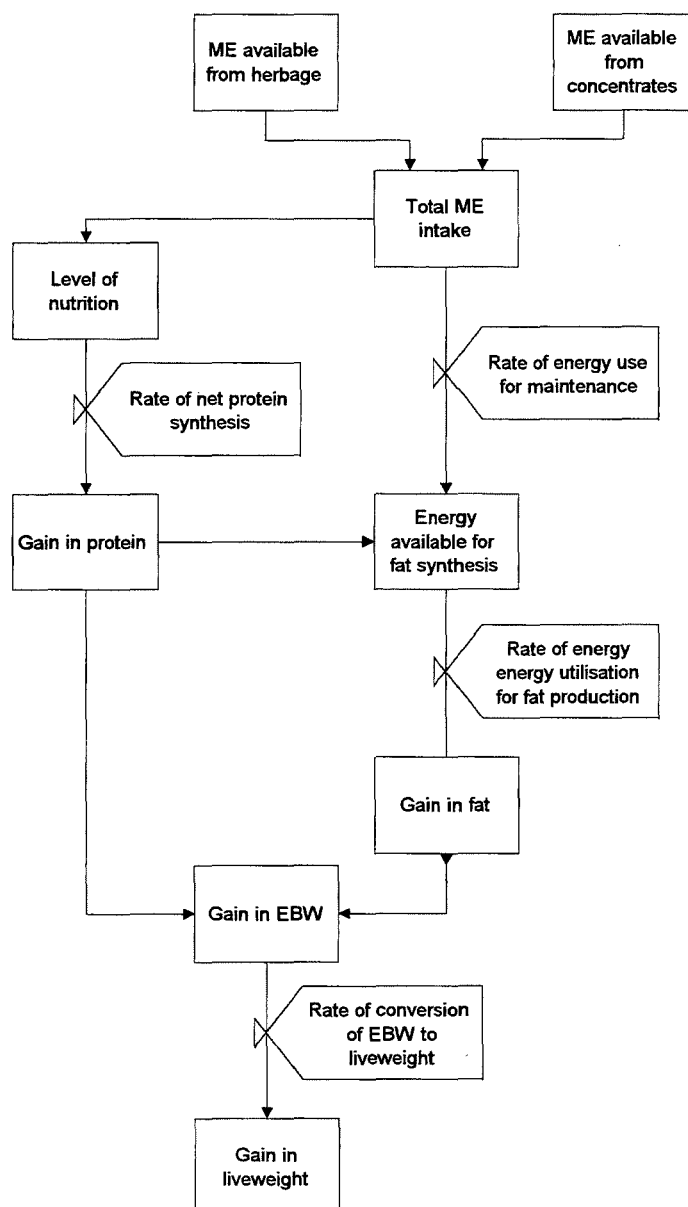


Figure 4-2 A schematic diagram of the partitioning of metabolisable energy in the beef steer

#### **4.4 Sheep Model**

The sheep flock is assumed to be lambled in a shed in the spring, and the date of lambing is presumed to be 15 March. In the model, the flock is represented by the 'average ewe' with the 'average number of lambs at foot'. The percentage of lambs weaned per ewe, in the model, is presumed to be no greater than 200%, although the lambing percentage is determined by the user. It is assumed that half the lambs are castrated males and the other half are females. The lambs are solely dependent on milk until they are five weeks old. After that period, if there is insufficient energy available from milk for potential growth, it is assumed that they would consume herbage. The lambs are assumed to be weaned at 16 weeks of age. It is presumed within the model that the date of turn-out is after the date of lambing and dependent on there being sufficient herbage on the paddocks to allow grazing.

The time interval within the model is a day. For convenience the model may be divided into five sub-models concerned with:

1. initial liveweight of the lambs;
2. factors controlling herbage intake;
3. calculation of the herbage intake;
4. partitioning of the metabolisable energy in sheep; and finally
5. partitioning of the metabolisable energy in lambs.

##### **4.4.1 Sub-model 1 – Initial Liveweight of the Lambs**

Dickenson, Hancock, Hovell, Taylor and Wiener (1962) predicted from egg transfer experiments that the lamb litter weight was dependent on the weights of both the

donor and recipient ewe at mating as well as the lamb litter size. France, Neal, Probert and Pollott (1983) assumed that the donor weight of the ewe at mating could be described by the average weight of the sire and dam breeds. The weight of the dam was presumed to specify the weight of the recipient ewe. Consequently, the lamb litter weight ( $Wt_L$ , kg litter<sup>-1</sup>) is defined as:

$$Wt_L = 0.089 * n * (Wt_D)^{0.83} * \left(1 - 10^{-(1.96 * V1/n)}\right) \quad (4.45)$$

where

$$Wt_D = Wt + Wt_S \quad (4.46)$$

and

$$V1 = \left(\frac{Wt}{Wt_D}\right)^{0.83} \quad (4.47)$$

where  $Wt$  (kg ewe<sup>-1</sup>) is the liveweight of the ewe at mating,  $Wt_S$  (kg ewe<sup>-1</sup>) is liveweight of ewe of the sire breed and  $n$  is the number of lambs in the litter. In the model the lamb litter weight is calculated for litter sizes of one and two lambs. The weight of the 'average lamb' is then calculated by weighting the lamb litter weights by the number of ewes with single and twin lambs. Following France *et al.* (1983), the liveweight of the ewe at lambing (LWT, kg ewe<sup>-1</sup>) is presumed to be described by:

$$LWT = Wt * Wt\% \quad (4.48)$$

where  $Wt\%$  represents the maternal liveweight at lambing as a percentage of the liveweight at mating.

#### **4.4.2 Sub-model 2 – Factors Controlling Herbage Intake**

In the model of the sheep flock it is assumed that the lambs' diet will consist only of milk for the first five weeks. If there is sufficient herbage available they will then start to graze and will be weaned at 16 weeks. After weaning it is assumed that the sheep and the lambs will be grazing different paddocks. The lambs are assumed to graze the paddock with either sufficient herbage to meet their requirements or the greatest herbage mass and the ewes will graze the paddock that the lambs previously grazed. In the model the factors limiting intake must be described for the ewes and lambs independently as the factor limiting the dry-matter intake of ewes is not the same as that for lambs.

##### **4.4.2.1 Feed Availability**

During the period when the sheep and lambs are both grazing the same paddock it is assumed that they are equally competitive for herbage. The herbage required for maximum intake constrained by feed availability is determined from equation (3.34) for both the sheep and the lambs. The daily allowance of green herbage ( $H$ , kg DM (ewe + lambs)<sup>-1</sup> day<sup>-1</sup>) on the paddock that is being grazed is divided between the ewes and the lambs in the proportion of their maximum daily intake. The maximum daily intake for the ewe ( $I_{E, \max}$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) and lambs ( $I_{L, \max}$ , kg DM head<sup>-1</sup> day<sup>-1</sup>) is calculated from equation (3.30), and thus the maximum daily intake for the lambs per ewe ( $I_{EL, \max}$ , kg DM litter<sup>-1</sup> day<sup>-1</sup>) is given by:

$$I_{EL, \max} = I_{L, \max} * \frac{L\%}{100} \quad (4.49)$$

where L% represents the lambing percent. The daily allowance of green herbage for the lambs per ewe ( $H_{EL}$ , kg DM litter<sup>-1</sup> day<sup>-1</sup>) is therefore described as:

$$H_{EL} = \frac{I_{EL, \max}}{I_{EL, \max} + I_{E, \max}} * H \quad (4.50)$$

Hence the daily allowance per lamb ( $H_L$ , kg DM lamb<sup>-1</sup> day<sup>-1</sup>) and per ewe ( $H_E$ , kg DM ewe<sup>-1</sup> day<sup>-1</sup>) are:

$$H_L = H_{EL} * \frac{100}{L\%} \quad (4.51)$$

$$H_E = H - H_{EL} \quad (4.52)$$

The feed availability limit to intake for the sheep ( $I_{E, F}$ , kg DM ewe<sup>-1</sup> day<sup>-1</sup>) and lambs ( $I_{L, F}$ , kg DM lamb<sup>-1</sup> day<sup>-1</sup>) are therefore described by:

$$I_{E, F} = I_{E, \max} * \left(1 - \exp(-H_E / I_{E, \max})^{b1}\right)^{1/b1} \quad (4.53)$$

$$I_{L, F} = I_{L, \max} * \left(1 - \exp(-H_L / I_{L, \max})^{b1}\right)^{1/b1} \quad (4.54)$$

where b1 is a constant.

#### **4.4.2.2 Physiological Limit**

##### **4.4.2.2.1 Physiological Limit to Intake for Ewes**

The metabolisable energy requirements (ME, MJ ewe<sup>-1</sup> day<sup>-1</sup>) of the ewe determine the physiological limit to intake, where the energy demands are divided into those for maintenance (E<sub>M</sub>, MJ ewe<sup>-1</sup> day<sup>-1</sup>), pregnancy (E<sub>P</sub>, MJ ewe<sup>-1</sup> day<sup>-1</sup>), milk production (E<sub>L</sub>, MJ ewe<sup>-1</sup> day<sup>-1</sup>) and growth and fattening (E<sub>F</sub>, MJ ewe<sup>-1</sup> day<sup>-1</sup>).

##### **4.4.2.2.1.1 Energy Requirements for Maintenance**

The energy requirements for maintenance include fasting heat production (M<sub>B</sub>, MJ head<sup>-1</sup> day<sup>-1</sup>) and the increase in heat production associated with muscular activity (M<sub>W</sub>, MJ head<sup>-1</sup> day<sup>-1</sup>). The following relationships described by Agricultural Research Council (1980) are used to determine the maintenance requirements (E<sub>M</sub>, MJ head<sup>-1</sup> day<sup>-1</sup>) of the sheep:

$$M_B = 0.245 - 0.02164 * \ln(\text{Age}) * \left( \frac{Wt}{108} \right)^{0.75} \quad (4.55)$$

$$M_W = \frac{31}{1000} * Wt \quad (4.56)$$

$$E_M = \frac{M_B + M_W}{k_m} \quad (4.57)$$

where the Age is the average age of the 'average ewe' in years, which is assumed to be three and Wt (kg ewe<sup>-1</sup>) is the liveweight. The proportionate net efficiency of use of ME for maintenance is represented by k<sub>m</sub>, which is related to the metabolisability of

the feed and is defined by equation (4.20). The factor 1.08 converts liveweight to fasted weight.

#### **4.4.2.2.1.2 Energy Requirements for Pregnancy**

Following the Agricultural Research Council (1980) the daily energy requirements for pregnancy ( $E_p$ , MJ ewe<sup>-1</sup> day<sup>-1</sup>) have been derived using relationships for a 4 kg lamb and are described as:

$$E_p = \frac{E_p * 0.07372 * \exp(-0.00643 * \text{DayP})}{k_c} \quad (4.58)$$

where

$$\log(E_p) = 3.322 - 4.979 * \exp(-0.00643 * \text{DayP}) \quad (4.59)$$

where DayP is the number of days since conception and  $k_c$  is the net utilisation efficiency of ME for pregnancy.

#### **4.4.2.2.1.3 Energy Requirements for Milk Production**

In order to estimate the potential energy requirements for milk production the potential milk yield ( $Y$ , kg head<sup>-1</sup> day<sup>-1</sup>) must be determined. Following France *et al.* (1983), the relationship described by Wood *et al.* (1980) which was derived for dairy cows is used to describe the lactation curve for ewes. Hence the potential milk yield is described as:

$$Y = \text{Pot} * d_L^{w_b} * \exp(-Wc * d_L) \quad (4.60)$$

where  $Pot$  ( $\text{kg head}^{-1} \text{ day}^{-1}$ ) represents the scale parameter,  $W_b$  and  $W_c$  are constants describing the shape of the lactation curve and  $d_L$  represents the number of days post partum. The potential milk yield of the ewe and thus the scale parameter ( $Pot$ ,  $\text{kg head}^{-1} \text{ day}^{-1}$ ) is dependent on the size of the litter (Meat and Livestock Commission, 1981). Consequently the milk yield for the 'average ewe' ( $Y$ ,  $\text{kg head}^{-1} \text{ day}^{-1}$ ) is average milk yield of a ewe with a single lamb and a ewe with twin lambs weighted by the number ewes with single and twin lambs.

The energy content of the milk ( $E_{ML}$ ,  $\text{MJ kg}^{-1}$ ) produced by ewes is defined by the Agricultural Research Council (1980) as:

$$E_{ML} = 0.3280 * F + 0.0025 * d_L + 2.303 \quad (4.61)$$

where  $F$  is the percentage fat content of the milk, and has a value of 7% (Agricultural Research Council, 1980). Hence the energy content of the milk ( $Y_E$ ,  $\text{MJ ewe}^{-1} \text{ day}^{-1}$ ) is:

$$Y_E = Y * E_{ML} \quad (4.62)$$

and the ME required for milk production ( $E_L$ ,  $\text{MJ head}^{-1} \text{ day}^{-1}$ ) is described by:

$$E_L = \frac{Y_E}{k_i} \quad (4.63)$$

where  $k_i$  is the proportionate efficiency with which ME is utilised for milk production.

#### **4.4.2.2.1.4 Energy Requirements for Growth and Fattening**

Within the model it is assumed that the potential growth of a ewe can be described by the Gompertz equation and therefore the potential gain in liveweight ( $\Delta_w$ , kg head<sup>-1</sup> day<sup>-1</sup>) is presumed to be described by equations (4.8) and (4.9), section 4.2.1.2. Accordingly, the daily energy requirement for growth and fattening ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is described as:

$$E_F = \frac{\Delta_w * N_w}{k_{eff}} \quad (4.64)$$

where  $N_w$  (MJ kg<sup>-1</sup>) is the net energy requirement for 1 kg of liveweight gain and the variable  $k_{eff}$  represents the proportionate efficiency of ME utilisation for growth and fattening. During the lactation phase of production,  $k_{eff}$  is designate by  $k_{fl}$ , whereas during the dry phase of production it is denoted by  $k_f$ , which is defined by equation (4.27).

#### **4.4.2.2.1.5 Physiological Energy Requirements**

The physiological energy requirements ( $E_{Ph}$ , MJ ewe<sup>-1</sup> day<sup>-1</sup>) of the ewe are therefore described by:

$$E_{Ph} = E_M + E_L + E_F + E_P \quad (4.65)$$

The determination of the physiological limit to intake corrected for feeding level ( $I_{E, Ph}$ , MJ ewe<sup>-1</sup> day<sup>-1</sup>) is described by equations (4.11)—(4.13).

#### **4.4.2.2.2 Physiological limit to intake for lambs**

The physiological limit to herbage intake for lambs gaining part of their energy requirements from forage is regulated by the energy requirements for maintenance ( $L_M$ , MJ lamb<sup>-1</sup> day<sup>-1</sup>), and growth and fattening ( $L_F$ , MJ lamb<sup>-1</sup> day<sup>-1</sup>).

##### **4.4.2.2.2.1 Energy Requirements for Maintenance**

It is assumed in the model, when the lambs start consuming herbage, that their maintenance requirements ( $L_M$ , MJ lamb<sup>-1</sup> day<sup>-1</sup>) are described by equations (4.55)—(4.57).

##### **4.4.2.2.2.2 Energy Requirements for Growth and Fattening**

In the model it is assumed that the potential growth of lambs ( $\Delta_{WL}$ , kg head<sup>-1</sup> day<sup>-1</sup>) can be described by the Gompertz equation which is represented by equations (4.8) and (4.9), section 4.2.1.2. The actual daily energy requirement for growth and fattening ( $L_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is therefore represented by:

$$L_F = \frac{\Delta_{WL} * N_S}{k_e} \quad (4.66)$$

where  $k_e$  denotes the proportionate efficiency of use of ME for growth and fattening. When the lamb is on an all-milk diet the proportionate efficiency of conversion is represented by  $k_{flb}$  while the efficiency of conversion for a lamb consuming solid feed is represented by  $k_f$  and defined by equation (4.27). The energy content of the liveweight gain ( $N_S$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is dependent on the liveweight of the lamb, and following the Agricultural Research Council (1980) is described by:

$$N_s = G1 + G2 * LWT_L \quad (4.67)$$

where G1 and G2 are constants and  $LWT_L$  ( $\text{kg lamb}^{-1}$ ) is the liveweight of the lamb. The Agricultural Research Council (1980) give values for the constants for lambs on all-milk diets and lambs on all-solid diets. When the lambs are consuming herbage the constants for lambs on all-solid diets are used. The energy values of the liveweight gain for castrate lambs are greater than those for female lambs. Within the model, it is assumed that the ratio of castrates to females is one. Consequently, the average of the energy values for castrates and females are used to determine the energy requirements for liveweight gain ( $L_F$ ,  $\text{MJ head}^{-1} \text{ day}^{-1}$ ).

#### **4.4.2.2.3 Physiological Energy Requirements**

The physiological energy requirements are obtained by summing the elements ( $L_M$  and  $L_F$ ,  $\text{MJ lamb}^{-1} \text{ day}^{-1}$ ) which are then corrected for feeding level, and are described by equations (4.11) and (4.12). It is assumed when calculating the physiological limit to intake for lambs ( $I_{L, Ph}$ ,  $\text{kg DM lamb}^{-1} \text{ day}^{-1}$ ) that they are on an all-solid diet which is described in equation (4.13).

#### **4.4.2.3 Physical Limit to Intake**

In the model, it is presumed that the intake can be constrained by the physical characteristics of the animal. As Blaxter, Wainman and Wilson (1961) estimated the dry-matter content of the digestive tract per kilogram of metabolic weight, equation (4.14) has been expressed in terms of metabolic liveweight. The physical limit to intake for sheep is therefore described by:

$$I_{E, A} = \frac{d_{\max} * LWT^{0.734}}{1 - dg_{\text{Diet}}} \quad (4.68)$$

where  $d_{\max}$  (kg DM (kg liveweight)<sup>-0.734</sup> day<sup>-1</sup>) represents the ability of the digestive tract to process and void undigested feed residues and  $dg_{\text{Diet}}$  represents the average digestibility of the feed in terms of the proportion of digestible organic matter in the dry matter. The physical limit is corrected for the intake of concentrates to give the physical limit to herbage intake ( $I_{E, A}$ , kg DM ewe<sup>-1</sup> day<sup>-1</sup>), which is described by equation (4.15). The physical limit to herbage intake for lambs ( $I_{L, A}$ , kg DM lamb<sup>-1</sup> day<sup>-1</sup>) is also described by equations (4.68) and (4.15), where LWT is replaced by  $LWT_L$ .

#### 4.4.3 Sub-model 3 – Calculation of Herbage Intake and Metabolisable Energy

The limits to intake for ewes and lambs are determined independently with the limit being the minimum of the feed availability, physiological limit to intake and the physical limit to intake. The methodology that is used to calculate actual intake and metabolisable energy has been described in section 4.2.2. The total intake of metabolisable energy is corrected for feeding level (Agricultural Research Council, 1980) to give the actual energy available for meeting the requirements of the animal. The quantity of the components consumed is then deducted from their respective components on the paddock being grazed.

#### 4.4.4 Sub-model 4 – Partitioning of the Energy in Sheep

During the grazing season the ewe will either be lactating or dry. However, the requirements for energy and the efficiencies of utilisation of the energy will differ between the two stages of production.

##### 4.4.4.1 Lactation Phase of Production

In the model, during the lactation phase of production, energy intake is partitioned between maintenance ( $E_M$ , MJ head<sup>-1</sup> day<sup>-1</sup>), milk production ( $E_L$ , MJ head<sup>-1</sup> day<sup>-1</sup>) and liveweight change ( $E_F$ , MJ head<sup>-1</sup> day<sup>-1</sup>). During the lactation phase of production, it is assumed that the ewe is not pregnant. Consequently, there are three different ME intake conditions which can occur and they are defined as:

$$MEI \geq C_{Ph} \quad (4.69)$$

$$E_M < MEI < C_{Ph} \quad (4.70)$$

$$MEI < E_M \quad (4.71)$$

where  $C_{Ph}$  (MJ head<sup>-1</sup> day<sup>-1</sup>) is the ME, corrected for feeding level, required for the daily physiological production of milk and growth, defined by equation (4.12). As for the dairy cow, Figure 4-1 describes the general rules used for partitioning the metabolisable energy in the lactating ewe. In the model it is presupposed that the maintenance requirements will have priority. Following the model of the dairy cow, it is assumed that if there is insufficient energy available to meet the potential energy requirements of the ewe then the requirements for milk and fattening will be reduced

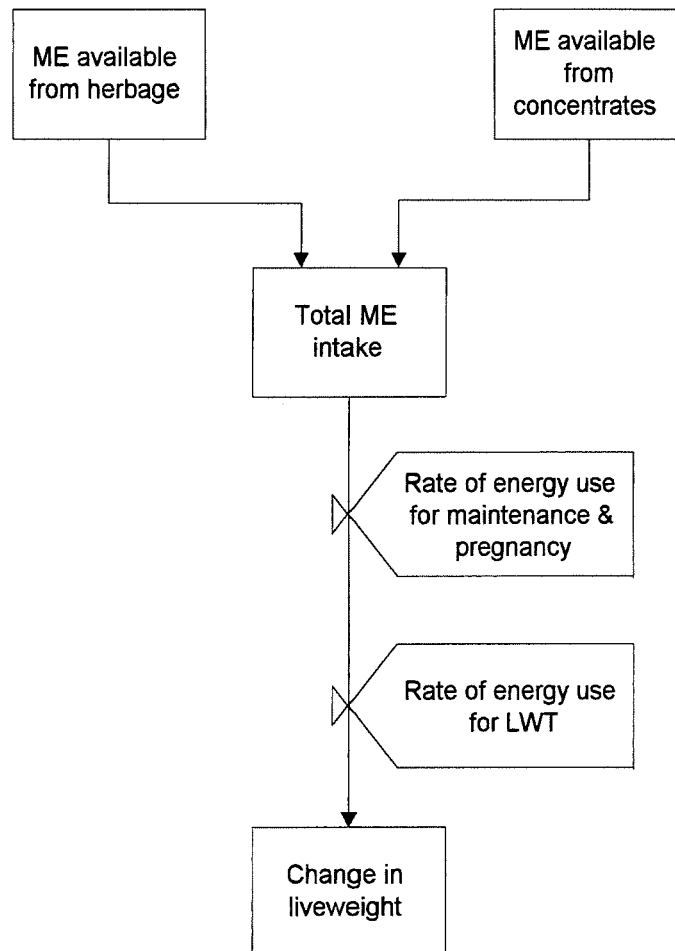
in equal amounts. The methodology for partitioning the energy in the ewe when the conditions outlined in equations (4.69), (4.70) and (4.71) are prevailing is described in Appendix VI.

#### **4.4.4.2 Dry Phase of Production**

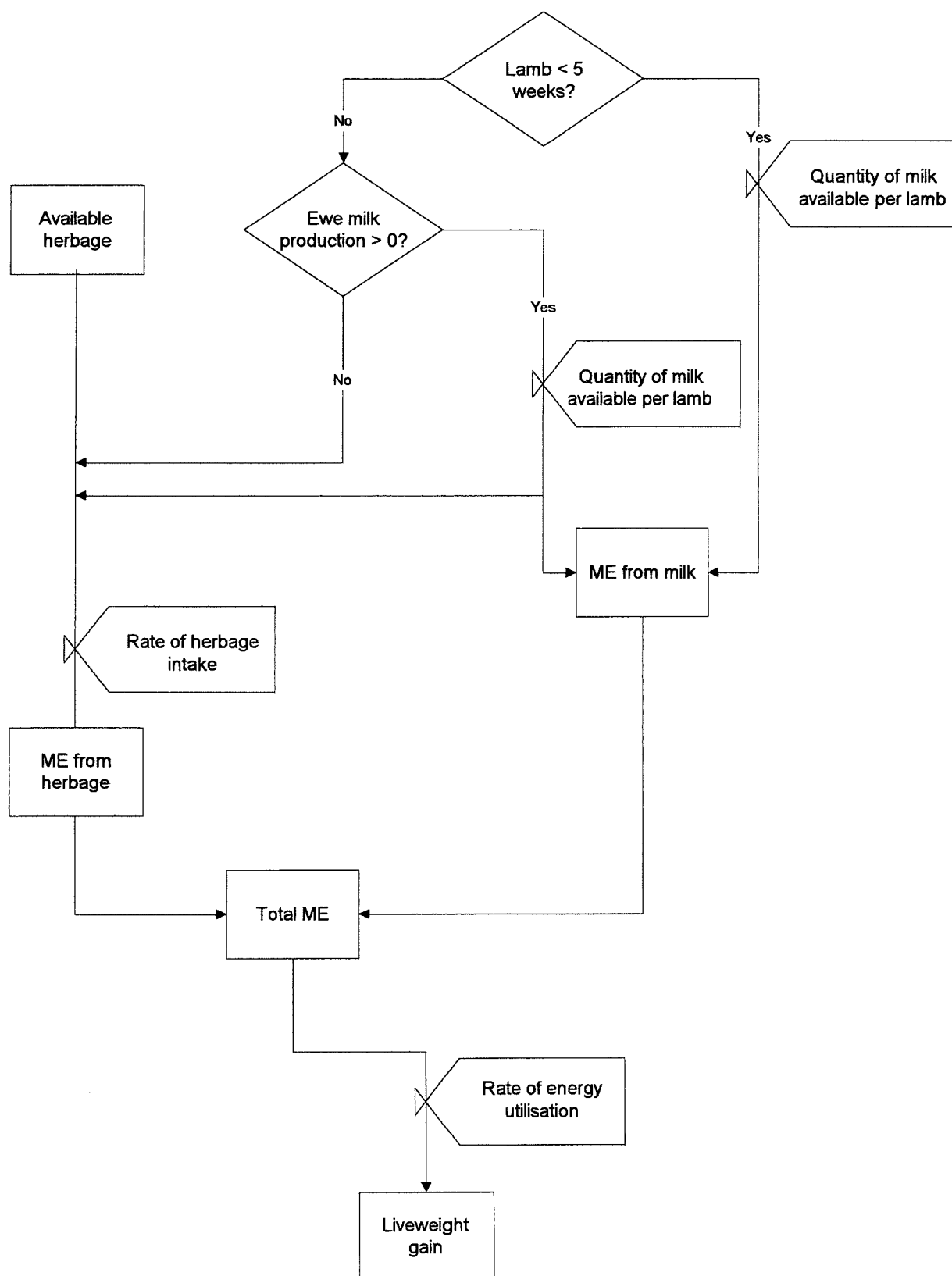
During the dry phase of production the partition of available energy between maintenance, pregnancy and liveweight gain is presented schematically in Figure 4-3. Specifically, it is assumed that maintenance and pregnancy are regarded to have priority. Any surplus energy is presumed to be used for liveweight gain. If there is insufficient energy to meet the maintenance and pregnancy requirements of the ewe, the deficit is met by catabolising maternal body. Hence the pregnancy requirements for energy from the maternal body are described by equations (VI.23) and (VI.24) in Appendix VI. As in the dairy cow model, it is assumed that the efficiency of utilisation of energy for maintenance is not affected by the source of the energy.

#### **4.4.5 Sub-model 5 – Partitioning of the Energy in Lambs**

The energy intake of the lambs is partitioned between maintenance and liveweight gain as shown in Figure 4-4. It is assumed within the model that the energy intake of the lamb will be sufficient to meet the maintenance requirements. The maintenance requirements and the efficiency of liveweight gain differ between lambs on an all-milk diet and those on an all-solid diet. The lambs consume an all-milk diet for the first five weeks and they are assumed to be weaned at 16 weeks of age. It is presumed that lambs consuming a proportion of herbage in the diet have similar efficiencies of conversion of ME as those on an all-solid diet.



**Figure 4-3** *A schematic diagram of the partitioning of metabolisable energy in the dry ewe*



**Figure 4-4** A schematic diagram of the partitioning of metabolisable energy in the lamb

#### 4.4.5.1 Milk Diet

The maintenance requirements of a lamb on an all-milk diet is composed of fasting heat production ( $M_B$ , MJ head<sup>-1</sup> day<sup>-1</sup>) and the heat production associated with muscular activity ( $M_W$ , MJ head<sup>-1</sup> day<sup>-1</sup>). Following the Agricultural Research Council (1980) the heat production associated with muscular activity is described by equation (4.56), while the fasting heat production ( $M_B$ , MJ head<sup>-1</sup> day<sup>-1</sup>) is defined as:

$$M_B = 0.35 * \left( \frac{LWT_L}{105} \right)^{0.75} \quad (4.74)$$

Accordingly, the maintenance requirements of the lamb ( $L_M$ , MJ head<sup>-1</sup> day<sup>-1</sup>) are described by:

$$L_M = \frac{M_B + M_W}{k_{mlb}} \quad (4.75)$$

where  $k_{mlb}$  is the proportionate efficiency of utilisation of milk for maintenance.

It is assumed that the milk produced by the 'average ewe' is shared equally among the 'average lambs at foot'. Accordingly, the actual milk energy consumed by each lamb ( $LM$ , MJ head<sup>-1</sup> day<sup>-1</sup>) can then be determined from the following equation:

$$LM = Y_E * \frac{L\%}{100} \quad (4.76)$$

where  $L\%$  represents the percentage of the number of live lambs per ewe at weaning and  $Y_E$  (MJ head<sup>-1</sup> day<sup>-1</sup>) is the energy content of the milk produced.

The surplus energy to maintenance which is used for liveweight gain ( $\Delta_w$ , kg head<sup>-1</sup> day<sup>-1</sup>) is therefore described by:

$$\Delta_w = \frac{(LM - L_M) * k_{fb}}{N_s} \quad (4.77)$$

The proportionate efficiency of utilisation of milk for liveweight gain is represented by  $k_{fb}$ , and  $N_s$  (MJ kg<sup>-1</sup>) is the average energy required for 1 kg of liveweight gain for a castrate and female lamb defined by equation (4.67).

#### **4.4.5.2 Solid Diet**

If the ewe is still lactating the total energy available for production consists of the energy obtainable from herbage and milk. The maintenance requirements of the lamb consuming herbage are described in equations (4.55)—(4.57). Hence, the liveweight gain ( $\Delta_w$ , kg head<sup>-1</sup> day<sup>-1</sup>) of the lamb can be described by the following equation:

$$\Delta_w = \frac{(MEI_L - L_M) * k_f}{N_s} \quad (4.78)$$

where  $MEI_L$  (MJ lamb<sup>-1</sup> day<sup>-1</sup>) is the total energy consumed after correcting for feeding level and  $k_f$  is the proportionate efficiency of ME utilisation for growth.

## **4.5 Initial Conditions and Parameter Values**

### **4.5.1 Dairy Cow Model**

The model of the 'average dairy cow' requires the specification of the initial conditions of three variables at the beginning of the grazing season which are listed in Table 4-1. The solution of the equations also requires the specification of parameters. The values ascribed to the parameters required for the milk production equations (equations (4.4)—(4.7)) are listed in Table 4-2 and Table 4-3, and the remaining parameters are listed in Table 4-4.

#### **4.5.1.1 Estimated Values and Fitted Equations**

The values for the average age (Age, yrs) and the mature weight ( $Wt_M$ , kg head<sup>-1</sup>) of the dairy cow cannot be derived directly from published sources and therefore they had to be estimated.

##### **4.5.1.1.1 Age of the 'Average Dairy Cow' (Age, yrs)**

Hulme *et al.* (1986) assumed that the first-year heifers are 2.5 years old and that the second-year heifers are 3.5 years old. It is therefore assumed in this model that the cows would be approximately 4.5 and 5.5 years old. As 25% of the cows are replaced annually, the average age of the herd is four years.

**Table 4-1** *Initial Conditions of the Variables at the Start of the Grazing Season*

Parameter	Value	Source <sup>1</sup>
$k_i$	0.63	1
$k_m$	0.7	2
LWT	525	3

Source<sup>1</sup> 1 Beever and Oldham (1986); 2 Hulme *et al.* (1986); 3 Østergaard (1979)

**Table 4-2** *Parameter Values Required to Define the Potential Level of Milk Production*

Parameters	Values		
	1 <sup>st</sup> Year Heifers	2 <sup>st</sup> Year Heifers	Cows
$Wb_i$	0.127	0.138	0.183
$Wc_i$	0.021	0.031	0.036
$Pot_i$	17.3	23.3	24.9

Source Mainland (1985)

**Table 4-3**    *The Monthly Values for the Seasonal and Calving effects on Milk Yield*

<b>Month</b>	<b>Seasonal Effect (S<sub>Y</sub>)</b>	<b>Calving Effect (C<sub>Y</sub>)</b>
1	-0.075	0.009
2	-0.045	-0.016
3	-0.027	-0.035
4	0.050	-0.033
5	0.111	-0.024
6	0.135	-0.026
7	0.083	-0.025
8	0.062	-0.006
9	0.026	0.016
10	-0.023	0.032
11	-0.071	0.044
12	-0.090	0.037
13	-0.092	0.029

Source    Mainland (1985)

**Table 4-4 Parameter Values**

Parameter	Value	Source <sup>1</sup>
Age	4	1
$dg_{Conc}$	0.82	2
$d_{max}$	0.0086	3
$F_{max}$	0.136	4
GE	18.4	5
$H_{Crit}$	900	6
$I_{C, I}$	0.15	7
$k_{bc}$	0.18	8
$k_{bl}$	0.84	5
$k_c$	0.133	5
$L_E$	3.1	5
$N_L$	19	9
$N_W$	19	9
$Wt_M$	672.5	1

Source<sup>1</sup> 1 See text; 2 Østergaard (1979); 3 Kahn and Spedding (1984); 4 McDonald *et al.* (1988); 5 Agricultural Research Council (1980); 6 Ministry of Agriculture and Fisheries (1985); 7 Hollinshead (1995); 8 Robinson, McDonald, Fraser and Gordon (1980); 9 Agricultural and Food Research Council (1993)

#### **4.5.1.1.2 Mature Weight of the 'Average Dairy Cow' ( $Wt_M$ , kg head<sup>-1</sup>)**

At the start of lactation Devir, Zur, Maltz, Genizi and Antler (1995) observed that the dairy cows lost approximately 5% of their body-weight. They also observed that the body weight of Israeli-Holstein cows at the end of the lactation was in the region of 115—129% of the initial body weight. However, this was affected by the date of calving. Accordingly, the mature body weight of the 'average dairy cow' has been assumed to be described by:

$$Wt_M = (LWT * 1.05) * 1.22 \quad (4.79)$$

where LWT represents the liveweight on the date of turn-out. The factor 1.05 and 1.22 respectively convert the liveweight at the date of turn-out to the liveweight just post calving, and the liveweight to the mature weight. This gives a mature weight of 672.5 kg which equates with the maximum body weight observed by Devir *et al.* (1995) of approximately 680 kg.

#### **4.5.2 Beef Model**

In the model the initial conditions of one variable and the values of twenty-seven parameters must be defined in order to solve the equations, which are shown in Table 4-5. Following Hulme *et al.* (1986), the initial value of the variable  $k_m$  is defined as 0.7.

**Table 4-5 Parameter Values**

Parameter	Value	Source <sup>1</sup>	Parameter	Value	Source <sup>1</sup>
Age	0.49	1	LEBW1	1.09	3
cal	4.184	2	LEBW2	14.0	3
d <sub>max</sub>	0.0086	3	LP1	0.8893	7
DNA1	0.32827	1	LP2	0.5037	7
DNA2	0.91183	1	N1	-0.7	4
DNA <sub>Max</sub>	385	4	N2	1.7	4
E2	0.73	4	N3	0.83	4
F <sub>E</sub>	39.3	3	N4	0.2	4
F <sub>max</sub>	0.1	5	N5	0.15	4
H <sub>Crit</sub>	750	6	Nm1	0.438	4
K1	0.00429	4	Nm2	0.2615	4
K2	0.0472	4	P <sub>E</sub>	23.6	3
K3	0.143	4	Wt <sub>M</sub>	750	4
K4	0.2201	4			

Source<sup>1</sup> 1 See text; 2 Agricultural Research Council (1980); 3 Kahn and Spedding (1984); 4 Oltjen *et al.* (1986); 5 McDonald *et al.* (1988); 6 Ministry of Agriculture and Fisheries (1985); 7 Agricultural Research Council (1980)

#### **4.5.2.1 Estimated Value and Fitted Equations**

The initial value for the average age (Age, yrs) and the initial quantity of DNA within the empty body cannot be derived directly from the text. Consequently the initial conditions of these variables have been estimated.

##### **4.5.2.1.1 Age of the 'Average Steer' (Age, yrs)**

In the model it is assumed that the beef cattle are 180 days old at turn-out.

##### **4.5.2.1.2 DNA Content at Turn-Out (DNA, kg head<sup>-1</sup>)**

The empty body protein content has been measured by Lobley *et al.* (1980) as 34.0 kg for a heifer weighing 209 kg empty body weight. It was assumed by Oltjen *et al.* (1986) that the initial protein content of an animal at 200 days old is 34.2 kg and the DNA content is 172 g. In order to estimate the initial DNA content, it is assumed that an animal weighing 200 kg empty body weight contains 172 g of DNA. The model is run for 180 days for an animal weighing 200 kg empty body weight at turn-out, assuming that it is growing at potential and therefore there is no effect of feeding. An equation of the same form as equation (4.33) is used to estimate the DNA (DNA, g head<sup>-1</sup>) of the 'average steer'. Accordingly, the equation is taken to be:

$$\text{Log (DNA)} = \text{DNA1} + \text{DNA2} * \text{Log (EBW)} \quad (4.80)$$

The relationship yielded from the regression procedure in SPSS (SPSS Inc, 1990) is:

$$\begin{aligned} \text{Log (DNA)} &= 0.14256 + 0.91183 * \text{Log (EBW)} \\ &\pm 0.0165 \quad \pm 0.0070 \end{aligned} \quad (4.81)$$

with an  $R^2$  equal to 0.998.

#### 4.5.3 Sheep Model

At the beginning of the grazing season the initial conditions of four variables are defined, and the values are listed in Table 4-6. The values ascribed to the parameters required for milk production (equation (4.60)) are listed in Table 4-7. The parameters required to determine the energy required for 1 kg of liveweight gain for ewe lambs and castrates on both milk and solid diets are defined in Table 4-8, and the remaining parameters required in the model are shown in Table 4-9.

**Table 4-6** *Initial Conditions of the Variables at the Start of the Grazing Season*

Variable	Value	Source <sup>1</sup>
$k_l$	0.63	1
$k_m$	0.7	2
Wt	60	3
Wt <sub>s</sub>	70	3

Source<sup>1</sup> 1 Beever and Oldham (1986); 2 Hulme *et al.* (1986); 3 See Text

**Table 4-7** *Parameter Values Required to Define the Potential Level of Milk Production*

Parameters	Values	
	Single Lambs	Twin Lambs
Wb	0.318	0.299
Wc	0.020	0.019
Pot <sup>1</sup>	1.024	1.170

Source Torres-Hernandez and Hohenboken (1980)

**Table 4-8** *Parameter Values Required to Define the Energy Required for 1 kg of Liveweight Gain*

	All Milk Diet		Solid Diet	
	Ewe Lambs	Castrate	Ewe Lambs	Castrate
G1	3.67	5.6	4.4	2.1
G2	0.472	0.338	0.32	0.45

Source Agricultural Research Council (1980)

**Table 4-9 Parameter Values**

Variable	Value	Source <sup>1</sup>
Age	3	1
$d_{\max}$	0.1	2
$F_{L, \max}$	0.130	3
$F_{S, \max}$	0.225	4
$H_{\text{Crit}}$	500	5
$k_{bl}$	0.84	6
$k_{flb}$	0.7	6
$k_{mlb}$	0.85	6
F	7	6
$N_L$	23.9	7
$N_W$	23.9	7
$Wt_M$	75	1

Source<sup>1</sup> 1 See Text; 2 Blaxter *et al.* (1961); 3 Elsen, Wallach and Charpentreau (1988); 4 Penning, Parsons, Orr and Hooper (1994); 5 Ministry of Agriculture and Fisheries (1985); 6 Agricultural Research Council (1980); 7 Agricultural and Food Research Council (1993)

#### **4.5.3.1 Estimated Value and Fitted Equations**

The values for the density of sheep milk, the average age (Age, yrs), the liveweights of the dam ( $Wt$ , kg head<sup>-1</sup>) and the dam of the sire breed ( $Wt_S$ , kg head<sup>-1</sup>), and the

mature weight ( $Wt_M$ , kg head<sup>-1</sup>) of the sheep cannot be derived directly from published sources, and therefore they have had to be estimated.

#### **4.5.3.1.1 Density of Sheep Milk**

It is assumed that the composition of sheep milk is 7.15 fat and 18.2% total solids (Harding, 1995). The density ( $d$ , kg l<sup>-1</sup>) of sheep milk is determined from (British Standards Institution, 1959)

$$d = 1 + \frac{T - 1.22 * F - 0.72}{0.25 * 1000} \quad (4.82)$$

where T and F are the percentages of total solids and fat in the milk. Consequently the density was estimated to be 1.035 kg l<sup>-1</sup>.

#### **4.5.3.1.2 Age the 'Average Ewe' (Age, yrs)**

It is assumed that in a low-ground sheep system that the ewe will have its first lamb crop at one year old and that it will have five lamb crops. Hence the average age of the ewe is three years.

#### **4.5.3.1.3 Liveweights of the Dam and the Dam of the Sire Breed ( $Wt$ , kg head<sup>-1</sup>, $LWT_S$ , kg head<sup>-1</sup>)**

In the model, it is assumed that the lambs produced are from Scottish Blackface ewes crossed with Suffolk rams. It is presumed that the average weight of the Scottish Blackface ewe is 60 kg and that the average weight of the Suffolk is 70 kg.

#### **4.5.3.1.4 Mature Weight of the 'Average Ewe' ( $Wt_M$ , kg head<sup>-1</sup>)**

The mature weight of crossbreeds range from 72 to 80 kg (Meat and Livestock Commission, 1986). In the model, a mature weight of 75 kg is used for the breeding ewe.

### ***4.6 Conclusions***

The models of forage production and the grazing dairy cows, beef cattle and sheep that have been described in this chapter and Chapter 3 are validated in Chapter 5. The partitioning of energy within the dairy cow has also been validated and is described in Chapter 5.

## CHAPTER 5

### VALIDATION OF THE FORAGE AND LIVESTOCK MODELS

#### 5.1 Introduction

This chapter outlines the statistical technique used to assess the ability of the forage and livestock sub-models to predict production. The validation of the sub-models will be divided into the following sections:

1. herbage production;
2. dairy production;
3. beef production; and finally
4. sheep production.

#### 5.2 Statistical Technique

The statistical technique used to assess the ability of the forage and livestock models to simulate production is Theil's inequality coefficient ( $u$ ), which was defined by Theil (1970) as:

$$u = \frac{\sqrt{\frac{1}{n} \sum_{n=1}^n (Y_P - Y_O)^2}}{\sqrt{\frac{1}{n} \sum_{n=1}^n (Y_P)^2} + \sqrt{\frac{1}{n} \sum_{n=1}^n (Y_O)^2}} \quad (5.1)$$

where  $Y_P$  and  $Y_O$  are the predicted and observed values respectively and  $n$  is the number of observations. The numerator of this equation is the root mean square error, while the denominator scales Theil's inequality statistics so that it always falls

between zero and one, with zero indicating a perfect fit. If the value of Theil's inequality is one the simulated values are:

1. always zero when actual values are non-zero; or
2. non-zero when actual values are zero; or
3. positive (negative) when actual values are negative (positive).

As the difference between the actual and the simulated values are squared, large errors are penalised more than small errors. This technique also assesses the model's ability to duplicate turning points or rapid changes in the data.

Theil's inequality coefficient can be decomposed into the following equation:

$$\frac{1}{n} \sum_{n=1}^n (Y_P - Y_O)^2 = (\bar{Y}_P - \bar{Y}_O)^2 + (\sigma_P - \sigma_O)^2 + 2 * (1 - \rho) * \sigma_P * \sigma_O \quad (5.2)$$

where  $\bar{Y}_P$ ,  $\bar{Y}_O$ ,  $\sigma_P$ , and  $\sigma_O$  are the means and standard deviations of the predicted and observed series respectively, and  $\rho$  is the correlation coefficient between the two series. The bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the inequality coefficient are therefore defined as:

$$u_M = \frac{(\bar{Y}_P - \bar{Y}_O)^2}{\frac{1}{n} \sum_{n=1}^n (Y_P - Y_O)^2} \quad (5.3)$$

$$u_S = \frac{(\sigma_P - \sigma_O)^2}{\frac{1}{n} \sum_{n=1}^n (Y_P - Y_O)^2} \quad (5.4)$$

$$u_c = \frac{2 * (1 - \rho) * \sigma_p * \sigma_o}{\frac{1}{n} \sum_{n=1}^n (Y_p - Y_o)^2} \quad (5.5)$$

The bias proportion ( $u_M$ ) is an indication of the systematic error, while the variance proportion ( $u_S$ ) represents the ability of the model to replicate the degree of variability in the observed data. The covariance proportion represents the error remaining after accounting for the bias and variance proportions. The ideal distribution of inequality over the three sources is  $u_M = u_S = 0$ , and  $u_C = 1$  (Pindyck and Rubinfeld, 1981). They regarded values of  $u_M$  and  $u_S$  greater than 0.2 as large.

