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

by

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TABLE OF CONTENTS

Volume 2

Appendix I

List of variables in the model

Variable	Description	Units
α	Photochemical efficiency at atmospheric CO_2 concentration	kg CO_2 MJ^{-1}
ϕ_j	Effect of water and nutrient availability on the proportionate rate of dry-matter production of crop j	
Δ	Slope of the saturation vapour pressure	mbars $°C^{-1}$
ℓ	Cumulative leaf area index	ha (leaf) ha^{-1} (ground)
ℓ_j	Cumulative leaf area index for crop j	ha (leaf) ha^{-1} (ground)
λ	Defined by equation (3.50)	
AET	Actual evapotranspiration	mm
alpha	Angstrom coefficient	
Atm	Atmospheric pressure	Pa
beta	Angstrom coefficient	
BrutE	Effects of vapour pressure on total radiation	J m^{-2}
BrutS	Effects of cloud cover on total radiation	J m^{-2}
BrutT	Upward total radiation	J m^{-2}
C_{dg}	Proportionate digestibility of the white clover component	
$C_{L,j}$	Quantity of the leaf component removed from the sward for crop j	kg DM ha^{-1}

Variable	Description	Units
$C_{Replace}$	Rate of substitution of forage by concentrates	kg DM herbage (kg DM concentrates)$^{-1}$
CO_2	Atmospheric concentration of CO_2	kg CO_2 m^{-3}
$CO_{2,\ ppmv}$	Atmospheric concentration of CO_2	ppmv
D_D	Dead dry matter	kg DM ha^{-1}
d_g	Proportionate digestibility of the herbage	
D_L	Leaf dry matter	kg DM ha^{-1}
D_R	Root dry matter	kg DM ha^{-1}
D_S	Stem dry matter	kg DM ha^{-1}
$D_{L,\ j}$	Leaf dry matter for crop j	kg DM ha^{-1}
Day	Day number since 1 January	day
DayLen	Effective day length	h
$delta_D$	Daily change in the quantity of dead material	kg DM ha^{-1}
$delta_L$	Daily change in the quantity of leaf dry-matter	kg DM ha^{-1}
$delta_S$	Daily change in the quantity of stem dry-matter	kg DM ha^{-1}
E	Potential evapotranspiration	mm day^{-1}
ES	Saturation vapour pressure	mbars
F_{max}	Maximum daily dry-matter intake of herbage per kg of metabolic weight	kg DM (liveweight$^{0.75}$)$^{-1}$ head^{-1} day^{-1}
G_{dg}	Proportionate digestibility of the grass component	
H	Daily allowance of green herbage	kg DM head^{-1}

Variable	Description	Units
H_{Move}	Quantity of herbage required to consume 95% of the maximum daily intake per paddock	kg DM paddock^{-1} day^{-1}
$HPad_{Crit}$	Minimum critical herbage mass per paddock required for grazing to occur	kg DM paddock^{-1}
H_{Req}	Quantity of herbage required to maintain maximum intake	kg DM head^{-1} day^{-1}
g_d	Amount of grass harvested	kg DM ha^{-1}
g_s	Amount of grass in the sward	kg DM ha^{-1}
I	Daily intake of herbage	kg DM head^{-1} day^{-1}
I_D	Daily intake of dead material	kg DM head^{-1} day^{-1}
$I_{D,j}$	Daily intake of dead material for crop j	kg DM head^{-1} day^{-1}
I_F	Herbage intake	kg DM head^{-1}
I_L	Daily intake of leaf dry matter	kg DM head^{-1} day^{-1}
$I_{L,j}$	Daily intake of leaf dry matter for crop j	kg DM head^{-1} day^{-1}
I_{max}	Maximum daily dry-matter intake of herbage	kg DM head^{-1}
I_O	Actual daily radiation	MJ ha^{-1} (ground) day^{-1}
I_S	Daily intake of stem dry matter	kg DM head^{-1} day^{-1}
$I_{S,j}$	Daily intake of stem dry matter for crop j	kg DM head^{-1} day^{-1}
L	Leaf area index	ha (leaf) ha^{-1} (ground)
L_j	Leaf area index of crop j	ha (leaf) ha^{-1} (ground)
Lat	Latitude of the site	degrees

Variable	Description	Units
LatRad	Latitude of the site	rad
L_S	Quantity of leaf material remaining in the sward after cutting	kg DM ha^{-1}
LWT	Liveweight	kg $head^{-1}$
M_{Conc}	ME value of 1 kg of ingested concentrates	MJ $(kg\ DM)^{-1}$
M_{Fod}	ME value of 1 kg of ingested herbage	MJ $(kg\ DM)^{-1}$
M_j	Total dry weight of crop component j	kg DM ha^{-1}
ME_C	MEI value of the diet	MJ $head^{-1}$ day^{-1}
N	Daily available nitrogen	kg N ha^{-1} day^{-1}
NL	Night length	h
P	Canopy gross rate of photosynthesis	kg CO_2 ha^{-1} (ground) day^{-1}
P_j	Canopy gross rate of photosynthesis of crop j	kg CO_2 ha^{-1} (ground) day^{-1}
P^T_{max}	Leaf photosynthetic rate at saturating light levels modified for the effect of temperature	kg CO_2 ha^{-1} (leaf) day^{-1}
P_{max}	Leaf photosynthetic rate at saturating light levels	kg CO_2 ha^{-1} (leaf) day^{-1}
P_n	Canopy net rate of photosynthesis	kg CO_2 ha^{-1} (ground) day^{-1}
PAR	Photosynthetically active radiation	MJ ha^{-1} (ground) day^{-1}
PET	Potential evapotranspiration	mm

Variable	Description	Units
Prop	proportion of white clover leaf area at a given leaf area of the sward	
R_0	Radiation corrected for the soil heat flux	J m^{-2}
R	Growth and maintenance respiration	kg CO_2 ha^{-1} (ground) day^{-1}
R_j	Growth and maintenance respiration for crop j	kg CO_2 ha^{-1} (ground) day^{-1}
RX	Daily clear sky radiation	MJ ha^{-1} (ground) day^{-1}
SolarDec	Solar constant	degrees
SolarDecR	Solar constant	rad
Solcon	Solar constant	J m^{-2} (ground) day^{-1}
S_S	Quantity of stem material remaining in the sward after cutting	kg DM ha^{-1}
T	Mean daily temperature	°C
T_{Conc}	ME value of the intake of concentrates	MJ $head^{-1}$
T_{Fod}	ME value of the intake of herbage	MJ $head^{-1}$
V	Evaporation component due to the wind and the vapour pressure deficit	kg m^{-2}
WtGain	Daily gain in the above-ground herbage	kg DM ha^{-1}
W	Available soil water	mm
w_d	Amount of white clover harvested	kg DM ha^{-1}
w_s	Amount of white clover in the sward	kg DM ha^{-1}

Variable	Description	Units
YearAng	year angle	degrees

List of parameters in the model

Parameter	Description	Units
α_{max}	Maximum value of the photochemical efficiency	kg CO_2 MJ^{-1}
β_1—β_4	Constants in equations (3.26) and (3.27)	
ε	Rate of decline of P^0_{max} with irradiance	
γ_D	Proportionate daily rate of dead matter decomposing	
γ_L	Proportionate daily senescence rate of leaf matter	
γ_S	Proportionate daily senescence rate of stem matter	
$\gamma_{D,j}$	Proportionate daily rate of dead matter decomposing for crop j	
$\gamma_{L,j}$	Proportionate daily senescence rate of leaf matter for crop j	
$\gamma_{S,j}$	Proportionate daily senescence rate of stem matter for crop j	
θ	Efficiency of converting CO_2 to dry matter	kg CH_2O (kg CO_2)$^{-1}$
Θ	Leaf photosynthesis parameter	
κ	Constants in equation (3.28)	
λ	Proportion of the daily gain in above ground dry matter partitioned to leaves	
λ_j	Proportion of the daily gain in above ground dry matter partitioned to leaves for crop j	
ν	Selection coefficient for the preferential removal of white clover	