### 5.3 *Herbage Growth Validation*

The ability of the model to simulate grass and grass – white clover production between sites and at different fertiliser nitrogen rates were investigated for three sites using data from the GM20 (Morrison *et al.*, 1980) and GM23 (J.Gilbey, *personal communication*) trials. The GM20 trial and GM23 trials were conducted during the periods 1970—1973 and 1978—1981 respectively. The sward types used in the validation process were based on S23 perennial ryegrass for the grass model and a Blanca and S23 mixture for the grass – white clover model. The first criterion in choosing the sites was that daily weather data was obtainable from the BBSRC ARCMET database. The sites, shown in Figure 5-1, were also chosen to represent northern, central and southern locations and they had a range of available soil water capacities. Consequently High Mowthorpe and Rosemaund, situated in northern and central England respectively and used in both the GM20 and GM23 trials, were employed to validate the grass and grass – white clover models. The southern site

was represented by Seale Hayne for the grass model and Liscombe for the grass – white clover model. The weather data were obtained for High Mowthorpe, Rosemaund, Starcross and Hawkrigde (Biotechnology and Biological Research Council (BBSRC)), with the latter two being in the vicinity of Seale Hayne and Liscombe respectively.

In both trials, the herbage was cut between five and seven times per year. The seventh cut was taken at the end of the growing season if there was sufficient herbage to harvest. For the purpose of validation, the cuts were grouped into three: the first and second cuts; the third and fourth cuts; and the remaining cuts. The dates of the actual cuts are shown in Table 5-1 and Table 5-2 for the grass and the grass – white clover swards respectively. The fertiliser rates from the GM20 trial used to validate the grass model were 0, 150, 300, 450 and 600 kg nitrogen ha<sup>-1</sup> yr<sup>-1</sup>, with a sixth of the application applied at each dressing. In the GM23 trial, the nitrogen fertiliser application rate of 0 kg ha<sup>-1</sup> yr<sup>-1</sup> was tested in the model at all three sites, namely High Mowthorpe, Liscombe and Rosemaund. For all years at High Mowthorpe and Liscombe 200 kg ha<sup>-1</sup> yr<sup>-1</sup> of nitrogen were applied. However, at Rosemaund 300 kg ha<sup>-1</sup> yr<sup>-1</sup> of nitrogen were applied in 1978 and 1979, whereas in 1980 and 1981 the application rate was 200 kg ha<sup>-1</sup> yr<sup>-1</sup>. Accordingly, the appropriate rates were used for each year at each site to validate the model. In both trials, the nitrogen was applied as six equal dressings with the first application in the spring and the remaining applications after cuts 1—5.



*Figure 5-1 The location of the sites used to validate the grass and grass – white clover model*

**Table 5-1**    *The dates of cutting at High Mowthorpe, Rosemaund and Seale Hayne for the GM20 trial*

<b>Cut</b>	<b>High Mowthorpe</b>	<b>Rosemaund</b>	<b>Seale Hayne</b>
1	14 May	10 May	6 May
2	11 June	7 June	3 June
3	9 July	5 July	1 July
4	6 August	2 August	29 July
5	3 September	30 August	26 August
6	1 October	27 September	23 September
7	10 November	10 November	10 November

Source: Morrison *et al.* (1980)

*Table 5-2 The dates of cutting at High Mowthorpe, Liscombe and Rosemaund for the GM23 trial*

Site	Cut	1978	1979	1980	1981
High Mowthorpe	1	10 May	16 May	12 May	13 May
	2	8 June	13 June	11 June	11 June
	3	5 July	9 July	9 July	9 July
	4	5 August	8 August	5 August	10 August
	5	30 August	3 September	3 September	11 September
	6	25 September	27 September	30 September	15 October
Liscombe	1	8 May	8 May	8 May	6 May
	2	5 June	5 June	5 June	3 June
	3	3 July	3 July	3 July	1 July
	4	1 August	31 July	31 July	28 July
	5	29 August	28 August	28 August	26 August
	6	15 November	16 November	25 September	23 September
Rosemaund	1	9 May	8 May	8 May	8 May
	2	5 June	5 June	5 June	5 June
	3	3 July	3 July	3 July	3 July
	4	2 August	31 July	31 July	31 July
	5	29 August	28 August	28 August	28 August
	6	25 September	25 September	25 September	25 September
	7			17 November	

The data required to run the model are the latitude of the site, the available water capacity and the available soil nitrogen (see Table 5-3 and Table 5-4). The available water capacity was measured in the GM20 trial. However, this data were not obtainable from the GM23 trial. Nevertheless, all the sites used for the validation process were in the locality of sites used in the GM20 trial. It was therefore assumed that, although the water capacities might differ for the two trials, they would be representative of the soils within that region. Consequently the available water capacity for High Mowthorpe and Rosemaund was presumed to be the same in both trials, and it was assumed that the Liscombe site could be represented by Cannington from the GM20 trial. In the GM20 trial, it was assumed that the available soil nitrogen could be approximated from the annual yield of nitrogen harvested in the grass that had had no nitrogen fertiliser applications (see Table 5-4). In the GM23 trial, pure swards of S23 had been grown at a range of nitrogen levels including  $0 \text{ kg ha}^{-1} \text{ yr}^{-1}$ . It was therefore assumed that the nitrogen removed in the harvested grass from the sward that had had no nitrogen fertiliser applied, averaged over the four years of the experiment, would give an estimate of the amount of soil nitrogen that would be available for the growth of the sward, as shown in Table 5-4. Accordingly these values were used in the model as the quantity of available soil nitrogen for crop growth.

The grass model was specifically run for the period 1970—1973 for Seale Hayne and High Mowthorpe at the five nitrogen levels. However, as the 1973 grass yield data for Rosemaund was unobtainable, the model was only run for the period 1970—1972 for this site. The period used to test the grass – white clover model at High Mowthorpe, Rosemaund and Liscombe was 1978—1981.

**Table 5-3** *The latitude and the available water capacity of the sites*

Site	Latitude (°)	Available Water Capacity (mm) <sup>1</sup>
High Mowthorpe	54.0	86
Rosemaund	52.0	132
Seale Hayne	50.5	109
Liscombe	51.0	66

Source: <sup>1</sup> Morrison *et al.* (1980)

**Table 5-4** *The available soil nitrogen for the grass and grass – white clover swards at High Mowthorpe, Rosemaund, Seale Hayne and Liscombe*

Sward Type	Year	High Mowthorpe (N kg ha <sup>-1</sup> )	Rosemaund (N kg ha <sup>-1</sup> )	Seale Hayne (N kg ha <sup>-1</sup> )	Liscombe (N kg ha <sup>-1</sup> )
Grass <sup>1</sup>	70	22	98	40	
	71	14	44	58	
	72	41	47	75	
	73	109		59	
Grass – white clover <sup>2</sup>	78–81	76	37		105

Source: <sup>1</sup> Morrison *et al.* (1980); <sup>2</sup> J. Gilbey (*personal communication*)

### 5.3.1 Results for Grass Validation

The value of Theil's inequality coefficient, and the bias, variance and covariance proportions of the coefficients over the four years and five nitrogen levels for Seale Hayne and High Mowthorpe are shown in Table 5-5. The corresponding values for Rosemaund measured over three years and five nitrogen levels are also shown in Table 5-5. The results indicate that the proportions of Theil's inequality coefficient due to bias and variance at High Mowthorpe are large. Nevertheless, this is not the case for Seale Hayne and Rosemaund. The ratios of the predicted to observed dry-matter yields averaged over years for each cut and nitrogen level are shown for the three sites in Table 5-6—Table 5-8. A breakdown by year of the observed and predicted dry-matter yields is given in Appendix VII. There is a tendency for the model to under-predict at nitrogen fertiliser application levels of zero kg ha<sup>-1</sup> yr<sup>-1</sup> and 150 kg ha<sup>-1</sup> yr<sup>-1</sup>. However, at High Mowthorpe the dry-matter yield obtained from the second and third cuts, when no fertiliser nitrogen had been applied, was under-estimated while at Seale Hayne the dry-matter yield was under-estimated for all cuts. In contrast at Rosemaund there was no distinct pattern. At fertiliser application rates of 150 kg ha<sup>-1</sup> yr<sup>-1</sup>, with the exception of the first cut at Rosemaund and the third cut at High Mowthorpe, which were always under-predicted for all years, the dry-matter yields were both under- and over- predicted for all cuts and all sites, see Appendix VII. However at fertiliser application rates 300—600 kg ha<sup>-1</sup> yr<sup>-1</sup> the dry-matter yields tended to be over-estimated (see Table 5-6—Table 5-8).

**Table 5-5** *Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for High Mowthorpe, Seale Hayne and Rosemaund*

<b>Site</b>	<b>Inequality Coefficient</b>	<b>Bias proportion</b>	<b>Variance proportion</b>	<b>Covariance proportion</b>
High Mowthorpe	0.23	0.225	0.205	0.570
Seale Hayne	0.18	0.000	0.015	0.985
Rosemaund	0.18	0.009	0.042	0.949

**Table 5-6** *The ratio of the predicted yield:observed yield averaged over years for each cut and nitrogen level at High Mowthorpe*

<b>Nitrogen Level</b>	<b>Cut</b>			
<b>(N kg ha<sup>-1</sup> yr<sup>-1</sup>)</b>	<b>1</b>	<b>2</b>	<b>3</b>	<b>Total</b>
0	2.27	0.10	0.00	0.79
150	1.28	0.88	0.55	0.90
300	1.13	1.30	1.07	1.17
450	1.32	1.97	2.06	1.78
600	1.35	2.54	2.83	2.24
<b>Total</b>	<b>1.47</b>	<b>1.36</b>	<b>1.30</b>	<b>1.38</b>

**Table 5-7** *The ratio of the predicted yield:observed yield averaged over years for each cut and nitrogen level at Rosemaund*

Nitrogen Level (N kg ha <sup>-1</sup> yr <sup>-1</sup> )	Cut			
	1	2	3	Total
0	0.99	0.14	0.00	0.38
150	0.78	1.01	0.49	0.76
300	0.94	1.41	0.85	1.07
450	1.04	1.87	0.92	1.28
600	1.13	2.69	1.23	1.68
Total	0.98	1.42	0.70	1.03

**Table 5-8** *The ratio of the predicted yield:observed yield averaged over years for each cut and nitrogen level at Seale Hayne*

Nitrogen Level (N kg ha <sup>-1</sup> yr <sup>-1</sup> )	Cut			
	1	2	3	Total
0	0.71	0.18	0.00	0.30
150	0.84	1.01	1.04	0.96
300	0.89	1.11	1.09	1.03
450	1.04	1.39	1.51	1.31
600	0.92	1.61	1.53	1.35
Total	0.88	1.07	1.03	0.99

### 5.3.2 Results for Grass – White Clover Validation

The values of Theil's inequality coefficient over the four years and two nitrogen levels are shown in Table 5-9—Table 5-11 for the grass, white clover and combined dry-matter yields for High Mowthorpe, Liscombe and Rosemaund respectively. The results reveal that systematic bias only occurred at the Rosemaund site. The ratios of the predicted to the observed dry-matter yields averaged over years are presented in Table 5-12—Table 5-14, while the annual values are given in Appendix VII. At all sites and all fertiliser application rates, there was a tendency for the dry-matter yield of grass from the second cut to be over-estimated. The grass yield from the third cut at the zero nitrogen application rate was under-estimated at High Mowthorpe (see Table 5-12). Theil's inequality coefficient and the ratio of the predicted to the observed dry-matter yield have rather high values for the white clover yield at Liscombe for both fertiliser application rates. However, the observed dry-matter yield of white clover at this site in 1981 for 0 and 200 kg nitrogen ha<sup>-1</sup> yr<sup>-1</sup> was practically zero (0.045 t ha<sup>-1</sup> and 0.008 t ha<sup>-1</sup> respectively). In contrast the white clover yields in 1979 were particularly high. The model also failed to adequately predict the white clover yields at Rosemaund. At this site, the reason why the model failed to predict the yield of white clover adequately was that the total yield tended to be composed of predominately white clover, whereas the yield at the other two sites was dominated by grass. The model also failed to predict the observed white clover yields of 4.5 t DM ha<sup>-1</sup> and 5.3 t DM ha<sup>-1</sup> at Rosemaund for 1978 and 1979 at fertiliser application rates of 300 kg ha<sup>-1</sup>. However, white clover was usually projected to disappear at nitrogen fertiliser levels of 150—250 kg ha<sup>-1</sup> (Williams, 1980). Nevertheless, the model in general proved to be reasonably valid for the grass and the combined yield. Even in the case of white

clover, although the model did not accurately predict the dry-matter yield, both under- and over- predicting at all sites, it did give reasonable predictions in terms of the general trends of white clover yield.

**Table 5-9** *Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for the grass, white clover and combined dry-matter yields at High Mowthorpe*

<b>Component</b>	<b>Nitrogen Level (N kg ha<sup>-1</sup>)</b>	<b>Inequality Coefficient</b>	<b>Bias proportion</b>	<b>Variance proportion</b>	<b>Covariance proportion</b>
Grass	0	0.20	0.017	0.021	0.962
White clover		0.26	0.051	0.001	0.948
Combined		0.19	0.055	0.143	0.802
Grass	200	0.19	0.137	0.290	0.573
White clover		0.28	0.015	0.425	0.560
Combined		0.16	0.110	0.276	0.614

*Table 5-10 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for the grass, white clover and combined dry-matter yields at Liscombe*

Component	Nitrogen Level (N kg ha <sup>-1</sup> )	Inequality Coefficient	Bias proportion	Variance proportion	Covariance proportion
Grass	0	0.25	0.008	0.196	0.796
White clover		0.50	0.001	0.073	0.926
Combined		0.26	0.000	0.406	0.594
Grass	200	0.21	0.012	0.504	0.484
White clover		0.64	0.153	0.526	0.321
Combined		0.17	0.179	0.403	0.418

*Table 5-11 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for the grass, white clover and combined dry-matter yields at Rosemaund*

Component	Nitrogen Level (N kg ha <sup>-1</sup> )	Inequality Coefficient	Bias proportion	Variance proportion	Covariance proportion
Grass	0	0.16	0.307	0.161	0.532
White clover		0.43	0.352	0.134	0.514
Combined		0.28	0.452	0.386	0.162
Grass	200/300 <sup>1</sup>	0.21	0.007	0.643	0.350
White clover		0.62	0.681	0.105	0.214
Combined		0.23	0.303	0.476	0.221

Note 1 The nitrogen application rate was 300 kg ha<sup>-1</sup> yr<sup>-1</sup> in 1978 and 1979, and 200 kg ha<sup>-1</sup> yr<sup>-1</sup> in 1980 and 1981.

*Table 5-12 The ratio of the predicted yield:observed yield averaged over years for each cut and nitrogen level at High Mowthorpe*

<b>Nitrogen Level</b> <b>(N kg ha<sup>-1</sup>)</b>	<b>Cut</b>	<b>Grass</b>	<b>White Clover</b>	<b>Combined</b>
<b>0</b>	<b>1</b>	<b>1.10</b>	<b>0.65</b>	<b>0.92</b>
	<b>2</b>	<b>1.55</b>	<b>1.02</b>	<b>1.20</b>
	<b>3</b>	<b>0.37</b>	<b>1.41</b>	<b>0.99</b>
<b>Total</b>		<b>1.01</b>	<b>1.03</b>	<b>1.04</b>
<b>200</b>	<b>1</b>	<b>0.78</b>	<b>1.29</b>	<b>0.82</b>
	<b>2</b>	<b>1.55</b>	<b>1.30</b>	<b>1.35</b>
	<b>3</b>	<b>0.82</b>	<b>1.73</b>	<b>0.92</b>
<b>Total</b>		<b>1.05</b>	<b>1.44</b>	<b>1.03</b>
<b>Grand Total</b>		<b>1.03</b>	<b>1.23</b>	<b>1.03</b>

**Table 5-13** *The ratio of the predicted yield:observed yield averaged over years for each cut and nitrogen level at Liscombe*

<b>Nitrogen Level</b> <b>(N kg ha<sup>-1</sup>)</b>	<b>Cut</b>	<b>Grass</b>	<b>White Clover</b>	<b>Combined</b>
<b>0</b>	<b>1</b>	<b>1.00</b>	<b>119.56</b>	<b>0.91</b>
	<b>2</b>	<b>1.78</b>	<b>9.54</b>	<b>1.52</b>
	<b>3</b>	<b>0.76</b>	<b>5.53</b>	<b>1.59</b>
<b>Total</b>		<b>1.18</b>	<b>44.87</b>	<b>1.34</b>
<b>200</b>	<b>1</b>	<b>0.84</b>	<b>0.57</b>	<b>0.82</b>
	<b>2</b>	<b>1.27</b>	<b>4.67</b>	<b>0.96</b>
	<b>3</b>	<b>1.31</b>	<b>81.67</b>	<b>1.04</b>
<b>Total</b>		<b>1.14</b>	<b>28.97</b>	<b>0.94</b>
<b>Grand Total</b>		<b>1.16</b>	<b>36.92</b>	<b>1.14</b>

*Table 5-14 The ratio of the predicted yield:observed yield averaged over years for each cut and nitrogen level at Rosemaund*

Nitrogen Level (N kg ha <sup>-1</sup> )	Cut	Grass	White Clover	Combined
0	1	0.85	0.32	0.59
	2	1.03	0.67	0.72
	3	0.39	2.73	1.68
Total		0.76	1.24	1.00
200/300 <sup>1</sup>	1	0.84	0.39	0.71
	2	1.47	0.25	0.81
	3	2.66	1.35	2.02
Total		1.66	0.66	1.18
Grand Total		1.21	0.95	1.09

Note <sup>1</sup> The nitrogen application rate was 300 kg ha<sup>-1</sup> yr<sup>-1</sup> in 1978 and 1979, and 200 kg ha<sup>-1</sup> yr<sup>-1</sup> in 1980 and 1981.

### 5.3.3 Herbage Production Under Enhanced Atmospheric CO<sub>2</sub>

The ability of the forage model to simulate production under enhanced atmospheric CO<sub>2</sub> conditions was investigated by running the model at CO<sub>2</sub> concentrations of 520 ppmv and 700 ppmv for High Mowthorpe, Liscombe, Rosemaund and Seale Hayne. The annual dry-matter yields obtained for the grass and grass – white clover swards at CO<sub>2</sub> concentrations of 520 and 700 ppmv have been expressed as a proportion of the yield obtained at a CO<sub>2</sub> concentration of 350 ppmv (see Table 5-15 and Table 5-16). With a doubling of CO<sub>2</sub> concentrations, enhancements in annual dry-matter yield of

between 8% and 28% for swards that had an annual nitrogen application of 600 kg N ha<sup>-1</sup> and were not subjected to water stress were reported (Jones *et al.*, 1996b). Nevertheless, enhancements in yield of 43% for young plants (Jones *et al.*, 1996b) at double current concentrations of CO<sub>2</sub>, and 48% (Casella *et al.*, 1996) and 54% (Jones *et al.*, 1996a) for yields obtained during part of the season have been reported. Increases in yield of white clover plants of between 45% (Ryle and Powell, 1992) and 229% (Ryle *et al.*, 1992b) have been observed when CO<sub>2</sub> concentrations have been elevated to 680 ppmv. On the other hand, the yield from a mixed sward containing a 1:1 mixture of grass white clover was enhanced by 58% when CO<sub>2</sub> concentrations were elevated from 300 ppmv to 620 ppmv (Overdieck and Reining, 1986). Nevertheless, Jongen *et al.* (1995) observed changes of +13% and -7% for the yield of the grass harvested in August and November respectively. The comparable figures for the white clover component were +24% and +39%. The enhancement in yield from the grass and the grass – white clover sward predicted by the model falls within the ranges quoted in the literature. Consequently, it is assumed that the model of the grass and grass – white clover swards can adequately predict the effect of enhanced CO<sub>2</sub> levels on production.

*Table 5-15 The ratio of the yield obtained at CO<sub>2</sub> concentrations of 520 ppmv to the yield obtained at CO<sub>2</sub> concentrations of 350 ppmv and the ratio of the yield obtained at CO<sub>2</sub> concentrations of 700 ppmv to the yield obtained at CO<sub>2</sub> concentrations of 350 ppmv for High Mowthorpe, Seale Hayne and Liscombe for each nitrogen level*

Nitrogen Level (N kg ha <sup>-1</sup> )	Yield at 520 ppmv:Yield at 350 ppmv			Yield at 700 ppmv:Yield at 350 ppmv		
	High Mowthorpe	Rosemaund	Seale Hayne	High Mowthorpe	Rosemaund	Seale Hayne
0	1.06	1.39	1.37	1.09	1.60	1.56
150	1.43	1.35	1.34	1.70	1.55	1.55
300	1.30	1.28	1.26	1.47	1.43	1.41
450	1.26	1.25	1.23	1.40	1.35	1.36
600	1.24	1.23	1.21	1.37	1.35	1.33
Total	1.26	1.30	1.28	1.40	1.46	1.44

*Table 5-16 The ratio of the yield obtained at CO<sub>2</sub> concentrations of 520 ppmv to the yield obtained at CO<sub>2</sub> concentrations of 350 ppmv and the ratio of the yield obtained at CO<sub>2</sub> concentrations of 700 ppmv to the yield obtained at CO<sub>2</sub> concentrations of 350 ppmv for grass, white clover and the combined yield at High Mowthorpe, Liscombe and Rosemaund*

Site	Nitrogen Level (N kg ha <sup>-1</sup> )	Yield at 520 ppmv:Yield at 350 ppmv			Yield at 700 ppmv:Yield at 350 ppmv		
		Grass	White Clover	Combined	Grass	White Clover	Combined
High Mowthorpe	0	1.14	1.50	1.39	1.21	1.73	1.56
	200	1.28	1.19	1.26	1.44	1.28	1.41
Liscombe	0	1.25	1.30	1.28	1.35	1.48	1.44
	200	1.27	0.93	1.23	1.42	0.97	1.37
Rosemaund	0	1.17	1.54	1.45	1.22	1.78	1.64
	200/300 <sup>1</sup>	1.28	1.04	1.26	1.44	1.01	1.40

Note <sup>1</sup> The nitrogen application rate at Rosemaund was 300 kg ha<sup>-1</sup> yr<sup>-1</sup> in 1978 and 1979, and 200 kg ha<sup>-1</sup> yr<sup>-1</sup> in 1980 and 1981.

## **5.4 Dairy Model**

The ability of the model to simulate milk production was investigated for a non-grazing and a grazing situation, and are described in this section.

### **5.4.1 Non-Grazing Validation**

Østergaard (1979) reported a four-year experiment on the effect of different levels of concentrate feeding on the food intake and liveweight change of dairy cows and milk production. This data were used to assess the model's ability to predict the liveweight change of the dairy cows and monthly milk production. The experimental period was for 36 weeks from on average seven days after parturition. Each cow was fed a basal diet through the lactation which is described in Table 5-17, and the cows were allocated to one of eight concentrate feeding regimes (see Table 5-18). The strategies for the concentrate feeding regime were:

- L0 — low level of concentrates with an equal quantity fed daily;
- L05 — low level of concentrates with the quantity fed being reduced by 0.5 kg every four weeks;
- M0 — medium level of concentrates with an equal quantity fed daily;
- M05 — medium level of concentrates with the quantity fed being reduced by 0.5 kg every four weeks;
- M1 — medium level of concentrates with the quantity fed being reduced by 1.0 kg every four weeks;
- M21 — medium level of concentrates with the quantity fed being increased over the first twelve weeks, and thereafter reduced;
- H0 — high level of concentrates with an equal quantity fed daily; and
- H15 — high level of concentrates with the quantity fed being increased over the first twelve weeks, and thereafter reduced.

The quantity of concentrates fed during each of the 36 weeks of the experiments is shown in Table 5-18—Table 5-20 . Østergaard (1979) reported that the dry-matter percentage of the concentrates was 0.87, while the energy value was 13.23 MJ kg<sup>-1</sup>. The liveweights of the heifers and cows post partum for each of the feeding regimes are shown in Table 5-21. For each of the concentrate feeding regimes the silage was fed *ad libitum*. Østergaard (1979) described the voluntary intake of silage (SI, kg fresh weight head<sup>-1</sup> day<sup>-1</sup>) by:

$$SI = a - b * e^{cx} + d * x \quad (5.6)$$

where x denotes the week of lactation and the coefficients a, b, c and d are given for heifers and cows, and for each concentrate regime in Table 5-22. In the model it is presumed that the dry-matter percentage of the silage is 22% (Østergaard, 1979).

**Table 5-17 Components, quantity and energy value of the basal diet**

Component	Quantity kg DM head <sup>-1</sup> day <sup>-1</sup>	Energy Value MJ kg <sup>-1</sup> DM
Fodder Beet	2.7	10.73
Molasses	1.0	11.92
Beet-top silage	1.0	8.94
Barley straw	0.7	3.34

Source Østergaard (1979)

*Table 5-18 Feeding regime strategies and quantity of concentrates fed during the first 12 weeks of the experiment*

Week of		Concentrate Feeding Regime (kg fresh weight head <sup>-1</sup> day <sup>-1</sup> )						
Lactation	L0	L05	M0	M05	M1	M21	H0	H15
1	4.5	6.5	6.0	8.0	10.5	3.0	7.5	6.0
2	4.5	6.5	6.0	8.0	10.0	3.5	7.5	6.5
3	4.5	6.5	6.0	8.0	10.0	4.0	7.5	6.5
4	4.5	6.5	6.0	8.0	9.5	4.5	7.5	7.0
5	4.5	6.0	6.0	7.5	9.5	5.0	7.5	7.0
6	4.5	6.0	6.0	7.5	9.0	5.5	7.5	7.5
7	4.5	6.0	6.0	7.5	9.0	6.5	7.5	7.5
8	4.5	6.0	6.0	7.5	8.5	7.0	7.5	8.0
9	4.5	5.5	6.0	7.0	8.5	7.5	7.5	8.0
10	4.5	5.5	6.0	7.0	8.0	8.0	7.5	8.5
11	4.5	5.5	6.0	7.0	8.0	8.5	7.5	8.5
12	4.5	5.5	6.0	7.0	7.5	9.0	7.5	9.0

Source Østergaard (1979)

*Table 5-19 Feeding regime strategies and quantity of concentrates fed during the second 12 weeks of the experiment*

Week of		Concentrate Feeding Regime (kg fresh weight head <sup>-1</sup> day <sup>-1</sup> )						
Lactation	L0	L05	M0	M05	M1	M21	H0	H15
13	4.5	5.0	6.0	6.5	7.5	9.0	7.5	9.0
14	4.5	5.0	6.0	6.5	7.0	8.5	7.5	9.0
15	4.5	5.0	6.0	6.5	7.0	8.5	7.5	8.5
16	4.5	5.0	6.0	6.5	6.5	8.0	7.5	8.5
17	4.5	4.5	6.0	6.0	6.5	8.0	7.5	8.5
18	4.5	4.5	6.0	6.0	6.0	7.5	7.5	8.5
19	4.5	4.5	6.0	6.0	6.0	7.5	7.5	8.0
20	4.5	4.5	6.0	6.0	5.5	7.0	7.5	8.0
21	4.5	4.0	6.0	5.5	5.5	7.0	7.5	8.0
22	4.5	4.0	6.0	5.5	5.0	6.5	7.5	8.0
23	4.5	4.0	6.0	5.5	5.0	6.5	7.5	7.5
24	4.5	4.0	6.0	5.5	4.5	6.0	7.5	7.5

Source Østergaard (1979)

*Table 5-20 Feeding regime strategies and quantity of concentrates fed during the third 12 weeks of the experiment*

Week of Lactation	Concentrate Feeding Regime (kg fresh weight head <sup>-1</sup> day <sup>-1</sup> )							
	L0	L05	M0	M05	M1	M21	H0	H15
25	4.5	3.5	6.0	5.0	4.5	6.0	7.5	7.5
26	4.5	3.5	6.0	5.0	4.0	5.5	7.5	7.5
27	4.5	3.5	6.0	5.0	4.0	5.5	7.5	7.0
28	4.5	3.5	6.0	5.0	3.5	5.0	7.5	7.0
29	4.5	3.0	6.0	4.5	3.5	5.0	7.5	7.0
30	4.5	3.0	6.0	4.5	3.0	4.5	7.5	7.0
31	4.5	3.0	6.0	4.5	3.0	4.5	7.5	6.5
32	4.5	3.0	6.0	4.5	2.5	4.0	7.5	6.5
33	4.5	2.5	6.0	4.0	2.5	4.0	7.5	6.5
34	4.5	2.5	6.0	4.0	2.0	3.5	7.5	6.5
35	4.5	2.5	6.0	4.0	2.0	3.5	7.5	6.0
36	4.5	2.5	6.0	4.0	1.5	3.0	7.5	6.0

Source Østergaard (1979)

*Table 5-21 Liveweight of the herd post partum, kg head<sup>1</sup>*

	<b>L0</b>	<b>L05</b>	<b>M0</b>	<b>M05</b>	<b>M1</b>	<b>M21</b>	<b>H0</b>	<b>H15</b>
Heifers	480	481	477	473	479	473	485	484
Cows	547	540	530	538	537	547	537	529

Source Østergaard (1979)

*Table 5-22 Estimates of the coefficients for the model of silage intake (equation (5.6))*

		<b>a</b>	<b>b</b>	<b>c</b>	<b>d</b>
Heifers	L0	28.0	13.5	-0.234	-0.045
	L05	28.7	13.1	-0.154	0.077
	M0	26.7	15.5	-0.228	0.065
	M05	18.5	7.9	-0.396	0.266
	M1	15.1	4.6	-0.287	0.370
	M21	25.2	16.1	-0.789	0.101
	H0	108.8	96.0	-0.035	-1.657
	H15	22.5	9.1	-0.262	0.084
Cows	L0	34.2	21.2	-0.298	-0.066
	L05	37.7	21.9	-0.188	-0.207
	M0	26.7	12.1	-0.287	0.025
	M05	28.6	15.8	-0.265	-0.004
	M1	33.2	21.4	-0.163	-0.012
	M21	28.5	12.4	-0.656	0.074
	H0	28.5	14.7	-0.213	-0.111
	H15	27.6	14.7	-0.307	-0.035

Source Østergaard (1979)

Although the experimental groups were not composed of 43% heifers, the reported milk yields and liveweights are for a herd of that composition. Hence during the validation this was the assumed herd composition in the model. The predicted milk yields were compared with the average daily 4% fat corrected milk yield over three 12 week periods and over nine four week periods (see Figure 5-2). The values of the Theil's inequality coefficients for the fat corrected milk yield and the liveweight change of the dairy herd are shown in Table 5-23. The bias, variance and covariance proportions of the coefficients are also shown in Table 5-23. For all the concentrate regimes, milk production was under-estimated which is revealed in the estimation of bias ( $u_M$ ). Nevertheless the predicted milk yield was at least 90% of the observed yield during the first two of the 12 week periods, although this fell to approximately 80% for the third period. In contrast the magnitude of the liveweight change was over-estimated for all the concentrate regimes during the first 24 weeks of the experiment, and under-estimated for the final 12 weeks.

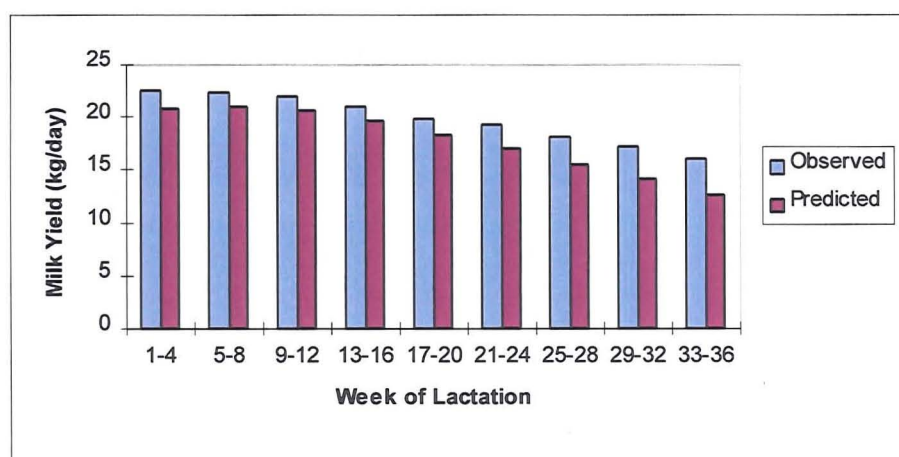


Figure 5-2 The observed and predicted fat corrected milk yield averaged over the eight concentrate feeding regimes.

*Table 5-23 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for the milk yield and liveweight change*

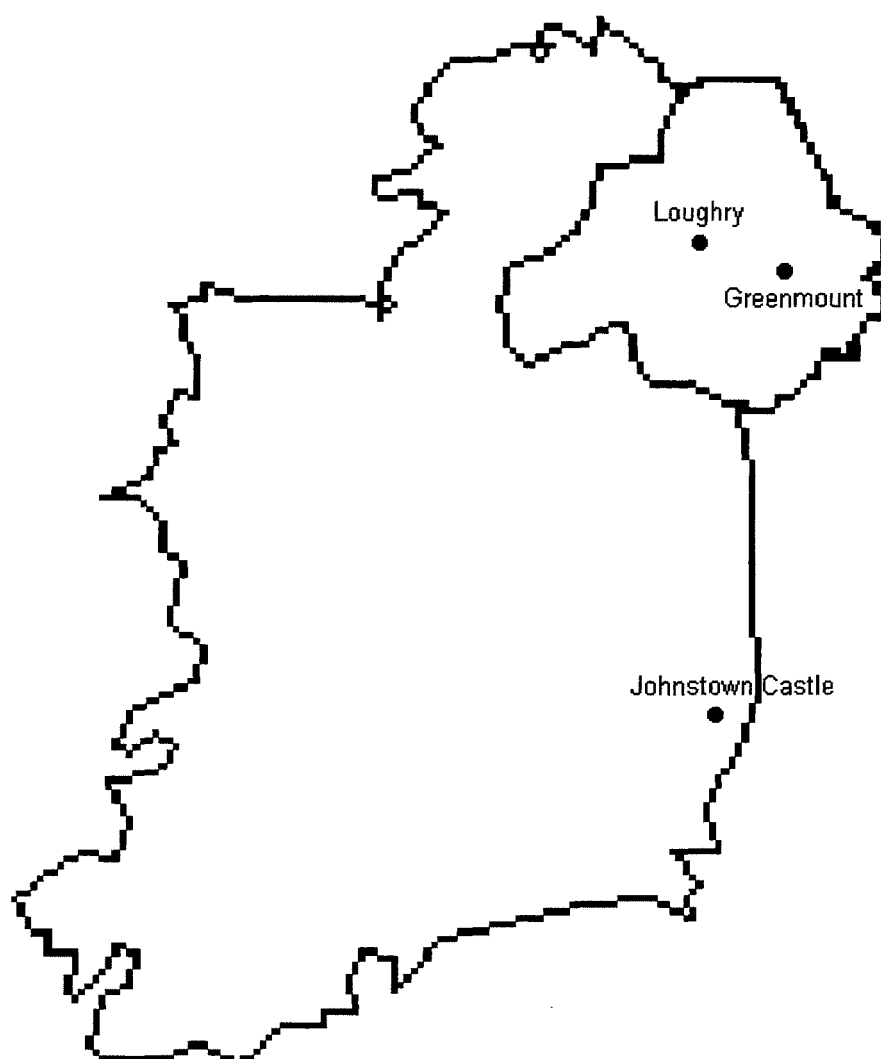
Variable	Measurement Period	Inequality Coefficient	Bias proportion	Variance proportion	Covariance proportion
Milk Yield	3*9 weeks	0.602	0.800	0.087	0.113
Milk Yield	12*4 weeks	0.604	0.834	0.080	0.086
Liveweight	3*9 weeks	0.207	0.04	0.042	0.949

However, the under-estimation of milk yield may be due to the potential milk yield of the Danish cows and heifers being approximately 10% higher during the first two weeks of the lactation than the potential yield parameter defined for cows in the South-West of Scotland. Increasing the potential milk yield by 10% resulted in a Theil's inequality coefficient of 0.037 with a bias proportion of 0.363.

#### **5.4.2 Grazing Validation**

The ability of the model to simulate milk production from a dairy herd grazing pasture was investigated using data from a trial carried out during the period 1983—1987 at An Foras Taluntais, Johnstown Castle, Wexford (M. Ryan, *personal communication*) as shown in Figure 5-3. The trial was conducted on grass and grass – white clover swards with a high and low stocking density for each sward type. The dairy herds were rotationally grazed round a twelve-paddock system. On the grass – based system in the trial, half the area was set aside for first-cut silage production and a third for the second cut. With respect to the grass – white clover system, nitrogen was

applied to the four paddocks that were set aside for silage production, whereas no nitrogen was applied to the grazed paddocks. The mean date of calving was early February and the mean date of turn-out was the 9 April, with the mean experimental period running from 18 April to 15 October (Ryan, 1989).



*Figure 5-3 The location of Johnstown Castle used to validate the dairy model, and Greenmount and Loughry used to validate the beef model*

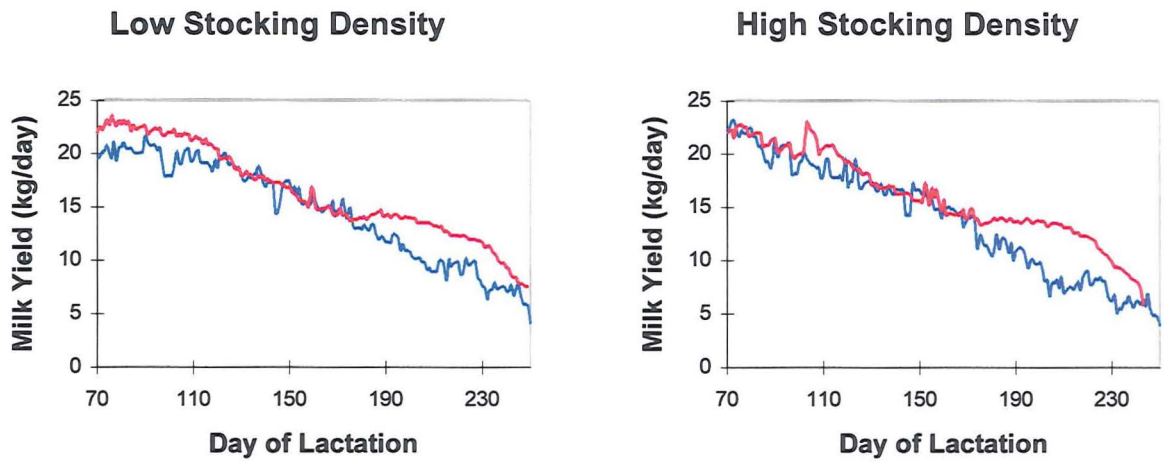
For the validation process the model was specifically run for the period 1985—1987 for dairy herds on both sward types. Calving was assumed to occur on 7 February and the dates of turn-out and yarding were presumed to be 9 April and 15 October respectively. The nitrogen rates and the stocking densities used in the model for each year are shown in Table 5-24 (Ryan, 1988; Ryan, 1989). The 'average dairy cow' was assumed to weigh 525 kg at turnout. In the model it was also assumed that the quantity of concentrates fed per day was determined by the milk yield and consequently the 'average cow' was fed 0.15 kg fresh weight of concentrates per litre of milk (Hollinshead, 1995). The weather data for the site were provided by the Irish Meteorological Office, Dublin (*personal communication*). The soil type was assumed to be either a shallow soil over chalk or rock or a gravel or coarse sandy soil with an available water capacity of between 40 and 80 mm (Baker, Doyle and Lidgate, 1991). The sward type was presumed to be permanent grassland. Hence it was assumed in the model that the available water capacity of the soil was 60 mm and the soil nitrogen status was 120 kg ha<sup>-1</sup>. In the model it was presumed that the dates of the conservation cuts were 1 June and 27 July.

*Table 5-24 The rates of nitrogen application and stocking densities for each sward type for each year*

Year	Low Stocking Density		High Stocking Density	
	Nitrogen	Density	Nitrogen	Density
	(kg ha <sup>-1</sup> )	(cows ha <sup>-1</sup> )	(kg ha <sup>-1</sup> )	(cows ha <sup>-1</sup> )
Grass				
1985	354	2.49	352	3.23
1986	329	2.49	329	3.23
1987	307	2.36	307	3.10
Grass – White Clover				
1985	399	2.10	399	2.55
1986	327	2.10	327	2.55
1987	366	1.98	366	2.4

With respect to the grass – based system, there was a tendency to over-predict towards the end of the grazing season at both stocking densities (see Figure 5-4—Figure 5-6). This trend was also apparent for the predicted milk yields from the grass – white clover based system for both stocking densities in 1985 (see Figure 5-4) and 1986 (see Figure 5-5). Nevertheless, the values of Theil's inequality coefficient for both systems, shown in Table 5-25 and Table 5-26, indicated a reasonably good fit, although there was a tendency for bias.