Parameter	Description	Units
ν_{Cow}	Selection coefficient for the preferential removal of white clover by grazing ruminants	
ν_D	Selection coefficient for the preferential removal of white clover dry matter	
ν_L	Selection coefficient for the preferential removal of white clover leaf material	
ξ_L	Proportion of the total pasture by weight accounted for by leaf material	
ξ_S	Proportion of the total pasture by weight accounted for by leaf material	
ρ	Proportion of the assimilate partitioned to the root	
ρCO_2	Density of CO_2 at 1 atmosphere	kg CO_2 m^{-3}
τ	CO_2 conductance parameter	m s^{-1}
ϖ	Photorespiration constant	kg m^{-2} s^{-1}
A	Specific leaf area	ha leaf (kg DM)$^{-1}$
a1—a2	Constants in equation (3.24)	
A1—A2	Constants in equation (3.2)	
Atm_{Sea}	Atmospheric pressure at sea-level	Pa
AWC	Available water capacity	mm
B1—B2	Constants in equation (3.3)	
b1	Constant in equation (3.53)	
be1—be2	Constant in equation (3.34)	

Parameter	Description	Units
bs1—bs2	Constant in equation (3.35)	
bt1	Constant in equation (3.32)	
c	white clover	
D0	Albedo factor for water	
d1	Constant in equation (3.31)	
D8	Constant in equation (3.37)	
$dg_{D,j}$	Proportionate digestibility of the dead material for crop j	
$dg_{L,j}$	Proportionate digestibility of the leaf component for crop j	
$dg_{S,j}$	Proportionate digestibility of the stem component for crop j	
End	Temperature which defines the end of the growing season	°C
es1—es2	Constant in equation (3.32)	
ev1—ev2	Constant in equation (3.37)	
g	Grass	
H_{Crit}	Minimum critical herbage mass per hectare required for grazing to occur	kg DM ha^{-1}
I_{Conc}	Dry-matter intake of concentrates	kg DM $head^{-1}$ day^{-1}
j	Component of the crop	
k	Light extinction coefficient	
k_j	Light extinction coefficient for crop j	

Parameter	Description	Units
K	Average daily temperature	K
K_0	0°C expressed in degrees Kelvin	K
KP_{max}	CO_2 concentration at which $P_{max}^{CO_2}$ is half its maximal value	kg CO_2 m^{-3}
L_v	Latent heat of vaporisation of water	J kg^{-1}
m	Leaf transmission coefficient	
m_j	Leaf transmission coefficient for crop j	
M_j	Total dry-matter weight of crop j	kg DM ha^{-1}
N_{max}	Saturating level of nitrogen	kg N ha^{-1} day^{-1}
P_{ha}	Area per paddock	ha $paddock^{-1}$
$P_{max}^{CO_2}$	Maximum hourly rate of leaf photosynthesis	kg CO_2 ha (leaf) hr^{-1}
P_{max}^{0}	Maximum hourly rate of leaf photosynthesis at atmospheric CO_2	kg CO_2 ha (leaf) hr^{-1}
r_j	Respiration maintenance coefficient	kg CO_2 kg DM^{-1} day^{-1}
Rdg_L	Proportionate reduction in the digestibility of the leaf component	
$Rdg_{L,j}$	Proportionate reduction in the digestibility of the leaf component for crop j	
Rdg_S	Proportionate reduction in the digestibility of the stem component	

Parameter	Description	Units
$Rdg_{S,j}$	Proportionate reduction in the digestibility of the stem component for crop j	
S_2	Number of days since the fraction of available soil water fell below 0.5	day
S	Psychrometric constant	mbars °C^{-1}
SR	Stocking rate per hectare	stock ha^{-1}
S_{R1}—S_{R2}	Constants in equation (3.55)	
St_j	Temperature which defines the start of the growing season for crop j	°C
T_0	Temperature at which photosynthesis ceases	°C
T_{Ref}	Temperature at which photosynthesis is maximal	°C
W_{max}	Available soil water at field capacity	mm
Y_j	Respiration growth conversion efficiency of crop j	kg CO_2 (kg CO_2)$^{-1}$
z	Zenith angle	degrees

Appendix II

II.1 Calculation of Day Length and Daily Clear Sky Radiation

II.1.1 Calculation of Solar Constant and Declination

In order to calculate the daily clear sky radiation, the solar constant and solar declination must be determined. The solar constant (SolCon, J m^{-2} (ground) day^{-1}) is defined as the irradiancy of 1 cm^2 perpendicular to the sun rays at the top of the atmosphere, and has been calculated from the following formula (Hume and Corrall, 1986):

$$\mathrm{SolCon} = 1360 * \left(1 + 0.0335 * \cos\left(2 * \pi * \mathrm{Day}/365\right)\right) \tag{II.1}$$

where Day represents the day number measured from 1 January. In the sward model, the solar constant is converted to MJ ha^{-1}. The definition of the solar declination is the angle between the line joining the sun and the earth, and the equatorial plane. The solar declination is 0° at the equinoxes, and +23.45° on the 21 June and -23.45° on the 21 December. One year corresponds to 360° and it is assumed that the year angle is 0° on the 21 March, and thus the year angle (YearAng, degrees) for a given day is expressed by the following relationship:

$$\mathrm{YearAng} = \left[\frac{\mathrm{Day} - 21}{365}\right] * 360 \tag{II.2}$$

In the sward model, the year angle is converted into radians. The following equation, which was defined by Usher (1970), was used to calculate the solar declination (SolarDec, degrees):

$$\begin{aligned} \text{SolarDec} = 0.38092 &- 0.76996 * \cos(\text{YearAng}) \\ &+ 23.265 * \sin(\text{YearAng}) \\ &+ 0.36958 * \cos(2 * \text{YearAng}) \\ &+ 0.10868 * \sin(2 * \text{YearAng}) \\ &+ 0.01834 * \cos(3 * \text{YearAng}) \\ &- 0.16650 * \sin(3 * \text{YearAng}) \\ &- 0.00392 * \cos(4 * \text{YearAng}) \\ &+ 0.00072 * \sin(4 * \text{YearAng}) \\ &- 0.00051 * \cos(5 * \text{YearAng}) \\ &+ 0.00250 * \sin(5 * \text{YearAng}) \\ &+ 0.00442 * \cos(6 * \text{YearAng}) \end{aligned} \tag{II.3}$$

II.1.2 Calculation of Effective Day Length, DayLen

The effective day length must also be determined in order to calculate the actual and clear sky radiation. Following France and Thornley (1984), the effective day length, DayLen (h), is calculated from the following equations:

$$\text{DayLen} = \frac{\arccos(\text{ccos} - \text{ttan}) * 24}{\pi} \tag{II.4}$$

where:

$$\text{ccos} = \frac{\cos(z * \text{Rad})}{\cos(\text{LatRad}) * \cos(\text{SolarDecR})} \tag{II.5}$$

$$\text{ttan} = \tan(\text{LatRad}) * \tan(\text{SolarDecR}) \quad (II.6)$$

where z (degree) is the zenith angle, Rad converts degrees to radians, LatRad is the latitude of the specified site in radians and SolarDecR denotes the solar declination (radians) which has been converted from degrees (SolarDec) to radians. Within the model, it is assumed that the definition of sunset and sunrise is determined by civil twilight and thus the sun sets and rises at 6° below the horizon. The zenith angle (z, degrees) is therefore defined as 96°.