## Grass – Based System



## Grass – White Clover Based System

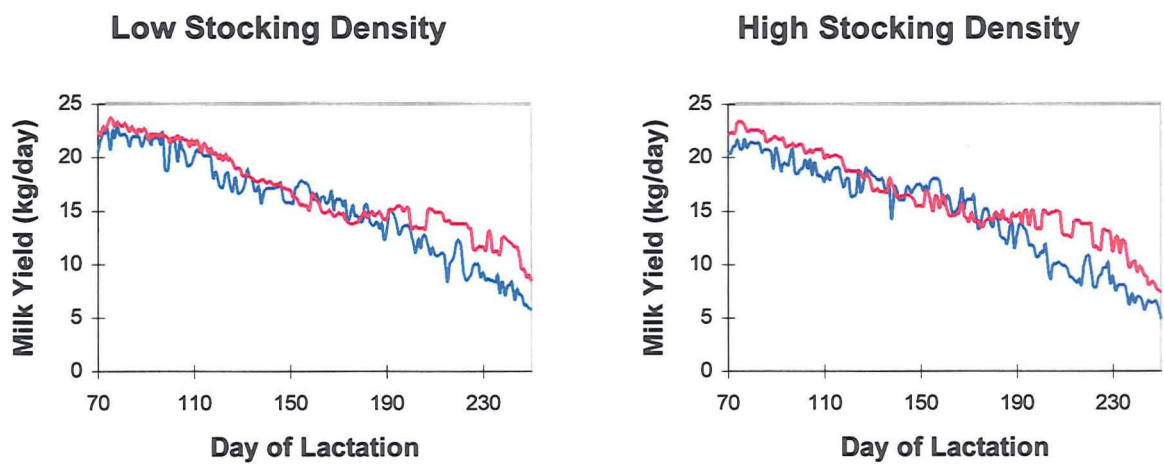
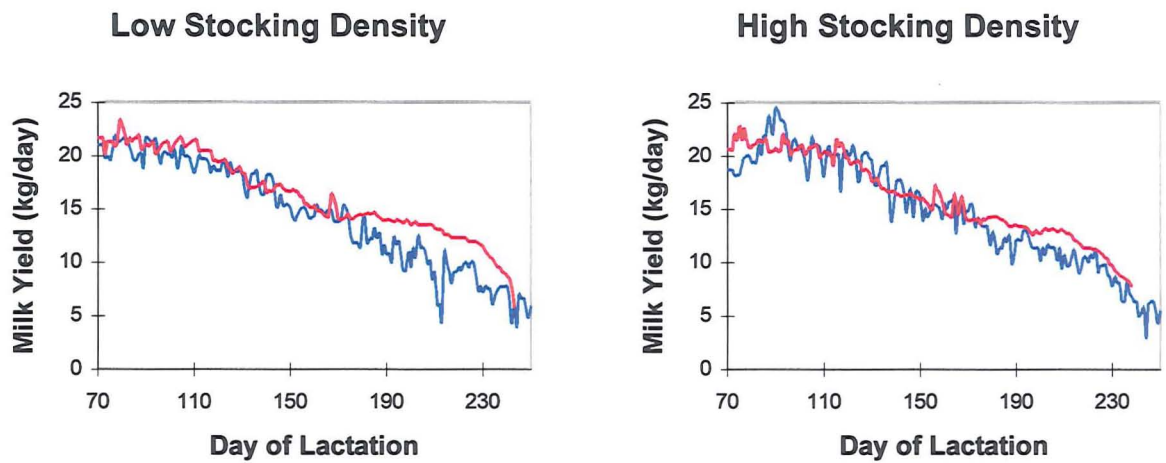


Figure 5-4 Observed and predicted daily milk yields for the 'average cow' at An Foras Taluntais, Johnstown Castle, 1985

## Grass – Based System



## Grass – White Clover Based System

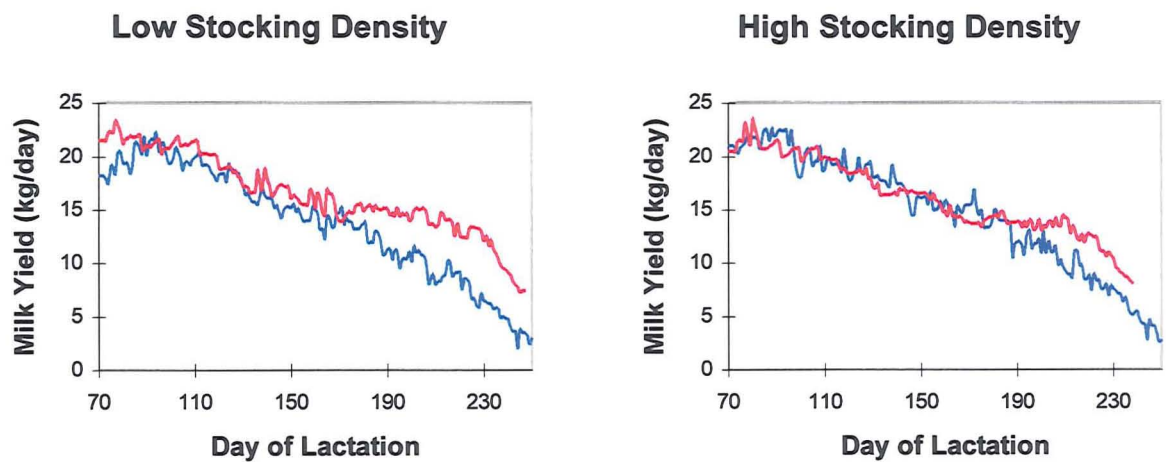
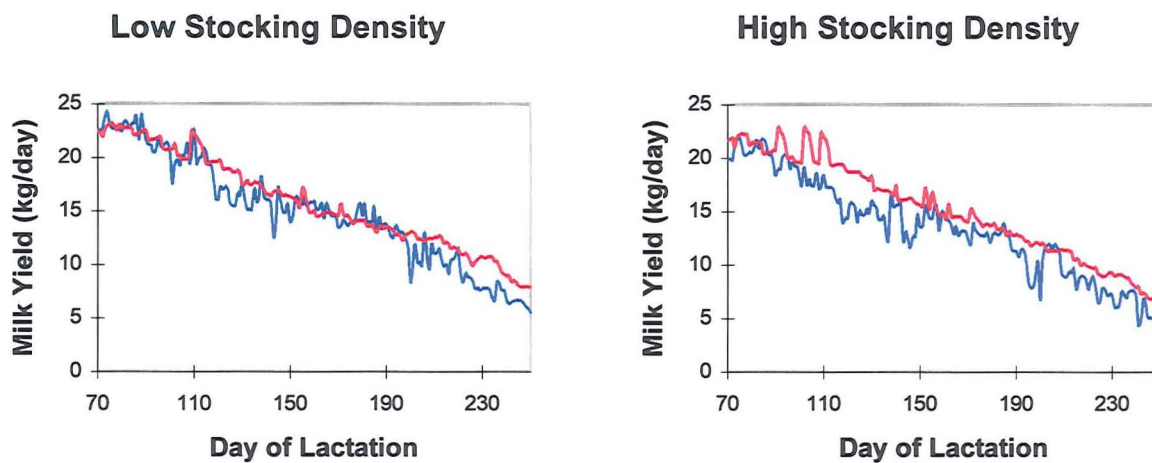


Figure 5-5 Observed and predicted daily milk yields for the 'average cow' at An Foras Taluntais, Johnstown Castle, 1986

## Grass – Based System



## Grass – White Clover Based System

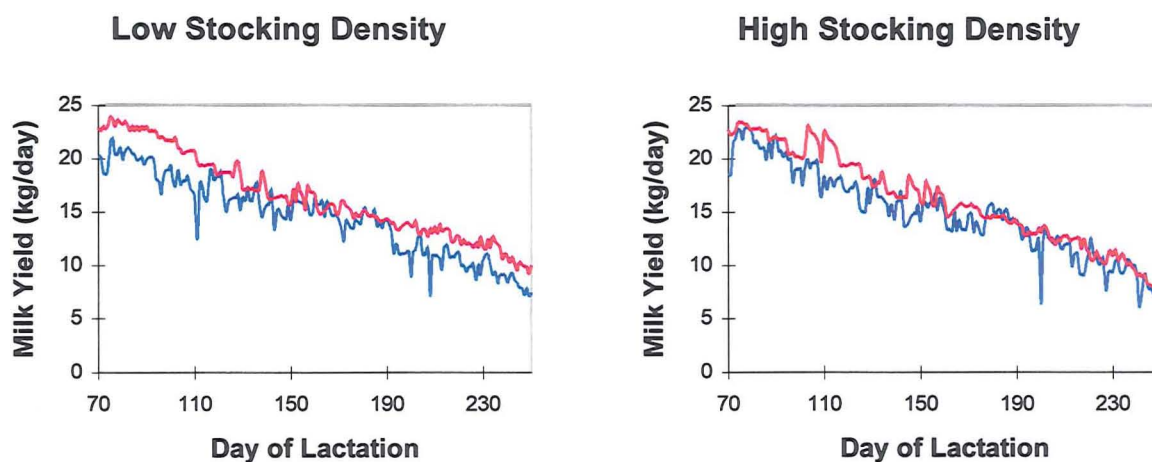


Figure 5-6 Observed and predicted daily milk yields for the 'average cow' at An Foras Taluntais, Johnstown Castle, 1987

*Table 5-25 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for grass – based dairy systems*

<b>Stocking Density</b>	<b>Year</b>	<b>Theil Statistic</b>	<b>Bias</b>	<b>Variance</b>	<b>Covariance</b>
Low	1985	0.069	0.575	0.020	0.405
	1986	0.070	0.470	0.184	0.346
	1987	0.051	0.291	0.131	0.578
	1985—1987	0.064	0.443	0.084	0.473
High	1985	0.082	0.494	0.168	0.338
	1986	0.053	0.154	0.141	0.705
	1987	0.075	0.622	0.000	0.378
	1985—1987	0.071	0.418	0.075	0.507

*Table 5-26 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for grass – white clover based dairy systems*

Stocking Density	Year	Theil Statistic	Bias	Variance	Covariance
Low	1985	0.064	0.370	0.117	0.507
	1986	0.100	0.629	0.175	0.196
	1987	0.075	0.647	0.007	0.346
	1985—1987	0.081	0.535	0.070	0.395
High	1985	0.076	0.367	0.094	0.539
	1986	0.059	0.132	0.352	0.516
	1987	0.058	0.463	0.028	0.509
	1985—1987	0.065	0.306	0.061	0.633

## **5.5 Beef Cattle Model**

Data from a trial conducted at Greenmount and Loughry, Northern Ireland (Stewart and Haycock, 1984) were used to investigate the ability of the beef model to simulate production from a grazing beef herd (see Figure 5-3). During the period 1977—1982, a typical high nitrogen 18 – month beef system was compared with a system that was dependent on white clover and a low input of nitrogen. In the trial, each system was divided into ten equally sized paddocks which were rotationally grazed. The first-cut silage, which was approximately two thirds of the area, was cut in the third or fourth week in May and further cuts were taken later in the summer. The calves were turned

out to grass in April. At Greenmount, the mean weight at turn-out over the trial period was 180 kg, whereas at Loughry it was 200 kg. The land area per system and the stocking densities used during the experimental period at each site are shown in Table 5-27.

*Table 5-27 The area per system and the stocking densities at Greenmount and Loughry for the grass and grass – white clover systems*

Site	Area per system (ha)	Stocking Density (Cattle ha <sup>-1</sup> )	
		Grass	Grass – White Clover
Greenmount	7.5	4.53	3.33
Loughry	7.0	4.57	3.29

For the validation process, the model was specifically run for the period 1978—1982. Turn-out and yarding were assumed to occur on the 14 April and 31 October respectively. Following the recommendations of the Meat and Livestock Commission, (1982), the calves were fed 0.86 kg DM of concentrates per day for the three weeks after turn-out and for the months of September and October. The application rates of nitrogen are shown for each year in Table 5-28. While the rates are shown per hectare in the grass – white clover system, approximately 30 kg ha<sup>-1</sup> was applied to the areas intended for grazing, and the remaining nitrogen was applied to the areas selected for first-cut silage production. The weather data for Cookstown, which was obtained from the BBSRC ARCMET database, were used to represent the conditions at the Loughry site, whereas the weather station at Hillsborough was assumed to represent the weather at the Greenmount site. The soil at the Greenmount site was

described as a dull reddish brown clay and at Loughry the soil was a dark red – brown clay loam or a sandy silt loam (Stewart and Haycock, 1984). Accordingly, the available soil water capacity was assumed to be 120 mm. The sward type was presumed to be permanent grassland and therefore the soil nitrogen status had a value of 120 kg ha<sup>-1</sup>. The dates of the conservation cuts were taken to be 1 June and 27 July.

The liveweight gains observed and predicted by the model are shown in Table 5-29. The observed and predicted number of paddocks harvested for the first and second cuts and the quantity of silage harvested per head are shown in Table 5-30 and Table 5-31 respectively. Specifically, if no grazing had occurred twenty paddocks were recorded as being cut for silage, as each of the ten paddocks were cut twice. Apart from the grass – white clover system at Loughry, there was a tendency to under-predict daily liveweight gain. In contrast the number of paddocks harvested for silage for the grass and the grass – white clover based systems at both Greenmount and Loughry tended to be over-predicted (see Table 5-30), although the quantity of silage harvested was always under-predicted (see Table 5-31). The tendency to underestimate silage production was also apparent in the proportion of Theil's inequality coefficient accounted for by bias (see Table 5-32 and Table 5-33). However, the values of Theil's inequality coefficient for both systems over the five – year period reveal that the model predictions for liveweight gain, the number of paddocks cut for silage and the quantity of silage harvested per head are reasonable (see Table 5-32 and Table 5-33).

*Table 5-28 The rates of nitrogen application for each sward type for each year.*

<b>Year</b>	<b>Greenmount</b>	<b>Loughry</b>
	<b>Nitrogen (kg ha<sup>-1</sup>)</b>	<b>Nitrogen(kg ha<sup>-1</sup>)</b>
<b>Grass</b>		
1978	275	299
1979	297	299
1980	302	299
1981	307	299
1982	362	299
<b>Grass – White Clover</b>		
1978	48	33
1979	48	45
1980	51	45
1981	51	45
1982	52	53

*Table 5-29 The observed and predicted liveweight daily liveweight gain at Greenmount and Loughry for the grass and grass – white clover systems*

Year	Liveweight Gain (kg head <sup>-1</sup> day <sup>-1</sup> )			
	Greenmount		Loughry	
	Observed	Predicted	Observed	Predicted
<b>Grass</b>				
1978	0.73	0.63	0.77	0.60
1979	0.86	0.66	0.90	0.67
1980	0.94	0.68	0.79	0.72
1981	0.78	0.68	0.75	0.69
1982	0.92	0.69	0.75	0.69
<b>Grass – White Clover</b>				
1978	0.91	0.82	0.85	0.84
1979	0.92	0.88	0.99	0.91
1980	1.01	0.88	0.83	0.88
1981	0.81	0.90	0.75	0.89
1982	0.93	0.89	0.69	0.84

*Table 5-30 The observed and predicted number of paddocks cut for silage at Greenmount and Loughry for the grass and grass – white clover systems*

Year	Number Paddocks Cut for Silage			
	Greenmount		Loughry	
	Observed	Predicted	Observed	Predicted
<b>Grass</b>				
1978	10	9	11	10
1979	5	12	12	11
1980	11	14	16	11
1981	8	13	12	12
1982	12	13	10	10
<b>Grass – White Clover</b>				
1978	10	10	13	9
1979	8	13	11	12
1980	8	13	13	10
1981	6	14	10	12
1982	12	13	13	10

**Table 5-31** *The observed and predicted quantity of silage per head at Greenmount and Loughry for the grass and grass – white clover systems*

Year	Quantity of Silage (t head <sup>-1</sup> )			
	Greenmount		Loughry	
	Observed	Predicted	Observed	Predicted
<b>Grass</b>				
1978	0.69	0.58	1.05	0.47
1979	0.62	0.62	1.09	0.69
1980	1.13	0.70	1.47	1.03
1981	0.88	0.72	1.12	0.88
1982	1.03	0.54	1.00	0.85
<b>Grass – White Clover</b>				
1978	0.81	0.48	1.69	0.53
1979	1.11	0.67	1.50	0.71
1980	1.18	0.54	1.48	0.86
1981	0.78	0.79	1.30	0.95
1982	0.89	0.52	1.49	0.79

*Table 5-32 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for the liveweight gain and the number of paddocks cut for silage for grass – based systems.*

	<b>Theil Statistic</b>	<b>Bias</b>	<b>Variance</b>	<b>Covariance</b>
<b>Greenmount</b>				
Liveweight gain	0.094	0.892	0.065	0.043
Number Paddocks	0.164	0.229	0.335	0.436
Silage head <sup>-1</sup>	0.226	0.684	0.185	0.131
<b>Loughry</b>				
Liveweight gain	0.063	0.599	0.133	0.268
Number Paddocks	0.077	0.000	0.035	0.965
Silage head <sup>-1</sup>	0.174	0.795	0.013	0.192

*Table 5-33 Theil's inequality coefficient and bias ( $u_M$ ), variance ( $u_S$ ) and covariance ( $u_C$ ) proportions of the coefficients for the liveweight gain and the number of paddocks cut for silage for grass – white clover based systems.*

	<b>Theil Statistic</b>	<b>Bias</b>	<b>Variance</b>	<b>Covariance</b>
<b>Greenmount</b>				
Liveweight gain	0.042	0.178	0.340	0.482
Number Paddocks	0.177	0.266	0.072	0.662
Silage head <sup>-1</sup>	0.292	0.788	0.020	0.192
<b>Loughry</b>				
Liveweight gain	0.077	0.281	0.407	0.312
Number Paddocks	0.097	0.062	0.002	0.936
Silage head <sup>-1</sup>	0.291	0.715	0.031	0.254

## **5.6 Sheep Model**

### **5.6.1 Experimental Data Used for Validation**

The ability of the sheep model to simulate production was only tested for grass swards as no data were available to compare the model results with production from a grass – white clover sward. The production from grass swards was tested against two sets of experimental data. The first experiment was conducted at the Hartwood Research Station, Scotland (Maxwell, Sibbald, Dalziel, Agnew and Elston, 1994) and the second was conducted at the Bronydd Mawr Research Station, Wales (Sibbald, Maxwell, Morgan, Jones and Rees, 1994), as shown in Figure 5-7.



*Figure 5-7 The location of Harthill and Bronydd Mawr*

Maxwell *et al.* (1994) conducted the experiment at Hartwood during the period 1983—1985 at two sward heights. The ewes were stocked at either 10 or 15 ha<sup>-1</sup> and the mean date of turnout was 5 and 27 April for the low and high sward heights respectively. In the experiment mating commenced on the 26 October, and consequently the mean date of lambing was presumed to be 27 March. The lambing percentage for the high stocking density (15 ewe ha<sup>-1</sup>) was 137, while it was 150 for the low stocking density (10 ewe ha<sup>-1</sup>). As the lambs were weaned during mid July, it was assumed in the model that the date of weaning was 15 July. The quantity of nitrogen fertiliser applied to the sward was 153 kg ha<sup>-1</sup> which was assumed to have been utilised by the sward by the 30 September. During the trial, silage cuts were taken in the first week of June and by the 10 August. Hence in the model the silage was assumed to be cut on 1 June and 10 August. For the validation process the model was specifically run for the period 1983—1985 at two stocking densities and for turnout dates of 5 and 27 April. It was assumed in the model that the sheep were rotationally grazed, using a twelve – paddock system. The soil water capacity was presumed to be 60 mm, while the available soil nitrogen was taken to be 120 kg ha<sup>-1</sup>. Weather data for Blyth Bridge was obtained from the BBSRC ARCMET database to represent the climatic conditions at Hartwood. The latitude of the site is 56 degrees.

The trial at Bronydd Mawr Research Station was only conducted for the year 1984 (Sibbald *et al.*, 1994). The experiment consisted of four treatments which were:

1. nitrogen fertiliser application rate of 100 kg ha<sup>-1</sup> plus a stocking density of 12 ewe ha<sup>-1</sup>;
2. nitrogen fertiliser application rate of 100 kg ha<sup>-1</sup> plus a stocking density of 20 ewe ha<sup>-1</sup>;

3. nitrogen fertiliser application rate of 200 kg ha<sup>-1</sup> plus a stocking density of 12 ewe ha<sup>-1</sup>; and finally
4. nitrogen fertiliser application rate of 200 kg ha<sup>-1</sup> plus a stocking density of 20 ewe ha<sup>-1</sup>.

As the first and second silage cuts at the site were taken in early June and 10 August respectively, it was assumed in the model that the dates of silage cuts were the 1 June and 10 August. In 1984 the ewes were mated from 20 October and thus it was assumed that the ewes had been mated from the same date in the previous year. Assuming a gestation period of 142 days and that lambing occurs over a three-week period it was presupposed in the model that the average date of lambing was 21 March. For both stocking densities the lambing percentage was 120%. The date of turnout was the 9 May, while the date of weaning was 21 July. The weight of the average lamb at turnout at a stocking density of 12 ewe ha<sup>-1</sup> was 12.4 kg. This was increased to 12.9 kg for the higher stocking density (20 ewe ha<sup>-1</sup>). As with the Hartwood site it was assumed in the model that soil contained 120 kg of nitrogen that could be utilised by the crop and that the soil water capacity was 60 mm. The latitude of the site was taken to be 52 degrees and weather data from the Trawscoed meteorological weather station (BBSRC ARCMET database) was taken to represent the weather at Bronydd Mawr Experimental Station.

### **5.6.2 Validation of Model**

The results for the experiment conducted at Hartwood (Maxwell *et al.*, 1994) were averaged over the two sward heights which are shown along with the predicted values in Table 5-34. Sibbald *et al.* (1994) reported the proportion of paddocks harvested and the liveweight of the lambs at weaning for both stocking densities averaged over

the two fertiliser nitrogen application rates for the trial conducted at Bronydd Mawr. On the other hand the quantity of silage available per ewe was reported for each stocking density at each nitrogen fertiliser. The observed and predicted results are given in Table 5-35. Theil's inequality coefficient for the proportion of paddocks harvested, the liveweight of the lambs and the silage produced per ewe for Bronydd Mawr and Hartwood are shown in Table 5-36. As some of the data reported by Maxwell *et al.* (1994) and Sibbald *et al.* (1994) had been averaged over years or treatments, the bias, variance and covariance proportions of Theil's inequality coefficients were not calculated.

**Table 5-34** *The predicted and observed results from the experiment conducted at Hartwood*

	Stocking Density			
	10 ewe ha <sup>-1</sup>		15 ewe ha <sup>-1</sup>	
	Observed	Predicted	Observed	Predicted
<hr/>				
Liveweight lamb (kg head <sup>-1</sup> )				
1983	27.9	32.2	26.8	32.9
1984	34.4	32.2	31.6	32.7
1985	33.1	30.2	30.2	30.2
Silage (kg DM ewe <sup>-1</sup> ), 1983–1985	213	389	39	91
Proportion of paddocks harvested, 1983–1985	0.278	0.299	0.076	0.097
<hr/>				

**Table 5-35** *The predicted and observed results from the experiment conducted at Bronydd Mawr*

	Stocking Density			
	12 ewe ha <sup>-1</sup>		20 ewe ha <sup>-1</sup>	
	Observed	Predicted	Observed	Predicted
Proportion paddocks harvested	0.429	0.333	0.075	0.063
Liveweight lamb (kg head <sup>-1</sup> )	29.5	30.8	29.1	29.2
Silage (kg DM ewe <sup>-1</sup> )				
100 kg N ha <sup>-1</sup>	130	82	0	0
200 kg N ha <sup>-1</sup>	238	184	54	34

**Table 5-36** *Theil's inequality coefficients*

	Bronydd Mawr	Hartwood
Proportion paddocks harvested	0.120	0.295
Liveweight lamb (kg head <sup>-1</sup> )	0.015	0.052
Silage (kg DM ewe <sup>-1</sup> )	0.154	0.297

The results of the validation indicate that at the Hartwood site there was a tendency to over-estimate the liveweight of the lambs, but only at the higher stocking density (15 ewe ha<sup>-1</sup>). The prediction of the quantity of silage was high at both stocking densities at the Hartwood site. However, in contrast, silage production was under-estimated at Bronydd Mawr. Nevertheless, in general the results indicate that the model gives

reasonable predictions for the weight of the lambs at weaning and the quantity of silage produced.

### ***5.7 Conclusions***

The models of forage and livestock production based on grass and grass – white clover swards give reasonable predictions of actual productions. These models are therefore suitable to be used to assess the effects of changes in temperature, rainfall and atmospheric CO<sub>2</sub> concentrations on forage and livestock production within Scotland. Chapter 6 will assess how the changes in climate will affect livestock farming.

## CHAPTER 6

### *RESULTS*

#### **6.1 Introduction**

The effect of global warming and increases in the atmospheric concentration of CO<sub>2</sub> on grass and grass – white clover production and livestock production have been explored. The scenarios used have consisted of ten years of data for current climatic conditions and for seven global warming scenarios at two levels of CO<sub>2</sub> concentration for five sites within Scotland. The sites were chosen as representative of the main areas of livestock production which utilise improved pastures in Scotland. Nevertheless, the choice of sites was restricted by the availability of weather data. This chapter analyses how temperature, rainfall and CO<sub>2</sub> affect herbage and livestock production, while Chapter 7 assesses how livestock production will be affected by the combined effects associated with global warming.

Under global warming, the expected concentration of CO<sub>2</sub>, when all the radiative forcing effects of all the “greenhouse” gases including CO<sub>2</sub> is double the pre-industrial level, is 520 ppmv (Wigley and Raper, 1992). The concentrations used in the model are thus 350 ppmv, representing current levels, and 520 ppmv. As the temperature changes predicted by Viner *et al.* (1995) are similar for the winter and summer period, the average daily temperatures throughout the year were increased by the same daily increase. The temperature changes used to simulate the effect of global warming were current temperatures +1°C, +2°C, and +3°C, as this permitted an assessment of the effect of temperature on livestock production. For the climate change scenarios

the rainfall on rainy days was increased according to estimates by Viner and Hulme (1994) and is shown in Table 6-1. The scenarios were therefore created by increasing the daily temperature and rainfall measurements for the base climate by the appropriate amounts. The base climate was obtained from the BBSRC ARCMET database for period 1979—1988 for five sites, namely Auchincruive (Auch), Blyth Bridge (Blyth), Craibstone (Craib), Drummond Castle (Drum) and Wick (Wick) and are shown in Figure 6-1. The sixteen scenarios used in the model are described in Table 6-2.

#### **6.1.1 Soil Characteristics**

The volumetric water content and the stoniness of the soil have been obtained from the soil association maps (Macaulay Institute for Soil Research, 1982). Following Bibby, Douglas, Thomasson and Robertson (1991), this information has been used to calculate the available water capacity of the soil at each site and is shown in Table 6-3. It is assumed that the rooting depth is 1 metre. It has also been assumed that all sites are under predominately permanent grassland, so that available soil nitrogen was taken to be 120 kg ha<sup>-1</sup> (Baker *et al.*, 1991).



*Figure 6-1 The location of the sites*

**Table 6-1**    *The change in the rain on rainy days predicted under a doubling of the atmospheric CO<sub>2</sub> concentration*

Month	Change rainfall (mm)	Month	Change rainfall (mm)
January	1.5	July	0.1
February	1.3	August	0.0
March	1.0	September	-0.2
April	0.7	October	1.1
May	0.8	November	1.0
June	0.4	December	1.1

*Table 6-2 Temperature, rainfall and CO<sub>2</sub> concentrations for the climate scenarios*

Scenario	Temperature	Rainfall Change	CO <sub>2</sub> Concentration (ppmv)
0A3	+0	No	350
0A5	+0	No	520
0B3	+0	Yes	350
0B5	+0	Yes	520
1A3	+1	No	350
1A5	+1	No	520
1B3	+1	Yes	350
1B5	+1	Yes	520
2A3	+2	No	350
2A5	+2	No	520
2B3	+2	Yes	350
2B5	+2	Yes	520
3A3	+3	No	350
3A5	+3	No	520
3B3	+3	Yes	350
3B5	+3	Yes	520

*Table 6-3 The available water capacity of the sites*

Site	Available water capacity (mm)
Auchincruive	160
Blyth Bridge	161
Craibstone	104
Drummond Castle	189
Wick	149

## **6.2 Statistical Analysis**

The differences between the treatment effects, namely temperature, rainfall and ambient concentration of CO<sub>2</sub>, have been assessed using analysis of variance. Although this technique is fairly robust, the data should meet the following criteria:

1. the distribution of the population of observations is normal;
2. the treatment and environmental effects are additive; and
3. experimental errors are random, independently and normally distributed about the zero mean and with a common variance.

If these assumptions are not met, the level of significance and sensitivity of the F-test can be affected. In most cases, with non-normality of the data the true level of significance is greater than the apparent level (Steel and Torrie, 1981) and thus the null hypothesis is rejected when it is true. In the case of non-additivity, the components of error contributed by the various observations do not supply estimates of a common variance and thus the error is heterogeneous. Hence, non-additivity of

the data results in false significance levels for certain specific comparisons of treatment means. Nevertheless, the significance level for the F-test may be little affected. The final assumption implies that the experimental error should be normally distributed and the errors have a common variance. However if the distributions of the experimental errors are skewed, the error component of a treatment tends to be a function of the treatment mean and hence the error is heterogeneous, which may arise due to the erratic behaviour of the response to certain treatments. Consequently, when a 5% level of significance is being used as the criteria for detecting differences between the populations, the actual level of significance actually being detected may be 7% or 8% (Steel and Torrie, 1981). However, Steel and Torrie (1981) indicate that for most biological data that the failure of the data to fulfil the above criteria are usually unimportant. On the other hand, the process of randomisation of experimental treatments results in the errors being independent of each other.

On examination of the data it is apparent that the treatments are non-additive, and that there is a tendency for the distribution of the error to be skewed. Nevertheless, transforming the data did not appear to improve either the additivity assumption or the normality of the distribution of the errors. Accordingly, while the size of the F-ratios predicted from the analysis of variance will be used to assess whether the treatment effects were significant, it is recognised that the level of significance may actually be slightly higher than 5%. As a consequence, there is the possibility of acceptance of some non-existent significant differences. However, it is not possible to make specific comparisons between treatment levels. Significance at the 5% level is indicated by “★★★”. Where there is a significant interaction between factors, only the interaction

effects will be noted and described. The effects of climate change on livestock production within Scotland are analysed separately in terms of:

1. forage production; and
2. livestock production.

### **6.3 Impact of Global Warming on Forage Production**

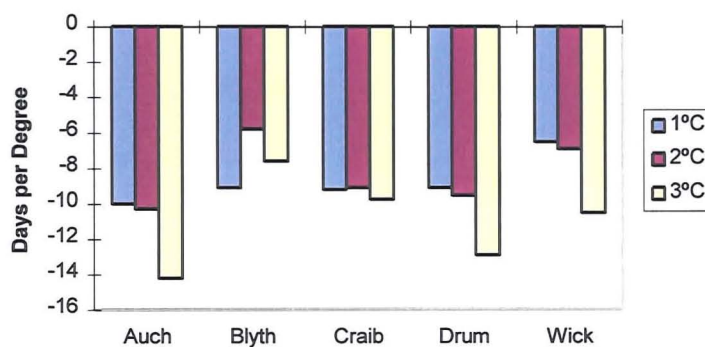
The quantity of nitrogen applied to the pure grass sward is 300 kg ha<sup>-1</sup>, with a third applied in the spring and a third after both the first cut and second cuts. In the spring 50 kg ha<sup>-1</sup> of nitrogen is applied to the grass – white clover swards. For dairy enterprises based on a two-cut pasture system, the dates for the first cut range from the end of May to the beginning of June with the second cut taken approximately eight weeks later at Auchincruive, Blyth Bridge, Craibstone and Drummond Castle (A. Gill, D. Younie, A. Waterhouse, *personal communication*). At Wick, the first cut on dairy farms tends to be taken in mid-June (D. Birkbeck, *personal communication*). Accordingly, the silage cuts were assumed to be taken on the 1 June and eight weeks later on the 27 July for both the pure grass and the grass – white clover swards. However, it is recognised that the cutting dates for beef and sheep enterprises compared to the dairy enterprise tend to be later in the season. On farms with predominately grass – white clover swards the silage dates tend to be approximately a week later than those utilising pure grass swards (K. Leach, *personal communication*). Nevertheless, the same cutting dates for all enterprises, swards and locations were used, as these permitted comparisons to be made. It also allowed comparisons to be made between grazed and ungrazed swards.

### **6.3.1 Effect of Global Warming on the Length of the Growing Season**

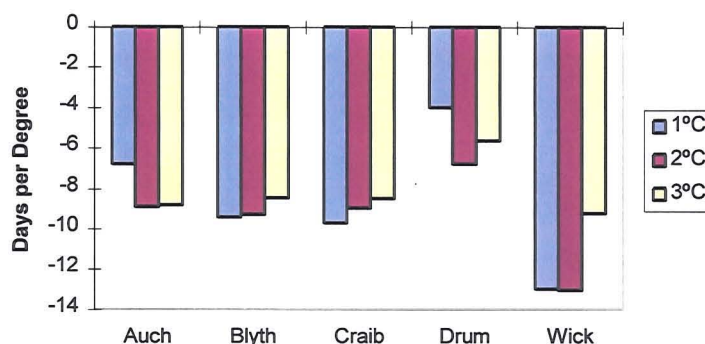
Generally, increases in temperature resulted in the growing season starting earlier and finishing later in the year. Consequently the length of the growing season for grass and white clover also increased with temperature as underlined in Table 6-4. Site also had a significant effect on the commencement and the termination of the growing season. However, as regards the date when growth commenced and the length of the growing season for pure grass and for the grass component of the mixed swards, there was a significant interaction between site and temperature. Similarly, there was a significant interaction between temperature and site for the commencement of white clover growth. Nevertheless, temperature did not have a linear effect on the start date of the growing season for both grass and white clover and for the length of the growing season for grass (see Figure 6-2—Figure 6-4). On the other hand, the effect of temperature on the end date of the growing season for both grass and white clover was approximately linear with an increase of 10 days per degree temperature rise. Similarly, the length of the growing season for white clover was also linearly affected by temperature, with an increase of approximately 19 days per degree of temperature increase. The temperature constraint for the end of the growing season is the same for both the grass and white clover components.

*Table 6-4 The effect of site and temperature on the start and end dates and the length of the growing season for grass and white clover*

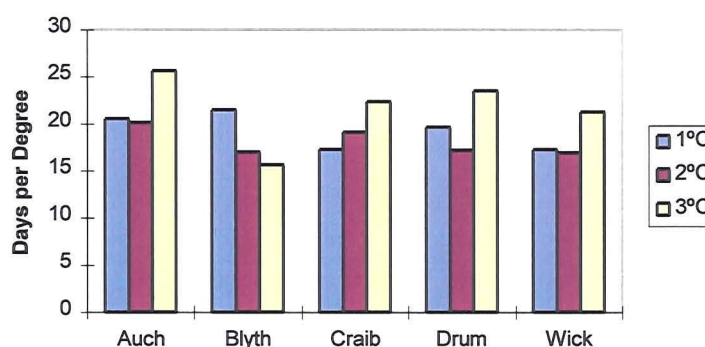
Component	Factors	Start Date	End Date	Length
Grass	Site	★★★	★★★	★★★
	Temperature	★★★	★★★	★★★
	Site * Temperature	★★★		★★★
White Clover	Site	★★★	★★★	★★★
	Temperature	★★★	★★★	★★★
	Site * Temperature	★★★		



*Figure 6-2 The change in the commencement of the growing season per degree of temperature change at each site for grass*



*Figure 6-3 The change in the commencement of the growing season per degree of temperature change at each site for white clover*



*Figure 6-4 The change in the length of the growing season per degree of temperature change at each site for grass*

### 6.3.2 Effect of Global Warming on the Yield

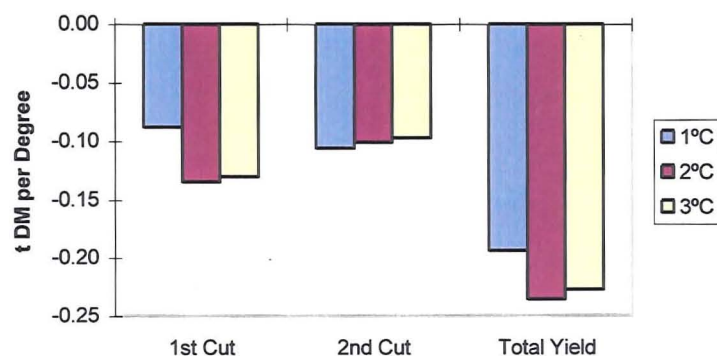
#### 6.3.2.1 Grass Swards

The dry-matter yield of herbage from the pure grass sward for the first and second cuts and hence the total yield differed between sites. The main effects of CO<sub>2</sub>, temperature and rainfall also significantly affected yield, although there were no interaction effects. Increasing the ambient concentration of CO<sub>2</sub> or presuming a change in the rainfall pattern increased production throughout the season (see Table 6-5), whereas increasing the temperature resulted in decreasing yields. Although the

change in yield per degree was approximately linear for the second-cut yield, this was not the case for the first-cut yield (see Figure 6-5). Hence the change in total yield did not decrease linearly with temperature. Nevertheless, the change in yield for a 2°C and 3°C increase in temperature resulted in similar decreases per degree of temperature increase for all cuts. The proportion of the total yield harvested at the first cut was significantly decreased from 60.4% to 59.4% by elevating the ambient concentration of CO<sub>2</sub>.

**Table 6-5** *The increase in dry-matter yield from changing the rainfall pattern and increasing the ambient concentration of CO<sub>2</sub>*

Cut	Percentage increase in DM yield from base level	
	Climate change rainfall pattern	Elevated CO <sub>2</sub> (520 ppmv)
1 <sup>st</sup>	3.0	19.7
2 <sup>nd</sup>	2.8	25.0
Total	3.0	21.8



**Figure 6-5** *The change in the dry-matter yield per degree of temperature change*

#### **6.3.2.2 Grass – White Clover Yields**

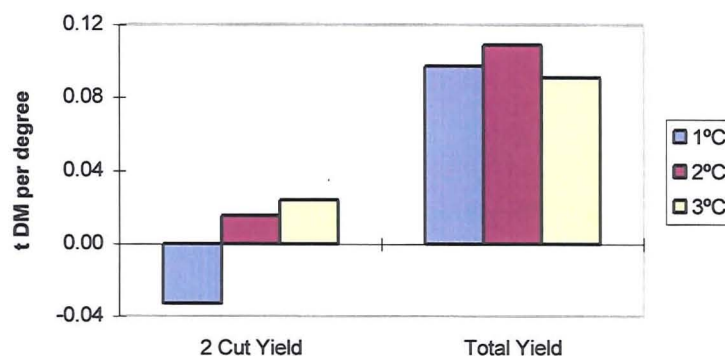
The combined and the component dry-matter yields of the grass – white clover sward were significantly affected by site, temperature, and rainfall pattern. However, in contrast to the pure grass sward, the site \* temperature and the temperature \* CO<sub>2</sub> interactions were significant for some of the components of yield. The percentage changes in the components of yield, relative to the base conditions for a change in the rainfall pattern and the CO<sub>2</sub> concentration, are shown in Table 6-6. The seasonality of production was also significantly affected by enhanced CO<sub>2</sub> concentration. Thus, the percentage of total yield and total grass yield harvested from the first cut was decreased by 1.1% and 2.0% respectively. In contrast the percentage of the total white clover yield obtained from the first cut was enhanced by 2.5% by augmenting the CO<sub>2</sub> conditions. The effect of temperature on the second cut and total combined yields was not linear and indeed the effect was not consistent between these two components of yield (see Figure 6-6). The percentage of grass and white clover harvested from the first cut was significantly increased with elevated temperatures (see Figure 6-7).

**Table 6-6** *The percentage change in the components of dry-matter yield from the base level for the components significantly affected by rainfall and CO<sub>2</sub> level*

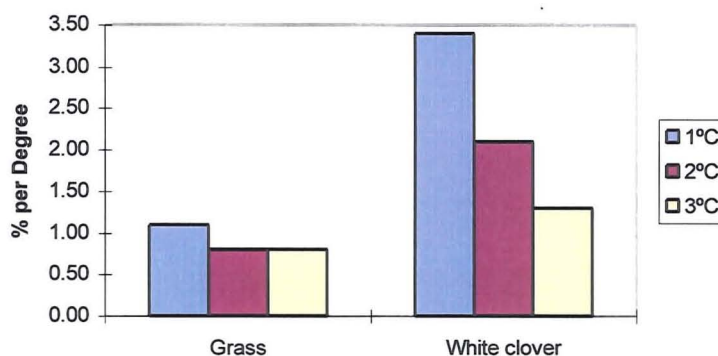
Cut	Component	Percentage increase in dry-matter yield from base level	
		Climate change rainfall pattern	Elevated CO <sub>2</sub> (520 ppmv)
First	grass	2.23	18.39
	white clover	9.27	25.79 <sup>1</sup>
	combined	3.63	19.86
	% white clover	5.49	4.48
Second	grass	2.42	30.86 <sup>1</sup>
	white clover	13.66	17.02
	combined	6.26	25.76
	% white clover	6.65	-7.63
Total	grass	2.29	21.72
	white clover	11.23	21.75
	combined	4.47	21.72
	% white clover <sup>2</sup>	6.45	

Note: <sup>1</sup> There was a significant interaction between temperature and CO<sub>2</sub> concentration.

<sup>2</sup> The effect of CO<sub>2</sub> concentration on the percentage of white clover in the total yield was not significant.



*Figure 6-6 The change in the dry-matter yield per degree of temperature change for the combined second cut and total yield*



*Figure 6-7 The change in the percentage of grass and white clover harvested from the first cut per degree of temperature change*

#### **6.3.2.2.1 Site – Temperature Interactions on Yields**

There was a significant interaction between site and temperature for the first-cut yield of grass, white clover and the combined yield (see Figure 6-8 and Figure 6-9). The yield of grass obtained from the first cut tended to decrease with increased temperature (see Figure 6-8). The exceptions were at a 1°C temperature increase at Auchincruive, Craibstone and Drummond Castle and at a 2°C temperature increase at Craibstone. In contrast, the first-cut yield of white clover was increased by temperature at all sites (see Figure 6-9). The net result of increasing the temperature

on the first-cut combined yield was that the yield was increased at all sites and for all scenarios, except for a 1°C temperature increase at Wick. Nevertheless, the effect of temperature at each site on the components of the first-cut yield and the combined yield is not linear. The percentage of white clover in the material harvested from the first cut is increased with elevated temperatures, although the effect per degree was not linear (see Table 6-7). In contrast to the first-cut, the second-cut white clover yield was decreased for a 1°C temperature increase at Auchincruive and Drummond Castle (see Figure 6-10). This resulted in the percentage of white clover harvested from the second cut remaining unchanged at Auchincruive and decreasing at Drummond Castle for a 1°C temperature increase (see Table 6-7). The total yield of grass and white clover was also significantly affected by a site \* temperature interaction. The total grass tended to decrease with elevated temperatures, although an increase of 1°C enhanced the grass yield at Craibstone and Drummond Castle (see Figure 6-11). On the other hand, the total yield of white clover was increased at all sites, except at a 1°C decrease at Drummond Castle (see Figure 6-12).

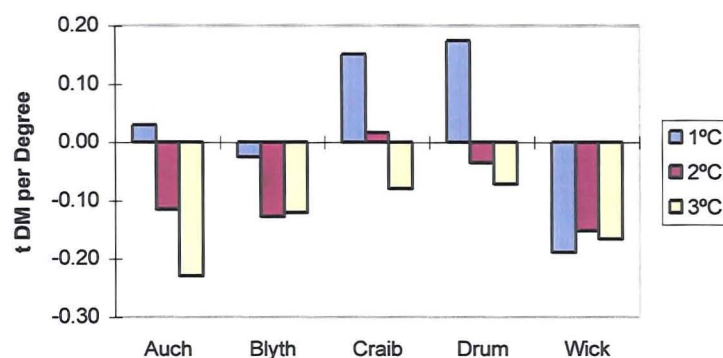


Figure 6-8 The change in the first-cut grass dry-matter yield per degree of temperature change

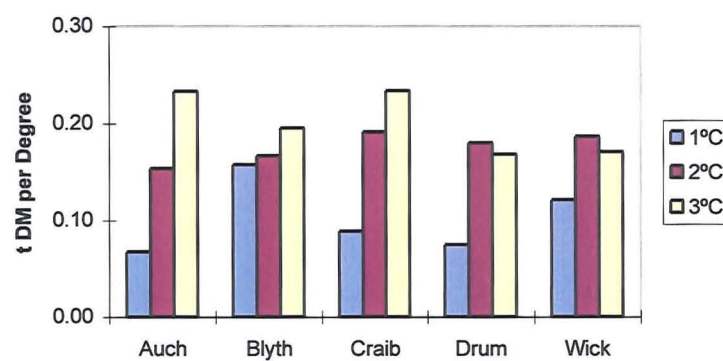


Figure 6-9 The change in the first-cut white clover yield per degree of temperature change.

*Table 6-7 The change in the percentage of white clover in the harvested material per degree of temperature change at each site*

Cut	Site	Change per degree of temperature change (t)		
		1°C	2°C	3°C
1 <sup>st</sup> cut yield	Auchincruive	0.01	0.04	0.06
	Blyth Bridge	0.04	0.05	0.05
	Craibstone	0.01	0.04	0.05
	Drummond Castle	0.01	0.04	0.04
	Wick	0.05	0.06	0.05
2 <sup>nd</sup> cut yield	Auchincruive	0.00	0.03	0.08
	Blyth Bridge	0.05	0.07	0.07
	Craibstone	0.02	0.05	0.07
	Drummond Castle	-0.03	0.03	0.04
	Wick	0.08	0.08	0.07
Total yield	Auchincruive	0.00	0.03	0.06
	Blyth Bridge	0.04	0.06	0.06
	Craibstone	0.01	0.04	0.06
	Drummond Castle	-0.01	0.03	0.03
	Wick	0.06	0.06	0.06

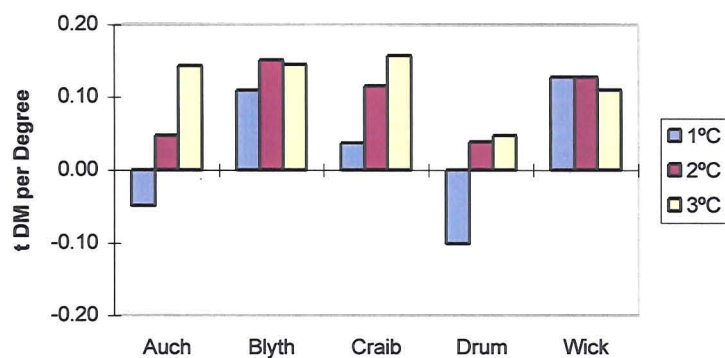


Figure 6-10 The change in the second-cut white clover yield per degree of temperature change at each site

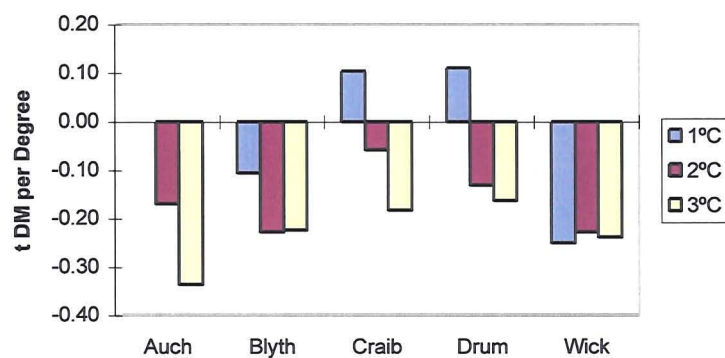
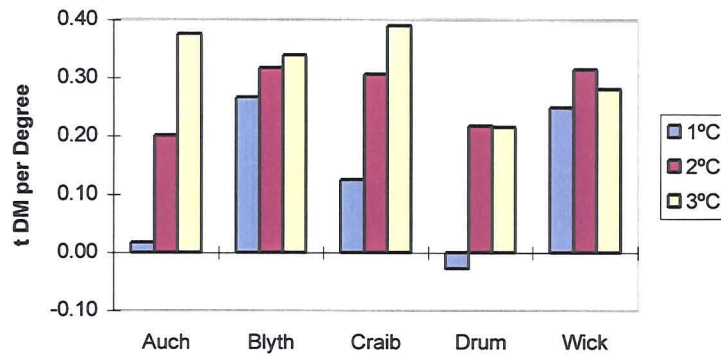


Figure 6-11 The change in the total grass yield per degree of temperature change at each site



*Figure 6-12 The change in the total white clover yield per degree of temperature change at each site*

#### **6.3.2.2.2 Temperature – CO<sub>2</sub> Interactions on Yields**

There was a significant interaction between temperature and ambient CO<sub>2</sub> level for the first-cut white clover yield, the second-cut grass yield and the total white clover yield (see Figure 6-13 and Table 6-8). At current climatic conditions, increasing the CO<sub>2</sub> concentrations resulted in an increase of 0.09 t DM, 0.14 t DM and 0.34 t DM for the first-cut and total white clover yields and the second-cut grass yields, respectively. The effect of enhanced CO<sub>2</sub> concentrations was to increase white clover yields, with the effect being more pronounced at higher temperatures. In contrast, the second-cut grass yield was decreased at current concentrations of CO<sub>2</sub> and the rate of decrease was greater at higher temperature levels (see Table 6-8). Nevertheless, increasing the ambient concentration of CO<sub>2</sub> increased the quantity of grass harvested in the second cut, although this effect diminished with increasing temperature.