II.1.3 Calculation of Clear Sky Radiation, RX

McGechan and Glasbey (1988) estimated the daily clear sky radiation (RX, MJ ha^{-1} (ground) day^{-1}) from the following equations:

$$\text{RX} = 3600 * \text{SolCon} * \text{RX1} \quad (II.7)$$

$$\text{RX1} = \text{ssin} * \text{DayLen} + \text{pif} * \text{ccos} * \sin(\text{NL}/\text{pif}) \quad (II.8)$$

where:

$$\text{ssin} = \sin(\text{LatRad}) * \sin(\text{SolarDecR}) \quad (II.9)$$

$$\text{NL} = 24 - \text{DayLen} \quad (II.10)$$

$$\text{pif} = 24/\pi \quad (II.11)$$

and SolCon is derived from equation (II.1), DayLen from equation (II.4), and ccos from equation (II.5).

Appendix III

III.1 Calculation of Slope of the Saturation Vapour Pressure

The slope of the saturation vapour pressure (Δ, mbars °C^{-1}) is defined as:

$$\Delta = \frac{d1 * ES}{T + 237.3} \qquad (III.1)$$

where d1 is a constant, T (°C) is the average daily temperature and ES (mbars) is the saturation vapour pressure which is described as:

$$ES = es1 * \exp * \left(\frac{es2 * T}{T + 237.3} \right) \qquad (III.2)$$

where es1 and es2 are constants.

III.2 Calculation of Net Radiation

The net radiation received (R_O, J m^{-2}) is defined as the total radiation corrected for the effects of the upward total radiation (BrutT, J m^{-2}), and the effects of vapour pressure (BrutE, J m^{-2}) and cloud cover (BrutS, J m^{-2}). The net radiation is thus defined as:

$$R_0 = SolR - BrutT * BrutE * BrutS \qquad (III.3)$$

where (SolR, J m^{-2}) is the actual daily radiation (I_O, MJ ha^{-1} (ground) day^{-1}) converted to J m^{-2} and multiplied by the proportionate albedo factor for water (D0). The factors BrutT (J m^{-2}), BrutE (J m^{-2}) and BrutS (J m^{-2}) are described by:

$$\mathrm{BrutT} = \mathrm{bt1} * \left(K_0 + T\right)^4 \qquad \text{(III.4)}$$

$$\mathrm{BrutE} = \mathrm{be1} - \mathrm{be2} * \sqrt{\mathrm{VP}} \qquad \text{(III.5)}$$

$$\mathrm{BrutS} = \mathrm{bs1} + \frac{\mathrm{bs2} * \mathrm{Sun}}{\mathrm{DayLen}} \qquad \text{(III.6)}$$

where bt1, be1, be2, bs1 and bs2 are constants. K_0 is 0°C measured in degrees Kelvin and T is the average daily temperature (°C), VP is the vapour pressure (mbars), Sun is the number of sunshine hours (h day^{-1}) and DayLen is the effective day length (h).

III.3 Calculation of Evaporation Due to Wind and Vapour Pressure

The evaporation component (V, kg m^{-2}) due to the wind (RunW, km day^{-1}) and vapour pressure deficit (vpd, mbars) is:

$$V = \mathrm{ev1} * \mathrm{vpd} * (\mathrm{D8} + (\mathrm{RunW} * \mathrm{ev2})) \qquad \text{(III.7)}$$

where ev1, ev2 and D8 are constants and vpd (mbars) is calculated from the following equations depending on the saturation vapour pressure (ES, mbars):

$$\begin{aligned} \mathrm{vpd} &= \mathrm{ES} - \mathrm{VP}; \quad \text{for ES} \geq \text{VP} \\ \mathrm{vpd} &= 0; \quad \text{for ES} < \text{VP} \end{aligned} \qquad \text{(III.8)}$$

Appendix IV

IV.1 Derivation of the Equation to Calculate the Quantities of Grass and White Clover Removed from the Herbage

In the model, equation (3.46) has been re-arranged in the following form so that the quantities of white clover and grass leaf mass harvested can be calculated:

$$\nu_L = \frac{C_{L,c} * A_c}{C_{L,g} * A_g} \Big/ \frac{D_{L,c} * A_c}{D_{L,g} * A_g} \qquad \text{(IV.2)}$$

where C_L (kg DM ha^{-1}) represent the quantity of the leaf component removed from the sward, D_L (kg DM ha^{-1}) represents the quantity of the leaf component in the sward prior to cutting, and A (ha (kg DM)$^{-1}$) is the specific leaf area. Subscript g and c refer to grass and white clover components respectively. The total quantity of white clover leaf area harvested from the sward ($C_{L,c}$, kg DM ha^{-1}) can be defined as:

$$C_{L,c} = D_{L,c} + D_{L,g} - L_S - C_{L,g} \qquad \text{(IV.3)}$$

where L_S (kg DM ha^{-1}) is the amount of leaf material in the sward after removal of the herbage. Rearranging equation (IV.2) and substituting for $C_{L,c}$ gives:

$$\nu_L = \frac{D_{L,c} + D_{L,g} - L_S - C_{L,g}}{C_{L,g}} \Big/ \frac{D_{L,c}}{D_{L,g}} \qquad \text{(IV.4)}$$

Rearranging equation (IV.4) gives:

$$\nu_L * D_{L,c} = \frac{D_{L,g} * \left(D_{L,c} + D_{L,g} - L_S\right)}{C_{L,g}} - D_{L,g} \qquad \text{(IV.5)}$$

and solving equation (IV.5) for the quantity of grass leaf area removed from the sward ($C_{L,g}$, kg DM ha^{-1}) gives:

$$C_{L,g} = \frac{D_{L,g} * (D_{L,c} + D_{L,g} - L_S)}{v_L * D_{L,c} + D_{L,g}} \tag{IV.6}$$

Once the quantity of white clover and grass leaf mass removed has been calculated, the quantity of white clover and grass dry matter removed can be determined. In order to calculate the white clover dry matter preferentially removed, the dry matter of the crop components is expressed in terms of the dry matter of the leaf and stem fractions and substituted into equation (IV.1), giving the following formula:

$$v_D = \frac{C_{L,c} + C_{S,c}}{C_{L,g} + C_{S,g}} \Bigg/ \frac{D_{L,c} + D_{S,c}}{D_{L,g} + D_{S,g}} \tag{IV.7}$$

where C_S (kg DM ha^{-1}) represents the quantity of the stem component removed from the sward and D_S (kg DM ha^{-1}) represents the quantity of the stem component in the sward prior to cutting. The total amount of stem material harvested ($C_{S,c}$ + $C_{S,g}$, kg DM ha^{-1}) is:

$$\begin{aligned} C_{S,c} + C_{S,g} &= D_{S,c} + D_{S,g} - S_S \\ &= C_S \end{aligned} \tag{IV.8}$$

where S_S (kg DM ha^{-1}) is the amount of stem material in the sward after the cutting of the herbage, and C_S (kg DM ha^{-1}) represents the amount of stem material removed. Rearranging equation (IV.7) and substituting for $C_{S,c}$ gives:

$$\nu_D = \frac{C_{L,c} + C_S - C_{S,g}}{C_{L,g} + C_{S,g}} \bigg/ \frac{D_{L,c} + D_{S,c}}{D_{L,g} + D_{S,g}} \tag{IV.9}$$