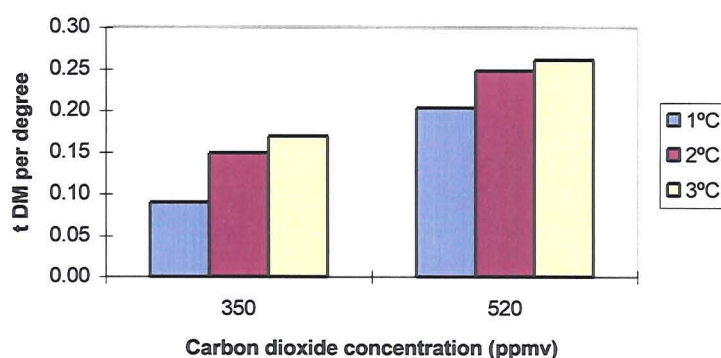


Figure 6-13 The change in the first-cut white clover yield per degree of temperature for each level of ambient CO<sub>2</sub> concentration relative to current climatic conditions

Table 6-8 The change in the first-cut and total white clover yield, and the second-cut grass yield per degree of temperature for each level of ambient CO<sub>2</sub> concentration relative to the base climate.

Cut	CO <sub>2</sub> Concentration (ppmv)	Change per degree of temperature change (t)		
		1°C	2°C	3°C
1 <sup>st</sup> white clover	350	0.09	0.15	0.17
	520	0.20	0.25	0.26
2 <sup>nd</sup> grass	350	-0.05	-0.07	-0.08
	520	0.28	0.08	0.00
Total white clover	350	0.12	0.23	0.27
	520	0.28	0.38	0.42

## 6.4 Livestock Production

Dairy cows, beef cattle and sheep were rotationally grazed on a twelve-paddock grass or grass – white clover system. The pure grass swards were grazed at three stocking densities which are typical values for United Kingdom farming systems (see Table 6-9). Following Ryan (1988) the stocking densities on the grass – white clover swards were reduced by approximately 16%. Nitrogen was applied throughout the season to the pure grass and the grass – white clover swards and the application rates are shown in Table 6-10. The silage cuts were presumed to be taken on 1 June and 27 July. In both the grass and the grass – white clover based system in the trial, half the area was set aside for first-cut silage production and a third for the second cut.

*Table 6-9 The stocking densities for the grass and grass – white clover swards for dairy cows, beef cattle and sheep.*

Sward Type	Dairy Cows (head ha <sup>-1</sup> )	Beef Cattle (head ha <sup>-1</sup> )	Sheep (head ha <sup>-1</sup> )
Grass	2.00	3.08	9.52
	2.25	3.46	12.50
	2.50	3.85	13.89
Grass – white clover	1.68	2.58	8.00
	1.89	2.91	10.50
	2.10	3.23	11.67

*Table 6-10 The nitrogen application rates for grass and grass – white clover swards for dairy cows, beef cattle and sheep.*

Sward Type	Dairy Cows (kg ha <sup>-1</sup> )	Beef Cattle (kg ha <sup>-1</sup> )	Sheep (kg ha <sup>-1</sup> )
Grass	300	300	150
Grass – white clover	50	50	50

The date of turnout was determined by the availability of herbage. Nevertheless, neither the dairy cattle nor the sheep were turned out if this was less than four days after the date of parturition. The date of calving was assumed to be 15 February whereas the date of lambing was presumed to be 15 March. In the beef enterprise, the average age of the cattle at turnout was assumed to be 180 days. At turnout the weights of dairy cows, beef cattle and ewes were assumed to be 525 kg head<sup>-1</sup>, 200 kg head<sup>-1</sup> and 60 kg head<sup>-1</sup> respectively. The lambing percentage for a lowground flock was taken to be 150%. The lambs were a product of a cross between a Scottish Blackfaced ewe and a Suffolk ram, with the average weight of the ewe and ram assumed to be 60 and 70 kg head<sup>-1</sup> respectively. The dates of yarding for the dairy and beef enterprises were determined by the herbage availability. On the other hand, the lambs were assumed to be sold at twenty weeks of age, and consequently the lambs were removed from the paddocks on the 2 August. The weight of the ewes is also reported for this date.

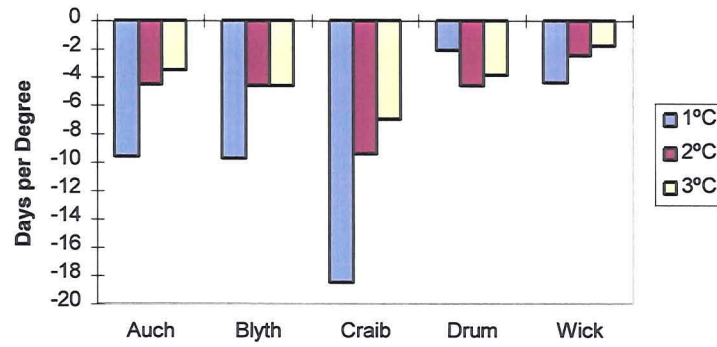
The dairy cows were assumed to be fed 0.15 kg fresh weight of concentrates per litre of milk produced per day. With respect to the beef enterprise, during the first three

weeks of grazing and from the first week in October the cattle were fed at a rate of 0.86 kg DM head<sup>-1</sup>. On the other hand, the ewes were not fed any concentrates during the grazing season.

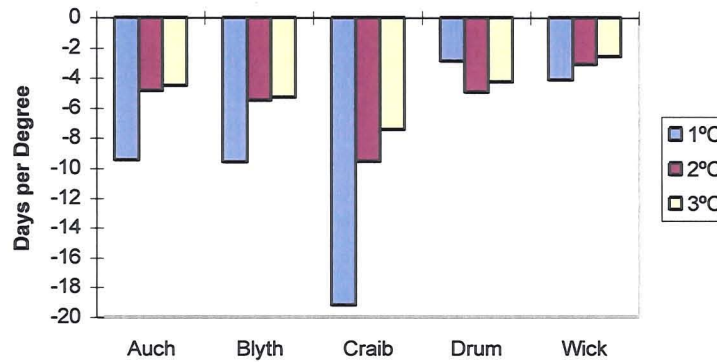
#### **6.4.1 The Effect of Global Warming on the Grazing Season**

##### **6.4.1.1 *Date of Turnout***

The date of turnout was significantly earlier in the season with increases in temperature and the ambient concentration of CO<sub>2</sub> for the dairy, beef and sheep enterprises. This occurred for both the grass and the grass – white clover based systems. However, there was a significant interaction between temperature and site, and temperature and CO<sub>2</sub> concentration for all livestock enterprises grazing both sward types. Although the effect of temperature differed at the five locations, the effect was similar across all the enterprises for both the grass and grass – white clover swards. This is illustrated for the dairy enterprise in Figure 6-14 and Figure 6-15. However, the temperature did not have a linear effect on the date of turnout at any site. Except for Drummond Castle, a 1°C increase in daily temperature had a larger effect per degree than either a 2°C or 3°C rise in temperature. Similarly, a 1°C increase in temperature had the greatest effect per degree change on the date of turnout on both grass and grass – white clover based systems (see Table 6-11). This effect was observed for both the current and elevated levels of the ambient concentration of CO<sub>2</sub>. The effect of temperature at each CO<sub>2</sub> level for all enterprises grazing both sward types was that turnout was earlier in the spring than at current temperatures. Nevertheless, the date of turnout was earlier for the elevated CO<sub>2</sub> than current CO<sub>2</sub> conditions for all temperature scenarios.



*Figure 6-14 The effect of change in the date of turnout per degree of temperature change at each site for the dairy enterprise on the grass – based systems*



*Figure 6-15 The effect of change in the date of turnout per degree of temperature change at each site for the dairy enterprise on the grass – white clover based systems*

#### **6.4.1.2 Date of Yarding**

With respect to the dairy and beef enterprises the date of yarding was determined by the model. In contrast to the effect of global warming on the date of turnout, the factors that were significant differed between sward types. Moreover, the factors that were significant differed between the dairy and beef enterprises grazing the pure grass sward, although this was not the case for the grass – white clover swards.

#### **6.4.1.2.1 Grass – Based Enterprises**

With respect to the dairy enterprise grazing the pure grass swards, the date of yarding was significantly affected by a site \* temperature \* CO<sub>2</sub> interaction, rainfall \* CO<sub>2</sub> interaction and the stocking density. In contrast the yarding date for beef enterprise was significantly affected by the two-way interactions between site and temperature, site and CO<sub>2</sub>, site and rainfall, temperature and CO<sub>2</sub>, and rainfall and CO<sub>2</sub>. Similarly for the dairy enterprise, stocking rate also had a significant effect.

At all sites increasing the ambient concentration of CO<sub>2</sub> resulted in the grazing season ending later in the season for the dairy enterprise than under current CO<sub>2</sub> conditions. Nonetheless, the effect of temperature within each CO<sub>2</sub> level differed between sites (see Figure 6-16). With a temperature increase of 0°C, increasing the ambient concentration of CO<sub>2</sub> resulted in the grazing season in the autumn being extended by between 4.1 and 13.6 days. In general, the change in the date of yarding was not linearly affected by temperature, although the effect was approximately linear at current CO<sub>2</sub> concentrations at the Wick site. In the same way, the date of yarding for the beef enterprise was later in the season for each temperature scenario at elevated CO<sub>2</sub> concentrations than at ambient levels (see Table 6-12). Increasing the concentration of CO<sub>2</sub> at current climate temperature levels resulted in the grazing season finishing 5 days later than under current concentrations of CO<sub>2</sub> (350 ppmv).

*Table 6-11 The effect of elevated CO<sub>2</sub> on the date of turnout for the grass and grass – white clover based systems*

Enterprise	Sward	CO <sub>2</sub> Level (ppmv)	Change in days per degree of temperature change		
			1°C	2°C	3°C
Dairy	Grass	350	-8.0	-4.2	-3.9
		520	-10.2	-6.3	-5.3
Beef		350	-8.0	-4.2	-3.4
		520	-10.2	-6.3	-5.1
Sheep		350	-7.0	-3.6	-2.7
		520	-10.0	-5.6	-4.3
Dairy	Grass – white clover	350	-8.5	-4.6	-4.1
		520	-10.4	-6.9	-5.7
Beef		350	-8.5	-4.6	-4.1
		520	-10.4	-6.9	-5.7
Sheep		350	-7.4	-4.4	-3.9
		520	-9.4	-6.3	-5.3

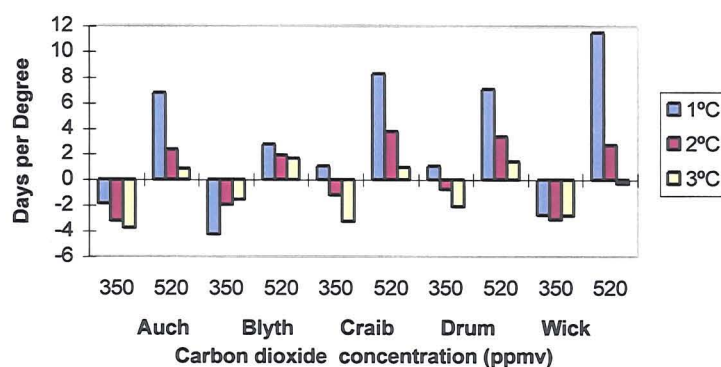
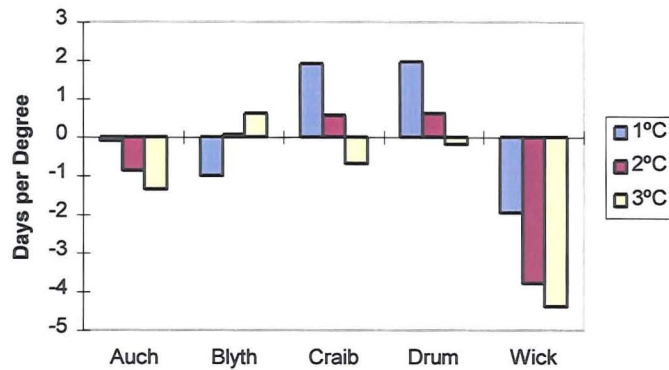


Figure 6-16 The effect of change in the date of yarding per degree of temperature change at each site and at CO<sub>2</sub> concentration for the dairy enterprise on the grass – based systems relative to current climatic conditions

Table 6-12 The change in the date of yarding for the beef enterprise grazing on a grass – based system at CO<sub>2</sub> concentrations of 350 and 520 ppmv

CO <sub>2</sub> Concentration (ppmv)	Change per degree of temperature change (days)		
	1°C	2°C	3°C
350	-0.5	-1.4	-2.1
520	5.8	2.5	1.4

However, the effect per degree increase in temperature tends to decrease with increasing temperature. The effect of temperature on the date of yarding at each site differed both in magnitude and direction (see Figure 6-17). The date of yarding was later in the season at all sites when the CO<sub>2</sub> concentration was increased to 520 ppmv (see Table 6-13). Nevertheless, the effect ranged from 5.1 days at Drummond Castle to 11.7 days at Wick (see Table 6-13).



*Figure 6-17 The change in the date of yarding per degree of temperature change at each site for the beef enterprise on the grass – based systems*

*Table 6-13 The effect of increasing the ambient concentration of CO<sub>2</sub> and changing to a global warming rainfall pattern on the date of yarding for the beef enterprises on the grass – based systems at each of the sites*

	Change in date of yarding with	
	elevated CO <sub>2</sub> concentrations (Days)	global warming rainfall patterns (Days)
Auchincruive	8.5	-2.9
Blyth Bridge	5.6	-2.7
Craibstone	6.2	-4.5
Drummond Castle	5.1	-3.7
Wick	11.7	-0.3

On the other hand, under the rainfall pattern associated with global warming, the date of yarding was earlier in the season than under current climatic conditions (see Table 6-13). The decrease ranged from 0.3 days at Wick to 4.5 days at Craibstone. For

both the dairy and beef enterprises changing the rainfall pattern resulted in the date of yarding being earlier in the season than for the current rainfall (see Table 6-14), due to an increased risk of poaching. This effect was apparent at both current and elevated ambient concentrations of CO<sub>2</sub>. Nevertheless, increasing the CO<sub>2</sub> concentration for both rainfall patterns resulted in yarding being later in the season than at current CO<sub>2</sub> levels.

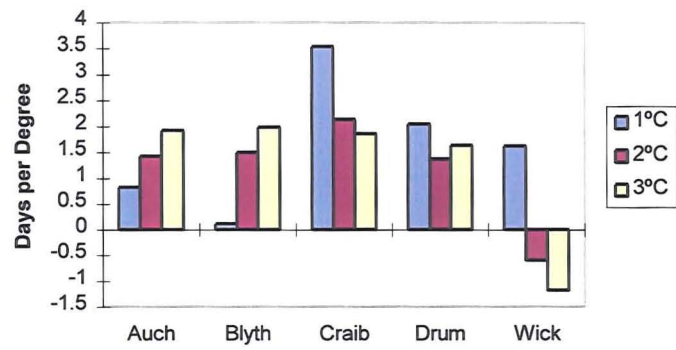
*Table 6-14 The effect of elevated CO<sub>2</sub> and changing to a global warming rainfall pattern on the date of yarding for the dairy and beef enterprises on the grass – based systems*

Enterprise	CO <sub>2</sub> Concentration (ppmv)	Change in date of yarding with changing rainfall patterns (Days)	
		Current	Global Warming
Dairy	350		-0.4
	520	9.9	7.8
Beef	350		-1.8
	520	8.5	4.6

Increasing the stocking rate resulted in the date of yarding being earlier in the season for both the dairy and beef enterprises. The change for the dairy enterprise was between -1.7 and -1.9 days when the stocking densities were increased by 0.25 dairy cows ha<sup>-1</sup>. The corresponding figure for the beef enterprise was -1.5 days when stocking density was increased by 0.38 steers ha<sup>-1</sup>.

#### **6.4.1.2.2 Grass – White Clover Swards**

In the grass – white clover based systems the factors that had a significant effect on the date of yarding for both the dairy and beef enterprises were site and temperature, site and CO<sub>2</sub>, site and rainfall, rainfall and CO<sub>2</sub> and stocking density. The date of yarding tended to be later in the season at elevated temperatures, which is illustrated for the dairy enterprise in Figure 6-18. Except for a temperature increase of 1°C at the Craibstone site, the effect of temperature on the date of yarding for the beef system tended to be marginally greater (0.08—1.15 days) than that experienced by the dairy enterprise. However, the exceptions were a 1°C and 2°C increase in temperature at Wick for the dairy enterprise, and a 2°C temperature increase at Wick for the beef enterprise. Nevertheless, the effect was not linear with temperature (see Figure 6-18). Increasing the ambient concentration of CO<sub>2</sub> resulted in the date of yarding being later in the season than under current CO<sub>2</sub> levels, although the magnitude of the effect varied between sites (see Table 6-15). On the other hand, except for Wick, the yarding date was earlier in the season when the rainfall was changed under global warming (see Table 6-15). The date of yarding was later in the season with elevated CO<sub>2</sub> concentrations, although this effect was diminished with a global warming rainfall pattern (see Table 6-16). At CO<sub>2</sub> concentrations of 350 ppmv changing the rainfall pattern resulted in an earlier removal of stock from the paddocks. Increasing the stocking density of the dairy herd by 0.21 cows ha<sup>-1</sup> resulted in the yarding date being 1.9 days earlier. Similarly for the beef enterprise, increasing the stocking density by 0.33 steers ha<sup>-1</sup> resulted in the stock being removed between 1.3 and 1.4 days earlier than for a stocking density of 2.58 steers ha<sup>-1</sup>.



*Figure 6-18 The change in the date of yarding per degree of temperature change at each site for the dairy enterprise on the grass – white clover based systems*

*Table 6-15 The effect of increasing the ambient concentration of CO<sub>2</sub> and changing to a global warming rainfall pattern on the date of yarding for the dairy and beef enterprises on the grass – white clover based systems at each of the sites*

Enterprise		Change in date of yarding with	
		elevated CO <sub>2</sub> concentrations (Days)	global warming rainfall patterns (Days)
Dairy	Auchincruive	7.8	-3.4
	Blyth Bridge	5.3	-2.6
	Craibstone	6.1	-5.3
	Drummond Castle	4.1	-3.8
	Wick	14.5	0.8
Beef	Auchincruive	5.4	-6.3
	Blyth Bridge	2.2	-3.8
	Craibstone	3.5	-8.2
	Drummond Castle	2.3	-5.4
	Wick	13.4	0.7

*Table 6-16 The effect of elevated CO<sub>2</sub> and changing to a global warming rainfall pattern on the date of yarding for the dairy and beef enterprises on the grass – white clover based systems*

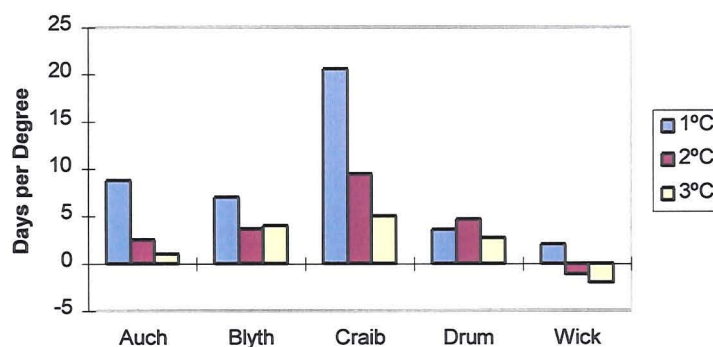
Enterprise	CO <sub>2</sub> Concentration (ppmv)	Change in date of yarding with changing rainfall patterns (Days)	
		Current	Global Warming
Dairy	350		-1.5
	520	8.9	4.7
Beef	350		-3.5
	520	6.4	0.8

#### **6.4.1.3 Length of the Grazing Season**

##### **6.4.1.3.1 Grass – Based Enterprises**

The length of the grazing season for both the dairy and beef enterprises on grass – based systems was significantly affected by stocking rate and rainfall pattern. The interactions between site and temperature, site and CO<sub>2</sub>, temperature and CO<sub>2</sub> were also significant for both enterprises. The effect of increasing the stocking density was to reduce the length of the grazing season by between 1.7 and 1.9 days for an increase of 0.25 cows ha<sup>-1</sup> for the dairy enterprise. The corresponding figure for the beef enterprise was an increase of 0.38 steers ha<sup>-1</sup> resulting in a reduction of 1.5 days in the length of grazing season. Changing the rainfall to a pattern associated with global warming resulted in the grazing being reduced by 1.2 and 2.7 days for the dairy and beef enterprises respectively. Except for temperature increase of 2°C and 3°C at

Wick, the length of the grazing season was increased at all sites for both the dairy (see Figure 6-19) and beef enterprises. A similar pattern was also predicted for the beef enterprise. Although temperatures have a similar effect on both the dairy and beef enterprises at each site, the effect on length of the grazing season is not linear with temperature. Elevating the CO<sub>2</sub> concentration from 350 ppmv to 520 ppmv resulted in the grazing season being extended at all sites, although the extension varied between sites (see Table 6-17). The length of the grazing season was also increased by enhanced CO<sub>2</sub> levels at all temperatures (see Table 6-18). At current temperatures the grazing season was lengthened by 7.4 and 5.4 days for the dairy and beef enterprises respectively with elevated concentrations of CO<sub>2</sub>. However, the increase in the length of the grazing season was greatest when the temperature was increased by 1°C and the rate of increase per degree increase in temperature diminished as the temperature was increased by 2°C and 3°C.



*Figure 6-19 The change in the length of the grazing season per degree of temperature change at each site for the dairy enterprise on the grass – based systems*

*Table 6-17 The effect of increasing the ambient concentration of CO<sub>2</sub> on the length of the grazing season for the dairy and beef enterprises on the grass – based systems at each of the sites*

Site	Change in length of the grazing season with elevated CO <sub>2</sub> concentrations (Days)	
	Dairy	Beef
Auchincruive	13.7	12.2
Blyth Bridge	8.2	6.7
Craibstone	13.5	11.0
Drummond Castle	9.9	7.5
Wick	14.5	14.4

*Table 6-18 The change in the length of the grazing season for the dairy and beef enterprise grazing on a grass – based system at CO<sub>2</sub> concentrations of 350 and 520 ppmv*

Enterprise	CO <sub>2</sub> Concentration (ppmv)	Change per degree of temperature change (days)		
		1°C	2°C	3°C
Dairy	350	6.7	2.2	0.7
	520	17.4	9.1	6.0
Beef	350	7.5	2.8	1.3
	520	16.0	8.8	6.5

#### **6.4.1.3.2 Grass – White Clover Based Swards**

With respect to the grass – white clover sward the length of the grazing season was significantly affected by the site \* CO<sub>2</sub> interaction, site \* temperature interaction, site \* rainfall and stocking density for both the dairy and beef enterprises. However, for the dairy enterprise the interactions between temperature and CO<sub>2</sub> and temperature and rainfall pattern were also significant. Increasing the stocking density reduced the length of the grazing season by 1.9 days for an increase of 0.21 cows ha<sup>-1</sup> and between 1.3 and 1.4 days for an increase of 0.33 steers ha<sup>-1</sup>. The effect on the length of grazing for the dairy and beef enterprises differed between sites, with the difference ranging from a reduction of 8.3 days at Blyth Bridge to an increase of 1.3 days at Wick (see Table 6-19). Nevertheless, the reduction in the length of the grazing season for the dairy enterprise with the global warming rainfall pattern was increased at elevated ambient concentrations of CO<sub>2</sub>. Enhancing the CO<sub>2</sub> concentration increased the length of the grazing season (see Table 6-20). However, the greatest increase per degree of temperature enhancement at both current and elevated CO<sub>2</sub> levels occurred when the temperature was increased by 1°C. Moreover the magnitude differed between sites (see Table 6-21). At all sites increasing the temperature increased the length of the grazing season, although the magnitude differed between sites for both the dairy (see Figure 6-20) and beef enterprises. A similar pattern to that illustrated for the dairy enterprise was also predicted in respect of the effect of temperature on the length of the grazing season for the beef enterprise.

*Table 6-19 The effect of changing from the current rainfall pattern to a rainfall under global warming on the length of the grazing season for the dairy and beef enterprises on the grass – based systems at each of the sites*

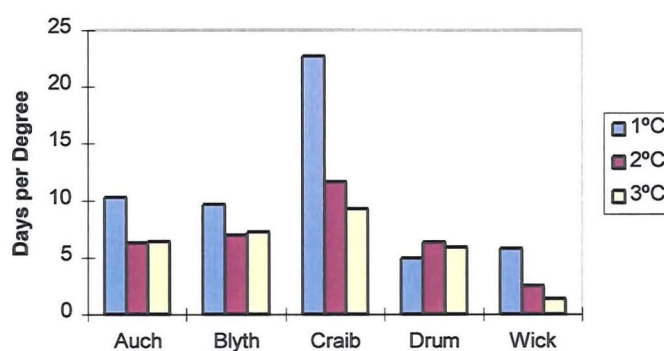
Site	Change in length of the grazing season (Days)	
	Dairy	Beef
Auchincruive	-3.2	-6.1
Blyth Bridge	-2.7	-3.9
Craibstone	-5.3	-8.3
Drummond Castle	-4.1	-5.6
Wick	1.4	1.3

*Table 6-20 The change in the length of the grazing season for the dairy and beef enterprise grazing on a grass – white clover based system at CO<sub>2</sub> concentrations of 350 and 520 ppmv*

Enterprise	CO <sub>2</sub> Concentration (ppmv)	Change in length of the grazing season per degree of temperature change (days)		
		1°C	2°C	3°C
Dairy	350	9.6	5.4	4.8
	520	18.7	11.5	9.6
Beef	350	9.8	5.6	5.4
	520	16.9	10.9	9.2

*Table 6-21 The effect of increasing the ambient concentration of CO<sub>2</sub> on the length of the grazing season for the dairy and beef enterprises on the grass – white clover based systems at each of the sites*

Site	Change in length of the grazing season with elevated CO <sub>2</sub> concentrations (Days)	
	Dairy	Beef
Auchincruive	11.2	8.8
Blyth Bridge	7.5	4.3
Craibstone	9.9	7.4
Drummond Castle	7.0	5.2
Wick	17.4	16.3



*Figure 6-20 The change in the length of the grazing season per degree of temperature change at each site for the dairy enterprise on the grass – white clover based systems*

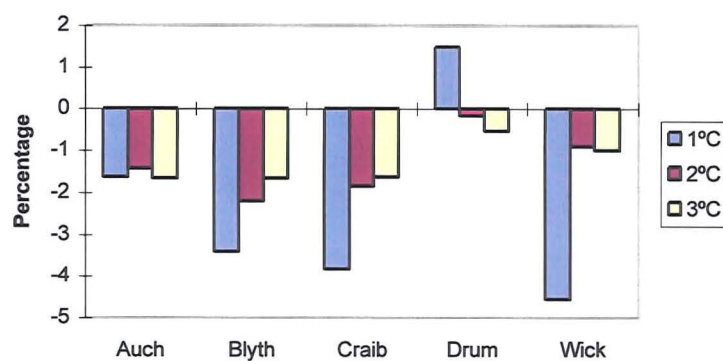
#### **6.4.1.4 Proportion of Paddocks Harvested**

##### **6.4.1.4.1 Grass – Based Enterprises**

The factors that significantly affected the proportion of paddocks cut over the grazing season were:

- Dairy – rainfall pattern, stocking rate and interactions between site and temperature, and site and CO<sub>2</sub>;
- Beef – rainfall pattern, and interactions between site and temperature, site and CO<sub>2</sub>, site and stocking rate, temperature and CO<sub>2</sub>, and CO<sub>2</sub> and stocking rate; and
- Sheep – rainfall pattern, and interactions between site and temperature, site and CO<sub>2</sub>, site and stocking rate, temperature and CO<sub>2</sub>, temperature and stocking rate, and CO<sub>2</sub> and stocking rate.

The effect of changing to a global warming rainfall pattern increased the percentage of paddocks cut by 1.1%, 1.6% and 1.7% for the beef, sheep and dairy enterprises respectively. Although there was an interaction effect between site and temperature, the response of the three enterprises was similar across all sites. Consequently, the results are only shown for the dairy enterprise (see Figure 6-21). On the other hand, the relative magnitudes of the effect of CO<sub>2</sub> at each site differed between enterprises (see Table 6-22). For the beef and sheep enterprises the effect of CO<sub>2</sub> on the percentage of paddocks harvested was also affected by the ambient temperature (see Table 6-23). Nevertheless, the effect of temperature per degree of increase tended to decline as the temperature increased.



*Figure 6-21 The change in the percentage of paddocks harvested throughout the season per degree increase in temperature for the grass – based dairy enterprise at each site*

*Table 6-22 The change in the percentage of paddocks harvested throughout the season with elevated CO<sub>2</sub> concentrations at each site for the grass – based enterprises*

Enterprise	Site (%)				
	Auch	Blyth	Craib	Drum	Wick
Dairy	10.6	9.2	9.0	9.8	6.8
Beef	6.7	6.0	5.3	5.4	9.1
Sheep	10.3	8.3	7.2	7.5	10.1

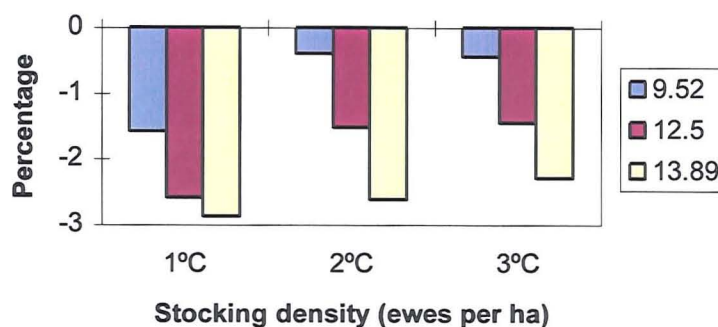
*Table 6-23 The change in the percentage of paddocks harvested for the beef and sheep enterprises grazing on a grass – based system at CO<sub>2</sub> concentrations of 350 and 520 ppmv*

Enterprise	CO <sub>2</sub> Concentration  (ppmv)	Change in the percentage of paddocks harvested per degree increase in temperature		
		1°C	2°C	3°C
Beef	350	-2.6	-1.3	-1.2
	520	3.8	1.9	1.3
Sheep	350	-2.8	-2.1	-1.9
	520	5.2	2.6	1.5

Increasing the dairy stocking rate from 2.0 to 2.25 cows ha<sup>-1</sup> reduced the percentage of paddocks harvested from 55.5% to 50.3%. Similarly increasing the stocking density to 2.5 cows ha<sup>-1</sup> resulted in the percentage of paddocks harvested declining to 45.7%. A similar reduction was observed for the beef enterprise when the stocking densities were increased from the low to the medium and to the high stocking densities, although the change differed between sites (see Table 6-24). Equally, the effect for the sheep enterprise also differed between sites, but the magnitude of the decrease was larger than that observed for the beef enterprise (see Table 6-24). As the stocking density increased, the enhancement in the percentage of paddocks harvested with CO<sub>2</sub> was increased for the beef and sheep enterprises. On the other hand, as the stocking density increased the reduction in the percentage of paddocks harvested per degree increase in temperature was enhanced (see Figure 6-22).

*Table 6-24 The change in the percentage of paddocks harvested relative to the lowest stocking density (3.08 steers ha<sup>-1</sup>, 9.52 ewes ha<sup>-1</sup>) at each site for the beef and sheep enterprises on the grass – based systems*

Enterprise		Change in percentage of paddocks harvested	
		medium stocking density	high stocking density
Beef	Auchincruive	-3.5	-8.4
	Blyth Bridge	-3.4	-7.1
	Craibstone	-4.2	-7.9
	Drummond Castle	-3.6	-7.3
	Wick	-4.8	-10.1
Sheep	Auchincruive	-13.0	-21.8
	Blyth Bridge	-11.7	-18.0
	Craibstone	-13.7	-21.5
	Drummond Castle	-11.0	-17.9
	Wick	-19.0	-27.4



*Figure 6-22 The change in the percentage of paddocks harvested per degree increase in temperature relative to the current temperature scenario for each stocking density*

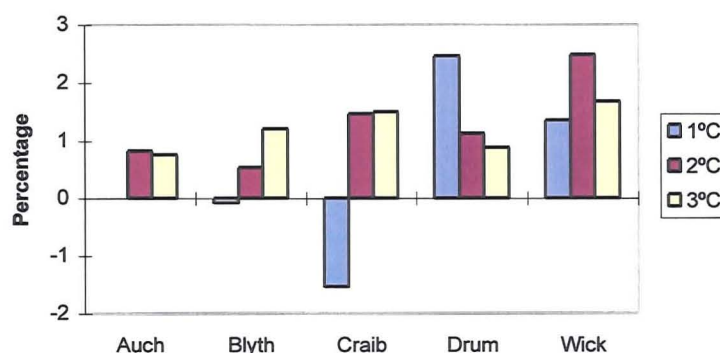
#### **6.4.1.4.2 Grass – White Clover Based Enterprises**

The factors that significantly affected the percentage of paddocks harvested throughout the season for all enterprises were rainfall and the interaction between site and temperature. In addition the following factors were also significant:

- Dairy – interaction between site and CO<sub>2</sub>;
- Beef – interaction between CO<sub>2</sub> and stocking rate; and
- Sheep – interaction between site and CO<sub>2</sub>, site and stocking rate, temperature and CO<sub>2</sub>, temperature and stocking rate.

The effect of changing to a global warming rainfall pattern increased the percentage of paddocks harvested by 1.1%, 2.1% and 2.2% for the sheep, beef and dairy enterprises respectively. The effect of temperature on the percentage of paddocks varied at each site (see Figure 6-23 and Figure 6-24). Although the effect was similar for the dairy and sheep enterprises, which tended to experience an increase, the effect for the beef enterprise was usually a decline (see Figure 6-24). Site also influenced the magnitude of the effect of elevating the ambient concentration of CO<sub>2</sub>

on the percentage of paddocks harvested for the dairy and sheep enterprises. The enhancement for the dairy enterprise ranged from 7.7% at Craibstone to 9.8% at Wick. The comparable figures for the sheep enterprise ranged from 3.9% at Craibstone to 6.5% at Wick. In the case of the beef enterprise, increasing the concentration of CO<sub>2</sub> increased the percentage of paddocks harvested by 7.0%. At the elevated concentrations of CO<sub>2</sub> the effect of temperature per degree increase on the percentage of paddocks harvested from the sheep system diminished as temperature increased (see Figure 6-25).



*Figure 6-23 The change in the percentage of paddocks harvested throughout the season per degree increase in temperature for the grass – white clover based dairy enterprise at each site*

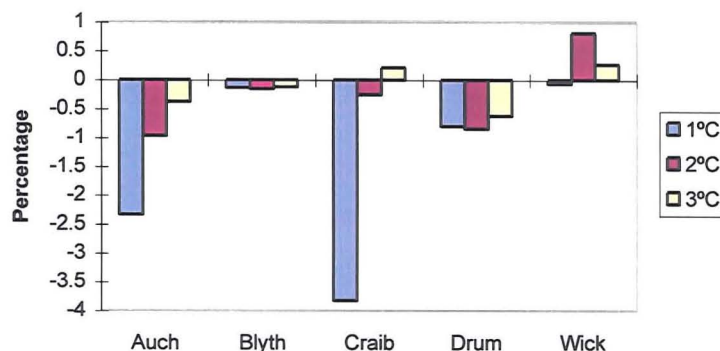


Figure 6-24 The change in the percentage of paddocks harvested throughout the season per degree increase in temperature for the grass – white clover based beef enterprise at each site

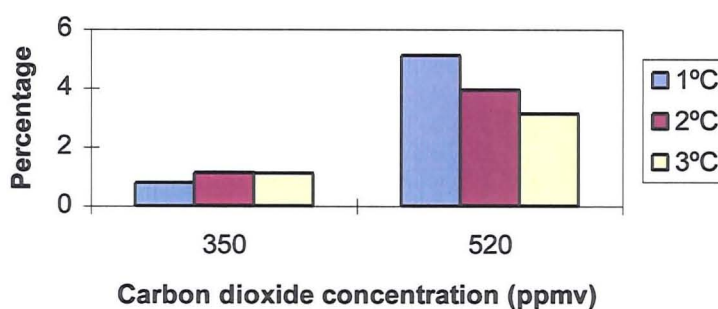
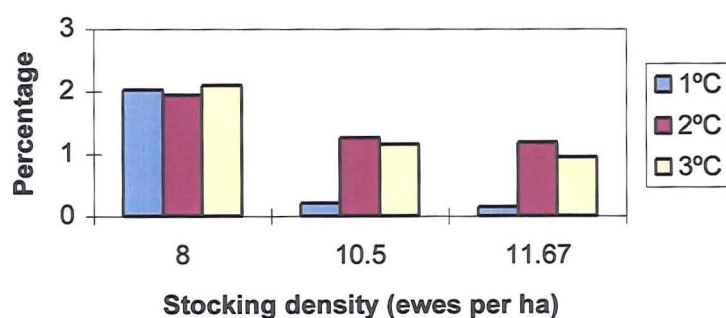


Figure 6-25 The change in the percentage of paddocks harvested throughout the season per degree increase in temperature for the grass – white clover based sheep enterprise at current and elevated CO<sub>2</sub> concentrations

Increasing the stocking density reduced the percentage of paddocks harvested (see Table 6-25), although the magnitude differed between sites for the sheep system. For the sheep enterprise, the change in the paddocks harvested per degree increase in temperature was approximately linear, at a stocking density of 8 ewes ha<sup>-1</sup>, as shown in Figure 6-26. However, this was not the case at the higher stocking densities.

*Table 6-25 The change in the percentage of paddocks harvested with increased stocking density relative to the base stocking density for all enterprises grazing on a grass – white clover based system*

Enterprise		Change in percentage of paddocks harvested	
		medium stocking density	high stocking density
Dairy		-5.4	-10.4
Beef		-3.7	-7.4
Sheep	Auchincruive	-11.3	16.1
	Blyth Bridge	-9.2	-12.8
	Craibstone	-10.0	-13.7
	Drummond Castle	-9.3	-14.0
	Wick	-10.4	-16.4



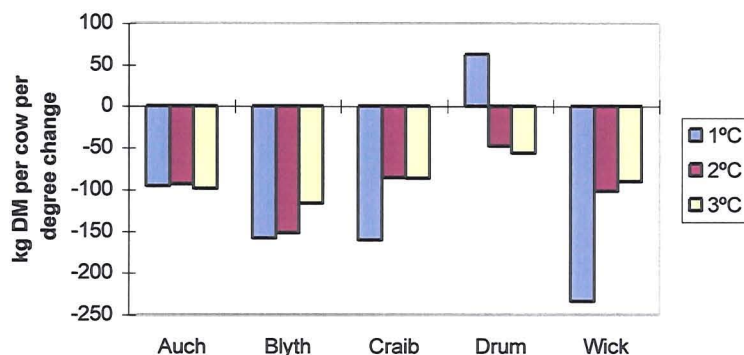
*Figure 6-26 The change in the percentage of paddocks harvested per degree increase in temperature relative to the current temperature scenario for each stocking density*

#### **6.4.1.5 Total Yield Per Head**

##### **6.4.1.5.1 Grass – Based Enterprises**

The total dry-matter yield per head from the grass – based system was significantly affected by rainfall pattern and interactions between site and temperature and CO<sub>2</sub> and stocking rate for all enterprises. In addition, the site \* CO<sub>2</sub> and site \* stocking rate effects were significant for the dairy and sheep enterprises. The global warming rainfall pattern resulted in the total yield harvested increasing by 86.2 kg DM cow<sup>-1</sup>, 60.4 kg DM steer<sup>-1</sup> and 14.5 kg DM ewe<sup>-1</sup>. Except for a temperature rise of 1°C at Drummond Castle, increasing the temperature reduced the yield for all enterprises, which corresponds to the pattern observed for the cut swards (see Figure 6-5). A similar pattern to that illustrated for the dairy enterprise (see Figure 6-27) was also predicted for the beef and sheep enterprises, although the magnitude of the absolute changes differed. Nevertheless, the percentage changes in dry-matter yield per head for the dairy, beef and sheep enterprises were of a similar magnitude ranging from -18.4—3.4%, -15.0—2.5% and -17.3—7.5% per degree increase in temperature respectively. Elevating the concentration of CO<sub>2</sub> increased the total yield, whereas increasing the stocking density reduced the total yield (see Table 6-26). Consequently, for all enterprises increasing the CO<sub>2</sub> levels at the highest stocking density resulted in a lower yield than the lowest stocking density at current concentrations of CO<sub>2</sub> (see Table 6-26). This was also the case for the medium stocking density for the sheep enterprise. At all sites for the dairy and sheep enterprises increasing the stocking rate decreased the yield per head (see Table 6-27). On the other hand, increasing the ambient concentration of CO<sub>2</sub> increased the yield by between 40.2% at Craibstone and 46.0% at Auchincruive for the dairy

enterprise, while for the sheep enterprise the range was from 42.0% at Drummond Castle to 60.5% at Wick.



*Figure 6-27 The change in the total dry-matter yield per cow per degree increase in temperature at each site for the dairy enterprise on the grass – based systems*

*Table 6-26 The change in the total dry-matter yield per head at current and elevated concentrations of CO<sub>2</sub> for all grass – based enterprises*

Enterprise	CO <sub>2</sub> Concentration (ppmv)	Change in the total dry-matter yield (kg DM head <sup>-1</sup> )		
		Low	Medium	High
Dairy	350		-290.0	-505.6
	520	634.9	234.4	-76.1
Beef	350		-221.0	-401.1
	520	416.2	153.0	-64.4
Sheep	350		-126.4	-167.8
	520	96.7	-47.5	-97.6

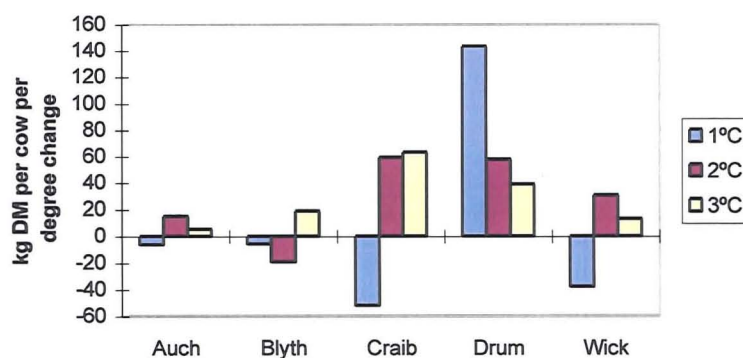
*Table 6-27 The change in total yield per head relative to the base stocking density for the dairy and sheep enterprises grazing on a grass – based system*

Enterprise	Site	Change in the total dry-matter yield per head (kg DM head <sup>-1</sup> )	
		Medium	High
Dairy	Auchincruive	-349.8	-593.4
	Blyth Bridge	-381.6	-664.0
	Craibstone	-354.0	-631.0
	Drummond Castle	-394.5	-709.8
	Wick	-246.3	-443.3
Sheep	Auchincruive	-132.0	-181.5
	Blyth Bridge	-139.8	-184.1
	Craibstone	-143.7	-192.5
	Drummond Castle	-143.0	-193.6
	Wick	-118.0	-153.6

#### **6.4.1.5.2 Grass – White Clover Based Enterprises**

The harvested dry-matter yield from the grass – white clover based systems was significantly affected by rainfall pattern for all enterprises. The interactions that were significant for the dairy, beef and sheep enterprises were between site and temperature, site and CO<sub>2</sub> level, site and stocking rate and CO<sub>2</sub> level and stocking rate. In addition the interaction between temperature and CO<sub>2</sub> level was significant for the sheep enterprise. Under the rainfall pattern associated with global warming, the

total dry-matter yield per head for the dairy, beef and sheep enterprises was increased by 7.1%, 6.9% and 6.8% respectively. The direction and magnitude of the change per head were dependent on site and enterprise (see Figure 6-28—Figure 6-30). Increasing the stocking density at all sites for all enterprises decreased the yield per head (see Table 6-28), although increasing the CO<sub>2</sub> concentration resulted in an increase in the yield (see Table 6-29). However, the increase varied substantially between sites. At all stocking densities, increasing the level of CO<sub>2</sub> enhanced the yield harvested (see Table 6-30). Nonetheless, only at the medium stocking density for the dairy enterprise did the effect of increasing the CO<sub>2</sub> concentration mitigate the effect of increasing the stocking density from the base level. For the sheep enterprise the effect of enhanced CO<sub>2</sub> levels per degree of temperature increase was reduced as temperature increased (see Figure 6-31). Increasing the ambient concentration of CO<sub>2</sub> at current temperatures resulted in the yield per ewe increasing by 35%.



*Figure 6-28 The change in the total dry-matter yield per cow per degree increase in temperature at each site for the dairy enterprise on the grass – white clover based systems*

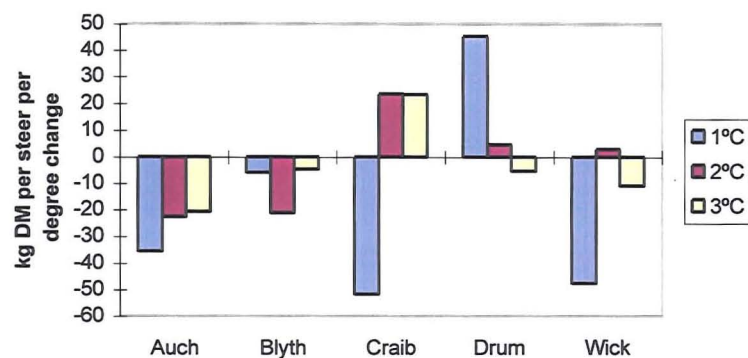


Figure 6-29 The change in the total dry-matter yield per steer per degree increase in temperature at each site for the beef enterprise on the grass – white clover based systems

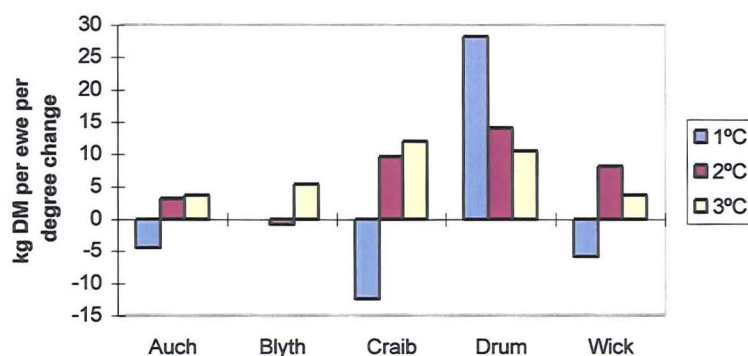


Figure 6-30 The change in the total dry-matter yield per ewe per degree increase in temperature at each site for the sheep enterprise on the grass – white clover based systems

*Table 6-28 Effect of change in stocking rate on the percentage change in total dry-matter yield per head relative to the base stocking density for the dairy, beef and sheep enterprises grazing on a grass – white clover based system*

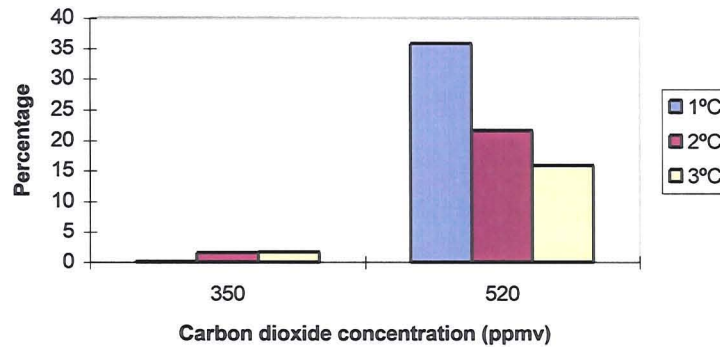
Enterprise	Site	Change in the total dry-matter yield per head (%)	
		Medium Stocking Rate	High Stocking Rate
Dairy	Auchincruive	-18.0	-32.3
	Blyth Bridge	-19.4	-33.8
	Craibstone	-19.6	-34.4
	Drummond Castle	-18.1	-32.3
	Wick	-21.6	-37.9
Beef	Auchincruive	-15.4	-27.0
	Blyth Bridge	-15.0	-27.0
	Craibstone	-15.8	-27.5
	Drummond Castle	-14.8	-26.8
	Wick	-16.1	-29.3
Sheep	Auchincruive	-39.0	-51.1
	Blyth Bridge	-37.3	-48.5
	Craibstone	-38.2	-49.8
	Drummond Castle	-37.3	-49.0
	Wick	-40.3	-53.5

**Table 6-29** *Effect of change in CO<sub>2</sub> concentration on the percentage change in total dry-matter yield per head relative to the current CO<sub>2</sub> concentrations for all enterprises grazing on a grass – white clover based system for each site*

Site	Change in the total dry-matter yield per head (%)		
	Dairy	Beef	Sheep
Auchincruive	39.7	32.2	40.1
Blyth Bridge	39.9	30.0	35.0
Craibstone	38.5	30.6	34.5
Drummond Castle	36.9	29.3	36.3
Wick	52.1	34.6	44.5

**Table 6-30** *Effect of changes in stocking rate and CO<sub>2</sub> concentration on the change in the total yield per head at current and elevated concentrations of CO<sub>2</sub> for all grass – white clover based enterprises*

Enterprise	CO <sub>2</sub> Concentration (ppmv)	Change in the total dry-matter yield (%)		
		Low	Medium	High
Dairy	350		-20.4	-35.7
	520	37.4	12.3	-7.2
Beef	350		-15.7	-27.8
	520	30.4	10.7	-4.9
Sheep	350		-39.7	-51.5
	520	34.5	-15.6	-31.6



*Figure 6-31 The percentage change in the total dry-matter yield per ewe per degree increase in temperature for current and elevated CO<sub>2</sub> concentrations for the sheep enterprise on the grass – white clover based systems*

The percentage of white clover in the harvested yield was significantly affected by rainfall pattern and an interaction between site and temperature for all enterprises. The CO<sub>2</sub> concentration was also significant for the dairy and beef enterprises, while stocking rate had a significant effect on the percentage of white clover in the beef enterprise. The rainfall pattern increased the percentage of white clover by 1.36%, 1.44% and 1.93% for the dairy, beef and sheep enterprises respectively. Except for a 1°C rise at Auchincruive and Drummond Castle, increasing the temperature increased the percentage of white clover in the sward, as illustrated for the dairy enterprise in Figure 6-32. The pattern of the results for the beef and sheep enterprises was similar, although the change per degree increase in temperature for a 1°C rise at Drummond Castle for the beef enterprise was close to zero. The effect of increasing the CO<sub>2</sub> levels resulted in the percentage increasing by 0.59% for the dairy system and by 0.68% for the beef system. On the other hand, the percentage was reduced by between 0.48% and 0.52% for an increase of 0.33 steers ha<sup>-1</sup>.

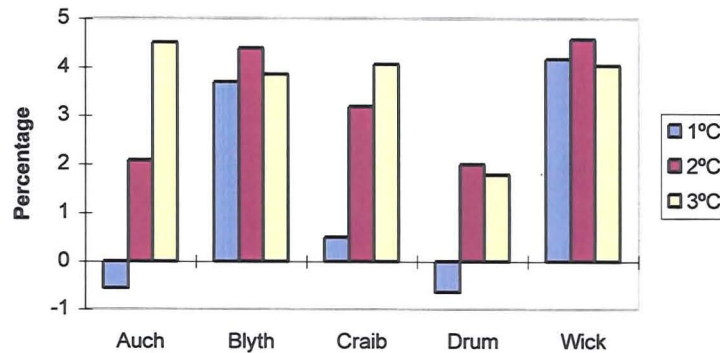


Figure 6-32 The change in the percentage of white clover in the harvested yield per degree increase in temperature at each site for the dairy enterprise

## 6.5 Animal Production

### 6.5.1 Dairy Farming

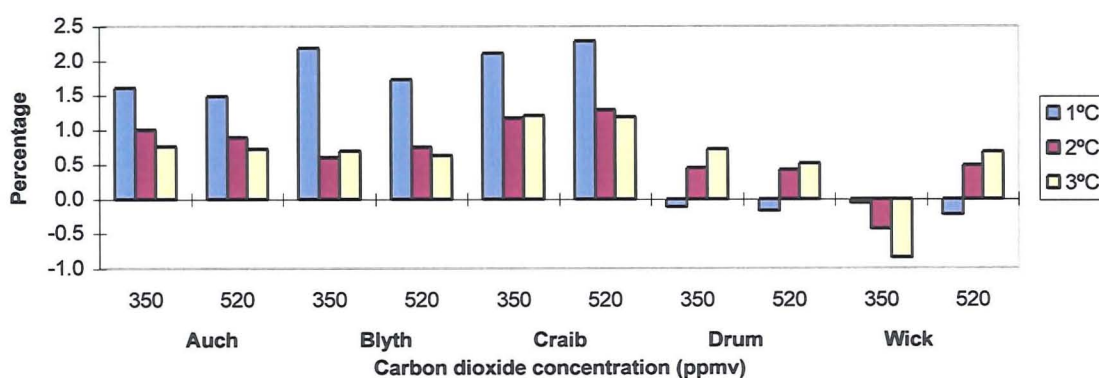
#### 6.5.1.1 Grass – Based Systems

The milk yield per dairy cow grazing on a grass sward was affected by rainfall pattern and interactions between site and stocking rate, CO<sub>2</sub> concentration and stocking rate, and site, temperature and CO<sub>2</sub> concentration. The global warming rainfall pattern increased the yield per day by 0.51%. However, increasing the stocking rate reduced the milk yield, although the rate of decrease differed between sites (see Table 6-31). The milk yield tended to be increased with elevated temperatures and augmented CO<sub>2</sub> levels (see Figure 6-33). Nevertheless, at Drummond Castle the yield was decreased for temperature scenario 1 at current CO<sub>2</sub> levels and for temperature scenario 1 at elevated CO<sub>2</sub> concentrations. A similar pattern was observed at Wick, but in this case the milk yield was only increased when the temperature was elevated by 2°C or 3°C at a CO<sub>2</sub> concentration of 520 ppmv. At current temperatures increasing the ambient concentration of CO<sub>2</sub> changed the milk yield between -1.03% at Wick to +0.23% at

Blyth Bridge. Increasing the CO<sub>2</sub> concentration at the medium and high stocking density reduced the decrease in the milk yield that occurred, compared to the low stocking rate at current concentrations of CO<sub>2</sub> (see Table 6-32). However, at the low stocking rate increasing the CO<sub>2</sub> concentration resulted in a decrease in the yield.

*Table 6-31 The percentage change in the milk yield for the dairy herd grazing a grass – based system for each site*

Site	Percentage change in the milk yield per day	
	Medium	High
Auchincruive	-0.17	-0.56
Blyth Bridge	-0.29	-0.51
Craibstone	-0.29	-0.69
Drummond Castle	-0.17	-0.34
Wick	-0.91	-1.76



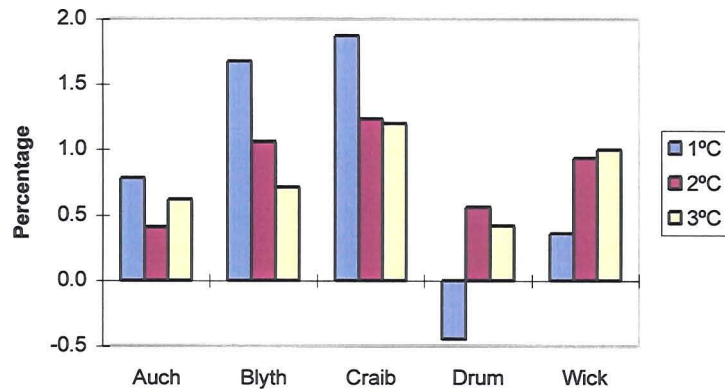
*Figure 6-33 The percentage change in the daily milk yield per degree increase in temperature at each level of CO<sub>2</sub> concentration for each site*

*Table 6-32 The percentage change in the daily milk yield per head at current and elevated concentrations of CO<sub>2</sub> at all stocking densities grazing a grass – white clover sward*

CO <sub>2</sub> Concentration (ppmv)	Percentage change in the milk yield (%)		
	Low	Medium	High
350		-0.57	-1.25
520	-0.28	-0.40	-0.57

#### **6.5.1.2 Grass – White Clover Based Systems**

In the case of the dairy herd grazing the grass – white clover sward the significant factors were rainfall pattern, stocking rate and CO<sub>2</sub> levels. There was also a significant interaction between site and temperature. As with the grass – based system, changing to a global warming rainfall pattern increased the daily milk yield by 1.12%. The effect of increasing the atmospheric CO<sub>2</sub> levels resulted in an increase of 0.89%. On the other hand, increasing the stocking density from 1.68 cows ha<sup>-1</sup> to 1.89 cows ha<sup>-1</sup> reduced the milk yield by 0.33%. The milk yield was reduced by 0.82% when the stocking density was increased from 1.68 cows ha<sup>-1</sup> to 2.1 cows ha<sup>-1</sup>. Except for a 1°C rise in temperature at Drummond Castle, increasing the temperature increased the milk yield, although the effect per degree of temperature increase was not linear (see Figure 6-34).

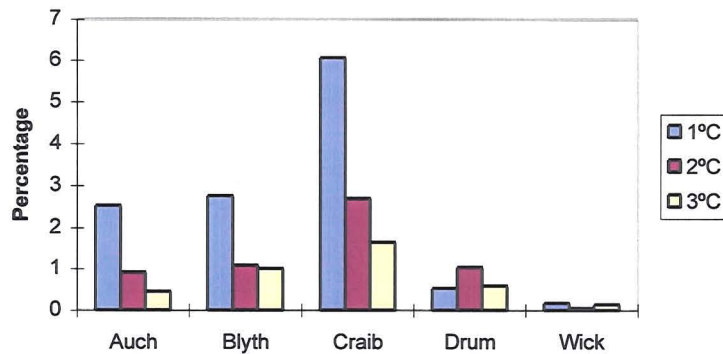


*Figure 6-34 The percentage change in the daily milk yield per degree increase in temperature for each site*

## 6.5.2 Beef Production

### 6.5.2.1 Grass – Based Systems

For the grass – based beef enterprise, the daily gain in liveweight of the steers was significantly affected by the rainfall pattern, CO<sub>2</sub> concentration, stocking rate and the interaction between site and temperature. Increasing the stocking rate from 3.08 steers ha<sup>-1</sup> to 3.46 steers ha<sup>-1</sup> and from 3.08 steers ha<sup>-1</sup> to 3.85 steers ha<sup>-1</sup> reduced the daily gain in liveweight by -0.65% and -1.45% respectively. On the other hand increasing the CO<sub>2</sub> concentration increased the daily gain by 2.31%, while changing to a global warming rainfall pattern resulted in an increase of 0.79%. The percentage increase in the daily gain varied between sites, and at four of the five sites the increase per degree was greatest when the temperature was increased by 1°C (see Figure 6-35).



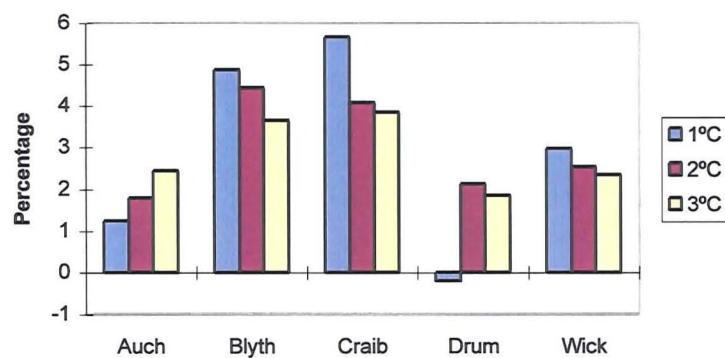
*Figure 6-35 The percentage change in the liveweight gain per day per degree increase in temperature at each site for a grass – based beef system*

#### **6.5.2.2 Grass – White Clover Based Systems**

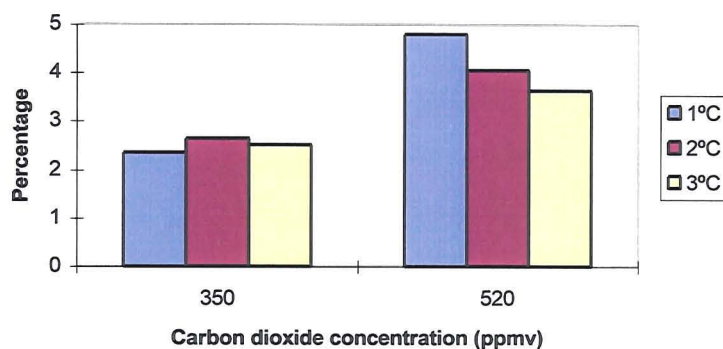
On grass – white clover based systems the factors that were significant were rainfall pattern and the interactions between site and temperature, site and CO<sub>2</sub> level, temperature and CO<sub>2</sub> level and CO<sub>2</sub> level and stocking density. The global warming rainfall pattern increased the daily gain by 1.45%. Similarly, the effect of elevating the CO<sub>2</sub> conditions to 520 ppmv increased the daily gain but the percentage enhancement differed between sites (see Table 6-33). At current temperatures increasing the CO<sub>2</sub> concentration increased the percentage daily gain by 1.4%. Except for a 1°C increase at Drummond Castle, daily gain was increased with temperature (see Figure 6-36). Nevertheless, the effect was not linear with temperature. The effect of temperature on daily gain at current concentrations of CO<sub>2</sub> was similar for each degree increase (see Figure 6-37). However, this was not the case at CO<sub>2</sub> concentrations of 520 ppmv. At both current and elevated CO<sub>2</sub> concentrations increasing the stocking rate reduced the percentage gain (see Table 6-34). However, at elevated CO<sub>2</sub> levels the daily gain was higher than at the lowest stocking density for current CO<sub>2</sub> levels (see Table 6-34).

*Table 6-33 The percentage change in the daily gain of the beef steer with elevated concentrations of CO<sub>2</sub> at each site*

CO <sub>2</sub> Concentration (ppmv)	Percentage change in the liveweight (%)				
	Auch	Blyth	Craib	Drum	Wick
520	2.46	1.91	1.47	0.84	5.66



*Figure 6-36 The percentage change in the liveweight gain per day per degree increase in temperature at each site for a grass – white clover based beef system*



*Figure 6-37 The percentage change in the liveweight gain per day per degree increase in temperature at each CO<sub>2</sub> level for a grass – white clover based beef system*

*Table 6-34 The percentage change in the liveweight daily gain of the steer at current and elevated concentrations of CO<sub>2</sub> at all stocking densities for a grass – white clover based beef enterprise*

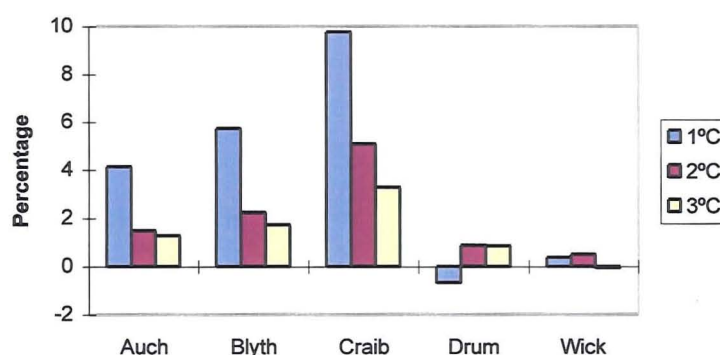
CO <sub>2</sub> Concentration (ppmv)	Percentage change in the liveweight (%)		
	Low	Medium	High
350		-1.39	-3.12
520	1.45	0.90	0.26

### 6.5.3 Sheep Production

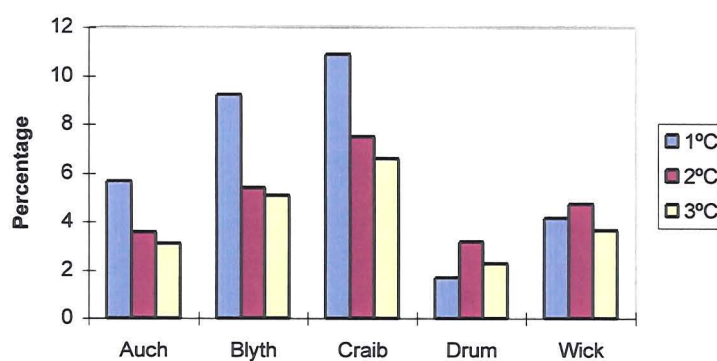
#### 6.5.3.1 Liveweight of Lambs on Grass and Grass – White Clover Based Systems

The daily gain in liveweight of lambs reared on grass and grass – white clover based systems was significantly affected by rainfall pattern and the interactions between site and temperature and site and CO<sub>2</sub> level. In the case of the grass – white clover sward stocking rate was also significant. The effect of rainfall was to increase the daily

liveweight gain by 1.07% and 2.17% for grass and grass – white clover systems respectively. The percentage increase per degree increase in temperature was higher for the grass – white clover swards (see Figure 6-39) than the pure grass (see Figure 6-38). However, a 1°C increase at Drummond Castle and a 3°C increase at Wick for the grass – based system actually reduced the daily gain in liveweight. The percentage increase with elevated CO<sub>2</sub> levels was greater for the grass – white clover swards than for the pure grass swards (see Table 6-35). The daily weight gain of lambs grazing the grass – white clover pasture was reduced by 2.63% as stocking rate was increased from the low to the medium rate. The comparable figure for increasing from the low to the high rate was a reduction of 3.28%.



*Figure 6-38 The percentage change in the liveweight gain per day per degree increase in temperature at each site for a grass – based sheep system*



*Figure 6-39 The percentage change in the liveweight gain per day per degree increase in temperature at each site for a grass – white clover based sheep system*

*Table 6-35 The percentage change in the daily gain of the lamb with elevated concentrations of CO<sub>2</sub> at each site for the grass and the grass – white clover based system*

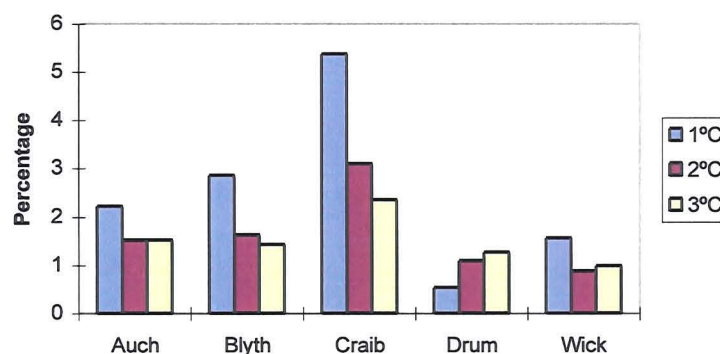
Sward	Percentage change in the liveweight with elevated CO <sub>2</sub> (%)				
	Auch	Blyth	Craib	Drum	Wick
Grass	6.46	6.82	5.42	5.64	11.81
Grass – white clover	11.67	9.75	10.47	7.48	18.54

### **6.5.3.2 Liveweight of Ewes on Grass and Grass – White Clover Based Systems**

The liveweight of the ewe was significantly affected by the two-way interaction of site with temperature for both the grass and grass – white clover based systems. In the grass – based system, the interaction between site, CO<sub>2</sub> and stocking density, and temperature and stocking density were also significant. The other factors that were significant for the grass – white clover system was the interactions of CO<sub>2</sub> and

stocking density with site, and the interaction between stocking density and CO<sub>2</sub> level. The rainfall factor was also significant for the grass – white clover based enterprise.

The ewe liveweight for the grass – based system increased with temperature at all sites, although the magnitude differed between sites (see Figure 6-40). Increasing the stocking rate increased the liveweight of the ewe at each site (see Figure 6-41). At elevated CO<sub>2</sub> concentrations increasing the stocking level increased the percentage change. Nevertheless, except for the highest stocking density at Wick, the increase with stocking density was greater at current concentrations of CO<sub>2</sub> (see Figure 6-41). At elevated temperatures increasing the stocking rate was associated with enhanced liveweight of the ewe (see Figure 6-42).



*Figure 6-40 The percentage change in the liveweight of the ewe per degree increase in temperature at each site for a grass – based sheep system*

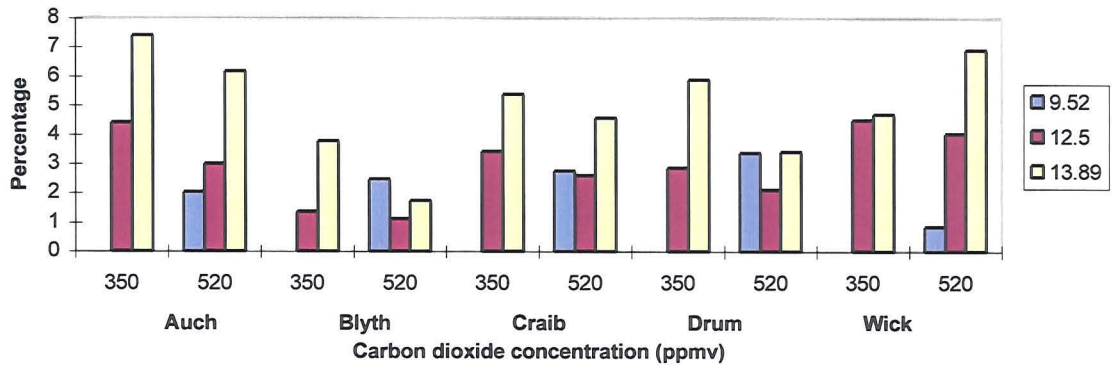


Figure 6-41 The percentage change in the liveweight of the ewe for each stocking density at current and elevated CO<sub>2</sub> level at each site for a grass – based sheep system

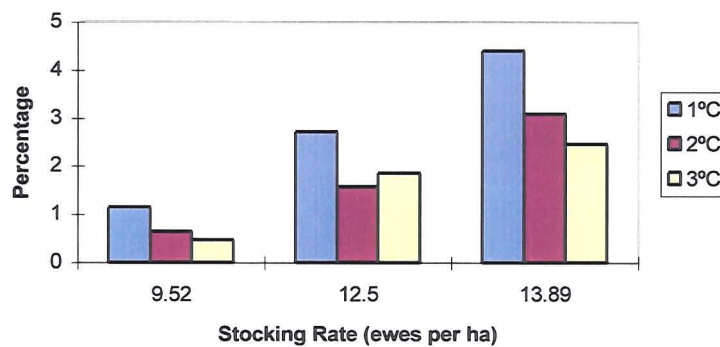
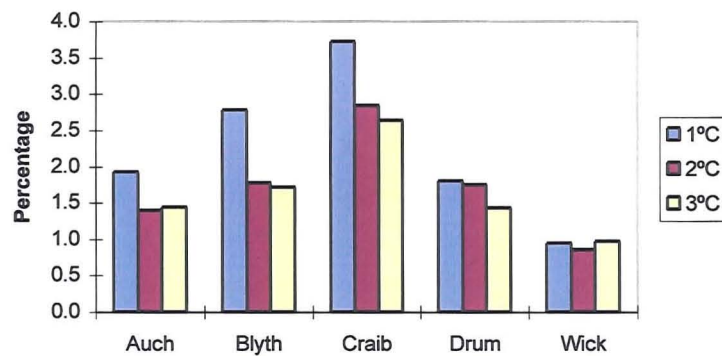


Figure 6-42 The percentage change in the liveweight of the ewe per degree increase in temperature at each stocking density for a grass – based sheep system

Changing to a global warming rainfall pattern on grass – white clover sward increased the liveweight of the ewe by 0.52%. The liveweight was also increased by increasing temperatures at each site (see Figure 6-43). In contrast to the ewes grazing the pure grass swards, increasing the stocking rate tended to decrease the liveweight (see Table 6-36). Nevertheless, the magnitude of the reduction was decreased as the stocking density was increased and the ewe liveweight was actually increased for the

Craibstone and Wick sites. Increasing the ambient concentration  $\text{CO}_2$  also increased the liveweight at all sites (see Table 6-37). However, as stocking rate increased the reduction in liveweight was increased, although the difference compared to the lowest stocking rate at ambient concentrations of  $\text{CO}_2$  was reduced by elevating the  $\text{CO}_2$  levels (see Table 6-38).



*Figure 6-43 The percentage change in the liveweight of the ewe per degree increase in temperature at each site for a grass - white clover based sheep system*

*Table 6-36 The percentage change in the liveweight of the ewe at each site for the medium and high stocking densities on a grass – white clover based system for each site*

Site	Percentage change in the liveweight of the ewes	
	From 8 to 10.5 ewes ha <sup>-1</sup>	From 10.5 to 11.67 ewes ha <sup>-1</sup>
Auchincruive	-5.62	-0.26
Blyth Bridge	-5.03	-0.45
Craibstone	-5.05	0.44
Drummond Castle	-5.90	-0.78
Wick	-1.29	1.02

*Table 6-37 The percentage change in the liveweight of the ewe with elevated concentrations of CO<sub>2</sub> at each site*

CO <sub>2</sub> Concentration (ppmv)	Percentage change in the liveweight (%)				
	Auch	Blyth	Craib	Drum	Wick
520	4.24	3.35	4.08	3.57	2.41

*Table 6-38 The percentage change in the liveweight of the ewe at current and elevated concentrations of CO<sub>2</sub> at all stocking densities for a grass – white clover based sheep enterprise*

CO <sub>2</sub> Concentration  (ppmv)	Percentage change in the liveweight (%)		
	Low	Medium	High
350		-3.38	-2.96
520	5.58	-0.55	-0.99

## 6.6 Conclusions

The consequences of global warming for livestock production occur primarily through its effect on forage production. Relative to current climatic conditions the enhancement in harvestable yield range from 20% to nearly 60% and the percentage of white clover in the harvested material can increase by up to 126%. Equally, the model has shown that livestock production can also be enhanced. Thus, the increase in milk production, and the daily gains in liveweight for the beef steers and lambs range from 3%—13%, 1%—12%, and 4%—28% respectively. The larger increases tend to occur on grass – white clover swards. However, the increases in harvestable forage yield per livestock unit on grass swards with enhanced CO<sub>2</sub> concentration diminish with temperature. In contrast, the effect of CO<sub>2</sub> concentrations on the yield obtained from grass – white clover swards tend to increase marginally with temperature.

The increased length of the grazing season for both grass and grass – white clover swards will reduce the need for winter forage, although global warming appears to

increase the production of silage. This may reduce the requirement for concentrate feeding for livestock production, especially for the beef and sheep systems. As the yields from the grass – white clover swards under global warming are similar to those obtained from grass – based systems under current conditions there may be a switch from grass – based systems to mixed grass – legume production. This would have the added benefit of reducing fertiliser nitrogen inputs into the system which may result in environmental benefits. Nevertheless, the environmental consequences of fertiliser nitrogen and nitrogen fixed by the white clover have not been included in the model. Similarly, a switch to grass – white clover swards coupled with the increase in the percentage of white clover in the harvested material would be expected to increase livestock production during the winter feeding period. This is due to white clover having a higher nutritive value than grass and it also tends to stimulate herbage intake (Thomson, 1984). This may again reduce the quantity of concentrates that are required during the winter period. Nevertheless, the model simulations have not been extended to cover the winter period, so the effects of global warming on livestock production during this period remain a matter for inference.

The enterprise with the most benefits from global warming is the sheep system, and therefore farmers may switch to sheep production from other livestock enterprises. There will also be a tendency for the production from all the livestock enterprises to increase so that there will tend to be an increase in the quantity of the products available for sale. This could lead to declining product prices, although reduced costs through reduced use of purchased feed and fertilisers may be sufficient for farm profitability to be maintained. However, this economic consequence has not been explored. In Chapter 7 the effect of global warming on livestock production in relation

to the hypothesis outlined in Chapter 1, and the effects that climate change will have on livestock production in Scotland will be discussed.

## **CHAPTER 7**

### ***DISCUSSION***

#### ***7.1 Introduction***

This chapter will discuss the results analysed in Chapter 6 against the background of the original hypotheses outlined in Chapter 1. In particular it will draw together the findings in order to ascertain the effects of global warming on Scottish livestock production. This chapter will then outline the consequences of global warming for livestock production, further developments of the model that could be made and the advancement to knowledge made by the model.

#### ***7.2 Hypothesis One: The Effect of Temperature on the Length of the Growing Season***

This hypothesis recognises that temperature has an impact on when the herbage mass in the paddocks starts to grow in the spring and when growth ceases in the winter. It states that the growing season will be lengthened by increases in the annual average temperature. Although it must be recognised that temperature controls the period of growth in the forage model, the results for both the grass and white clover components indicated that the length of the growing season was increased (see Figure 6-4). However, for the grass component the effect differed between sites and the effect was not a linear function of rising temperature (see Figure 6-4). The increase in the length of the growing season was between 15.6 and 25.6 days per degree increase for an overall increase of 3°C in temperature. The range was

reduced to 16.8 to 20.5 per degree increase for the 1°C and 2°C elevation in temperature. On the other hand, the effect on the length of the growing season for the white clover component was approximately linear with the increase of between 18.8 and 19.1 days per degree increase in temperature. These results are in broad agreement with the results of Flohn (1985), who stated that, in high latitudes, a 1°C change in the global mean air temperature could change the length of the growing season by three to four weeks. However, the results suggest that the change would be slightly less. In contrast, Hanson *et al.* (1993) predicted that the length of the growing season would increase in the Great Plains of America by about 30 days with mean annual temperature enhancements of 4.9°C—6.3°C. Nevertheless, it must be recognised that the effect on length of the growing season is due to both an earlier commencement and a later cessation of growth. The commencement of growth for both the grass and white clover components differed between sites, while cessation of growth did not differ across the five locations.

### **7.3 Hypothesis Two: The Effect of Global Warming on Forage Production**

The second hypothesis states that increases in CO<sub>2</sub>, rises in temperature, and anticipated changes in the rainfall pattern will all combine to increase the harvestable dry-matter yield from both the grass and grass – white clover swards.

#### **7.3.1 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>**

With the exception of the first-cut white clover yield, the yield of all the cuts for both the grass and grass – white clover swards were enhanced by elevated CO<sub>2</sub>. Similarly, the experiments of Schenk *et al.* (1997a), Jones *et al.* (1996a), Jones *et al.* (1996b) and

Schapendonk *et al.* (1996), Casella *et al.* (1996), Schenk *et al.* (1995), Nijs *et al.* (1989a) for grass showed that yield was increased when the ambient concentration of CO<sub>2</sub> was increased. Evidence from the model predictions of Thornley and Cannell (1997) also suggests that increasing the ambient CO<sub>2</sub> will increase herbage mass production. This also occurred with white clover stands (Schenk *et al.*, 1997a, Schenk *et al.*, 1995; Ryle and Powell, 1992) and mixed swards (Schenk *et al.*, 1997a, Hardacre *et al.*, 1986). The level of increase under enhanced CO<sub>2</sub> conditions is also in a similar range to the predictions of Kimball (1983), who stated that the average increase in yield for C<sub>3</sub> crops would be 33% as CO<sub>2</sub> concentrations increased from 330 ppmv to 660 ppmv. In contrast, the model of Hanson *et al.* (1993) predicted no change in yield under enhanced CO<sub>2</sub>. Similarly, Newton *et al.* (1995) observed little change in the yield from mixed swards when the CO<sub>2</sub> concentration was elevated. Nevertheless, the effect on the predicted yield varied throughout the season, as also occurred in experiments (Casella *et al.*, 1996; Jones *et al.*, 1996a; Schapendonk *et al.*, 1996). In contrast to Schenk *et al.* (1997a) and Hardacre *et al.* (1986), the percentage increase in total yield was similar for the grass and the grass – white clover swards. Nevertheless, the magnitude of the increase was less for the mixed swards as the harvestable yield under current conditions is greater for pure grass swards.

The prime reason for the increased yield with elevated CO<sub>2</sub> concentration is due to the augmenting effect that the enhanced levels have on the rate of photosynthesis (Ryle *et al.*, 1992a; Ryle *et al.*, 1992b; Nijs *et al.*, 1989a, Nijs *et al.*, 1989b). However, the augmentation effect is greater for the rate of photosynthesis than dry-matter production (Nijs *et al.*, 1989a). Nevertheless, acclimation can occur (Ryle *et al.*,

1992a; Jones *et al.*, 1996b; Casella and Soussana, 1997) and so reduce the effect of the enhanced concentration of CO<sub>2</sub>. But this consequence has not been observed in mixed swards (Newton *et al.*, 1996) and does not always occur for pure grass swards (Jones *et al.*, 1996a).

### **7.3.2 Effect of Increasing the Temperature on Yield**

Contrary to expectations, the effect of increasing the average daily temperature reduced the harvestable dry-matter yield for all cuts from the pure grass sward (see Figure 6-5). Nevertheless, there is experimental evidence for this phenomenon (Nijs and Impens, 1996; Nijs and Impens, 1997). The model developed by Thornley and Cannell (1997) also predicts that the production of grass will decline with increased ambient temperatures, although Armstrong's (1996) model predicts increased yields. In contrast, the total dry-matter yield harvested from the grass – white clover sward was enhanced with elevated temperatures, although a 1°C increase did reduce the yield from the second cut. Elevating the daily temperature, below the optimum temperature for the process, increased the rates of photosynthesis and respiration. The rate of transpiration will also increase under elevated temperatures, which may increase the stress experienced by the plant and hence decrease the rate of dry-matter production. Consequently, the net effect on the dry-matter yield can either be an increase or a decrease depending on the balance of the processes. Casella *et al.* (1996) observed no change in the harvested yield obtained with increased temperature during the summer months in France and decreases in yield have also been reported (Nijs and Impens, 1996; Nijs and Impens, 1997). Furthermore, there is no evidence of changes in temperature at current ambient concentrations of CO<sub>2</sub>

increasing yield. In contrast, the reduction in yield that can occur with elevated concentrations of CO<sub>2</sub> can be reduced when the ambient temperature is elevated (Nijs and Impens, 1996), but it must be recognised that the opposite effect can also occur (Nijs and Impens, 1997).

### **7.3.3 Effect of Changing to a Global Warming Rainfall Pattern**

The importance of the rainfall pattern is noted by Ojima, Parton, Schimel, Scurlock and Kittel (1993) who showed that their predictions of forage production across seven ecoregions for climate change without enhanced ambient CO<sub>2</sub> conditions were correlated to the changes in rainfall. The model simulation predicted that the effect of changing the rainfall pattern to one associated with global warming was to increase the dry-matter yield of all cuts from the grass and the grass – white clover swards. The yield enhancement for the pure grass swards was similar for all cuts (see Table 6-5). In contrast, the enhancement for the grass – white clover sward was higher for the second cut than the first (see Table 6-6). Although, the enhancement for the grass component was lower (2.2%—2.4%) than that observed for the pure grass swards (2.8% —3.0%), the increase in the white clover yield was much higher (9.3%—13.7%). As the daily rainfall on rainy days is increased, except for August and September, under the global warming rainfall pattern, the harvestable yield is increased as the stress experienced by the crop is reduced. Although increasing the ambient concentration of CO<sub>2</sub> reduces the stomatal conductance and hence the rate of transpiration, this effect is not included in the model of forage production (Ryle *et al.*, 1992a; Ryle *et al.*, 1992b; Nijs *et al.*, 1989b). Consequently, the effect of changing the

rainfall pattern under enhanced ambient concentrations of CO<sub>2</sub> is likely to understate the change in yield.

#### **7.3.4 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>, Temperature and Changing to a Global Warming Rainfall Pattern**

The effect of increasing the ambient concentration of CO<sub>2</sub> coupled with changing to the rainfall pattern associated with global warming resulted in the dry-matter yield from the grass sward increasing (see Table 7-1). The increase in the ambient concentration of CO<sub>2</sub> resulted in enhancement of the yield relative to only changing the weather variables. This is a result that was also reported by Ojima *et al.* (1993). Nevertheless, the rate of increase declined as the temperature increased. Similarly, Thornley and Cannell (1997) observed that the enhancement in production resulting from elevated CO<sub>2</sub> levels was reduced as the ambient temperature increased. Equally, the enhancement in dry-matter yield of the grass component from the mixed sward also tended to decline with increases in temperature (see Table 7-2). On the other hand, the white clover and the combined yields increased with increases in temperature. There is experimental evidence for increases in ambient temperature coupled with elevated CO<sub>2</sub> levels both increasing (Nijs and Impens, 1996) and decreasing (Nijs and Impens, 1997) the yield of perennial ryegrass compared to that obtained when only the CO<sub>2</sub> conditions were enhanced. Nevertheless, Nijs and Impens (1996) reported a decrease in yield when the temperature was elevated by 4°C and the atmospheric concentration of CO<sub>2</sub> was enhanced.

**Table 7-1**    *The percentage increase in dry-matter yield for the elevated CO<sub>2</sub> levels and the global warming rainfall pattern relative to current conditions for the grass sward*

Cut	Percentage Change			
	0°C	1°C	2°C	3°C
1 <sup>st</sup>	21.0	19.1	14.6	11.7
2 <sup>nd</sup>	28.3	23.6	19.1	15.2
Total	23.9	20.9	16.4	13.1

*Table 7-2 The percentage increase in dry-matter yield for the elevated CO<sub>2</sub> levels and the global warming rainfall pattern relative to current conditions for the grass – white clover sward*

Component	Cut	Percentage Change			
		0°C	1°C	2°C	3°C
Grass	1 <sup>st</sup>	21.0	22.7	14.4	4.6
	2 <sup>nd</sup>	37.8	30.9	17.6	2.5
	Total	25.6	24.9	15.3	4.0
White clover	1 <sup>st</sup>	29.5	58.0	131.8	203.7
	2 <sup>nd</sup>	25.0	32.4	83.3	134.0
	Total	27.2	45.3	107.7	169.1
Combined	1 <sup>st</sup>	22.1	27.3	30.0	31.0
	2 <sup>nd</sup>	34.1	31.3	36.2	39.8
	Total	25.9	28.6	31.9	33.8

#### **7.4 Hypothesis Three: The Effect of Changes in Temperature on Yield**

The third hypothesis states that the increases in annual average temperature will not result in linear changes in the yield from grass swards or the components of yield from grass – white clover swards. It recognises that many of the processes involved in plant growth have an optimum temperature.

For the pure grass swards the increases in the dry-matter yield harvested at the first cut were approximately linear for temperature increase of 2°C and 3°C with a

decrease of  $0.13 \text{ t DM ha}^{-1} \text{ }^{\circ}\text{C}^{-1}$  (see Figure 6-5). On the other hand, a temperature increase of  $1^{\circ}\text{C}$  resulted in a higher yield with a decrease of  $0.09 \text{ t DM ha}^{-1}$ . In contrast the decrease in yield for the second cut was approximately linear for all temperature increases (see Figure 6-5). The net effect on the total yield was that a  $1^{\circ}\text{C}$  increase resulted in significantly higher yield than either the  $2^{\circ}\text{C}$  or  $3^{\circ}\text{C}$  increase in temperature which had an approximately linear effect. Similarly, temperature increases of  $2^{\circ}\text{C}$  and  $3^{\circ}\text{C}$  resulted in an approximately linear increase in the combined second-cut yield harvested from the grass – white clover sward (see Figure 6-6), although the percentage increase differed by 0.5%. However, a  $1^{\circ}\text{C}$  increase resulted in a decrease in the harvested yield. Although the increase in the total yield per degree of temperature increase was approximately linear for the total combined yield, the  $2^{\circ}\text{C}$  and  $3^{\circ}\text{C}$  scenarios were +0.2% and -0.2% different respectively from the predicted change in yield for a  $1^{\circ}\text{C}$  temperature increase.

As the annual average temperature for the study sites ranged from  $7.0^{\circ}\text{C}$  at Blyth Bridge to  $8.7^{\circ}\text{C}$  at Auchincruive, it was not expected that location would significantly influence the yield. Nevertheless, the different responses of yield to increases in temperature indicate that the balance of changes that occur are effected by the response of the different processes to changes in temperature. With respect to transpiration the availability of water interacts with temperature to determine the level of stress experienced by the crop and consequently the rate of dry-matter production.

## **7.5 Hypothesis Four: The Effect of Global Warming on the Percentage of White Clover in the Sward**

The hypothesis is concerned with the effect changes in CO<sub>2</sub>, temperature, and changes in rainfall pattern will have on the proportion of white clover in the harvested yield obtained from mixed swards. The combined effects of changes in CO<sub>2</sub>, temperature and the rainfall pattern are also discussed. The hypothesis states that the percentage of white clover in the harvested material will be augmented by changes in the climatic conditions associated with global warming and elevated CO<sub>2</sub> concentrations.