Rearranging equation (IV.9) gives:

$$\nu_D * \frac{(D_{L,c} + D_{S,c})(C_{L,g} + C_{S,g})}{D_{L,g} + D_{S,g}} = C_{L,c} + C_S - C_{S,g} \tag{IV.10}$$

Defining λ as:

$$\lambda = \nu_D * \frac{D_{L,c} + D_{S,c}}{D_{L,g} + D_{S,g}} \tag{IV.11}$$

and substituting into equation (IV.10) gives:

$$\lambda * (C_{L,g} + C_{S,g}) = C_{L,c} + C_S - C_{S,g} \tag{IV.12}$$

Equation (IV.11) is rearranged to give an equation for $C_{S,g}$:

$$C_{S,g} = \frac{C_{L,c} + C_S - \lambda * C_{L,g}}{\lambda + 1} \tag{IV.13}$$

Appendix V

List of variables in the dairy cow model

Variable	Description	Units
Δ_E	Metabolisable energy available for growth	MJ head^{-1} day^{-1}
Δ_W	Potential growth	kg head^{-1} day^{-1}
B_M	Metabolisable energy required from the maternal body to meet the energy requirements of maintenance	MJ head^{-1} day^{-1}
B_P	Metabolisable energy required from the maternal body to meet the energy requirements of pregnancy	MJ head^{-1} day^{-1}
C_{Ph}	Daily physiological energy requirements after correcting for feeding level	MJ head^{-1} day^{-1}
$C_{Replace}$	Rate of substitution of forage by concentrates	kg DM herbage (kg DM concentrates)$^{-1}$
DayP	Day number from the date of conception	day
dg_{Diet}	Proportionate digestibility of the diet	
E_{AL}	Metabolisable energy available for milk production	MJ head^{-1} day^{-1}
E_F	Daily energy requirements for potential growth and fattening	MJ head^{-1} day^{-1}
E_L	Daily energy requirements for potential milk yield	MJ head^{-1} day^{-1}
E_{Loss}	Metabolisable energy deficit for potential growth and fattening, and milk production	MJ head^{-1} day^{-1}
E_M	Daily energy requirements for maintenance	MJ head^{-1} day^{-1}

Variable	Description	Units
E_P	Daily energy requirements for pregnancy	MJ head^{-1} day^{-1}
E_{Ph}	Daily physiological energy requirements before correcting for feeding level	MJ head^{-1} day^{-1}
E_{Prod}	Metabolisable energy required for actual production on the previous day	MJ head^{-1} day^{-1}
i	age cohort	
I	Actual intake	kg DM head^{-1} day^{-1}
I_A	Physical limit to herbage intake	kg DM head^{-1} day^{-1}
$I_{C, kg}$	Dry-matter quantity of concentrates fed per kilogram of milk	kg DM concentrates kg^{-1} milk
I_{Conc}	Intake of concentrates per day	kg DM head^{-1} day^{-1}
I_F	Herbage intake	kg DM head^{-1} day^{-1}
I_{Ph}	Physiological limit to herbage intake	kg DM head^{-1} day^{-1}
k_{fl}	Proportionate efficiency of metabolisable energy for growth and fattening for a lactating cow	
k_l	Proportionate efficiency of metabolisable energy for milk production	
k_m	Proportionate efficiency of metabolisable energy for maintenance	
L_D	Energy released for milk production from that day's intake of metabolisable energy	MJ head^{-1} day^{-1}
Level	Level of feeding in terms of multiples of maintenance	

Variable	Description	Units
LWT	Liveweight of the 'average dairy cow'	kg $head^{-1}$
M_{Conc}	Daily metabolisable energy intake of concentrates	MJ $head^{-1}$ day^{-1}
M_E	Metabolisability of the feed	MJ $(kg\ DM)^{-1}$
ME	Daily physiological energy requirements corrected for feeding level	MJ $head^{-1}$ day^{-1}
ME_C	Total energy intake per head	MJ $head^{-1}$ day^{-1}
MEI	Total energy available for energy requirements after correcting for feeding level	MJ $head^{-1}$ day^{-1}
M_{Fod}	Metabolisable energy value of 1 kg of dry matter	MJ kg^{-1}
Mn	Month number since the start of the year	
T_{Conc}	Metabolisable intake of concentrates	MJ $head^{-1}$ day^{-1}
T_{Fod}	Metabolisable intake of forage	MJ $head^{-1}$ day^{-1}
t	Number of weeks since the start of lactation	week
Y	Potential milk yield	kg $head^{-1}$ day^{-1}

List of parameters in the dairy cow model

Parameter	Description	Units
Age	Average age of the 'average cow'	yrs
C_Y	Percentage deviation in the lactation curve per month due to date of calving	%
dg_{Conc}	Proportionate digestibility of concentrates	
DM_C	Dry-matter weight of 1 kilogram of fresh weight concentrates	kg DM kg^{-1} fresh weight
d_{max}	Limit of the digestive tract's ability to process feed	kg DM (kg liveweight)$^{-1}$ day^{-1}
F_{max}	Maximum intake per kilogram of metabolic weight	kg DM (kg liveweight)$^{-0.75}$
GE	Gross energy of the feed	MJ (kg DM)$^{-1}$
H_{Crit}	Minimum critical herbage mass per hectare required for grazing to occur	kg DM ha^{-1}
$I_{C,\,l}$	Fresh weight quantity of concentrates fed per litre of milk	kg $head^{-1}$ l^{-1} milk
k_{bc}	Proportionate utilisation efficiency of maternal body for pregnancy	
k_{bl}	Proportionate utilisation efficiency of maternal body for milk production	
k_c	Proportionate utilisation efficiency of metabolisable energy for pregnancy	
kg_l	Weight of 1 litre of milk	kg l^{-1}

Parameter	Description	Units
L_E	Net energy value of 1 kg of milk containing 4% fat	MJ kg^{-1}
N_L	Net energy released from 1 kg of liveweight loss	MJ kg^{-1}
N_W	Net energy requirement for 1 kg of liveweight gain	MJ kg^{-1}
Pot	Scale parameter in equation (4.4)	kg $head^{-1}$ day^{-1}
S_Y	Percentage deviation in the lactation curve per month due to seasonal variation	
Wb	Constant in equation (4.4)	
Wc	Constant in equation (4.4)	
Wt_M	Mature weight of the 'average cow'	kg $head^{-1}$

List of variables in the beef model

Variable	Description	Units
Δ_{DNA}	Change in the DNA content of the 'average steer'	g head^{-1} day^{-1}
Δ_{EBW}	Change in empty body weight	kg head^{-1} day^{-1}
Δ_{F}	Potential gain in fat	kg head^{-1} day^{-1}
Δ_{P}	Potential gain in protein	kg head^{-1} day^{-1}
Δ_{W}	Potential growth	kg head^{-1} day^{-1}
C_{Ph}	Daily physiological energy requirements after correcting for feeding level	MJ head^{-1} day^{-1}
$C_{Replace}$	Rate of substitution of forage by concentrates	kg DM herbage (kg DM concentrates)$^{-1}$
DNA	DNA content of the 'average steer'	g head^{-1}
dg_{Diet}	Proportionate digestibility of the diet	
EB	Potential empty body weight of the 'average steer' assuming it had grown at the normative growth rate	kg head^{-1}
EBW	Actual empty body weight of the 'average steer'	kg head^{-1}
EBW_{M}	Mature empty body weight of the 'average steer'	kg head^{-1}
E_{F}	Daily energy requirements for potential growth and fattening	MJ head^{-1} day^{-1}
E_{M}	Daily energy requirements for maintenance	MJ head^{-1} day^{-1}
E_{Ph}	Daily physiological energy requirements before correcting for feeding level	MJ head^{-1} day^{-1}

Variable	Description	Units
E_{Prod}	Metabolisable energy required for actual production on the previous day	MJ head^{-1} day^{-1}
I_A	Physical limit to herbage intake	kg DM head^{-1} day^{-1}
I_{Conc}	Intake of concentrates per day	kg DM head^{-1} day^{-1}
I_F	Herbage intake	kg DM head^{-1} day^{-1}
I_{Ph}	Physiological limit to herbage intake	kg DM head^{-1} day^{-1}
k_f	Proportionate efficiency of metabolisable energy for growth and fattening	
k_m	Proportionate efficiency of metabolisable energy for maintenance	
Level	Level of feeding in terms of multiples of maintenance	
L_N	Level of feeding in terms of the energy requirements required for normal growth of the steer	
LWT	Liveweight of the 'average steer'	kg head^{-1}
M_{Conc}	Daily metabolisable energy intake of concentrates	MJ head^{-1} day^{-1}
M_E	Metabolisability of the feed	MJ (kg DM)$^{-1}$
ME	Daily physiological energy requirements corrected for feeding level	MJ head^{-1} day^{-1}
ME_C	Total energy intake per head	MJ head^{-1} day^{-1}
MEI	Total energy available for energy requirements after correcting for feeding level	MJ head^{-1} day^{-1}

Variable	Description	Units
MEI_N	Total energy available requirements for the normal growth of the 'average steer'	MJ $head^{-1}$ day^{-1}
M_{Fod}	Metabolisable energy value of 1 kg of dry matter	MJ kg^{-1}
Nut1—Nut2	Nutritional effects on DNA accumulation	
P	Protein content of the 'average steer'	kg $head^{-1}$
P_D	Potential rate of protein degradation	kg $head^{-1}$ day^{-1}
P_S	Potential rate of protein synthesis	kg $head^{-1}$ day^{-1}
T_{Conc}	Metabolisable intake of concentrates	MJ $head^{-1}$ day^{-1}
T_{DNA}	DNA content of the 'average steer' assuming that the steer attains the potential liveweight gain	g $head^{-1}$
T_{Fod}	Metabolisable intake of forage	MJ $head^{-1}$ day^{-1}
Wt_N	Liveweight of the 'average steer' if it had grown at the normative growth rate	kg $head^{-1}$

List of parameters in the beef model

Parameter	Description	Units
Age	Average age of the 'average steer'	yrs
cal	Converts megacolories to megajoules	MJ $MCal^{-1}$
dg_{Conc}	Proportionate digestibility of concentrates	
DM_C	Dry-matter weight of 1 kilogram of fresh weight concentrates	kg DM kg^{-1} fresh weight
DNA1	Constant in equation (4.69)	
DNA2	Constant in equation (4.69)	
DNA_{max}	DNA content of the 'average steer' at maturity	g $head^{-1}$
d_{max}	Limit of the digestive tract's ability to process feed	kg DM $(kg\ liveweight)^{-1}$
E2	Constant that converts liveweight to metabolic weight	
F_E	Net energy value of 1 kg of fat	MJ kg^{-1}
F_{max}	Maximum intake per kilogram of metabolic weight	kg DM $(kg\ liveweight)^{-0.75}$
GE	Gross energy of the feed	MJ $(kg\ DM)^{-1}$
H_{Crit}	Minimum critical herbage mass per hectare required for grazing to occur	kg DM ha^{-1}
K1	Constant in equation (4.52)	
K2	Constant in equation (4.53)	
K3	Constant in equation (4.55)	
K4	Constant in equation (4.61)	
LP1	Constant in equation (4.33)	

Parameter	Description	Units
LP2	Constant in equation (4.57)	
LEBW1	Constant in equation (4.58)	
LEBW2	Coefficient in equation (4.58) appropriate for cattle with an initial gut fill of 300 g kg^{-1} empty body weight	
LP1	Constant in equation (4.57)	
LP2	Constant in equation (4.57)	
N1	Constant in equation (4.63)	
N2	Constant in equation (4.63)	
N3	Constant in equation (4.64)	
N4	Constant in equation (4.64)	
N5	Constant in equation (4.64)	
Nm1	Constant in equation (4.66)	
Nm2	Constant in equation (4.66)	
P_E	Net energy value of 1 kg of protein	MJ kg^{-1}
Wt_M	Mature weight of the 'average steer'	kg $head^{-1}$

List of variables in the sheep model

Variable	Description	Units
Δ_E	Metabolisable energy available for growth	kg head^{-1} day^{-1}
Δ_W	Potential growth of ewe	kg ewe^{-1} day^{-1}
Δ_{WL}	Potential growth of lamb	kg lamb^{-1} day^{-1}
B_M	Metabolisable energy required from the maternal body to meet the energy requirements of maintenance	MJ head^{-1} day^{-1}
C_{Ph}	Daily physiological energy requirements after correcting for feeding level	MJ head^{-1} day^{-1}
$C_{Replace}$	Rate of substation of forage by concentrates	kg DM herbage (kg DM concentrates)$^{-1}$
DayP	Day number from the date of conception	day
dg_{Diet}	Proportionate digestibility of the diet	
d_L	Number of days since the start of lactation	day
E_{AL}	Metabolisable energy available for milk production	MJ head^{-1} day^{-1}
E_F	Daily energy requirements for potential growth and fattening	MJ head^{-1} day^{-1}
E_L	Daily energy requirements for potential milk yield	MJ ewe^{-1} day^{-1}
E_{Loss}	Metabolisable energy deficit for potential growth and fattening, and milk production	MJ head^{-1} day^{-1}
E_M	Daily energy requirements for maintenance	MJ ewe^{-1} day^{-1}
E_{ML}	Net energy value of 1 kg of milk	MJ kg^{-1}
E_P	Daily energy requirements for pregnancy	MJ ewe^{-1} day^{-1}

Variable	Description	Units
E_{Ph}	Daily physiological energy requirements before correcting for feeding level	MJ ewe^{-1} day^{-1}
H	Daily allowance of green herbage by the 'average ewe + lambs at foot'	kg DM (ewe + $lambs)^{-1}$ day^{-1}
H_E	Daily allowance of green herbage by the 'average ewe'	kg DM ewe^{-1} day^{-1}
H_{EL}	Daily allowance of green herbage by the lambs at foot for the 'average ewe'	kg DM $litter^{-1}$ day^{-1}
H_L	Daily allowance of green herbage by the 'average lamb'	kg DM $lamb^{-1}$ day^{-1}
I_{Conc}	Intake of concentrates per day	kg DM $head^{-1}$ day^{-1}
$I_{E, A}$	Physical limit to herbage intake for the 'average ewe'	kg DM ewe^{-1} day^{-1}
$I_{E, F}$	Daily intake of herbage by the 'average ewe'	kg DM ewe^{-1} day^{-1}
$I_{E, Ph}$	Physiological limit to herbage intake for the 'average ewe'	kg DM ewe^{-1} day^{-1}
$I_{E, max}$	Maximum daily dry-matter intake of herbage by the 'average ewe'	kg DM ewe^{-1} day^{-1}
$I_{EL, max}$	Maximum daily dry-matter intake of herbage by the lambs at foot for the 'average ewe'	kg DM $litter^{-1}$ day^{-1}
$I_{L, A}$	Physical limit to herbage intake for the 'average lamb'	kg DM $lamb^{-1}$ day^{-1}
$I_{L, F}$	Daily intake of herbage by the 'average lamb'	kg DM $lamb^{-1}$ day^{-1}
$I_{L, max}$	Maximum daily dry-matter intake of herbage by the 'average lamb'	kg DM $lamb^{-1}$ day^{-1}