### **7.5.1 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>**

Elevating the concentration of CO<sub>2</sub> resulted in the percentage of white clover harvested in the total dry-matter yield being neither increased nor decreased. This is contrary to the experimental evidence of Schenk *et al.* (1997a), Clark *et al.* (1997), Stewart and Potvin (1996), Campbell *et al.* (1995), Newton *et al.* (1995) and Newton *et al.* (1994). In particular, Clark *et al.* (1997) observed that the percentage of white clover in the sward declined as the CO<sub>2</sub> concentration was increased from 525 ppmv to 700 ppmv. Against this, Overdieck and Reining (1986) observed that the above-ground dry-matter production of white clover did not respond to enhanced concentrations of CO<sub>2</sub> after the first cut, whereas the dry-matter yield of the perennial ryegrass component from a mixed sward tended to increase with elevated CO<sub>2</sub> after this cut. Although, the first-cut grass yield and the second-cut white clover yield were significantly increased by elevated CO<sub>2</sub>, the percentage of white clover in the first cut

was increased from 19.7% to 20.6% with elevated CO<sub>2</sub>, whereas the percentage harvested in the second cut was decreased from 34.9% to 32.2%.

However, the results of Newton *et al.* (1994) and Campbell *et al.* (1995) also indicated that there was an interaction between the temperature and the ambient concentration of CO<sub>2</sub> on the dry-matter yield response and consequently the percentage of white clover in the harvested material. Against this, the model assumes that elevating the concentration of CO<sub>2</sub> influences the rate of photosynthesis of both the grass and white clover components in the same manner. Furthermore, it does not describe the effects of CO<sub>2</sub> enhancement on the rates of branching and tillering of the grass and white clover components. This may be critical, as Newton *et al.* (1995) relate the increase in the percentage of white clover in the harvested material to the effects that CO<sub>2</sub> has on the axillary buds and consequently on rates of branching and tillering.

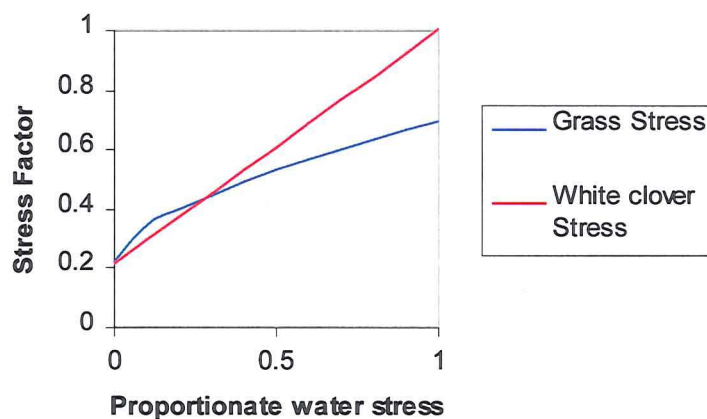
### **7.5.2 Effect of Increasing the Temperature**

In contrast to the effect of CO<sub>2</sub> on the percentage of white clover in the harvested yield, the effect of temperature was dependent on the location of the site (see Table 6-7). Nevertheless, with the exception of the Wick site, there was a general tendency for the percentage of white clover harvested in all cuts per degree of temperature increase to be enhanced as temperature was elevated. There was a tendency for the 2°C and 3°C increase to result in a similar increase per degree of temperature change in the percentage of white clover within the harvested material. In contrast, the percentage increase per degree of temperature change was enhanced as the temperature increase was elevated from +1°C to +2°C. Nevertheless, the changes in the percentage of white clover harvested were small. This tendency for the

percentage of white clover in the sward to increase as the temperature increased is evident in the experiments of Newton *et al.* (1994) and Campbell *et al.* (1995).

### 7.5.3 Effect of Changing to a Global Warming Rainfall Pattern

Changing to a global warming rainfall pattern also resulted in the percentage of white clover increasing in the harvested material (see Table 6-6). The availability of water is increased under the global warming rainfall pattern, as the rainfall is increased in ten months of the year. The percentage change is a result of the reduction in water stress having greater impact on the white clover component than the grass component (see Figure 7-1).



*Figure 7-1 The effect of water stress on the grass and white clover components at a proportionate nitrogen stress level of 0.5.*

### 7.5.4 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>, Temperature and Changing to a Global Warming Rainfall Pattern

Under all climate scenarios, the percentage of white clover in the sward increases when the temperature is elevated (see Table 7-3). On the other hand, elevating the CO<sub>2</sub> levels reduces the percentage of white clover in the sward at temperature

changes of 0°C and 1°C. Consequently, the increase in the percentage of white clover in the sward under the global warming rainfall pattern and current concentrations of CO<sub>2</sub> is mitigated when the concentration of CO<sub>2</sub> is elevated at temperature changes of 0°C and 1°C. Indeed, at temperature increases of 0°C and 1°C the global warming scenario results in a decrease in the percentage of white clover in the harvested second-cut yield.

*Table 7-3 The percentage of white clover in the sward*

Climate	Cut	Percentage			
		0°C	1°C	2°C	3°C
Ambient CO <sub>2</sub> and current rainfall	1 <sup>st</sup>	13	15	21	27
	2 <sup>nd</sup>	27	29	36	44
	Total	18	20	26	32
Ambient CO <sub>2</sub> and global warming rainfall	1 <sup>st</sup>	14	16	22	29
	2 <sup>nd</sup>	28	31	38	47
	Total	19	21	28	35
Elevated CO <sub>2</sub> and current rainfall	1 <sup>st</sup>	13	16	22	29
	2 <sup>nd</sup>	23	25	34	43
	Total	17	19	26	34
Elevated CO <sub>2</sub> and global warming rainfall	1 <sup>st</sup>	14	16	24	31
	2 <sup>nd</sup>	24	27	36	46
	Total	18	20	28	36

## ***7.6 Hypothesis Five: The Effect of Global Warming on the Length of the Grazing Season for Livestock Systems***

This hypothesis recognises that the length of the growing season is lengthened as the ambient temperature increases, and that the yield of herbage is elevated under the growing conditions associated with global warming. Consequently, this hypothesis examines how the grazing season will be affected by CO<sub>2</sub> concentrations, increases in the ambient temperature and changing to a global warming rainfall pattern. The hypothesis will also consider how the combined changes of CO<sub>2</sub>, temperature and rainfall will affect the length of the grazing season. As the sheep were removed during the summer, the effect of climate change on the date of yarding and the length of the grazing season will only be examined for the dairy and beef enterprises, although the effects on the date of turnout will be discussed for the three enterprises.

### **7.6.1 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>**

Although the effect of CO<sub>2</sub> on the date of turnout was similar for all enterprises on both the grass and grass – white clover swards, there was an interaction between CO<sub>2</sub> level and temperature (see Table 6-11). The effect of increasing the ambient concentration of CO<sub>2</sub> resulted in the livestock being turned out earlier in the season than under current climatic conditions, although the increase at each level of temperature was reduced as the ambient temperature was elevated. Against this, the effect of CO<sub>2</sub> concentrations on the date of yarding was dependent on enterprise, although the general trend was for elevated CO<sub>2</sub> concentrations to result in yarding occurring later in the season than under current climatic conditions. Furthermore, the change in the date of yarding differed between the sites (see Figure 6-16, Table 6-13

and Table 6-15). As with to the date of turnout, elevating the temperature on the grass – based system resulted in a smaller increase in the date yarding (see Figure 6-16 and Table 6-12). Equally, on both the grass and the grass – white clover based systems the effect of elevating the CO<sub>2</sub> concentration was also reduced under the rainfall pattern associated with global warming for both the dairy and beef enterprises (see Table 6-14 and Table 6-16). The net result for the dairy and beef enterprises was that elevating the CO<sub>2</sub> concentration lengthened the grazing season, although the magnitude of the change differed between sites (see Table 6-17 and Table 6-19). The level of enhancement at each level of temperature also decreased as the temperature increased (see Table 6-18). The prime reason for this result, as well as the earlier turnout date for the sheep enterprise, is that enhanced concentrations of CO<sub>2</sub> increase the herbage production and thus the availability of herbage for consumption.

#### **7.6.2 Effect of Increasing the Temperature**

Increasing the ambient temperature resulted in the grazing starting earlier in the season than under current climatic conditions for all enterprises on both the grass and grass – white clover swards (see Figure 6-14 and Figure 6-15), although the magnitude of the change differed between sites. Nonetheless, the greatest effect per degree of temperature increase occurred when the elevation in ambient temperature was 1°C at all sites and at both the CO<sub>2</sub> concentrations associated with current and global warming climates (see Table 6-11).

In respect of the yarding date for the dairy and beef enterprises on a grass – based system, at elevated concentrations of CO<sub>2</sub>, increasing the ambient temperature reduced the number of days increase per degree of temperature change (see Figure

6-16 and Table 6-12). Nevertheless, for the dairy enterprise, in general, this effect was not apparent at current concentrations of CO<sub>2</sub> (see Figure 6-16). In contrast, for the beef enterprise increasing the temperature at current concentrations of CO<sub>2</sub> increased the reduction in the number of days per degree of temperature change (see Table 6-12). In addition, the effect of temperature on the date of yarding, for the beef and dairy systems based on pure and mixed swards differed between sites and enterprises in the magnitude and the direction of the change (see Figure 6-16, Figure 6-17 and Figure 6-18).

The effect of temperature elevation on the length of the grazing season differed between sites (see Figure 6-19 and Figure 6-20). In general, a temperature elevation of 1°C resulted in a larger increase than changes of 2°C and 3°C in the length of the grazing season per degree increase in temperature. Nevertheless, the Drummond Castle site did not exhibit this pattern for all enterprises and both sward types. Furthermore, for the grass – based dairy and beef systems reductions in the length of the grazing season occurred at the Wick site for temperature elevations of 2°C and 3°C (see Figure 6-19). The effect of temperature was also increased when the CO<sub>2</sub> concentration was augmented for the grass – based dairy and beef enterprises (see Table 6-18).

Although increasing the ambient temperature extends the growing season, the herbage yield from the grass – based systems declined as temperature was elevated. This is a result of the net effect of elevated temperature on the processes of photosynthesis, respiration and transpiration. Nevertheless, at the beginning and end of the season, water stress is unlikely to occur. The effect of temperature on the

length of the grazing season will be determined by how herbage growth is affected. As the temperature was increased the difference between the length of the grazing and growing season was also increased, although this was more apparent for the grass – based systems than for those based on a mixed sward (see Table 7-4 and Table 7-5). It must be recognised that the start of the growing season is defined as when continuous growth commences. Hence, if the daily air temperature requirement is attained and then falls below the threshold, growth ceases and recommences when the temperature requirement has been re-attained for growth. Consequently, grazing can commence before the growing season has been recorded as commencing. This would indicate that the prime reason for the length of the grazing season to increase is the enhanced rate of photosynthesis that occurs with elevated temperatures. Nevertheless, as the increase in the length of the growing season declines as temperature elevation increases, the rate of dry-matter production approaches an asymptotic value. Consequently, the increase in herbage mass available for consumption, and thus the increase in the length of the grazing season, decrease with temperature elevation.

**Table 7-4** *The difference in the length of the growing and grazing seasons for the grass – based enterprises*

Enterprise	Site	Difference between length of growing and grazing season (days)			
		0°C	1°C	2°C	3°C
Dairy	Auch	4	15	39	78
	Blyth	-14	1	13	21
	Drum	-11	-15	8	41
	Craib	-13	3	12	50
	Wick	-5	11	31	65
Beef	Auch	-2	9	31	69
	Blyth	-17	-4	7	14
	Drum	-16	-19	2	32
	Craib	-16	-1	7	43
	Wick	-14	0	22	57

**Table 7-5** *The difference in the length of the growing and grazing seasons for the grass – white clover based enterprises*

Enterprise	Site	Difference between length of growing and grazing season (days)			
		0°C	1°C	2°C	3°C
Dairy	Auch	-31	-22	-5	7
	Blyth	-14	-5	10	20
	Drum	-22	-26	-8	6
	Craib	-28	-14	-2	11
	Wick	-19	-6	14	33
Beef	Auch	-35	-27	-10	1
	Blyth	-18	-8	7	16
	Drum	-26	-29	-12	2
	Craib	-30	-16	-5	8
	Wick	-28	-16	3	22

### **7.6.3 Effect of Changing to a Global Warming Rainfall Pattern**

Changing the rainfall pattern to one associated with global warming had no effect on the date of turnout for any of the enterprises based on both pure grass and grass – white clover swards. On the other hand, the date of yarding for both the dairy and beef enterprises in respect of both sward types was earlier in the season than under current rainfall patterns (see Table 6-14 and Table 6-16). However, at elevated CO<sub>2</sub>

concentrations changing to a global warming rainfall pattern resulted in the difference in the date of yarding between current and global warming rainfall patterns being larger than for current ambient concentrations of CO<sub>2</sub>. With respect to the dairy and beef grass – based systems, the length of the grazing season was reduced by the global warming rainfall pattern. Although the effects of changing the rainfall pattern on the length of the grazing season for grass – white clover based systems differed between sites, the general trend was a reduction (see Table 6-19). However, the length of the grazing season was increased at the Wick site. Nevertheless, the reductions varied between sites for both the dairy and beef enterprises.

Armstrong (1996) also predicted a reduction in the length of the grazing season, although the climate change scenario was based on a 10% increase in winter rain and a 10% decrease in summer rainfall. However, since changing to a global warming rainfall pattern resulted in enhanced yields, the probable reason for the reduction in the length of the grazing season was due to the ground becoming waterlogged and hence the livestock being removed from the paddocks.

#### **7.6.4 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>, Temperature and Changing to a Global Warming Rainfall Pattern**

There are some site differences in the response of the length of the grazing season to the changes in the climatic conditions for the both the grass and grass – white clover systems for both the dairy and beef enterprises. These are illustrated for the dairy enterprise in Table 7-6—Table 7-7. However, the general trend across sites for all the enterprise systems is that the rate of increase in the length of the grazing season with temperature is enhanced at elevated ambient concentrations of CO<sub>2</sub>. Similarly, the

reduction in the length of the grazing season with the global warming rainfall pattern is increased at augmented CO<sub>2</sub> levels. With respect to the turnout date for the sheep enterprises, the general trend is that the temperature response is increased with elevated CO<sub>2</sub> concentrations. The response for the grass – white clover based systems for all enterprises to changing the climate was greater than that for the grass – based systems (see Table 7-6—Table 7-7).

**Table 7-6** *The length of the grazing season for the dairy herd based on a grass sward for each climate scenario*

Site	Climate	Length of Grazing Season (Days)			
		0°C	1°C	2°C	3°C
Auch	Ambient CO <sub>2</sub> and current rainfall	175	181	176	171
	Ambient CO <sub>2</sub> and global warming rainfall	174	181	176	171
	Elevated CO <sub>2</sub> and current rainfall	184	194	191	191
	Elevated CO <sub>2</sub> and global warming rainfall	180	191	190	191
Blyth	Ambient CO <sub>2</sub> and current rainfall	165	170	169	173
	Ambient CO <sub>2</sub> and global warming rainfall	165	170	170	173
	Elevated CO <sub>2</sub> and current rainfall	170	178	180	188
	Elevated CO <sub>2</sub> and global warming rainfall	168	177	178	181
Craib	Ambient CO <sub>2</sub> and current rainfall	170	187	183	177
	Ambient CO <sub>2</sub> and global warming rainfall	169	187	182	176
	Elevated CO <sub>2</sub> and current rainfall	176	201	201	198
	Elevated CO <sub>2</sub> and global warming rainfall	173	196	198	197

Table 7-6 Continued

Site	Climate	Length of Grazing Season (Days)			
		0°C	1°C	2°C	3°C
Drum	Ambient CO <sub>2</sub> and current rainfall	177	180	182	173
	Ambient CO <sub>2</sub> and global warming rainfall	175	177	181	179
	Elevated CO <sub>2</sub> and current rainfall	183	188	195	195
	Elevated CO <sub>2</sub> and global warming rainfall	179	183	193	192
Wick	Ambient CO <sub>2</sub> and current rainfall	162	163	159	156
	Ambient CO <sub>2</sub> and global warming rainfall	163	164	160	158
	Elevated CO <sub>2</sub> and current rainfall	176	180	175	169
	Elevated CO <sub>2</sub> and global warming rainfall	176	179	175	171

**Table 7-7**    *The length of the grazing season for the dairy herd based on a grass – white clover sward for each climate scenario*

Site	Climate	Length of Grazing Season (Days)			
		0°C	1°C	2°C	3°C
Auch	Ambient CO <sub>2</sub> and current rainfall	181	188	190	194
	Ambient CO <sub>2</sub> and global warming rainfall	178	187	190	195
	Elevated CO <sub>2</sub> and current rainfall	190	202	203	212
	Elevated CO <sub>2</sub> and global warming rainfall	183	195	199	207
Blyth	Ambient CO <sub>2</sub> and current rainfall	164	174	176	186
	Ambient CO <sub>2</sub> and global warming rainfall	164	173	175	181
	Elevated CO <sub>2</sub> and current rainfall	170	179	187	198
	Elevated CO <sub>2</sub> and global warming rainfall	168	178	184	189
Craib	Ambient CO <sub>2</sub> and current rainfall	174	195	194	197
	Ambient CO <sub>2</sub> and global warming rainfall	171	192	190	193
	Elevated CO <sub>2</sub> and current rainfall	180	205	208	215
	Elevated CO <sub>2</sub> and global warming rainfall	174	198	201	205
Drum	Ambient CO <sub>2</sub> and current rainfall	179	185	189	195
	Ambient CO <sub>2</sub> and global warming rainfall	176	181	187	191
	Elevated CO <sub>2</sub> and current rainfall	185	190	199	207
	Elevated CO <sub>2</sub> and global warming rainfall	181	185	196	198

Table 7-7 Continued

Site	Climate	Length of Grazing Season (Days)			
		0°C	1°C	2°C	3°C
Wick	Ambient CO <sub>2</sub> and current rainfall	165	168	166	164
	Ambient CO <sub>2</sub> and global warming rainfall	166	169	168	166
	Elevated CO <sub>2</sub> and current rainfall	177	186	185	185
	Elevated CO <sub>2</sub> and global warming rainfall	179	186	186	186

## **7.7 Hypothesis Six: The Effect of Global Warming on Livestock Production**

As global warming has effects on the length of the grazing season and the yield of herbage from ungrazed swards, this hypothesis examines the knock-on effects of these changes on the saleable products from the livestock enterprises. It will also consider the consequence for the forage production per head that is produced for winter feeding of the stock, and changes in the proportion of paddocks harvested. This hypothesis will therefore discuss the effect of elevated CO<sub>2</sub> levels, changes in temperature, changes in rainfall pattern and the changes associated with a global warming climate scenario on livestock production.

### **7.7.1 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>**

#### **7.7.1.1 Forage Production and the Proportion of Paddocks Harvested**

At all stocking rates for all enterprises on both the grass and grass – white clover based systems increasing the concentration of CO<sub>2</sub> in the atmosphere increased the

dry-matter yield of herbage per head (see Table 6-26 and Table 6-30). Thornley and Cannell (1997) also predicted that enhancing the CO<sub>2</sub> concentration would increase the yield under a grazing simulation. However, with the exception of the beef enterprise grazing a pure grass sward, the magnitude of the response differed between sites (see Table 6-27 and Table 6-29). In respect of the difference in response between grass and grass – white clover swards, except for the dairy enterprise at Wick, the percentage increase in the harvested yield was higher for grass swards than for grass – white clover swards. Nevertheless, at the enhanced atmospheric concentrations of CO<sub>2</sub> the response of the harvested yield per ewe on grass – white clover based systems declined as temperature increased (see Figure 6-31). Increasing the ambient concentration of CO<sub>2</sub> also had an enhancing effect on the proportion of white clover harvested per livestock unit from the mixed swards for the dairy and beef enterprises, although in both cases the change was less than 1%. This effect was not apparent for the sheep system.

The percentage of paddocks harvested increased with elevated CO<sub>2</sub> concentration for all enterprises grazing the grass swards. Nevertheless, the magnitude of the response differed between sites for all enterprises (see Table 6-22). However, for the beef and sheep enterprises the rate of increase was reduced when the temperature was elevated by 2°C or 3°C, compared to a temperature elevation of 1°C (see Table 6-23). On the other hand, the enhancement in the percentage of paddocks harvested decreased with stocking density for the beef and sheep enterprises (see Table 6-24). Equally, the percentage of paddocks harvested for the grass – white clover based systems increased with the elevated CO<sub>2</sub>, although the magnitude of the increase was

affected by the location of the site for the dairy and sheep enterprises. On the other hand, at elevated ambient CO<sub>2</sub> concentrations, the rate of increase declined with increased temperature for the sheep enterprise (see Figure 6-25).

These results indicate that the increase in the conserved herbage yield per livestock unit at the CO<sub>2</sub> concentration associated with global warming is partly due to the increased yield per paddock as well as an increase in the number of paddocks available for taking conservation cuts.

#### **7.7.1.2 Livestock Production**

Although the total milk yield throughout the grazing season was increased with enhanced atmospheric CO<sub>2</sub> conditions, both the direction and magnitude of the effect on the average daily milk yield were also influenced by the location of the site and the presumed temperature scenario (see Figure 6-33). In contrast, the daily milk yield from cows grazing a grass – white clover sward increased with elevated ambient concentrations of CO<sub>2</sub>. Nevertheless, the increases in total milk yield ranged between 4.7%—10.9% and 4.9%—10.3% for the grass and grass – white clover swards respectively, while the change in the daily milk yield for the grass and grass – white clover based systems tended to be less than  $\pm 2\%$  and  $+1\%$  respectively. The increase in the total milk yield is therefore partly due to the increase in daily milk yield, where it occurred, and partly to a consequence of the increased length of the grazing season.

The daily gain in liveweight of the beef steers was elevated under enhanced CO<sub>2</sub> conditions. However, the rate of increase varied between sites for the grass – white clover systems (see Table 6-33), and the enhancement with temperature was also

greater at elevated concentrations of CO<sub>2</sub> (see Figure 6-37). On the other hand, the rate of enhancement with elevated CO<sub>2</sub> increased with stocking density (see Table 6-34). This increased gain in liveweight occurred as a result of the enhanced forage production that took place on ungrazed swards. Accordingly, the enhancement in forage production resulted in increased rates of intake and consequently liveweight gain. There was a tendency for the percentage of white clover in the harvested material from grazed swards to increase with elevated CO<sub>2</sub> conditions, although the rate of enhancement declined with temperature. It is therefore likely the proportion of white clover in the grazed swards was affected in a similar manner. As white clover has a higher nutritive value than grass (Thomson, 1984), the increased percentage of white clover in the sward is likely to result in this pattern of liveweight change for grass – white clover swards.

As for the sheep systems, increasing the ambient concentration of CO<sub>2</sub> increased the rate of daily liveweight gain of the lambs grazing both the grass and grass – white clover systems (see Table 6-35). In contrast, with the exception of the lowest stocking density on the grass – based system, increasing the CO<sub>2</sub> concentration tended to decrease the liveweight of the ewe (see Figure 6-41). However, on the grass – white clover system the ewe liveweight increased with elevated CO<sub>2</sub> concentrations, although the magnitude varied with site (see Table 6-37). As the percentage of white clover in the harvested material from the sheep system was not affected by CO<sub>2</sub> concentrations, the increased ewe liveweight and daily liveweight gain of the lambs was probably due to the enhanced yield of grazed herbage. Although this was not measured, the harvested yield was observed to increase (see Table 6-29).

Nevertheless, although the harvested yield from the grass sward was increased (see Table 6-26), this did not result in increased ewe liveweights, although the lamb liveweight gain was enhanced.

## **7.7.2 Effect of Increasing the Temperature**

### **7.7.2.1 Forage Production and the Proportion of Paddocks Harvested**

The response of harvestable yield per unit of livestock to elevating the ambient temperature differed between the grass and the grass – white clover swards, and also differed between sites. In general, on the grass – based systems increasing the ambient temperature reduced the harvestable yield (see Figure 6-27). Thornley and Cannell (1997) also predicted the decline in yield with elevated temperatures for a grazed sward. Nevertheless, although increasing the temperature reduced the total harvestable yield from the ungrazed grass swards, elevating the ambient temperature by 1°C at the Drummond Castle site increased the dry-matter yield per livestock unit. Similarly, for the same temperature scenario, the yield was also increased at that site for the grass – white clover swards, although the total yield from ungrazed swards was enhanced at all locations with elevated temperatures. On the other hand, at current concentrations of CO<sub>2</sub>, increasing the temperature had little effect on the harvestable yield per ewe from the grass – white clover swards, but at enhanced concentrations the temperature had the effect of reducing the augmentation of yield (see Figure 6-31).

The effect of elevating the ambient temperature on the percentage of white clover in the material harvested per livestock unit was similar to that for the ungrazed swards. Accordingly, the general trend was for elevated temperatures to increase the

percentage of white clover, although reductions in the percentage occurred for a 1°C increase in temperature at some locations.

For the dairy, beef and sheep enterprises on the grass – based system, increasing the temperature reduced the percentage of paddocks harvested. The rate of decrease tended to decline as temperature was increased (see Figure 6-21). However, the magnitude of the response differed between sites for all enterprises. On the other hand, the reduction with temperature was increased at elevated CO<sub>2</sub> concentrations for the beef and sheep enterprises (see Table 6-23). With respect to the sheep enterprise, as the stocking density increased the reduction per degree increase in temperature was increased. In contrast, the percentage of paddocks harvested from the grass – white clover swards tended to increase for the dairy and sheep enterprises, although the pattern and the magnitude for each temperature rise differed between sites (see Figure 6-23). Nevertheless, at current concentrations of CO<sub>2</sub> the change per degree increase in temperature was approximately linear for the sheep enterprise, although the rate declined at the higher concentrations of CO<sub>2</sub> (see Figure 6-25). However, the general trend for the beef enterprise was a reduction (see Figure 6-24). In contrast to grass swards, the rate of increase per degree increase in temperature declined as the ewe stocking density increased.

Consequently, the reduction in the herbage yield per livestock unit for the grass – based systems (see Figure 6-27) may be caused by two factors. The first, and the more significant effect, is the reduction in dry-matter yield from grass swards that occurs when the temperature is elevated (see Figure 6-5). Secondly, the number of paddocks harvested was reduced by enhanced temperatures (see Figure 6-21). This

resulted in a further reduction in the harvestable yield per livestock unit. Similarly, the herbage yield per livestock unit obtained on grass – white clover swards was the result of both changes in the harvested material obtained from ungrazed swards and in the percentage of paddocks harvested. Nevertheless, augmenting the temperature tended to increase the total dry-matter yield from ungrazed grass – white clover swards (see Figure 6-6). The general tendency was for enhanced temperature to increase the percentage of paddocks harvested for the dairy and sheep enterprises (see Figure 6-23). Nevertheless, this was not the case for the beef enterprise (see Figure 6-24). Consequently, the general trend for the dairy and sheep enterprises was for the dry-matter yield per livestock unit to increase (see Figure 6-28 and Figure 6-30). On the other hand, the reduction in the percentage of paddocks harvested for the beef enterprise tended to result in a decline in the herbage yield per head (see Figure 6-29). However, the response varied between sites.

#### **7.7.2.2 Livestock Production**

In general the rate of enhancement in the daily milk yield declined as temperature increased for both the grass and grass – white clover based systems (see Figure 6-33 and Figure 6-34) and a similar pattern was also evident for the total milk yield. However, in some locations the daily milk yield declined with some of the temperature scenarios, even though this did not necessarily result in a decline in total milk yield. Milk yield has been reported to increase as the temperature is elevated to 15°C—20°C, although this effect does not occur when the daily rainfall is greater than 5 mm per day (D'Hour and Coulon, 1994).

In the model, the effect of increasing the ambient temperature resulted in the liveweight gain of the beef steers increasing, although the effect varied between sites for both sward types (see Figure 6-35 and Figure 6-36). However, at some localities, the magnitude of the response differed between the grass and the grass – white clover systems. In general, the rate of the change declined with temperature. Nevertheless, for the grass – white clover systems this tended only to occur at augmented CO<sub>2</sub> levels (see Figure 6-37).

The response of the liveweight gain of lambs for both sward types was similar to that which occurred for the beef system (see Figure 6-38 and Figure 6-39). However, the response of the weight gain in lambs to temperature did not alter with the ambient concentration of the CO<sub>2</sub>. Similarly, temperature enhanced the ewe liveweight at the end of the season (see Figure 6-40 and Figure 6-43). On pure grass swards the percentage enhancement in the ewe liveweight increased with stocking density (see Figure 6-42). However, the increase in the liveweight of the ewes and lambs with temperature was not associated with increased harvestable yields per head from the grass – based system. On the other hand, the yield harvested from the grass – white clover system did tend to increase with elevated temperatures and therefore the growth rate on the pastures utilised for grazing may have also been enhanced (see Figure 6-30). Similarly, the percentage of white clover in the harvested material also tended to increase with elevated temperatures. Hence the nutritive value of the dry matter consumed would have been increased and this would have led to higher liveweight gains.

### **7.7.3 Effect of Changing to a Global Warming Rainfall Pattern**

#### ***7.7.3.1 Forage Production and the Proportion of Paddocks Harvested***

Under a global warming rainfall pattern, the herbage yield per unit of livestock was increased. Nevertheless, the percentage increase in yield was greater for the grass – white clover sward than for the grass sward for both the dairy and beef enterprises. In contrast, this was not the case for the sheep enterprise. With respect to the grass – based systems, the sheep enterprise experienced the greatest increase, while the beef enterprise had the smallest response. On the other hand, the greatest increase occurred for the dairy system, while the sheep enterprise showed the smallest response for grass – white clover based systems. This pattern of response was also observed for the percentage of paddocks harvested.

In general changing to a global warming rainfall pattern resulted in the percentage of paddocks harvested increasing. Except for the dairy enterprise based on the grass system, this trend was repeated for all enterprises on both sward types. Nevertheless, the effect was most pronounced for increases in the ewe stocking density on the grass – white clover swards. The global warming rainfall pattern resulted in a higher dry-matter yield from both grass and grass – white clover ungrazed swards, and the percentage of paddocks harvested tended to increase under grazing. Accordingly, these two factors are probably the cause of the enhanced yield per unit of livestock that occurs under a global warming rainfall pattern.

#### ***7.7.3.2 Livestock Production***

The daily milk yield for both the grass and grass – white clover swards increased when the rainfall was changed from the current pattern to one associated with global

warming. Nevertheless, the magnitudes of the changes were small at 0.51% and 1.12% for the grass and the grass – white clover swards respectively.

There was generally a tendency for the liveweight for steers to increase when the rainfall pattern was altered to one associated with global warming as the daily gain in liveweight was increased by 0.79% and 1.45% for the grass and mixed forage systems respectively. However, the rate of increase was elevated at enhanced CO<sub>2</sub> concentrations. The comparable increases under a changed rainfall pattern on the change in liveweight gain for the lambs were 1.07% and 2.17%, although CO<sub>2</sub> concentration had no effect in this case. In contrast, the ewe liveweight for the grass – based system was not influenced by the rainfall pattern, although the effect for the grass – white clover systems was an increase of 0.52%. In all cases, the enhancement in liveweight was coupled with an increase in the harvested yield per head and thus the growth rate on the grazed paddocks was probably augmented, which resulted in an increased dry-matter intake. Added to this, for grass – white clover swards, is the increase in the percentage of white clover, with a higher nutritive value, when the rainfall pattern was changed to one associated with global warming.

#### **7.7.4 Effect of Increasing the Ambient Concentration of CO<sub>2</sub>, Temperature and Changing to a Global Warming Rainfall Pattern**

##### ***7.7.4.1 Forage Production and the Proportion of Paddocks Harvested***

The production of herbage per livestock unit increases as CO<sub>2</sub> is elevated on both the grass and grass – white clover based systems. Similarly, changing to a global warming rainfall pattern also increases the dry-matter yield, albeit a smaller increase. These findings are illustrated for the dairy enterprise in Table 7-8. The model

predictions of Hanson *et al.* (1993) and Baker *et al.* (1993) also predicted that the climate scenarios associated with the GFDL, GISS and UKMO Global Circulation Models would enhance the standing green biomass in the United States. The general effect of temperature on the herbage yield per unit of livestock for the grass – based systems declined with temperature elevation (see Table 7-8), although it must be recognised that at some sites under certain temperature scenarios the yield increased with temperature. However, the general trend was contrary to the results of Thornley and Cannell (1997), who predicted that the rate of decrease in yield would increase as the temperature increased. In contrast, the herbage yield per dairy cow and per ewe on grass – white clover swards generally tended to increase, although the variations between sites was greater than on pure grass swards. Similarly, the herbage yield for the beef system was dependent on the location of the site.

The major effects of global warming on the percentage of white clover in the harvested material are that elevating the temperature and changing to the rainfall pattern associated with global warming results in an enhancement of the white clover percentage for all enterprises. Nevertheless, the increase in temperature has a larger influence than changing the rainfall pattern. In contrast, increasing the ambient concentration of CO<sub>2</sub> has little effect on the composition of the harvested material. However, the rate of enhancement with temperature varies between the enterprises (see Table 7-9).

**Table 7-8** *The dry-matter yield of herbage per dairy cow for each sward type for each climate scenario*

Sward type	Climate	Herbage Mass (t DM ha <sup>-1</sup> )			
		0°C	1°C	2°C	3°C
Grass	Ambient CO <sub>2</sub> and current rainfall	1.35	1.25	1.19	1.12
	Ambient CO <sub>2</sub> and global warming rainfall	1.43	1.32	1.26	1.19
	Elevated CO <sub>2</sub> and current rainfall	1.91	1.77	1.68	1.61
	Elevated CO <sub>2</sub> and global warming rainfall	2.03	1.89	1.79	1.70
Grass – white clover	Ambient CO <sub>2</sub> and current rainfall	1.29	1.29	1.34	1.36
	Ambient CO <sub>2</sub> and global warming rainfall	1.39	1.39	1.44	1.46
	Elevated CO <sub>2</sub> and current rainfall	1.82	1.83	1.88	1.90
	Elevated CO <sub>2</sub> and global warming rainfall	1.94	1.95	2.01	2.05

*Table 7-9 The percentage of white clover in the harvested material for all enterprises for each climate scenario*

Enterprise	Climate	Percentage white clover			
		0°C	1°C	2°C	3°C
Dairy	Ambient CO <sub>2</sub> and current rainfall	11	12	12	13
	Ambient CO <sub>2</sub> and global warming rainfall	11	12	13	14
	Elevated CO <sub>2</sub> and current rainfall	17	18	21	23
	Elevated CO <sub>2</sub> and global warming rainfall	18	19	22	24
Beef	Ambient CO <sub>2</sub> and current rainfall	12	13	13	14
	Ambient CO <sub>2</sub> and global warming rainfall	12	13	13	14
	Elevated CO <sub>2</sub> and current rainfall	18	20	23	25
	Elevated CO <sub>2</sub> and global warming rainfall	19	21	24	26
Sheep	Ambient CO <sub>2</sub> and current rainfall	17	19	25	31
	Ambient CO <sub>2</sub> and global warming rainfall	19	21	27	34
	Elevated CO <sub>2</sub> and current rainfall	17	19	26	32
	Elevated CO <sub>2</sub> and global warming rainfall	19	20	26	34

The percentage of paddocks harvested under the grazing for the global warming scenario was primarily influenced by the ambient concentration of CO<sub>2</sub>, although changing the rainfall pattern also increased the percentages. However, in general, as the temperature increased the rate of response declined, although the direction of change differed at the five sites.

#### **7.7.4.2 Livestock Production**

Global warming and the associated changes in climate and ambient concentrations of CO<sub>2</sub> tend to result in small, but increasing changes to the daily milk yield. This contradicts the predictions of Klinedinst, Wilhite, Hahn and Hubbard (1993) who predicted that milk yield would decline across the United States with the climatic changes associated with the scenarios described by the GISS, GFDL and UKMO Global Circulation Models. Nevertheless, their predictions suggest that the decline in Europe would be of a smaller magnitude. Although the predictions of milk production from Hanson's *et al.* (1993) model for the GISS and UKMO scenarios also predicted a decline in milk yield, the results for the GFDL scenario predicted an enhancement during months two to six of the simulation. As the length of the grazing season is also increased with global warming, this tends to result in a greater rise in the total milk yield obtained during the grazing period than for the daily milk yield.

The general trend was for the rainfall and CO<sub>2</sub> effects of global warming to increase the liveweight of the dairy cows, although the CO<sub>2</sub> changes resulted in larger increases than changes to the rainfall pattern associated with global warming. Similarly, this pattern of effects also occurred for the beef and sheep enterprises. Baker *et al.* (1993) also provided evidence of global warming increasing animal production in the northern latitudes, although their model predictions were for rangeland situations in the United States. On the other hand, although the predictions of Hanson *et al.* (1993) suggested that global warming would increase forage production, the daily gain in the liveweight of mature cows was predicted to decline. However, elevating the temperature reduced the liveweight of the cows, although enhancing the ambient concentration of CO<sub>2</sub> more than compensated for the effects of

increasing the ambient temperature. In contrast, elevating the ambient temperature for the grass – white clover based beef system enhanced the daily liveweight gain, although the direction and magnitude of the effect for the grass – based system was dependent on the site, rainfall pattern and ambient concentration of CO<sub>2</sub>. On the other hand, increased temperature tended to increase the lamb liveweight gain and the ewe liveweight for both the grass and the grass – white clover based systems.

### ***7.8 Hypothesis Seven: The Differential Increase in the Response of the Grass and the Grass – White Clover Swards***

This hypothesis was concerned with whether there was a differential response of grass and grass – white clover swards to global warming. The rate of enhancement of the total dry-matter yield from grass – white clover swards was greater than for grass swards when the temperature was elevated and the rainfall pattern was changed to one associated with global warming (see Table 6-5, Table 6-6, Figure 6-5 and Figure 6-6). In terms of herbage yield per head of livestock, for the dairy and sheep enterprises the yield declined from the grass swards, whereas the yield from grass – white clover swards increased with elevated temperatures. Although the yield per steer declined for both systems, the reduction was less for the grass – white clover system. Except for the sheep enterprise, which revealed no difference, changing the rainfall had a larger percentage effect on the herbage yield per head from the mixed swards than from the pure grass system. However, in general, increasing the concentration of CO<sub>2</sub> resulted in the grass – based system having larger percentage increases in yield. With respect to the milk yields and the liveweight gains, the grass –

white clover system tended to respond more strongly to increases in temperature, rainfall pattern and ambient concentration of CO<sub>2</sub>.

### ***7.9 Hypothesis Eight: The Effect of the Location of the Site***

The issue here is whether the effects of climate change varied across the five sites. As the daily weather conditions averaged over the year across the five locations are fairly similar (see Table 7-10), it might be presumed that the results would not be affected by location. However, the general trends of the results indicate that there are differences in the response for both herbage and livestock production factors. Indeed, the effects of elevating the ambient concentration of the CO<sub>2</sub> and increasing the ambient temperature were dependent on the locality of the site. It is therefore concluded that the location of the site is an important factor in determining the response of livestock production in Scotland to the changes in CO<sub>2</sub> concentration and the associated changes in climate. The seasonal distribution of temperature, rainfall and sunshine hours may be partly responsible for these differences.

*Table 7-10 The average daily climate at the five sites*

Site	Temperature (°C)	Rain (mm)	Sunshine (h)
Auchincruive	8.7	2.8	3.5
Blyth Bridge	7.0	2.5	3.1
Craibstone	7.5	2.4	3.7
Drummond Castle	7.6	3.5	3.6
Wick	7.4	2.3	3.2

### **7.10 The Advantages of Developing A Systems Model**

Climate change is recognised to impact on forage production. As changes in grass production and availability of forage impact on the production potential of livestock, climate change will also modify the levels of livestock production. To assess this impact it is necessary to understand the linkages between climate change and livestock production. Accordingly, the development of the systems model has made it possible to assess the effects of global warming across a wide range of climatic and CO<sub>2</sub> changes. The interaction effects that occur between temperature, rainfall and ambient concentrations of CO<sub>2</sub> on livestock and forage production can also be evaluated. In addition, using a model has permitted the assessment to be made at a number of different sites and for the dairy, beef and sheep enterprises. Consequently, comparisons between sites and enterprises can be made. The effects vary not only between sites and enterprises but also between different levels of changes in climate. Thus, the model has highlighted the dangers of extrapolating from either an empirical model developed for specific conditions or an experimental site to a different location, which has slightly different base climatic conditions.

### **7.11 Further Developments Required**

There are several weaknesses in the model and therefore scope for future developments to be made. First, the model assumes that grass and white clover respond in the same manner to enhanced levels of CO<sub>2</sub>. Consequently, the increase in the percentage of white clover in the harvested material from the ungrazed swards does not increase. This is a situation that contradicts the results of Clark *et al.* (1997), Stewart and Potvin (1996), Campbell *et al.* (1995), Newton *et al.* (1995) and Newton *et*

*al.* (1994), who tend to predict increases in the percentage of white clover in the sward with enhanced CO<sub>2</sub>. Nevertheless, as the percentage of white clover in the grazed mixed swards did increase under the simulations, the increase would probably be enhanced if the different responses of grass and white clover to elevated CO<sub>2</sub> were included.

Second, the interaction between the nitrogen in the sward and the level of photosynthesis is not included. This is because the nitrogen uptake by the herbage is not described in the model. Nevertheless, the nitrogen in the sward can have knock-on effects on how the grass and grass – white clover swards respond to the changes in climate and CO<sub>2</sub> concentrations. In order to incorporate the effect of nitrogen on photosynthesis and herbage production in the model, a sub-model describing the nitrogen flows within the soil would be required. This is because the soil processes determine the quantity of nitrogen available for plant growth. This would have the added benefit of permitting the environmental effects of nitrogen in livestock systems to be studied. Thirdly, the description of the transfer of nitrogen from the white clover component to the grass component is weak, due to the paucity of data describing this function. If further data describing this relationship became available this linkage within the model could be improved.

Fourth, the processes of tillering in grass and stolon development in white clover are not described in the model. The model also assumes that the switch over dates from vegetative to reproductive growth are not dependent on temperature and are not affected by the ambient concentration of CO<sub>2</sub>. On the other hand, the results of Luo, Chen, Reynolds, Field and Mooney (1997) reveal that the extent to which grassland

growth is stimulated by elevated  $\text{CO}_2$  is dependent on the extent to which the physiological processes of plant growth are influenced by the enhanced  $\text{CO}_2$ . As the effect of elevated  $\text{CO}_2$  on the physiology and morphology of the plant to elevated  $\text{CO}_2$  varies with species and environmental conditions (Bazzaz, 1990, Field, Chapin, Matson and Mooney, 1992), the effect of elevated  $\text{CO}_2$  on forage production and hence livestock production may vary from the model predictions. Consequently, it would be an advantage to incorporate the effects of  $\text{CO}_2$  and temperature on the morphology of the sward. The morphology of the sward also has implications for livestock production as the tiller density in the spring is known to have knock-on effects on milk production later in the season (Dowdeswell and Fisher, 1992).

Fifth, the effect of the nitrogen concentration of the herbage on livestock production is not included in the model. The first step to incorporating these effects would be the inclusion of a sub-model describing the nitrogen flows within the soil and plant. Nevertheless, an additional sub-model describing the effects of nitrogen on animal production would be required. Sixth, the grazing action of the dairy, beef and sheep are described by the same function, although the mouth action of cattle and sheep differ (G. Fisher, *personal communication*). Consequently, the model could be improved by incorporating equations that describe the mouth action for each livestock type. Seventh, further data on the selection of leaf and stem as well as grass and white clover are required to improve the simulation of grazing. Eighth, the model could be extended to cover the winter feeding period so that the effect of global warming on livestock throughout the year could be assessed. Finally, it would be beneficial if an economic component could be added to the model in order to assess

for example the difference between the economic benefits accruing to the different livestock types.

### ***7.12 Advancement to Knowledge***

Although the model requires expansion, its development has permitted the effect of global warming on livestock production to be assessed for grass and grass – white clover swards. Consequently, the model describes the effects of temperature and CO<sub>2</sub> concentration on plant growth. The model also describes the effect of water and nutrient stress on plant development and thus the consequences of changes in plant stress on livestock production. In the grass – white clover sward a major advancement has been made as the model permits the sward to have different proportions of grass and white clover at each layer through the sward. Nonetheless, the model assumes that the sward is horizontally homogenous. The model has also advanced the state of knowledge by assuming that the livestock can preferentially select from grass – white clover swards. The development of the model has also identified areas where knowledge of forage growth and the interaction between the grazing animal and the sward require further research and data collection. This would result in an improvement in the understanding of livestock systems.

### ***7.13 Conclusions***

In conclusion, although climate change is predicted to increase forage and livestock production in Scotland, the effects were dependent on the actual level of the changes in temperature. Indeed, the magnitude and, in some cases, the directions of the changes were influenced by the location of the site. There were also interactions

between CO<sub>2</sub> concentration and both temperature and rainfall, as well as an interaction between temperature and rainfall. Consequently, extrapolating results from other sites, and to other levels of the temperature, rainfall and CO<sub>2</sub> may not give a true indication of how forage and livestock production actually reacts. There are also indications that the modelled responses of grazed and ungrazed swards have different reactions to climate change, and indeed there were also differences in the responses of the dairy, beef and sheep enterprises. Nevertheless, the general trends of the three livestock systems were similar. Within the context of current environmental concerns the greater enhancement of grass – white clover swards may result in farmers switching from grass to mixed sward production and thus reduce fertiliser nitrogen use. Similarly with enhanced yields and longer grazing season the requirement for concentrates may be reduced.