Variable	Description	Units
$I_{L, Ph}$	Physiological limit to herbage intake for the 'average lamb'	kg DM $lamb^{-1}$ day^{-1}
k_e	Proportionate efficiency of metabolisable energy for growth and fattening for the 'average lamb'	
k_{eff}	Proportionate efficiency of metabolisable energy for growth and fattening for the 'average ewe'	
k_f	Proportionate efficiency of metabolisable energy for growth and fattening	
k_{fl}	Proportionate efficiency of metabolisable energy for growth and fattening for a lactating ewe	
k_l	Proportionate efficiency of metabolisable energy for milk production	
k_m	Proportionate efficiency of metabolisable energy for maintenance	
L%	Lambing percentage	%
L_D	Energy released for milk production from that day's intake of metabolisable energy	MJ $head^{-1}$ day^{-1}
Level	Level of feeding in terms of multiples of maintenance	
L_F	Daily energy requirements for growth and fattening	MJ $lamb^{-1}$ day^{-1}
LM	Metabolisable energy obtained from milk consumed by the 'average lamb'	MJ $lamb^{-1}$ day^{-1}
L_M	Daily energy requirements for maintenance	MJ $lamb^{-1}$ day^{-1}

Variable	Description	Units
L_{Ph}	Daily physiological energy requirements before correcting for feeding level	MJ $lamb^{-1}$ day^{-1}
LWT	Liveweight of the 'average ewe'	kg ewe^{-1}
LWT_L	Liveweight of the 'average lamb'	kg $lamb^{-1}$
M_B	Fasting heat production	MJ $head^{-1}$ day^{-1}
M_{Conc}	Daily metabolisable energy intake of concentrates	MJ $head^{-1}$ day^{-1}
M_E	Metabolisability of the feed	MJ $(kg\ DM)^{-1}$
ME	Daily physiological energy requirements corrected for feeding level	MJ $head^{-1}$ day^{-1}
ME_C	Total energy intake	MJ $head^{-1}$ day^{-1}
MEI	Total energy consumed by the 'average ewe' available for energy requirements after correcting for feeding level	MJ ewe^{-1} day^{-1}
MEI_L	Total energy consumed by the 'average lamb' available for energy requirements after correcting for feeding level	MJ $lamb^{-1}$ day^{-1}
M_{Fod}	Metabolisable energy value of 1 kg of dry matter	MJ kg^{-1}
M_W	Heat production associated with muscular activity	MJ $head^{-1}$ day^{-1}
n	Number of lambs per litter	lambs $litter^{-1}$
N_S	Net energy requirement for 1 kg of liveweight gain for the 'average lamb'	MJ kg^{-1}
T_{Conc}	Metabolisable intake of concentrates	MJ $head^{-1}$ day^{-1}
T_{Fod}	Metabolisable intake of forage	MJ $head^{-1}$ day^{-1}
Wt_L	Lamb litter weight	kg $litter^{-1}$

Variable	Description	Units
Y	Potential milk yield	kg head^{-1} day^{-1}
Y_E	Net energy value of the milk produced by the 'average ewe'	MJ ewe^{-1} day^{-1}

List of parameters in the sheep model

Parameter	Description	Units
Age	Average age	yrs
b1	Constant in equations (4.79) and (4.80)	
d	Density of ewes' milk	kg l^{-1}
dg_{Conc}	Proportionate digestibility of concentrates	
DM_C	Dry-matter weight of 1 kilogram of fresh weight concentrates	kg DM kg^{-1} fresh weight
d_{max}	Limit of the digestive tract's ability to process feed	kg DM (kg liveweight)$^{-0.734}$ day^{-1}
F	Fat content of milk	%
G1	Constant in equation (4.93)	
G2	Constant in equation (4.93)	
GE	Gross energy of the feed	MJ (kg DM)$^{-1}$
H_{Crit}	Minimum critical herbage mass per hectare required for grazing to occur	kg DM ha^{-1}
k_{bl}	Proportionate utilisation efficiency of maternal body for milk production	
k_c	Proportionate utilisation efficiency of metabolisable energy for pregnancy	
k_{flb}	Proportionate utilisation efficiency of milk for growth and fattening by the 'average lamb'	

Parameter	Description	Units
k_{mlb}	Proportionate utilisation efficiency of milk for maintenance by the 'average lamb'	
N_L	Net energy released from 1 kg of liveweight loss	MJ kg^{-1}
N_W	Net energy requirement for 1 kg of liveweight gain	MJ kg^{-1}
Pot	Scale parameter in equation (4.86)	kg $head^{-1}$ day^{-1}
T	Percentage of total solids in ewe milk	%
Wb	Constant in equation (4.86)	
Wc	Constant in equation (4.86)	
Wt	Weight of the ewe at mating	kg $head^{-1}$
Wt%	Maternal liveweight at lambing as a percentage of the liveweight at mating	%
Wt_D	Weight of the ewe at mating plus the weight of the ewe from the sire breed at mating	kg $head^{-1}$
Wt_S	Weight of the ewe of the sire breed at mating	kg $head^{-1}$
Wt_M	Mature weight of the 'average ewe'	kg $head^{-1}$

Appendix VI

VI.1 Partitioning of the Metabolisable Energy

In the model, there are four different possible ME intake (MEI, MJ head^{-1} day^{-1}) conditions which can occur and they are defined as:

$$MEI \geq C_{Ph} \tag{VI.1}$$

$$E_M + E_P < MEI < C_{Ph} \tag{VI.2}$$

$$E_M < MEI < E_M + E_P \tag{VI.3}$$

$$MEI < E_M \tag{VI.4}$$

where E_M (MJ head^{-1} day^{-1}) and E_P (MJ head^{-1} day^{-1}) are the maintenance and the pregnancy requirements for metabolisable energy and C_{Ph} (MJ head^{-1} day^{-1}) is the metabolisable energy corrected for feeding level required for the daily physiological production of milk and growth.

VI.1.1 Metabolisable Energy Intake Meets the Physiological Requirements of the Dairy Cow ($MEI \geq C_{Ph}$)

If the intake of ME is described by equation (VI.1), potential milk and growth production are achieved. The actual milk yield is calculated from equation (4.7), and the change in liveweight is determined from equation (4.10).

VI.1.2 Metabolisable Energy Intake Meets the Maintenance and Pregnancy Requirements of the Dairy Cow ($E_M + E_P < MEI < C_{Ph}$)

Under these circumstances, the energy requirements of the cow for maintenance and pregnancy are met. The energy deficit (E_{Loss}, MJ head^{-1} day^{-1}) for milk, and growth and fattening is described by:

$$E_{Loss} = MEI - C_{Ph} \qquad \text{(VI.7)}$$

As the energy requirements for milk production, and growth and fattening are reduced by equal amounts, the energy available for liveweight change (Δ_E, MJ head^{-1} day^{-1}) is defined as:

$$\Delta_E = E_F - \frac{E_{Loss}}{2} \qquad \text{(VI.8)}$$

where E_F (MJ head^{-1} day^{-1}) represents the daily potential energy requirements for growth and fattening. If the energy available for growth and fattening is positive, then actual milk yield (Y, kg head^{-1} day^{-1}) and growth (Δ_W, kg head^{-1} day^{-1}) are defined as:

$$Y = \frac{k_l * \left(E_L - \frac{E_{Loss}}{2}\right)}{M_E} \qquad \text{(VI.9)}$$

$$\Delta_W = \frac{k_{fl} * \left(E_F - \frac{E_{Loss}}{2}\right)}{N_W} \qquad \text{(VI.10)}$$

where E_L (MJ head^{-1} day^{-1}) represents the daily potential energy requirements for milk, and k_l and k_{fl} are the proportionate efficiency of ME utilisation for milk production and growth and fattening for a lactating cow respectively. The metabolisability of the feed is denoted by M_E (MJ (kg DM)$^{-1}$ and N_W (MJ kg^{-1}) is the net energy requirement for 1 kg of liveweight gain. However, if the maternal body change is negative, the energy released from the catabolism is used in milk production. The energy released for milk production (L_D, MJ head^{-1} day^{-1}) from the daily metabolic energy intake is assumed to be:

$$L_D = E_L - \frac{E_{Loss}}{2} \tag{VI.11}$$

and thus the total energy available for milk production can be described by:

$$\begin{aligned} E_{AL} &= L_D - (-\Delta_E) \\ \Rightarrow E_{AL} &= L_D + \Delta_E \end{aligned} \tag{VI.12}$$

where $-\Delta_E$ (MJ head^{-1} day^{-1}) represents the energy released from the maternal body for milk production and E_{AL} (MJ head^{-1} day^{-1}) is the energy available for actual milk production. In order to determine the energy catabolised from the maternal body, equation (VI.12) is substituted into equation (4.25) to give:

$$\begin{aligned} L_D + D_E &= E_L - E_F + (-\Delta_E) \\ \Rightarrow \Delta_E &= \frac{E_L - E_F - L_D}{2} \end{aligned} \tag{VI.14}$$

The actual change in body weight (Δ_W, kg head^{-1} day^{-1}) and the milk yield produced (Y, kg head^{-1} day^{-1}) are thus defined as:

$$\Delta_W = -\frac{\Delta_E}{N_L} \tag{VI.15}$$

$$Y = k_l * (E_L - L_D) - \Delta_E * k_{bl} \tag{VI.16}$$

where k_{bl} represents the proportionate efficiency of utilisation of maternal body for milk production, and N_L (MJ kg^{-1}) is the net energy produced from the catabolism of 1 kg of liveweight.

VI.1.3 Metabolisable Energy Intake Meets the Maintenance but not the Pregnancy Requirements of the Dairy Cow ($E_M < MEI < E_M + E_P$)

If this condition prevails, this implies that there is catabolism of maternal body tissue to meet the energy requirements of pregnancy. The ME required from maternal body tissue to meet the pregnancy requirements (B_P, MJ $head^{-1}$ day^{-1}) of the animal can therefore be described as:

$$B_P = -(MEI - E_M - E_P) * \frac{k_c}{k_{bc}} \tag{VI.17}$$

where k_c and k_{bc} represent the proportionate utilisation efficiency of ME for pregnancy and maternal body for pregnancy respectively. The energy released from the catabolism of the maternal body of the cow (Δ_E, MJ $head^{-1}$ day^{-1}) will therefore be determined by the energy requirements for pregnancy that are not met from the diet and the actual energy requirements for milk production. Consequently the energy obtained from the maternal body (Δ_E, MJ $head^{-1}$ day^{-1}) is defined as:

$$\Delta_E = -(E_{AL} + B_P) \tag{VI.18}$$

where E_{AL}, MJ head^{-1} day^{-1} represents the energy used to produce milk which is derived from the maternal body. Substituting the expression for the energy utilised from the maternal body (Δ_E, MJ head^{-1} day^{-1}) into equation (4.25) which gives:

$$E_{AL} = E_L - E_F + \left[-\left(E_{AL} + B_P\right)\right]$$
$$\Rightarrow E_{AL} = \frac{E_L - E_F - B_P}{2} \tag{VI.20}$$

The actual milk production (Y, kg head^{-1} day^{-1}) and the reduction in the maternal body (Δ_W, kg head^{-1} day^{-1}) are described as:

$$Y = E_{AL} * k_{bl} \tag{VI.21}$$

$$\Delta_W = -\frac{E_{AL} + B_P}{N_L} \tag{VI.22}$$

If the energy available for milk production is less than zero, it is assumed that there is no milk production. Under these circumstances the weight loss is solely determined by the requirements from the maternal body for pregnancy.

VI.1.4 Metabolisable Energy Intake Does not Meet Either the Maintenance or Pregnancy Requirements of the Dairy Cow ($MEI < E_M$)

Where there is insufficient energy intake to meet maintenance requirements there is catabolism of maternal body tissue. The maintenance energy requirements that are not provided by the diet, as well as the pregnancy and milk production requirements, are obtained from the maternal body. The ME required from maternal body tissue to meet the maintenance (B_M, MJ head^{-1} day^{-1}) and pregnancy (B_P, MJ head^{-1} day^{-1}) requirements are:

$$B_M = -(MEI - E_M) \tag{VI.23}$$

$$B_P = E_P * \frac{k_c}{k_{bc}} \tag{VI.24}$$

It is assumed within the model that the efficiency of utilisation of energy for maintenance is independent of the source of the energy; thus, consumed energy and catabolised maternal tissue are used with the same efficiency for maintenance. Consequently, the energy released from the catabolism of the maternal body of the cow (Δ_E, MJ head^{-1} day^{-1}) is described as:

$$\Delta_E = -(E_{AL} + B_P + B_M) \tag{VI.25}$$

where E_{AL}, MJ head^{-1} day^{-1} represents the energy used to produce milk which is derived from the maternal body. Substituting the expression for the energy utilised from the maternal body (Δ_E, MJ head^{-1} day^{-1}) into equation (4.25) which gives:

$$\begin{aligned} E_{AL} &= E_L - E_F + \left[-(E_{AL} + B_P + B_M)\right] \\ \Rightarrow E_{AL} &= \frac{E_L - E_F - B_P - B_M}{2} \end{aligned} \tag{VI.27}$$

The actual milk production (Y, kg head^{-1} day^{-1}) is described by equation (VI.21) and the reduction in the maternal body (Δ_W, kg head^{-1} day^{-1}) is defined as:

$$\Delta_W = -\frac{E_{AL} + B_P + B_M}{N_L} \tag{VI.28}$$

Within the model, it is presumed that, if there is no energy available for milk production, no milk is produced and thus the weight loss is solely determined by the requirements from the maternal body for pregnancy and maintenance.