Although there are several areas within the model that could be improved with existing knowledge and data, it must be recognised that some of the potential improvements would require further experimental work and data collection. The creation of a model that is capable of simulating non-homogenous vertically distributed grass – white clover swards has added to the knowledge base. Another addition to the knowledge of the modelling of forage production has been the incorporation of stress effects. In addition the model permits the effect of changes in climate on livestock production across Scotland to be assessed.

## References

- Acock, B., Charles-Edwards, D. A., Fitter, D. J., Hand, D. W., Ludwig, L. J., Warren-Wilson, J. and Withers A. C. (1978) The contribution of leaves from different levels within a tomato crop to canopy net photosynthesis: an experimental examination of two different canopy models. *Journal of Experimental Botany*, **29**, 815—827.
- Adams, R. M., Fleming, R. A., Chang, C. C., McCarl, B. A. and Rosenzweig, C. (1995) A reassessment of the economic-effects of global climate-change on US agriculture. *Climatic Change*, **30**, 147–167.
- Agricultural and Food Research Council (1993) *Energy and Protein Requirements of Ruminants: an advisory manual prepared by the AFRC Technical Committee on Responses to Nutrients*. Commonwealth Agricultural Bureaux, Wallingford, UK, XXIV + 159pp.
- Agricultural and Food Research Council (1991) *METDATA User Guide*, Harpenden, 32pp.
- Agricultural Research Council (1980) *The Nutrient Requirements of Ruminant Livestock*. Commonwealth Agricultural Bureaux, Farnham Royal, UK, 351pp.
- Allen, L. H. Jr. (1991a) Effects of increasing carbon dioxide levels and climate change on plant growth, evapotranspiration, and water resources. In: *Managing Water Resources in the West under Conditions of Climate Uncertainty*, Proceedings of a Colloquium, 14—16 November 1990, Scottsdale, AZ. National Academy Press,

Washington, USA.

- Allen, L. H. Jr. (1991b) *Carbon dioxide effects on growth, photosynthesis, and evapotranspiration of rice at three fertilizer levels. Response of Vegetation to Carbon Dioxide*. Report **No. 62**. Plant Stress and Protection Unit, USDA-ARS, Gainesville, Florida, US.
- Amir, J. and Sinclair, T. R. (1991a) A model of the temperature and solar-radiation effects on spring wheat growth and yield. *Field Crops Research*, **28**, 47—58.
- Amir, J. and Sinclair, T. R. (1991b) A model of water limitation on spring wheat growth and yield. *Field Crops Research*, **28**, 59—69.
- Aphalo, P. J. and Jarvis, P. G. (1993) An analysis of Ball's empirical model of stomatal conductance. *Annals of Botany*, **72**, 321—327.
- Armstrong, A. C. (1996) The impact of climate change on grassland production and utilisation. In: R. J. Froud-Williams, R. Harrington, T. J. Hocking, H. G. Smith and T. H. Thomas (Editors) *Aspects of Applied Biology, Implications of "Global Environmental Change" for Crops in Europe*, **No 45**, 79—84.
- Armstrong, A. C. and Castle, D. A. (1995) Potential effects of climate change on the agricultural production and the hydrology of drained grassland in the UK. In: D. F. McGregor and D. A. Thompson (Editors) *Geomorphology and Land Management in a Changing Environment*, Wiley & Sons, pp139—151.
- Armstrong, H. and Sibbald, A. (1992) A model of pasture utilisation in the hill country of the U.K. *Agricultural Systems and Information Technology*, **4**, 11—13.
- Armstrong, H. M., Gordon, I. J., Hutchings, N. J., Illius, A. W., Milne, J. A. and Sibbald,

- A. R. (1997a) A model of the grazing of hill vegetation by sheep in the UK. I. The prediction of vegetation biomass. *Journal of Applied Ecology*, **34**, 166—185.
- Armstrong, H. M., Gordon, I. J., Hutchings, N. J., Illius, A. W., Milne, J. A. and Sibbald, A. R. (1997b) A model of the grazing of hill vegetation by sheep in the UK. II. The prediction of offtake by sheep. *Journal of Applied Ecology*, **34**, 186—207.
- Arnone, J. A. and Gordon, J. C. (1990) Effect of nodulation, nitrogen fixation and CO<sub>2</sub> enrichment on the physiology, growth and dry mass allocation of seedlings of *Alnus rubra* Bong. *New Phytologist*, **116**, 55—66.
- Baker, B. B., Hanson, J. D., Bourdon, R. M. and Eckert, J. B. (1993) The potential effects of climate change on ecosystem process and cattle production on US Rangelands. *Climatic Change*, **25**, 97—117.
- Baker B. B., Bourdon, R. M. and Hanson, J. D. (1992) FORAGE: a model of forage intake in beef cattle. *Ecological Modelling*, **60**, 257—279.
- Baker, D., Doyle, C. and Lidgate, H. (1991) Grass Production. In: C. Thomas, A. Reeve and G. E. J. Fisher (Editors) *Milk from Grass* (2<sup>nd</sup> Edition), Billingham Press, Cleveland, pp1—26.
- Baldocchi, D. (1994) An analytical solution for coupled leaf photosynthesis and stomatal conductance models. *Tree Physiology*, **14**, 1069—1079.
- Barry, R. G. and Chorley, R. J. (1992) *Atmosphere, weather and climate* (6<sup>th</sup> edition), Routledge, London, 392pp.
- Bazzaz, F. A. (1990) The response of natural ecosystems to the rising global CO<sub>2</sub> levels. *Annual Review of Ecology and Systematics*, **21**, 167—196.

- Beever, D. E. and Oldham, J. D. (1986) Nutrient supply and utilization. In: W. H. Broster, R. H. Phipps and C. L. Johnson (Editors) *Principles and Practice of Feeding Dairy Cows Technical Bulletin 8*, Reading UK.
- Bergthorsson, P., Björnsson, H., Dyrmondsson, O., Gudmundsson, B., Helgadóttir, A. and Jonmundsson, J. V. (1988) The effects of climatic variations on agriculture in Iceland. In: M. L. Parry, T. R. Carter and N. T. Konijn (Editors) *The Impact of Climatic Variations on Agriculture, Vol. 1, Assessments in Cool Temperate and Cold Regions*, Kluwer, Dordrecht, The Netherlands, pp383—509.
- Berry, J. A. and Björkman, O. (1980) Photosynthetic response and adaptation to temperature in higher plants. *Annual Review of Plant Physiology*, **31**, 491—543.
- Besford, R. T., Ludwig, L. J. and Withers, A. C. (1990) The greenhouse effect: Acclimation of tomato plants growing in high CO<sub>2</sub>, photosynthesis and ribulose-1,5-bisphosphate carboxylase protein. *Journal of Experimental Botany*, **41**, 925—931.
- Bibby, J. S., Douglas, H. A., Thomasson, A. J. and Robertson, J. S. (1991) *Land Capability Classification for Agriculture*. Macaulay Land Use Research Station, Aberdeen, 75pp
- Bindi, M., Fibbi, L., Gozzini, B., Orlandini, S. and Miglietta, F. (1996) Modelling the impact of future climate scenarios on the yield and yield variability of grapevine. *Climate Research*, **7**, 213—224.
- 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.
- Blaxter, K. L., Wainman, F. W. and Wilson, R. S. (1961) The regulation of food intake

- by sheep. *Animal Production*, **3**, 51—61.
- Bolorsetseg, B. and Tuvannsuren, G. (1996) The potential impacts of climate-change on pasture and cattle production in Mongolia. *Water Air and Soil Pollution*, **92**, 95—105.
- Bootsma, A. and Boisvert, J. (1991) Modelling methodology for estimating forage yield potential in Canada. *Agriculture Canada, Research Branch, Technical Bulletin*, 1991-6E, Ottawa, 33pp.
- Bootsma, A., Boisvert, J. and Dumanski, J. (1994) Climate-based estimates of potential forage yields in Canada using a crop growth model. *Agricultural and Forest Meteorology*, **67**, 151—172.
- Brereton, A. J. and Hope-Cawdery, M. (1988) Drumlin soils – The depression of herbage yield by shallow water table depth. *Irish Journal of Agricultural Research*, **27**, 167—178.
- Brereton, A. J. and Ryan, M. (1984) Weather, grass growth and milk production. In: H. Riley and A. O Skjelvåg (Editors) *The Impact of Climate on Grass Production and Quality*, Proceedings of the 10<sup>th</sup> General Meeting of the European Grassland Federation, Ås, Norway, 1984, pp505—509.
- British Standards Institution (1959) *Density Hydrometers for Use in Milk Part 2. Methods*, **734, Part 2**.
- Brklacich, M. and Stewart, R. B. (1995) Impacts of climate change on wheat yield in the Canadian prairies. *Climate change and agriculture: Analysis of potential international impacts*. Proceedings of a symposium sponsored by the American

- Society of Agronomy in Minneapolis, MN, 4-5 Nov. 1992. Organized by Division A-3 (Agroclimatology and Agronomic Modeling) and Division A-6 (International Agronomy). ASA-Special-Publication. **No. 59**, 147—162.
- Broad, H. J. and Hough, M. N. (1993) The growing and grazing season in the United Kingdom. *Grass and Forage Science*, **48**, 26—37.
- Brown, R. H. and Blaser, R. E. (1968) Leaf area index in pasture growth. *Herbage Abstracts*, **38**, 1—9.
- Bruce, J. M., Broadbent, P. J. and Topps, J. H. (1984) A model of the energy system of lactating and pregnant cows. *Animal Production*, **38**, 351—362.
- Buan, R. D., Maglinao, A. R., Evangelista, P. P. and Pajuelas, B. G. (1996) Vulnerability of rice and corn to climate-change in the Philippines. *Water Air and Soil Productivity*, **92**, 41—51.
- Bunce, J. A. and Caulfield, F. (1991) Reduced respiratory carbon dioxide efflux during growth at elevated carbon dioxide in three herbaceous perennial species. *Annals of Botany*, **67**, 325—330.
- Buxton, D. R. (1996) Quality-related characteristics of forages as influenced by plant and agronomic factors. *Animal Feed Science and Technology*, **59**, 37—49.
- Cacho, O. J., Finlayson, J. D. and Bywater, A. C. (1995) A simulation model of grazing sheep: II. Whole farm model. *Agricultural Systems*, **48**, 27—50.
- Caloin, M. (1994) Analysis of dry matter partitioning in *Dactylis glomerata* during vegetative growth using a carbon budget model. *Annals of Botany*, **73**, 665—669.

- Campbell, B. D., Laing, W. A., Greer, D. H., Crush, J. R., Clark, H., Williamson, D. Y. and Given, M. D. J. (1995) Variation in grassland populations and species and the implications for community responses to elevated CO<sub>2</sub>. *Journal of Biogeography*, **22**, 315—322
- Carter, D. R. and Peterson, R. M. (1983) Effects of a CO<sub>2</sub>-enriched atmosphere on the growth and competitive interaction of a C<sub>3</sub> and a C<sub>4</sub> grass. *Oecologia*, **58**, 188—193.
- Carter, T. R., Porter, J. H. and Parry, M. L. (1992) Some implications of climatic change for agriculture in Europe. *Journal of Experimental Botany*, **43**, 1159—1167.
- Carton, O. T., Brereton, A. J., O'Keeffe, W. F. and Keane, G. P. (1988) Effect of autumn closing date and grazing severity in a rotationally grazed sward during winter and spring. *Irish Journal of Agricultural Research*, **27**, 141—150.
- Casella, E. and Soussana, J. F. (1997) Long-term effects of CO<sub>2</sub> enrichment and temperature increase on the carbon balance of a temperate grass sward. *Journal of Experimental Botany*, **48**, 1309—1321.
- Casella, E., Soussana, J. F. and Loiseau, P. (1996) Long-term effects of CO<sub>2</sub> enrichment and temperature increase on a temperate grass sward. I. Productivity and water use. *Plant and Soil*, **182**, 83—99.
- Chapman, D. F., Robson, M. J. and Snaydon, R. W. (1991) Quantitative carbon distribution in clonal plants of white clover (*Trifolium repens*): source—sink relationships during undisturbed growth. *Journal of Agricultural Science*,

Cambridge, **116**, 229—238.

- 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 pasture. *New Zealand Journal of Agricultural Research*, **27**, 303—312.
- Chang, C. W. (1975) Carbonic anhydrase and senescence in cotton plants. *Plant Physiology*, **55**, 515—519.
- Chen, D.-X. and Coughenour, M. B. (1994) GEMTM: a general model for energy mass transfer of land surfaces and its application at the FIFE sites. *Agricultural and Forest Meteorology*, **68**, 145—171.
- Christian, K. R., Freer, M., Donnelly, J. R., Davidson, J. L. and Armstrong, J. S. (1978) *Simulation of grazing systems*, Pudoc, Wageningen, 115pp.
- Clark, H., Newton, P. C. D., Bell, C. C. and Glasgow, E. M. (1997) Dry matter yield, leaf growth and population dynamics in *Lolium perenne*/*Trifolium repens*-dominated pasture turves exposed to two levels of elevated CO<sub>2</sub>. *Journal of Applied Ecology*, **34**, 304—316.
- Clark, H., Newton, P. C. D., Bell, C. C. and Glasgow, E. M. (1995) The influence of elevated CO<sub>2</sub> and simulated seasonal changes in temperature on tissue turnover in pasture turves dominated by perennial ryegrass (*Lolium perenne*) and white clover (*Trifolium repens*). *Journal of Applied Ecology*, **32**, 128—136.
- Coffin, D. P. and Lauenroth, W. K. (1996) Transient responses of North American Grasslands to changes in climate. *Climatic Change*, **34**, 269—278.

- Combellas, J. and Hodgson, J. (1979) Herbage intake and milk production by grazing dairy cows. 1. The effects of variation in herbage mass and daily herbage allowance in a short-term trial. *Grass and Forage Science*, **34**, 209—214.
- Connor, D. J., Hall, A. J. and Sadras, V. O. (1993) Effect of nitrogen content on the photosynthetic characteristics of sunflower leaves. *Australian Journal of Plant Physiology*, **20**, 251—263.
- Conrad, H. R., Pratt, A. D. and Hibbs, J. W. (1964) Regulation of feed intake in dairy cows. I. Change in the importance of physical and physiological factors with increasing digestibility. *Journal of Dairy Science*, **47**, 54—62.
- Conroy, J., Barlow, E. W. R. and Bevege, D. I. (1986) Response of *Pinus radiata* seedlings to carbon dioxide enrichment at different levels of water and phosphorus: growth, morphology and anatomy. *Annals of Botany*, **57**, 165—177.
- Cooper, J. P. (1960) Short-day and low-temperature induction in *Lolium*. *Annals of Botany*, **24**, 232—246.
- Cooter, E. J. (1990) The impact of climate change on continuous corn production in the southern U.S.A. *Climatic Change*, **16**, 53—82.
- Corrall, A. J. (1984) Grass growth and seasonal pattern of production under varying climatic conditions. In: H. Riley and A. O Skjelvåg (Editors) *The Impact of Climate on Grass Production and Quality*, Proceedings of the 10<sup>th</sup> General Meeting of the European Grassland Federation, Ås, Norway, 1984, pp36—46.
- Cosgrove, G. P., Anderson, C. B. and Fletcher, R. H. (1996) Do cattle exhibit a preference for white clover? In: D. R. Woodfield (Editor) *White Clover: New*

*Zealand's Competitive Edge*, Joint symposium, Lincoln University, New Zealand, 21—22 November 1995; Agronomy Society of New Zealand Special Publication **No 11**, Grassland Research and Practice Series **No 6**, 83—88.

Cowling, D. W. (1982) Biological nitrogen fixation and grassland production in the United Kingdom. *Philosophical Transactions of the Royal Society of London Series B—Biological Sciences*, **296**, 397—404.

Crush, J. R. (1993) Hydrogen evolution from root nodules of *Trifolium repens* and *Medicago sativa* plants grown under elevated atmospheric CO<sub>2</sub>. *New Zealand Journal of Agricultural Research*, **36**, 177—183.

Cure, J. D. and Acock, B. (1986) Crop responses to carbon dioxide doubling: A literature survey. *Agricultural and Forest Meteorology*, **38**, 127—145.

Curry, R. B., Jones, J. W., Boote, K. J., Peart, R. M., Allen, L. H. Jr. and Pickering, N. B. (1995) Response of soybean to predicted climate change in the USA. *Climate change and agriculture: Analysis of potential international impacts*. Proceedings of a symposium sponsored by the American Society of Agronomy in Minneapolis, MN, 4-5 Nov. 1992. Organized by Division A-3 (Agroclimatology and Agronomic Modeling) and Division A-6 (International Agronomy). ASA-Special-Publication, **No. 59**, 163—182.

Davidson, I. A. and Robson, M. J. (1986) Effect of temperature and nitrogen supply on the growth of perennial ryegrass and white clover. 2. A comparison of monocultures and mixed swards. *Annals of Botany*, **57**, 709—719.

Davies, A. (1977) Structure of grass sward. *Proceedings of an International Meeting*

*on Animal Production from Temperate Grassland, Dublin*, pp36—44.

Davies, A. and Jones, D. R. (1992) The production of leaves and stolon branches on established white clover cuttings in relation to temperature and soil-moisture in the field. *Annals of Botany*, **69**, 515—521.

Davies, A., Jenkins, T., Pike, A., Shao, J., Carson, I., Pollock, C. J. and Parry, M. L. (1996) Modelling the predicted geographic and economic response of UK cropping systems to climate change scenarios: the case of potatoes. In: R. J. Froud-Williams, R. Harrington, T. J. Hocking, H. G. Smith and T. H. Thomas (Editors) *Aspects of Applied Biology, Implications of "Global Environmental Change" for Crops in Europe*, **No 45**, 63—70.

DeJong, T. M. (1982) Leaf nitrogen content and CO<sub>2</sub> assimilation capacity in peach. *Journal of the American Society of Horticultural Science*, **107**, 955—959.

Delecolle, R., Ruget, F., Ripoche, D. and Gosse, G. (1995) Possible effects of climate change on wheat and maize crops in France. *Climate change and agriculture: Analysis of potential international impacts*. Proceedings of a symposium sponsored by the American Society of Agronomy in Minneapolis, MN, 4-5 Nov. 1992. Organized by Division A-3 (Agroclimatology and Agronomic Modeling) and Division A-6 (International Agronomy). ASA-Special-Publication, **No. 59**, 241—257.

Delucia, E. H., Sasek, T. W. and Strain, B. R. (1985) Photosynthetic inhibition after long-term exposure to elevated levels of atmospheric carbon dioxide. *Photosynthesis Research*, **7**, 175—184.

- Devir, S., Zur, B., Maltz, E., Genizi, A. and Antler, A. (1995) A model for the prediction of a dairy cow body weight based on physiological timescale. *Journal of Agricultural Science, Cambridge*, **125**, 415—424.
- Díaz, S. (1995) Elevated CO<sub>2</sub> responsiveness, interactions at the community level and plant functional types. *Journal of Biogeography*, **22**, 289—295.
- Dickenson, A. G., Hancock, J. L., Hovell, G. J. R., Taylor, St. C. S. and Wiener, G (1962) The size of lambs at birth – A study involving egg transfer. *Animal Production*, **4**, 64—79.
- Dillon, J. L. and Anderson, J. R. (1990) *The Analysis of Response in Crop and Livestock Production*. (3<sup>rd</sup> Edition), Pergamon Press, Oxford, 251pp.
- D'Hour, P. and Coulon, J. B. (1994) Variations de la production et de la composition du lait au pâturage en fonction des conditions climatiques. *Annales de Zootechnie*, **43**, 105—109.
- Dowdeswell, A. and Fisher, G. E. J. (1992) The performance of summer calving cows on different grass swards. *British Grassland Society Third Research Conference, Greenmount College of Agriculture and Horticulture, Antrim, Northern Ireland, 2—4 September, 1992*.
- Dowle, K., Doyle, C. J., Spedding, A. W. and Pollott, G. E. (1988) A model for evaluating grassland management decisions on beef and sheep farms in the U.K. *Agricultural Systems*, **28**, 299—317.
- Doyle, C. J., and Edwards, C. (1986) A model for evaluating grassland management decisions on dairy farms in the UK. *Agricultural Systems*, **21**, 243—266.

- Doyle, C. J., and Lazenby, A. (1984) The effect of stocking rate and fertilizer usage on income variability for dairy farms in England and Wales. *Grass and Forage Science*, **39**, 117—127.
- Doyle, C. J. and Morrison, J. (1983) An economic assessment of the potential benefits of replacing grass by grass – clover mixtures for 18-month beef systems. *Grass and Forage Science*, **38**, 273—282.
- Doyle, C. J., Barrs, J. A. and Bywater, A. C. (1989) A simulation of bull beef production under rotational grazing in the Waikato region of New Zealand. *Agricultural Systems*, **31**, 247—278.
- Doyle C. J., Morrison, J. and Peel, S. (1987) Prospects for grass – clover swards in beef production systems: a computer simulation of the practical and economic implications. *Agricultural Systems*, **24**, 119—148.
- Doyle C. J., Ridout, M. S., Morrison, J. and Edwards, C. (1986) Predicting the response of perennial ryegrass to fertilizer nitrogen in relation to cutting interval, climate and soil. *Grass and Forage Science*, **41**, 303—310.
- Doyle, C. J., Corrall, A. J., Thomas, C, Le Du, Y. L. P. and Morrison, J. (1983) The integration of conservation with grazing for milk production: a computer simulation of the practical and economic implications. *Grass and Forage Science*, **38**, 261—272.
- Drake, B. G. and Leadley, P. W. (1991) Canopy photosynthesis of crops and native plant communities exposed to long term elevated CO<sub>2</sub> treatment. *Plant, Cell and Environment*, **14**, 853—860.

- Duru, M., Ducrocq, H. and Tirilly, V. (1995) Modeling growth of cocksfoot (*Dactylis glomerata* L.) and tall fescue (*Festuca arundinacea* Scrb.) at the end of spring in relation to herbage nitrogen status. *Journal of Plant Nutrition*, **18**, 2033—2047.
- Easterling, W. E., Crosson, P. R., Rosenberg, N. J. McKenney M. S., and Frederick, K. D. (1992) Methodology for assessing regional economic impacts of responses to climate change: The MINK study. In: J. M. Reilly and M. Anderson (Editors) *Economic Issues in Global Climate Change*, Westview press: Boulder, Colorado, pp168—199.
- Edwards, G. R., Newman, J. A., Parsons, A. J. and Krebs, J. R. (1997) Use of cues by grazing animals to locate food patches: An example with sheep. *Applied Animal Behaviour Science*, **51**, 59—68.
- Elsen J. M., Wallach, T. W. and Charpentreau, J. L. (1988) The calculation of herbage intake of grazing sheep: A detailed comparison between models. *Agricultural Systems*, **26**, 123—160.
- Fagerberg, B. and Nyman, P. (1995) Modelling weather effects on nutritional value of grass – clover leys. 2. Estimation and validation of parameters in a model for changes in crude protein content. *Swedish Journal of Agricultural Research*, **25**, 3—12.
- Fagerberg, B. and Nyman, P. (1994) Modelling weather effects on nutritional value of grass – clover Leys. 1. Estimation and validation of parameters in a model for changes in metabolizable energy content. *Swedish Journal of Agricultural Research*, **24**, 147—156.

- Farquhar, G. D. and Sharkey, T. D. (1982) Stomatal conductance and photosynthesis. *Annual Review of Plant Physiology*, **33**, 317—345.
- Farquhar, G. D. and von Caemmerer, S. (1982) Modelling of photosynthetic responses to environmental conditions. In: O. L. Lange, P. S. Nobel, C. B. Osmond and H. Ziegler (Editors) *Physiological Plant Ecology. II Encyclopedia of Plant Physiology, New Series*, Springer-Verlag, Berlin, **Vol. 12b** pp548—577.
- Farquhar, G. D., von Caemmerer, S. and Berry, J. A. (1980) A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta*, **149**, 78—90.
- Farrar, J. F. and Williams, L. (1991) The effects of increased atmospheric carbon dioxide and temperature on carbon partitioning, source-sink relations and respiration. *Plant, Cell and Environment*, **14**, 819—830.
- Faurie, O., Soussana, J. F. and Sinoquet, H. (1996) Radiation interception, partitioning and use in grass-clover mixtures. *Annals of Botany*, **77**, 35—45.
- Favis-Mortlock, D. T., Evans, R., Boardman, J., and Harris, T. M. (1991) Climate change, winter wheat yield and soil erosion on the English South Downs. *Agricultural-Systems*, **37**, 415—433.
- Ferris, R., Nijs, I., Behaeghe, T and Impens, I. (1996a) Elevated CO<sub>2</sub> and temperature have different effects on leaf anatomy of perennial ryegrass in spring and summer. *Annals of Botany*, **78**, 489—497.
- Ferris, R., Nijs, I., Behaeghe, T and Impens, I. (1996b) Contrasting CO<sub>2</sub> and temperature effects on leaf growth of perennial ryegrass in spring and summer. *Journal of Experimental Botany*, **47**, 1033—1043.

- Field, C. and Mooney, H. A. (1986) The photosynthesis–nitrogen relationship in wild plants. In: T. J. Givnish (Editor) *On the Economy of Form and Function*, Cambridge University Press, Cambridge, UK, pp25—55.
- Field, C., Chapin, F. S., III, Matson, P. A. and Mooney, H. A. (1992) Responses of terrestrial ecosystems to the changing atmosphere: A resource-based approach.. *Annual Review of Ecology and Systematics*, **23**, 201—235.
- Finlayson, J. D., Cacho, O. J. and Bywater, A. C. (1995) Simulation of sheep grazing: I. Individual animal growth. *Agricultural Systems*, **48**, 1—25.
- Flohn, H. (1985) *Das Problem der Klimaänderungen in der Vergangenheit und der Zukunft*. Wissenschaftliche Büchergesellschaft, Darmstadt.
- Forbes, J. M. (1980) A model of short term control of feeding in the ruminant: Effects of changing animal characteristics. *Appetite*, **1**, 21—40.
- Forbes, J. M. (1977) Interrelationships between physical and metabolic control of voluntary food intake in fattening, pregnant and lactating mature sheep: A model. *Animal production*, **24**, 91—101.
- Forbes, J. M. and Hodgson, J. (1985) Comparative studies of the influence of sward conditions on the ingestive behavior of cows and sheep. *Grass and Forage Science*, **40**, 69—77.
- Frame, J. and Boyd, A. G. (1987) The effect of fertiliser nitrogen rate, white clover variety and closeness of cutting on herbage productivity from perennial ryegrass/white clover swards. *Grass and Forage Science*, **42**, 85—96.
- France, J. and Thornley, J. H. M. (1984) *Mathematical Models in Agriculture*,

Butterworths, London, UK, 335pp.

France, J, Neal, H. D. St. C., Probert, D. W. and Pollott, G. E. (1983) A model for evaluating lamb production systems. *Agricultural Systems*, **10**, 213—244.

Francis, S. M. and Smetham, M. L. (1985) Pasture utilisation and its effect on herbage quality. *Proceedings of the New Zealand Grassland Association*, **46**, 221—225.

Friend, A. D. and Cox, P. M. (1995) Modelling the effects of atmospheric CO<sub>2</sub> on vegetation – atmosphere interactions. *Agricultural and Forest Meteorology*, **73**, 285—295.

Garwood, E. A., Tyson, K. C. and Sinclair, J. (1979) Use of water by six grasses: 1. Dry-matter yields and response to irrigation. *Journal of Agricultural Science, Cambridge*, **93**, 13—24.

Gastal, F. and Saugier, B. (1989) Relationships between nitrogen uptake and carbon assimilation in whole plants of tall fescue. *Plant, Cell and Environment*, **12**, 407—418.

Gates, D. M. (1993) *Climate change and its biological consequences*, Sinauer Associates, Inc., Sunderland, Massachusetts, 280pp.

Genin, D. and Quiroz, R. (1993) MIAMH, A predictive model of range ruminant diets in patchy environments. *Agricultural Systems*, **43**, 381—395.

Gifford, R. M. (1977) Growth pattern, CO<sub>2</sub> exchange and dry weight distribution in wheat growing under different photosynthetic environments. *Australian Journal of Plant Physiology*, **4**, 99—110.

- Ginnett, T. F. and Demment, M. W. (1995) The functional response of herbivores: analysis and test of a simple mechanistic model. *Functional Ecology*, **9**, 376—384.
- Givens, I. and Moss, A. R. (1990) *UK Tables of Nutritive Value and Chemical Composition of Feedingstuffs*. Holmes McDougal Ltd., UK, 420pp.
- Goldsberry, K. L. (1986) CO<sub>2</sub> fertilization of carnations and some other flower crops. In: H. Z. Enoch and B. A. Kimball (Editors) *Carbon Dioxide Enrichment of Greenhouse Crops. Vol. II. Status and CO<sub>2</sub> Sources*, CRC Press, Inc., Boca Raton, FL., **Chapter 9**, pp117—140.
- Gong, Y., Hodgson, J., Lambert, M. G. and Gordon, I. L. (1996) Short-term ingestive behaviour of sheep and goats grazing grasses and legumes. 1. Comparison of bite weight , bite rate, and bite dimensions for forages at two stages of maturity. *New Zealand Journal of Agricultural Research*, **39**, 63—73.
- Gourdriaan, J. and de Ruiter, H. E. (1983) Plant growth in response to CO<sub>2</sub> enrichment at two levels of nitrogen and phosphorus supply. I. Dry matter, leaf area and development. *Netherlands Journal of Agricultural Science*, **31**, 157—169.
- Graham, N. McC., Black, J. L. and Faichney, G. J. (1976) Simulation of growth and production in sheep-model 1: A computer program to estimate energy and nitrogen utilization, body composition and empty liveweight change, day by day for sheep of any age. *Agricultural Systems*, **1**, 113—138.
- Grainger, C. and Mathews, C. L. (1989) Positive relation between substitution rate

- and pasture allowance for cows receiving concentrates. *Australian Journal of Experimental Agriculture*, **29**, 355—360.
- Greer, D. H., Laing, W. A. and Campbell (1995) Photosynthetic responses of thirteen pasture species to elevated CO<sub>2</sub> and temperature. *Australian Journal of Plant Physiology*, **22**, 713—722.
- Gustavsson, A. -M. (1995) Predictions of growth and nutritional value of forage leys with a dynamic model. *Agricultural Systems*, **47**, 93—105.
- Gustavsson, A. -M., Angus, J. F. and Torrsell, B. W. R. (1995) An integrated model for growth and nutritional value of timothy. *Agricultural Systems*, **47**, 73—92.
- Hammit, J. K., Jain, A. K., Adams J. L. and Wuebbles, D. J. (1996) A welfare-based index for assessing environmental effects of greenhouse-gas emissions. *Nature*, **381**, 301—303.
- Hansen, J. E. and Lacis, A. A. (1990) Sun and dust versus greenhouse gases: an assessment of their relative roles in global climate change. *Nature*, **346**, 713—719.
- Hanson, J. D., Baker, B. B. and Bourdon, R. M. (1993) Comparison of the effects of different climate change scenarios on rangeland livestock production. *Agricultural Systems*, **41**, 487—502.
- Hanson, J. D., Skiles, J. W. and Parton, W. J. (1988) A multispecies model for rangeland plant communities. *Ecological Modelling*, **44**, 89—123.
- Hardacre, A. K., Laing, W. A. and Christeller, J. T. (1986) The response of simulated swards of perennial ryegrass and white clover to enriched atmospheric CO<sub>2</sub>:

- interaction with nitrogen and photosynthetic photon flux density. *New Zealand Journal of Agricultural Research*, **29**, 567—573.
- Harding, F. (1995) Milk from sheep and goats. In: F. Harding (Editor) *Milk Quality*, Blackie Academic and Professional, Imprint of Chapman and Hall, Glasgow, UK, pp97—101.
- Harris, W. (1987) Population dynamics and competition. In: M. J. Baker and W. M. Williams (Editors) *White Clover*, Commonwealth Agricultural Bureaux International, Wallingford, Oxon, pp 203—297.
- Harrison, P. A. and Butterfield, R. E. (1996) Effects of climate change on Europe-wide winter wheat and sunflower productivity. *Climate Research*, **7**, 225—241.
- Hart, A. L. (1987) Physiology. In: M. J. Baker and W. M. Williams (Editors) *White Clover*, Commonwealth Agricultural Bureaux International, UK, pp125—151.
- Hatch, D. J. and MacDuff, J. H. (1991) Concurrent rates of N<sub>2</sub> fixation, nitrate and ammonium uptake by white clover in response to growth at different root temperatures. *Annals of Botany*, **67**, 265—274.
- Hikosaka, K. and Terashima, I. (1995) A model of the acclimation of photosynthesis in the leaves of C<sub>3</sub> plants to sun and shade with respect to nitrogen use. *Plant, Cell and Environment*, **18**, 605—618.
- Hollinshead, P. (1995) Making more out of less milk. *Livestock (A supplement to Farming News)*, **May**, 12—13.
- Holmes, W. (1989) Introduction. In: W. Holmes (Editor) *Grass: Its Production and Utilization*, Blackwell Scientific Publications, Oxford, UK, pp1—6.

- Horie, T., Kropff, M. J., Centeno, H. G., Nakagawa, H., Nakano, J., Kim, H. Y. and Ohnishi, M. (1995) Effect of anticipated change in global environment on rice yields in Japan. In: S. Peng, K. T. Ingram, H. U. Neue and L. H. Ziska (Editors) *Climate Change and Rice*, Springer-Verlag, Berlin, Germany. pp291—302.
- Hulme, D. J., Kellaway, R. C. and Booth, P. J. (1986) The CAMDAIRY model for formulating and analysing dairy cow rations. *Agricultural Systems*, **22**, 81—108.
- Hume and Corrall (1986) A quantitative study of the effects of climate variability and climatic change on herbage production from intensively managed grassland in Western European Countries. *Final Report EEC Contract No CLI-058-81-UK(H)*.
- Hunt, H. W., Trilica, M. J., Redente, E. F., Moore, J. C., Detling, J. K., Kittel, T. G. F., Walter, D. E., Fowler, M. C., Klein, D. A. and Elliot, E. T. (1991) Simulation model for the effects of climate change on temperate grassland ecosystems. *Ecological Modelling*, **53**, 205—246.
- Idso, S. B. and Kimball, B. A. (1989) Growth response of carrot and radish to atmospheric CO<sub>2</sub> enrichment. *Environmental and Experimental Botany*, **29**, 135—139.
- Idso, S. B., Kimball, B. A. and Mauney, J. R. (1987a) Atmospheric carbon dioxide enrichment on cotton midday foliage temperature: Implications for plant water use and crop yield. *Agronomy Journal*, **79**, 667—672.
- Idso, S. B., Kimball, B. A., Anderson, M. G. and Mauney, J. R. (1987b) Effects of atmospheric CO<sub>2</sub> enrichment on plant growth: the interactive role of air temperature. *Agriculture, Ecosystems and Environment*, **20**, 1—10.

Iglesias, A. and Minguez, M. I. (1995) Prospects for maize production in Spain under climate change. *Climate change and agriculture: Analysis of potential international impacts*. Proceedings of a symposium sponsored by the American Society of Agronomy in Minneapolis, MN, 4-5 Nov. 1992. Organized by Division A-3 (Agroclimatology and Agronomic Modeling) and Division A-6 (International Agronomy). ASA-Special-Publication, **No. 59**, 259—273.

Intergovernmental Panel on Climate Change (1996) In: J. T. Houghton, L. G. Meira Filho, B. A. Callander, N. Harris, A. Kattenberg and K. Maskell (Editors) *Climate Change 1995: the Science of Climate Change*, Contribution of Working Group I to the second assessment report of the IPCC, Cambridge University Press, UK, XII + 572pp.

Intergovernmental Panel on Climate Change (1992) In: J. T. Houghton and B. A. Callander (Editors) *Climate Change 1992: The Supplementary Report to the IPCC Scientific Assessment*, Cambridge University Press, UK, XII + 200pp.

Intergovernmental Panel on Climate Change (1990) In: J. T. Houghton, G. J. Jenkins and J. J. Ephraums (Editors) *Climate Change: The IPCC Scientific Assessment*, Cambridge University Press, UK, XXXIX + 365pp.

Jamieson, W. S. and Hodgson, J. (1979) The effects of variation in the sward characteristics upon the ingestive behaviour and herbage intake of calves and lambs under a continuous stocking management. *Grass and Forage Science*, **34**, 273—282.

Jarvis, P. G. (1989) Atmospheric carbon dioxide and forests. *Philosophical*

*Transactions of the Royal Society of London Series B—Biological Sciences*, **324**, 369—392.

Jin, Z., Ge, D., Chen, H. and Zheng, X. (1995) Assessing impacts of climate change on rice production: strategies for adaptation in southern China. In: S. Peng, K. T. Ingram, H. U. Neue and L. H. Ziska (Editors) *Climate Change and Rice*, Springer-Verlag, Berlin, Germany, pp303—313.

Jin, Z. Q., Ge, D. K., Chen, H. and Zheng, X. L. (1994) Positive and negative effects of global climate change on soyabean production in China. *Soybean Science*, **13**, 302—311.

Johnson, H. B., Polley, H. W. and Mayeux, H. S. (1993) Increasing CO<sub>2</sub> and plant-plant interactions: effects on natural vegetation. *Vegetatio*, **104/105**, 157—170.

Johnson, I. R. and Parsons, A. J. (1985) A theoretical analysis of grass growth under grazing. *Journal of Theoretical Biology*, **112**, 345—367.

Johnson, I. R. and Thornley, J. H. M. (1985) Dynamic model of the response of a vegetative crop to light, temperature and nitrogen. *Plant, Cell and Environment*, **8**, 485—499.

Johnson, I. R. and Thornley, J. H. M. (1984) A model of instantaneous and daily canopy photosynthesis. *Journal of Theoretical Biology*, **107**, 531—545.

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.

Johnson, I. R., Parsons, A. J. and Ludlow, M. M. (1989) Modelling photosynthesis in

- monocultures and mixtures. *Australian Journal of Plant Physiology*, **16**, 501—516.
- Johnson, I. R., Ameziane, T. E. and Thornley, J. H. M. (1983) A model of grass growth. *Annals of Botany*, **51**, 599—609.
- Jollans, J. L. (1981) *Grassland in the British Economy*. CAS Paper No. 10. Centre for Agricultural Strategy, Reading, UK.
- Jolliffe, P. A. and Tregunna, E. B. (1968) Effect of temperature, CO<sub>2</sub> concentration, and light intensity on oxygen inhibition of photosynthesis in wheat leaves. *Plant Physiology*, **43**, 902—906.
- Jones, M. B. (1985) Plant Microclimate. In: J. Coombs, D. O. Hall, S. P. Long and J. M. O. Scurlock (Editors) *Techniques in Bioproductivity and Photosynthesis*, (2<sup>nd</sup> Edition), Pergamon Press, Oxford, **Chapter 3**, pp26—40.
- Jones, M. B., Jongen, M and Doyle, T. (1996a) Effects of elevated carbon dioxide concentrations on agricultural grassland production. *Agricultural and Forest Meteorology*, **79**, 243—252.
- Jones, M. B., Jongen, M., Garvey, L. and Baxter, R. (1996b) The physiological responses of European grassland species to elevated CO<sub>2</sub>. In: R. J. Froud-Williams, R. Harrington, T. J. Hocking, H. G. Smith and T. H. Thomas (Editors) *Aspects of Applied Biology, Implications of "Global Environmental Change" for Crops in Europe*, **No 45**, 155—161.
- Jones, P., Allen, L. H. Jr. and Jones, J. W. (1985) Responses of soybean canopy photosynthesis and transpiration to whole-day temperature changes in different CO<sub>2</sub> environments. *Agronomy Journal*, **77**, 242—249.

- Jongen, M., Jones, M. B., Hebeisen, T. and Blum, H. (1995) The effects of elevated CO<sub>2</sub> concentrations on the root growth of *Lolium perenne* and *Trifolium repens* grown in a FACE system. *Global Change Biology*, **1**, 361—371.
- Junttila, O., Svenning, M. M. and Solheim, B. (1990) Effects of temperature and photoperiod on vegetative growth of white clover (*Trifolium repens*) ecotypes. *Physiologia Plantarum*, **79**, 427—434.
- Kahn, H. E. and Spedding, C. R. W. (1984) A dynamic model for the simulation of cattle herd production systems: 2. An investigation of various factors influencing the voluntary intake of dry matter and the use of the model in their validation. *Agricultural Systems*, **13**, 63—82.
- Karim, Z., Hussain, S. G. and Ahmed, M. (1996) Assessing the impacts of climatic variations on foodgrain production. *Water Air and Soil Pollution*, **92**, 53—62.
- Kenny, G. J. and Harrison, P. A. (1992) Thermal and moisture limits of grain maize in Europe: model testing and sensitivity to climate change. *Climate Research*, **2**, 113—129.
- Kenny, G. J., Harrison, P. A. and Parry, M. L. (1993) *EPOCH Project: The Effect of Climate Change on Agricultural and Horticultural Potential in Europe*. Research Report **No. 2**, Environmental Change Unit, University of Oxford.
- Kimball, B. A. (1986a) CO<sub>2</sub> stimulation of growth yield under environmental restraints. In: H. Z. Enock and B. A. Kimball (Editors) *Carbon Dioxide Enrichment of Greenhouse Crops, Vol. II.*, CRC Press Inc., Boca Raton, Florida, **Chapter 5**, pp55—67.

- Kimball, B. A. (1986b) *Effects of increasing atmospheric CO<sub>2</sub> on the growth, water relation, and physiology of plants under optimal and limiting levels of water and nitrogen. Response of Vegetation to Carbon Dioxide*, Report No. 39. U. S. Water Conservation Laboratory, Phoenix, Arizona, US.
- Kimball, B. A. (1983) Carbon dioxide and agricultural yield: An assemblage and analysis of 430 prior observations. *Agronomy Journal*, **75**, 779—788.
- Kimball, B. A., Mauney, J. R., Nakayama, F. S. and Idso, S. B. (1993a) Effects of elevated CO<sub>2</sub> and climate variables on plants. *Journal of Soil and Water Conservation*, **48**, 9—14.
- Kimball, B. A., Mauney, J. R., Nakayama, F. S. and Idso, S. B. (1993b) Effects of increasing atmospheric CO<sub>2</sub> on vegetation. *Vegetatio*, **104/105**, 65—75.
- Klinedinst, P. L., Wilhite, D. A., Hahn, G. L. and Hubbard, K. G. (1993) The potential effects of climate change on summer season dairy cattle milk production and reproduction. *Climatic Change*, **23**, 21—36.
- Körner, Ch. (1995) Towards a better experimental basis for upscaling plant responses to elevated CO<sub>2</sub> and climate warming. *Plant, Cell and Environment*, **18**, 1101—1110.
- Kramer, P. J. (1981) Carbon dioxide concentration, photosynthesis, and dry matter production. *BioScience*, **31**, 29—33.
- La Marche, V. C., Jr., Graybill, D. A., Fritts, H. C. and Rose, M. R. (1984) Increasing atmospheric CO<sub>2</sub>: tree ring evidence for growth enhancement in natural vegetation. *Science*, **225**, 1019—1021.

- Laidlaw, A. S., Withers, J. A. and Watson, S. (1994) Estimating errors in calculating herbage growth from net herbage accumulation rates continuously stocked swards. In: L. 't Mannetje and J. Frame (Editors) *Grassland Society. Proceedings of the 15<sup>th</sup> General Meeting of the European Grassland Federation*, 6—9 June 1994, Wageningen Pers, Wageningen, The Netherlands, pp181—184.
- Lantinga, E. A. (1985) Simulation of herbage production and herbage intake during a rotational grazing period: An evaluation of Linehan's formula. *Netherlands Journal of Agricultural Science*, **33**, 385—403.
- Laurila, H. A. (1995) Modelling the effects of elevated CO<sub>2</sub> and temperature on Swedish and German spring wheat-varieties with CERES-WHEAT and AFRC--WHEAT crop models. *Journal of Biogeography*, **22**, 591—595.
- Lawlor, D. W. and Mitchell, R. A. C. (1991) The effects of increasing CO<sub>2</sub> on crop photosynthesis and productivity: a review of field studies. *Plant, Cell and Environment*, **14**, 807—818.
- Le Du, Y. L. P., Combellas, J., Hodgson, J. and Baker, R. D. (1979) Herbage intake and milk production by grazing cows. 2. The effects of level of winter feeding and daily herbage allowance. *Grass and Forage Science*, **34**, 249—260.
- Leemans, R. and Solomon, A. M. (1993) Modeling the potential change in yield and distribution of the earth's crops under a warmed climate. *Climate Research*, **3**, 79—96.
- Lemaire, G., Gosse, G. and Chartier, M. (1984) Modelling of the dry matter growth of a grass stand in spring. Interaction between climatic factors and nitrogen nutrition.

- In: H. Riley and A. O Skjelvåg (Editors) *The Impact of Climate on Grass Production and Quality*, Proceedings of the 10<sup>th</sup> General Meeting of the European Grassland Federation, Ås, Norway, 1984, pp515—519.
- Leuning, R. (1995) A critical appraisal of a combined stomatal-photosynthesis model for C<sub>3</sub> plants. *Plant, Cell and Environment*, **18**, 339—355.
- Leuning, R., Kelliher, F. M., De Pury, D. G. G. and Schulze, E. -D. (1995) Leaf nitrogen, photosynthesis, conductance and transpiration: scaling from leaves to canopies. *Plant, Cell and Environment*, **18**, 1183—1200.
- Lobley, G. E., Milne, V., Lovie, J. M., Reeds, P. J. and Pennie, K. (1980) Whole body and tissue synthesis in cattle. *British Journal of Nutrition*, **43**, 491—502.
- Long, S. P. (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations: Has its importance been underestimated. *Plant, Cell and Environment*, **14**, 729—739.
- Loewer, O. J., Smith, E. M., Gay, N. and Fehr, R. (1983) Incorporation of environment and feed quality into a net energy model of beef cattle. *Agricultural Systems*, **11**, 67—94.
- Ludlow, M. M. and Charles-Edwards, D. A. (1980) Analysis of the regrowth of a tropical grass/legume sward subjected to different frequencies and intensities of defoliation. *Australian Journal of Agricultural Research*, **31**, 673—692.
- Luo, Y., Chen, J. -L., Reynolds, J. F., Field, C. B. and Mooney, H. A. (1997) Disproportional increases in photosynthesis and plant biomass in a Californian grassland exposed to elevated CO<sub>2</sub>: a simulation analysis. *Functional Ecology*,

11, 696—704.

- Luo, Y, Field, C. B. and Mooney, H. A. (1994) Predicting responses of photosynthesis and root fraction to elevated  $[\text{CO}_2]_a$ : interactions among carbon, nitrogen, and growth. *Plant, Cell and Environment*, **17**, 1195—1204.
- Maas, S. (1993) Parameterized model of gramineous crop growth: I. Leaf area and dry mass simulation. *Agronomy Journal*, **85**, 348—353.
- Macaulay Institute for Soil Research (1982) *Soil Survey of Scotland Sheets 3, 5 and 6*, Ordnance Survey, London.
- Madore, M. and Grodzinski, B. (1985) Effects of  $\text{CO}_2$  enrichment on growth and photoassimilate transport in dwarf cucumber (*Cucumis sativus* L.) cultivar. *Journal of Plant Physiology*, **121**, 59—71.
- Mainland, D. D. (1985) A note on lactation curves of dairy cows in Scotland. *Animal Production*, **41**, 413—416.
- Makadho, J. M. (1996) Potential effects of climate-change on corn production in Zimbabwe. *Climate Research*, **6**, 147—151.
- Manderscheid, R., Bender, J., Schenk, U. and Weigel, H. -J. (1997) Response of biomass and nitrogen yield of white clover to radiation and atmospheric  $\text{CO}_2$  concentration. *Environmental and Experimental Botany*, **38**, 131—143.
- Marshall, B. and Biscoe, P. V. (1980) A model for  $\text{C}_3$  leaves describing the dependence of net photosynthesis on irradiance. *Journal of Experimental Botany*, **31**, 29—39.

- Marshall, P. R., McCall, D. G. and Johns, K. L. (1991) Stockpol: A decision support model for livestock farms. *Proceedings of the New Zealand Grassland Association*, **53**, 137—140.
- Matthews, R. B., Kropff, M. J., Bachelet, D. and Laar, H. H. van (1995) *Modeling the impact of climate change on rice production in Asia*. Commonwealth Agricultural Bureaux International; Wallingford; UK, xvi + 289 pp.
- Maxwell, T. J., Sibbald, A. R., Dalziel, A. J. I., Agnew, R. D. M. and Elston, D. A. (1994) The implications of controlling grazed sward height for the operation and productivity of upland sheep systems in the UK. 1. Effects of two annual stocking rates in combination with two sward height profiles. *Grass and Forage Science*, **49**, 73—88.
- Mayne, C. S. (1990) Effects of supplementation on the performance of both growing and lactating cattle at pasture. In: C. S. Mayne (Editor) *Management Issues for the Grassland Farmer in the 1990's*, British Grassland Occasional Symposium No. **25**, pp55—71.
- Maytin, C. E., Acevedo, M. F., Jaimez, R., Andressen, R., Harwell, M. A., Robock, A., and Azocar, A. (1995) Potential effects of global climate-change on the phenology and yield of maize in Venezuela. *Climatic Change*, **29**, 189—211.
- McCree, K. J. (1970) An equation for the rate of respiration of white clover plants grown under controlled conditions. In: I. Setlik (Editor) *Prediction and Measurement of Photosynthetic Productivity*, Centre for Agricultural Publishing and Documentation, Wageningen, pp221—229.

- McCree, K. J. and Amthor, M. E. (1982) Effects of diurnal variation in temperature on the carbon balances of white clover plants. *Crop Science*, **22**, 822—827.
- McCree, K. J. and Silsbury, J. H. (1978) Growth and maintenance requirements of subterranean clover. *Crop Science*, **18**, 13—18.
- McDonald, P., Edwards, R. A. and Greenhalgh, J. F. D. (1988) *Animal Nutrition* (4<sup>th</sup> Edition), John Wiley and Sons Inc., New York, US, VI + 543pp
- McGechan, M. B. and Glasbey, C. A. (1988) Estimates of solar radiation based on other meteorological parameters for use in simulations of swath drying. *Departmental Note 5*, Scottish Centre for Agricultural Engineering, Penicuik, UK.
- McMurtrie, R. and Wolf, L. (1983) Above- and below-ground growth of forest stands: a carbon budget model. *Annals of Botany*, **52**, 437—448.
- Mearns, L. O., Rosenzweig, C., Goldenberg, R. (1996) The effect of changes in daily and interannual climatic variability on CERES-Wheat: a sensitivity study. *Climatic Change*, **32**, 257—292.
- Meat and Livestock Commission (1986) *Lamb Carcase Production Planning to Meet Your Market* (2<sup>nd</sup> Edition), MLC Sheep Improvement Services, Milton Keynes, UK.
- Meat and Livestock Commission (1982) *Blueprints for Beef*, MLC Beef Improvement Services Milton Keynes, UK, 36pp.
- Meat and Livestock Commission (1981) *Feeding the ewe* (2<sup>nd</sup> Edition), MLC Sheep Improvement Services, Milton Keynes, UK, 78pp.
- Meijs, J. A. C. and Hoekstra, J. A. (1984) Concentrate supplementation of grazing

dairy cows. 1. Effect of concentrate intake and herbage allowance on herbage intake. *Grass and Forage Science*, **39**, 59—66.

Menzhulin, G. V. Koval, L. A., and Badenko, A. L. (1995) Potential effects of global warming and carbon dioxide on wheat production in the Commonwealth of Independent States. *Climate change and agriculture: Analysis of potential international impacts*. Proceedings of a symposium sponsored by the American Society of Agronomy in Minneapolis, MN, 4-5 Nov. 1992. Organized by Division A-3 (Agroclimatology and Agronomic Modeling) and Division A-6 (International Agronomy). ASA-Special-Publication, **No. 59**, 275—292.

Ministry of Agriculture and Fisheries (1985) *Controlled grazing systems: Feed intakes*. Farm production and practice notes, No. **845**. MAF Information Services, Wellington, 2pp.

Mitchell, R. A. C. (1996) Predicting the effects of environmental change on winter wheat yield in genotypes with different flowering dates. In: R. J. Froud-Williams, R. Harrington, T. J. Hocking, H. G. Smith and T. H. Thomas (Editors) *Aspects of Applied Biology, Implications of "Global Environmental Change" for Crops in Europe*, **No 45**, 133—138.

Mitchell, R. A. C., Lawlor, D. W., Mitchell, V. J., Gibbard, C. L., White, E. M. and Porter, J. R. (1995) Effects of elevated CO<sub>2</sub> concentration and increased temperature on winter-wheat – test of ARCWHEAT1 simulation-model. *Plant, Cell and Environment*, **18**, 736—748.

Mogensen, V. O. (1977) Field measurements of dark respiration rates of roots and

- aerial parts in Italian ryegrass and barley. *Journal of Applied Ecology*, **14**, 243—252.
- Monteith, J. L. (1965) Evaporation and Environment. The state and movement of water in living organisms. *Symposium of the Society of Experimental Biology*, **19**, 205—234. Cambridge University Press.
- Moot, D. J., Henderson, A. L., Porter, J. R. and Semenov, M. A. (1996) Temperature, CO<sub>2</sub> and the growth and development of wheat – changes in the mean and variability of growing conditions. *Climatic change*, **33**, 351—368.
- Morrison, J. I. L. (1987) Intercellular CO<sub>2</sub> concentration and stomatal response to CO<sub>2</sub>. In: E. Zeiger, G. D. Farquhar and I. R. Cowan (Editors) *Stomatal Functions*, Stanford University Press, Stanford, CA, pp 229—251.
- Morrison, J., Jackson, M. V. and Sparrow, P. E. (1980) The Response of Perennial Ryegrass to Fertiliser Nitrogen in Relation to Climate and Soil: Report of the Joint ADAS/GRI Grassland Manuring Trial – GM20. *Grassland Research Institute Technical report No. 27*. The Grassland Research Institute, Hurley, Maidenhead, Berkshire, UK.
- Munro, J. M. M. and Hughes, R. (1966) White clover and hill land improvement. *Journal of the British Grassland Society*, **21**, 224—230.
- Nafziger, E. D. and Keller, R. M. (1976) Influence of leaf starch concentration on CO<sub>2</sub> assimilation in soybean. *Plant Physiology*, **57**, 560—563.
- National Research Council (1976) *Nutrient Requirements of Beef Cattle* (6<sup>th</sup> Edition), National Academy of Science, Washington DC, US.

- Neftel, A., Moor, E., Oeschger, H. and Stuafer, B. (1985) Evidence from polar ice cores in atmospheric carbon dioxide in the past two centuries. *Nature*, **315**, 45—47.
- Neue, H. U., Ziska, L. H., Matthews, R. B. and Dai, Q. (1995) Reducing global warming - the role of rice. *Geojournal*, **35**, 351—362.
- Newman, J., Parsons, A. J., Thornley, J. H. M., Penning, P. D. and Krebs, J. R. (1995) Optimal diet selection by a generalist grazing herbivore. *Functional Ecology*, **9**, 255—268.
- Newton, P. C. D., Clark, H., Bell, C. C. and Glasgow, E. M. (1996) Interaction of soil moisture and elevated CO<sub>2</sub> on the above-ground growth rate, root length density and gas exchange of turves from temperate pasture. *Journal of Experimental Botany*, **47**, 771—779.
- Newton, P. C. D., Clark, H., Bell, C. C., Glasgow, E. M., Tate, K. R., Ross, D. J., Yeates G. W. and Sagger, S. (1995) Plant growth and soil processes in temperate grassland communities at elevated CO<sub>2</sub>. *Journal of Biogeography*, **22**, 235—240.
- Newton, P. C. D., Clark, H., Bell, C. C., Glasgow, E. M. and Campbell, B. D. (1994) Effects of elevated CO<sub>2</sub> and simulated seasonal changes in temperature on the species composition and growth rates of pasture turves. *Annals of Botany*, **73**, 53—59.
- Nijs, I. and Impens, I. (1997) An analysis of the balance between root and shoot activity in *Lolium perenne* cv. Melvina. Effects of CO<sub>2</sub> concentration and air temperature. *New Phytologist*, **135**, 81—91.

- Nijs, I. and Impens, I. (1996) Effects of elevated CO<sub>2</sub> concentration and climate-warming on photosynthesis during winter in *Lolium perenne*. *Journal of Experimental Botany*, **47**, 915—924.
- Nijs, I. and Impens, I. (1993) Effects of long-term elevated atmospheric carbon dioxide on *Lolium perenne* and *Trifolium repens*, using a simple photosynthesis model. *Vegetatio*, **104/105**, 421—431.
- Nijs, I., Behaeghe, T. and Impens, I. (1995) Leaf nitrogen content as a predictor of photosynthetic capacity in ambient and global change conditions. *Journal of Biogeography*, **22**, 177—183.
- Nijs, I., Impens, I. and Behaeghe, T. (1989a) Leaf and canopy responses of *Lolium perenne* to long-term elevated atmospheric carbon-dioxide concentration. *Planta*, **177**, 312—320.
- Nijs, I., Impens, I. and Behaeghe, T. (1989b) Effects of different CO<sub>2</sub> environments on the photosynthesis – yield relationship and the carbon and water balance of a white clover (*Trifolium repens* L. Cv. Blanca) sward. *Journal of Experimental Botany*, **40**, 353—359.
- Nikolov, N. T., Massman, W. J. and Schoettle, A. W. (1995) Coupling biochemical and biophysical model for leaves of C<sub>3</sub> plants. *Ecological Modelling*, **80**, 205—235.
- Nonhebel, S. (1996) Effects of temperature rise and increase in CO<sub>2</sub> concentrations on simulated wheat yields in Europe. *Climatic Change*, **34**, 73—90.
- Oberbauer, S. F., Strain, B. R. and Fletcher, N. (1985) Effects of CO<sub>2</sub> enrichment on seedling physiology and growth of two tropical species. *Physiologia Plantarum*,

65, 352—356.

Oechel, W. C. and Reichers, G. I. (1987) *Responses of a Tundra Ecosystem to elevated Atmospheric CO<sub>2</sub>*. U.S. Department of Energy: Washington, DC, USA.

Ojima, D. S., Parton, W. J., Schimel, D. S., Scurlock, J. M. O. and Kittel, T. G. F. (1993) Modelling the effects of climatic and CO<sub>2</sub> changes on the grassland storage of soil C. *Water, Air, and Soil Pollution*, **70**, 643—657.

Oltjen, J. W., Bywater, A. C., Baldwin, R. L. and Garrett, W. N. (1986) Development of a dynamic model of beef cattle growth and composition. *Journal of Animal Science*, **62**, 86—97.

Orr, R. J., Parsons, A. J., Penning, P. D. and Treacher, T. T. (1990) Sward composition, animal performance and the potential production of grass/white clover swards continuously stocked with sheep. *Grass and Forage Science*, **45**, 325—336.

Osbourn, D. F. (1980) Grazing management. In: W. Holmes (Editor) *Grass and Its Production and Utilization*, Blackwell Scientific Publications, London, pp70—124.

Østergaard, V. (1979) Strategies for concentrate feeding to attain optimum feeding in high level dairy cows. *Beretning fra Statens Husdyrbugs forsøg*, 482.

Overdieck, D. and Reining, F. (1986) Effects of atmospheric CO<sub>2</sub> enrichment on perennial ryegrass (*Lolium perenne* L.) and white clover (*Trifolium repens* L.) competing in a managed model-ecosystems I. — Phytomass production. *Acta Ecologica/Ecologia Plantarum*, **7**, 357—366.

Pachepsky, L. B., Haskett, J. D. and Acock, B. (1996) An adequate model of

photosynthesis – I. Parameterization, validation and comparison of models. *Agricultural Systems*, **50**, 209—225.

Parry, M. L. (1990) . *Climate Change and World Agriculture*, Earthscan Publications Ltd., London, 157pp.

Parry, M. L. and Carter, T. R. (1988) The assessment of effects of climatic variations on agriculture: aims, methods and summary of results. In: M. L. Parry, T. R. Carter & N. T. Konijn (Editors) *The Impact of Climatic Variations on Agriculture. Vol. 1: Assessment in Cool Temperate and Cold Regions*, Kluwer Academic Publishers, Dordrecht, The Netherlands, pp11—96.

Parry, M. L., Carter, T. R. and Porter, J. H. (1989) The greenhouse effect and the future of UK agriculture. *Journal of the Royal Agricultural Society of England*, **150**, 120—131.

Parsons, A. J., Thornley, J. H. M., Newman, J. and Penning, P. D. (1994a) A mechanistic model of some physical determinants of intake rate and diet selection in a two – species temperate grassland sward. *Functional Ecology*, **8**, 187—204.

Parsons, A. J., Newman, J. Penning, P. D. Harvey, A. and Orr, R. J. (1994b) Diet preference of sheep - effects of recent diet, physiological-state and species abundance. *Journal of Animal Ecology*, **63**, 465—478.

Parsons, A. J., Harvey, A. and Johnson, I. R. (1991) Plant – animal interactions in a continuously grazed mixture. II. The role of differences in the physiology of plant growth and of selective grazing on the performance and stability of species in a mixture. *Journal of Applied Ecology*, **46**, 635—658.

- Pearcy, R. W. and Björkman, O. (1983) Physiological effects. In: E. R. Lemon (Editor) *CO<sub>2</sub> and Plants*, Westview Press, Boulder, Colorado, USA, **Chapter 4**.
- Peart, R. M., Curry, R. B., Rosenzweig, C., Jones, J. W., Boote, K. J., Allen, L. H. Jr. (1995) Energy and irrigation in south eastern U.S. agriculture under climate change. *Journal of Biogeography*, **22**, 635—642.
- Peel, S. (1988) Varieties, establishment and management. In: *The Grassland Debate: White Clover versus Applied Nitrogen, Proceedings of a Conference held at the National Agricultural Centre, Stoneleigh, 19 October 1988*. Kenilworth: Royal Agricultural Society of England Agricultural Development and Advisory Service.
- Peiris, D. R., Crawford, J. W., Grashoff, C., Jefferies, R. A., Porter, J. R. and Marshall, B. (1996) A simulation study of crop growth and development under climate change. *Agricultural and Forest Meteorology*, **79**, 271—287.
- Penman, H. C. (1948) Natural evapotranspiration from open water, bare soil and grass. *Proceedings of the Royal Society of London, Series A-Mathematical Physical and Engineering Sciences*, **193**, 120—145.
- Penning, P. D., Parsons, A. J., Orr, R. J., Harvey, A. and Yarrow, N. H. (1995) Dietary preference of heifers for grass or clover, with and without romensin slow-release anti-bloat boluses. *Animal Production*, **60**, 550, Proceedings of the British Society of Animal Science: titles and abstract of papers for presentation at the 111th meeting of the British Society of Animal Science, Scarborough, 20—22 March, 1995.
- Penning, P. D., Parsons, A. J., Orr, R. J. and Hooper, G. E. (1994) Intake and

- behaviour responses by sheep to changes in sward characteristics under rotational grazing. *Grass and Forage Science*, **49**, 476—486.
- Penning, P. D., Parsons, A. J., Orr, R. J. and Treacher, T. T. (1991) Intake and behaviour responses by sheep to changes in sward characteristics under continuous stocking. *Grass and Forage Science*, **46**, 15—28.
- Pesaran, M. H. and Pesaran, B. (1991) Microfit 3.0 User Manual, Oxford University Press, UK, XVI + 277pp.
- Phillips, D. L., Lee, J. J. and Dobson, R. F. (1996) Sensitivity of the US corn-belt to climate-change and elevated CO<sub>2</sub>. 1. Corn and soybean yields. *Agricultural Systems*, **52**, 481—502.
- Pindyck, R. S. and Rubinfeld, D. L. (1981) *Econometric Models and Economic Forecasts*, (Second Edition) McGraw-Hill International Book Company, London, pp630.
- Poorter, H. (1993) Interspecific variation in the growth response of plants to an elevated ambient CO<sub>2</sub> concentration. *Vegetatio*, **104/105**, 77—97.
- Poorter, H., Gifford, R. M., Kriedemann, P. E. and Wong, S. C. (1992) A quantitative analysis of dark respiration and carbon content as factors in the growth response of plants to elevated CO<sub>2</sub>. *Australian Journal of Botany*, **40**, 501—513.
- Potvin, C. and Strain, B. R. (1985) Effects of CO<sub>2</sub> enrichment and temperature on growth of two C<sub>4</sub> weeds, *Echinochloa crus-galli* and *Eleusine indica*. *Canadian Journal of Botany*, **63**, 1495—1499.
- Rattray, P. V. and Clark, D. A. (1984) Factors affecting the intake of pasture. *New*

*Zealand Agricultural Science*, **18**, 141—146.

- Reynolds, J. F. and Acock, B. (1985) Predicting the response of plants to increasing carbon dioxide: a critique of plant growth models. *Ecological Modelling*, **29**, 101—129.
- Ridout, M. S. and Robson, M. J. (1991) Diet composition of sheep grazing grass/white clover swards: a re-evaluation. *New Zealand Journal of Agricultural Research*, **34**, 89—93.
- Riha, S. J., Wilks, D. S. and Simoens, P. (1996) Impact of temperature and precipitation variability on crop model predictions. *Climatic Change*, **32**, 293—311.
- Robinson, J. J., McDonald, I., Fraser, C. and Gordon, J. G. (1980) Studies on the reproduction in prolific ewes. 6. The efficiency of utilisation for conceptus growth. *Journal of Agricultural Science, Cambridge*, **94**, 331—338.
- Robson, M. J. (1981) Respiratory efflux in relation to temperature of simulated swards of perennial ryegrass with contrasting soluble carbohydrate contents. *Annals of Botany*, **48**, 269—273.
- Robson, M. J., Ryle, G. J. A. and Woledge, J. (1988) The grass plant – its form and function. In: M. B. Jones and A. Lazenby (Editors) *The Grass Crop The Physiological Basis of Production*, Chapman and Hall, London, UK, **Chapter 2**, pp25—83.
- Robson, M. J., Parsons, A. J. and Williams, T. E. (1989) Herbage production: grasses and legumes. In: W. Holmes (Editor) *Grass: Its Production and Utilization*, Blackwell Scientific Publications, Oxford, UK, pp7—88.

- Rodriguez, R. O. and Fernandez, N. R. (1995) Behavioural differences in some soils of the Argentinean Pampa in relation to possible climatic changes. *Secheresse*, **6**, 183—187.
- Rogers, H. H., Bingham, G. E., Cure, J. D., Smith, J. M. and Surano, K. A. (1983) Responses of selected plant species to elevated carbon dioxide in the field. *Journal of Environmental Quality*, **12**, 569—574.
- Rogers, H. H., Cure, J. D. and Smith, J. M. (1986) Soybean growth and yield response to elevated carbon dioxide. *Agriculture, Ecosystems and Environment*, **16**, 113—128.
- Rosenzweig, C. and Tubiello, F. N. (1996) Effects of changes in minimum and maximum temperature on wheat yields in central US – a simulation study. *Agricultural and Forest Meteorology*, **80**, 215—230.
- Rosenzweig, C. and Parry, M. L. (1994) Potential impact of climate change on world food supply. *Nature*, **367**, 133—138.
- Roumet, C. and Roy, J. (1996) Prediction of the growth response to elevated CO<sub>2</sub>: a search for physiological criteria in closely related grass species. *New Phytologist*, **134**, 615—624.
- Rounsevell, M. D. A., Brignall, A. P. and Siddons, P. A. (1996) Potential climate change effects on the distribution of agricultural grassland in England and Wales. *Soil Use and Management*, **12**, 44—51.
- Ryan, M. (1989) Development of a legume-based dairy system. In: P. Plancquaert and P. Hagger (Editors) *Legumes in Farming Systems*, Kluwer Academic

Publishers, Dordrecht, pp159—167

- Ryan, M. (1988) Irish studies on milk production from grass/white clover swards. In: *The Grassland Debate: White Clover versus Applied Nitrogen*, Proceedings of a Conference held at the National Agriculture Centre, Stoneleigh, 19 October. Kenilworth: Royal Agricultural Society of England, Agricultural Development and Advisory Service
- Ryle, G. J. A., and Powell, C. E. (1992) The influence of elevated CO<sub>2</sub> and temperature on biomass production of continuously defoliated white clover. *Plant, Cell and Environment*, **15**, 593—599.
- Ryle, G. J. A., Powell, C. E. and Tewson, V. (1992a) Effect of elevated CO<sub>2</sub> on the photosynthesis, respiration and growth of perennial ryegrass. *Journal of Experimental Botany*, **43**, 811—818.
- Ryle, G. J. A., Woledge, J., Tewson, V. and Powell, C. E. (1992b) Influence of elevated CO<sub>2</sub> and temperature on the photosynthesis and respiration of white clover dependent on N<sub>2</sub> fixation. *Annals of Botany*, **70**, 213—220.
- Ryle, G. J. A., Powell, C. E. and Davidson, I. A. (1992c) Growth of white clover, dependent on N<sub>2</sub> fixation, in elevated CO<sub>2</sub> and temperature. *Annals of Botany*, **70**, 221—228.
- Saarikko, R. A. and Carter, T. R. (1996) Estimating the development and regional thermal suitability of spring wheat in Finland and under climatic warming. *Climate Research*, **7**, 243—252.
- Sage, R. F., Sharkey, T. D. and Sieman, J. R. (1989) Acclimation of photosynthesis to

elevated CO<sub>2</sub> in five C<sub>3</sub> species. *Plant Physiology*, **89**, 590—596.

Sanders, J. O. and Cartwright, T. C. (1979) A general cattle production systems model. I. Description of the model. *Agricultural Systems*, **4**, 217—227.

Sands, P. J. (1996) Modelling canopy production. III. Canopy light – utilisation efficiency and its sensitivity to physiological and environmental variables. *Australian Journal of Plant Physiology*, **23**, 103—114.

Sands, P. J. (1995a) Modelling canopy production. II. From single – leaf photosynthetic parameters to daily canopy photosynthesis. *Australian Journal of Plant Physiology*, **22**, 603—614.

Sands, P. J. (1995b) Modelling canopy production. I. Optimal distribution of photosynthetic resources. *Australian Journal of Plant Physiology*, **22**, 593—601.

Sands, P. J., Cromer, R. N. and Kirschbaum, M. U. F. (1992) A model of nutrient response in *Eucalyptus grandis* seedlings. *Australian Journal of Plant Physiology*, **19**, 459—470.

Sasek, T. W., DeLucia, E. H. and Strain, B. R. (1985) Reversibility of photosynthetic inhibition in cotton after long-term exposure to elevated CO<sub>2</sub> concentrations. *Plant Physiology*, **78**, 619—622.

Saugier, B., Ripley, E. A. and Lueke, P. (1974) A mechanistic model of plant growth and water use for matador grassland. *Technical report 65*, Matador project, University of Saskatchewan, 1974.

Schapendonk, A. H. C. M., and Gourdriaan, J. (1995) The influence of increased CO<sub>2</sub> on the annual production of a *Lolium perenne* sward. In: P. Mathis (Editor)

*Photosynthesis: from Light to Biosphere*, Kluwer Academic Publishers, The Netherlands, **Vol. 5**, 779—784.

- Schapendonk, A. H. C. M., Dijkstra, P., Groenwold, J., Pot, C. S. and Van de Geijn, S. C. (1996) Implications of elevated carbon dioxide concentration on *Lolium perenne* L. swards. Growth analyses and carbon balance. In: R. J. Froud-Williams, R. Harrington, T. J. Hocking, H. G. Smith and T. H. Thomas (Editors) *Aspects of Applied Biology, Implications of "Global Environmental Change" for Crops in Europe*, **No 45**, 31—40.
- Scheidegger, U. C. and Nösberger, J. (1984) Influence of carbon dioxide concentration on growth, carbohydrate content, translocation and photosynthesis of white clover. *Annals of Botany*, **54**, 735—742.
- Schenk, U., Jäger, H. -J. and Weigel, H. -J. (1997a) The response of perennial ryegrass/white clover mini-swards to elevated atmospheric CO<sub>2</sub> concentrations: effects on yield and fodder quality. *Grass and Forage Science*, **52**, 232—241.
- Schenk, U., Jäger, H. -J. and Weigel, H. -J. (1997b) The response of perennial ryegrass/white clover swards to elevated CO<sub>2</sub> concentrations. I. Effects on competition and species composition and interaction with N supply. *New Phytologist*, **135**, 67—79.
- Schenk, U., Manderscheid, R., Hugen, J. and Weigel, H. -J., (1995) Effects of CO<sub>2</sub> enrichment and intraspecific competition on biomass carbon in soil of perennial ryegrass and white clover. *Journal of Experimental Botany*, **46**, 987—993.
- Schiemann, R., Jentsch, W. and Wittenburg H. (1971) Zur Abhängigkeit der

Verdaulichkeit der Energie und der Nährstoffe von der Höhe der Fetleraufnahme unter der Rationszusammensetzung bei Milchkühen. *Archiv für Tierernährung*, **21**, 223—240.

Schneider, S. H. 1990. *Global Warming. Are We Entering the Greenhouse Century?* Lutterworth Press, Cambridge, 343pp.

Scottish Office Agriculture, Environment and Fisheries Department (1995) *Economic Report on Scottish Agriculture 1995 Edition*, HMSO, Edinburgh, v + 67pp.

Seino, H. (1995) The impacts of climatic warming on cereal crop production in Japan. *Journal of Agricultural-Meteorology*, **51**, 131—138.

Semenov, M. A., Wolf, J., Evans, L. G., Eckersten, H. and Iglesias, A. (1996) Comparison of wheat simulation models under climate change. II. Application of climate change scenarios. *Climate Research*, **7**, 271—281.

Sheehy, J. E., Gastal, F., Mitchell, P. L., Durand, J.-L., Lemaire, G. and Woodward, F. I. (1996) A nitrogen-led model of grass growth. *Annals of Botany*, **77**, 165—177.

Sheehy, J. E., Mitchell, P. L., Durand, J.-L., Gastal, F. and Woodward, F. I. (1995) Calculation of translocation coefficients from phloem anatomy for use in crop models. *Annals of Botany*, **76**, 263—269.

Sheehy, J. E., Cobby, J. M. and Ryle, G. J. A. (1980) The use of a model to investigate the influence of some environmental factors on the growth of perennial ryegrass. *Annals of Botany*, **46**, 343—365.

Sheriff, D. W. (1992) Roles of carbon gain and allocation in growth at different nitrogen nutrition in *Eucalyptus globulus* seedlings. *Australian Journal of Plant*

*Physiology*, **19**, 637—652.

Sibbald, A. R., Maxwell, T. J., Morgan, T. E. H., Jones, J. R. and Rees, M. E. (1994)

The implications of controlling grazed sward height for the operation and productivity of upland sheep systems in the UK. 2. Effects of two annual stocking rates in combination with two levels of fertiliser nitrogen. *Grass and Forage Science*, **49**, 89—95.

Sinclair, J. and Corrall, A. J. (1978) Variation in grass production at Hurley and a

model of the influence of water availability on yield. *Journal of Science, Food and Agriculture*, **29**, 300—301.

Sinclair, T. R. and Horie, T. (1989) Leaf nitrogen, photosynthesis and crop radiation

use efficiency: A review. *Crop Science*, **29**, 90—98.

Siqueira, O. J. F. de, Farias, J. R. B. de and Sans, L. M. A. (1994) Potential effects of

global climate change on Brazilian agriculture and studies of adaptation for wheat, maize and soyabean. *Revista Brasileira de Agrometeorologia*, **2**, 115—129.

Song, H. and Dinkel, C. A. (1978) Mathematical models of postweaning growth, feed

intake, and carcass composition of beef cattle. I. Empirical predictive model of voluntary feed intake from weaning to slaughter. *Journal of Animal Science*, **47**, 56—69.

Soussana, J. F. and Hartwig, U. A. (1996) The effects of elevated CO<sub>2</sub> on symbiotic

N<sub>2</sub> fixation: a link between carbon and nitrogen cycles in grassland ecosystems. *Plant and Soil*, **187**, 321—332.

Soussana, J. F., Casella, E. and Loiseau, P. (1996) Long-term effects of CO<sub>2</sub>

enrichment and temperature increase on a temperate grass sward. II. Plant nitrogen budgets and root fraction. *Plant and Soil*, **182**, 101—114.

Spedding, C. R. W. and Diekmahns, E. C. (1972) *Grasses and Legumes in British Agriculture*. Commonwealth Agricultural Bureaux, Farnham Royal, 511pp.

SPSS Inc., (1990) SPSS/PC Advanced Statistics 4.0, Chicago, Illinois, US.

Steel, R. G. D. and Torrie, J. H. (1981) *Principles and Procedures of Statistics A Biometrical Approach* (2<sup>nd</sup> Edition), McGraw-Hill, London, 633pp.

Stewart, J. and Potvin, C. (1996) Effect of elevated CO<sub>2</sub> on artificial grassland community: competition, invasion and neighbourhood growth. *Functional Ecology*, **10**, 157—166.

Stewart, T. A. and Haycock, R. E. (1984) Beef production from low N and high N S24 perennial ryegrass/Blanca white clover swards – a six – year farmlet comparison. *Research and Development in Agriculture*, **1**, 103—111.

Stockle, C. O., Dyke, P. T., Williams, J. R., Jones, C. A. and Rosenberg, N. (1992) A method for estimating the direct and climatic effects of rising atmospheric carbon dioxide on growth and yield of crops: Part II – Sensitivity analysis at three sites in the midwestern USA. *Agricultural Systems*, **38**, 239—256.

Stulen, I. and den Hertog, J. (1993) Root growth and functioning under atmospheric CO<sub>2</sub> enrichment. *Vegetatio*, **104/105**, 99—115.

Szász, G. (1984) A simulation model of grass yields based on ecological factors. In: H. Riley and A. O Skjelvåg (Editors) *The Impact of Climate on Grass Production and Quality*, Proceedings of the 10<sup>th</sup> General Meeting of the European Grassland

Federation, Ås, Norway, 1984, pp525—529.

Taylor, St. C. S. (1968) Time taken to mature in relation to mature weight for sexes, strains and species of domesticated mammals and birds. *Animal Production*, **10**, 157—69.

Theil, H. (1970) *Economic Forecasts and Policy* (2<sup>nd</sup> edition), North Holland Publishing Company, Amsterdam.

Thomson, D. J. (1984) The nutritive value of white clover. *British Grassland Society Occasional Symposium*, **16**, 79—92.

Thornley, J. H. M. (1996) Modelling water in crops and plant ecosystems. *Annals of Botany*, **77**, 261—275.

Thornley, J. H. M. (1991) A transport - resistance model of forest growth and partitioning. *Annals of Botany*, **68**, 211—226.

Thornley, J. H. M. (1976) *Mathematical Models in Plant Physiology*. Academic press, London, UK, 317pp.

Thornley, J. H. M. and Cannell, M. G. R. (1997) Temperate grassland responses to climate change: an analysis using the Hurley pasture model. *Annals of Botany*, **80**, 205—221.

Thornley, J. H. M. and Cannell, M. G. R. (1992) Nitrogen relations in a forest plantation — soil organic matter ecosystem model. *Annals of Botany*, **70**, 137—151.

Thornley, J. H. M. and Johnson, I. R. (1990) *Plant and Crop Modelling: A*

*Mathematical Approach to Plant and Crop Physiology*, Clarendon Press, Oxford, UK, XV + 669pp.

- Thornley, J. H. M. and Verberne, E. L. J. (1989) A model of nitrogen flows in grassland. *Plant, Cell and Environment*, **12**, 863—886.
- Thornley, J. H. M., Bergelson, J. and Parsons, A. J. (1995) Complex dynamics in a carbon – nitrogen model of a grass – legume pasture. *Annals of Botany*, **75**, 79—94.
- Thornley, J. H. M., Parsons, A. J., Newman, J. and Penning, P. D. (1994) A cost – benefit model of grazing intake and diet selection in a two – species temperate grassland sward. *Functional Ecology*, **8**, 5—16.
- Thornley, J. H. M., Fowler, D. and Cannel, M. G. R. (1991) Terrestrial carbon storage resulting from CO<sub>2</sub> and nitrogen fertilization in temperate grasslands. *Plant, Cell and Environment*, **14**, 1007—1011.
- Tolbert, N. E. and Zelitch, I. (1983) Carbon Metabolism. In: E. R Lemon (Editor) *CO<sub>2</sub> and Plants*, **Chapter 3**, Westview Press, Boulder, Colorado, US.
- Tolley, L. C. and Strain, B. R. (1984) Effects of CO<sub>2</sub> enrichment on growth of *Liquidambar styraciflua* and *Pinus taeda* seedlings under different irradiance levels. *Canadian Journal of Forestry Research*, **14**, 343—350.
- Torres-Hernandez, G. and Hohenboken, W. D. (1980) Biometric properties of lactations in ewes raising single or twin lambs. *Animal Production*, **30**, 431—436.
- Torrsell, B. W. R. and Kornher, A. (1983) Validation of a yield prediction model for temporary grasslands. *Swedish Journal of Agricultural Research*, **13**, 125—135.

- Touré, A., Major, D. J. and Lindwall, C. W. (1994) Sensitivity of four wheat simulation models to climate change. *Canadian Journal of Plant Science*, **75**, 69—74.
- Usher, M. B. (1970) An algorithm for estimating the length and direction of shadows with reference to the shadows of shelter belts. *Journal of Applied Ecology*, **7**, 141—145.
- Vallis, I., Henzell, E. F. and Evans, T. R. (1977) Uptake of soil nitrogen by legumes in mixed swards. *Australian Journal of Agricultural Research*, **28**, 413—425.
- van Es, A. J. H. (1976) Factors influencing the efficiency of energy utilisation by beef and dairy cattle. In: H Swan and W. H. Broster (Editors) *Principles of Cattle Production*. London: Butterworths (Proceedings Easter School Agricultural Science University of Nottingham. 1975) pp237—253.
- Van Oosten, J. J. and Besford, R. T. (1996) Acclimation of photosynthesis to elevated CO<sub>2</sub> through feedback regulation of gene expression: Climate of opinion. *Photosynthesis Research*, **48**, 353—365.
- van Wijk, W. R. and Scholte Ubing, D. W. (1963) Radiation. In: W. R. van Wijk (Editor) *Physics of Plant Environment*, North Holland Publishing Company, Amsterdam, pp62—101.
- Viner, D. and Hulme, M. (1994) *The Climate Impacts LINK Project. Providing climate change scenarios for impacts assessment in the UK*. Climate Change Research Unit, University of East Anglia, UK.
- Viner, D., Hulme, M. and Raper, S. C. B. (1995) Climate change scenarios for the — assessments of the climate change on regional ecosystems. *Journal of Thermal*

*Biology*, **20**, 175—190.

- Walker, T. W., Adams, A. F. R. and Orchiston, H. D. (1956) Fate of labelled nitrate and ammonium nitrogen when applied to grass and clover grown separately and together. *Soil Science*, **81**, 339—351.
- Wang, J. H. and Lin, E. (1996) The impacts of potential climate-change and climate variability on simulated maize production in China. *Water Air and Soil Pollution*, **92**, 75—85.
- Wang, Y. P., Handoko Jr and Rimmington, G. M. (1992) Sensitivity of wheat growth to increased air temperature for different scenarios of ambient CO<sub>2</sub> concentration and rainfall in Victoria, Australia — a simulation study. *Climate Research*, **2**, 131—149.
- Wigley, T. M. L. and Raper, S. C. B. (1992) Implications for climate and sea level of revised IPCC emissions scenarios. *Nature*, **357**, 293—300.
- Wigley, T. M. L. and Raper, S. C. B. (1990) Thermal-expansion of sea-water associated with global warming. *Nature*, **330**, 127—131.
- Williams, T. E. (1980) Herbage production: grasses and leguminous crops. In: W. Holmes (Editor) *Grass and its Production and Utilization*, Blackwell Scientific Publications, London, pp6—69.
- Wilman, D. and Altimimi, M. A. K. (1984) The in-vitro digestibility and chemical composition of plant parts in white clover, red clover and lucerne during primary growth. *Journal of Science, Food and Agriculture*. **35**, 133—138.
- Wilman, D., Ojuederie, B. M. and Asare, E. O. (1976) Nitrogen and Italian ryegrass.
3. Growth up to 14 weeks: yields, proportions, digestibilities and nitrogen contents

- of crop fractions, and tiller populations. *Journal of the British Grassland Society*, **31**, 73—79.
- Wittwer, S. H. (1986) Worldwide status and history of CO<sub>2</sub> enrichment – an overview. In: H. Z. Enoch and B. A. Kimball (Editors) *Carbon Dioxide Enrichment of Greenhouse Crops. Vol. I. Status and CO<sub>2</sub> Sources*, CRC Press, Inc., Boca Raton, FL., pp3—15.
- Wittwer, S. H. and Robb, W. (1964) Carbon dioxide enrichment of greenhouse atmospheres for food crop production. *Economic Botany*, **18**, 34—56.
- Woledge, J. (1988) Competition between grass and clover in spring affected by nitrogen fertiliser. *Annals of Applied Biology*, **112**, 175—186.
- Woledge, J. (1971) The effects of light intensity during growth on the subsequent rate of photosynthesis. *Annals of Applied Biology*, **35**, 311—322.
- Woledge, J. and Pearse, P. J. (1985) The effect of nitrogenous fertilizer on the photosynthesis of leaves of a ryegrass sward. *Grass and Forage Science*, **40**, 305—309.
- Woledge, J. and Dennis, W. D. (1982) The effect of temperature on photosynthesis of ryegrass and white clover leaves. *Annals of Botany*, **50**, 25—35.
- Woledge, J., Reyner, A., Tewson, V. and Parsons, A. J. (1992) The effect of cutting on the proportions of perennial ryegrass and white clover mixtures. *Grass and Forage Science*, **47**, 169—179.
- Woledge, J., Bunce, J. A. and Tewson, V. (1989) The effect of air humidity on photosynthesis of ryegrass and white clover at three temperatures. *Annals of*

*Botany*, **63**, 271—279.

- Wolf, J. and Van Diepen, C. A. (1994) Effects of climate change on silage production potential in the European Community. *Agricultural and Forest Meteorology*, **71**, 33—60.
- Wolfe, D. W. and Erickson, J. D. (1993) Carbon dioxide effects on plants: uncertainties and implications for modelling crop response to climate change. In: H. M. Kaiser and T. E. Drennen (Editors) *Agricultural Dimensions of Global Climate Change*, St Lucie Press, Delray Beach, Florida, USA, **Chapter 8**, pp153—178.
- Wong, S. C. (1993) Interaction between elevated atmospheric partial pressure of CO<sub>2</sub> and humidity on plant growth: comparison between cotton and radish. *Vegetatio*, **104/105**, 211—221.
- Wong, S. C. (1979) Elevated atmospheric partial pressure of CO<sub>2</sub> and plant growth. I. Interactions of nitrogen nutrition and photosynthetic capacity in C3 and C4 plants. *Oecologia*, **44**, 68—74.
- Wong, S. C., Rowan, I. R. and Farquhar, G. D. (1979) Stomatal conductance correlates with photosynthetic capacity. *Nature*, **282**, 424—426.
- Wood, P. D. P. (1969) Factors affecting the shape of the lactation curve. *Animal Production*, **11**, 307—316.
- Wood, P. D. P., King, J. O. L. and Youdan, P. G. (1980) Relationships between size, live-weight change and milk production characters in early lactation in airy cattle. *Animal Production*, **31**, 143—151.

- Woodward, F. I. (1988) The response of stomata to changes in atmospheric levels of CO<sub>2</sub>. *Plants Today*, **1**, 132—135.
- Woodward, F. I. (1987) Stomatal numbers are sensitive to increases in CO<sub>2</sub> from pre-industrial levels. *Nature*, **327**, 617—618.
- Woodward, F. I. (1986) Ecophysiological studies on the shrub *Vaccinium myrtillus* L. Taken from a wide altitudinal range. *Oecologia*, **70**, 580—586.
- Woodward, F. I. and Bazzaz, F. A. (1988) The response of stomatal density to CO<sub>2</sub> partial pressure. *Journal of Experimental Botany*, **39**, 1771—1781.
- Woodward, F. I., Thompson, G. B. and McKee, I. F. (1991) The effects of elevated concentrations of carbon dioxide on individual plants, populations, communities and ecosystems. *Annals of Botany*, **67 (Supplement 1)**, 23—38.
- Woodward, S. J. R. and Wake, G. C. (1993) A simple model for optimizing rotational grazing. *Agricultural Systems*, **41**, 123—155.
- Woodward, S. J. R., Wake, G. C. and McCall, D. G. (1995) Optimal grazing of a multi-paddock system using a discrete time model. *Agricultural Systems*, **48**, 119—139.
- Xevi, E., Gilley, J. and Feyen, J. (1996) Comparative-study of 2 crop yield simulation-models. *Agricultural Water Management*, **30**, 155—173.
- Yelle, S., Beeson, R. C., Jr., Trudel, M. J. and Gosselin, A. (1989) Acclimation of two tomato species to high atmospheric CO<sub>2</sub>. I. Sugar and starch concentrations. *Plant Physiology*, **90**, 1465—1472.
- Zanetti, S., Hartwig, U. A., Lüscher, A., Hebeisen, T., Frehner, M., Fischer, B. U.,