Appendix VII

Table VII-1 The observed and predicted dry-matter yields for each cut, nitrogen level and year for the grass swards at High Mowthorpe

		Cut							
Nitrogen		1		2		3		Total	
		kg DM ha^{-1}		kg DM ha^{-1}		kg DM ha^{-1}		kg DM ha^{-1}	
kg ha^{-1}	Year	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
0	70	0.838	0.854	0.102	0.000	0.000	0.000	0.940	0.854
	71	0.163	0.833	0.266	0.000	0.152	0.000	0.581	0.833
	72	0.837	1.058	0.657	0.000	0.108	0.000	1.602	1.058
	73	0.813	1.368	1.318	0.513	1.326	0.000	3.457	1.881
0 Average		0.663	1.028	0.586	0.128	0.397	0.000	1.645	1.157
150	70	1.519	2.587	1.566	1.386	0.766	0.436	3.851	4.409
	71	2.089	2.102	1.657	1.083	1.191	0.516	4.937	3.701
	72	2.434	2.702	1.385	1.332	0.515	0.408	4.334	4.442
	73	2.446	3.168	1.928	1.988	2.316	0.905	6.690	6.061
150 Average		2.122	2.640	1.634	1.447	1.197	0.566	4.953	4.653
300	70	2.574	4.055	2.607	2.926	1.573	1.387	6.754	8.368
	71	3.654	3.232	2.272	2.464	2.300	1.398	8.226	7.094
	72	4.036	4.086	1.837	2.641	0.567	1.199	6.440	7.926
	73	3.792	3.958	2.106	3.299	2.688	1.771	8.586	9.028
300 Average		3.514	3.833	2.206	2.833	1.782	1.439	7.502	8.104

Table VII-1 Continued

		Cut							
Nitrogen		**1**		**2**		**3**		**Total**	
		kg DM ha^{-1}		**kg DM ha^{-1}**		**kg DM ha^{-1}**		**kg DM ha^{-1}**	
kg ha^{-1}	**Year**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**
450	70	3.098	5.409	2.831	4.340	1.531	2.260	7.460	12.009
	71	3.922	4.280	2.809	3.751	2.099	2.220	8.830	10.251
	72	4.167	5.352	1.870	3.842	0.419	2.022	6.456	11.216
	73	4.079	4.690	1.519	4.484	2.946	2.583	8.544	11.757
450 Average		3.817	4.933	2.257	4.104	1.749	2.271	7.823	11.308
600	70	4.001	6.459	3.235	5.627	1.101	3.082	8.337	15.168
	71	4.732	5.252	2.916	4.935	2.081	2.988	9.729	13.175
	72	4.601	6.526	1.698	4.934	0.479	2.810	6.778	14.270
	73	4.241	5.355	1.413	5.395	2.686	3.253	8.340	14.003
600 Average		4.394	5.898	2.316	5.223	1.587	3.033	8.296	14.154
0—600		14.509	18.332	8.998	13.735	6.711	7.310	30.218	39.376

Table VII-2 The observed and predicted dry-matter yields for each cut, nitrogen level and year for the grass swards at Rosemaund

Nitrogen		Cut 1 kg DM ha^{-1}		Cut 2 kg DM ha^{-1}		Cut 3 kg DM ha^{-1}		Total kg DM ha^{-1}	
kg ha^{-1}	Year	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
0	70	3.068	1.647	0.715	0.304	0.550	0.228	4.333	2.179
	71	1.470	1.328	0.428	0.000	0.326	0.000	2.224	1.328
	72	0.894	1.367	0.880	0.000	0.255	0.000	2.029	1.367
0 Average		1.811	1.447	0.674	0.101	0.377	0.076	2.862	1.625
150	70	4.978	3.267	2.469	1.906	2.924	1.524	10.371	6.697
	71	4.120	3.239	1.244	1.864	1.891	0.638	7.255	5.741
	72	3.685	3.266	2.493	1.887	1.076	0.651	7.254	5.804
150 Average		4.261	3.257	2.069	1.886	1.964	0.938	8.293	6.081
300	70	6.100	4.650	4.103	3.362	3.793	2.640	13.996	10.652
	71	5.100	4.817	1.608	3.498	2.525	1.595	9.233	9.910
	72	4.309	4.841	2.866	3.519	1.300	1.607	8.475	9.967
300 Average		5.170	4.769	2.859	3.460	2.539	1.947	10.568	10.176
450	70	6.437	5.786	3.890	4.682	4.996	3.657	15.323	14.125
	71	5.943	6.230	1.633	4.966	3.370	2.499	10.946	13.695
	72	5.304	6.252	3.677	4.986	1.944	2.512	10.925	13.750
450 Total		5.895	6.089	3.067	4.878	3.437	2.889	12.398	13.857

Table VII-2 Continued

		Cut							
Nitrogen		1		2		3		Total	
		kg DM ha^{-1}		kg DM ha^{-1}		kg DM ha^{-1}		kg DM ha^{-1}	
kg ha^{-1}	Year	Observed	Predicted	Observed	Predicted	Observed	Predicted	Observed	Predicted
600	70	7.190	6.583	3.732	5.874	5.317	4.508	16.239	16.965
	71	6.811	7.520	1.322	6.287	3.102	3.347	11.235	17.154
	72	5.501	7.540	3.610	6.303	1.899	3.359	11.010	17.202
600 Total		6.501	7.214	2.888	6.155	3.439	3.738	12.828	17.107
0—600		23.637	22.778	11.557	16.479	11.756	9.588	46.949	48.845

Table VII-3 The observed and predicted dry-matter yields for each cut, nitrogen level and year for the grass swards at Seale Hayne

		Cut							
Nitrogen		**1**		**2**		**3**		**Total**	
		kg DM ha^{-1}		**kg DM ha^{-1}**		**kg DM ha^{-1}**		**kg DM ha^{-1}**	
kg ha^{-1}	**Year**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**
0	70	1.501	0.738	0.447	0.000	0.302	0.000	2.250	0.738
	71	1.206	0.984	0.731	0.441	0.691	0.000	2.628	1.425
	72	2.668	1.722	0.988	0.130	0.125	0.000	3.781	1.852
	73	1.253	1.099	0.592	0.000	0.915	0.000	2.760	1.099
0 Average		1.657	1.136	0.690	0.143	0.508	0.000	2.855	1.279
150	70	4.269	2.335	2.095	1.447	2.086	1.085	8.450	4.867
	71	2.471	2.908	2.088	2.616	1.712	0.977	6.271	6.501
	72	3.363	3.432	2.200	1.890	0.475	1.151	6.038	6.473
	73	4.111	2.481	1.593	1.987	1.916	1.203	7.620	5.671
150 Average		3.554	2.789	1.994	1.985	1.547	1.104	7.095	5.878
300	70	5.853	3.727	3.446	3.018	4.666	2.246	13.965	8.991
	71	4.014	4.579	3.142	4.469	2.673	2.102	9.829	11.150
	72	4.183	4.905	3.515	3.434	1.009	2.383	8.707	10.722
	73	6.063	3.684	3.179	3.660	3.346	2.426	12.588	9.770
300 Average		5.028	4.224	3.321	3.645	2.924	2.289	11.272	10.158

Table VII-3 Continued

		Cut							
Nitrogen		**1**		**2**		**3**		**Total**	
		kg DM ha^{-1}		**kg DM ha^{-1}**		**kg DM ha^{-1}**		**kg DM ha^{-1}**	
kg ha^{-1}	**Year**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**	**Observed**	**Predicted**
450	70	6.696	5.011	3.651	4.561	5.351	3.310	15.698	12.782
	71	4.586	6.093	3.675	6.096	2.730	3.156	10.991	15.345
	72	4.650	6.238	4.144	4.844	1.108	3.552	9.902	14.634
	73	6.396	4.787	3.446	5.172	3.118	3.555	12.960	13.514
450 Average		5.582	5.532	3.729	5.143	3.077	3.393	12.388	14.069
600	70	7.086	6.207	4.193	5.773	5.459	4.283	16.738	16.263
	71	7.709	7.481	4.033	7.493	2.657	4.132	14.399	19.106
	72	6.711	7.457	5.199	6.129	1.680	4.647	13.590	18.233
	73	8.077	5.810	3.195	6.536	4.263	4.590	15.535	16.936
600 Average		7.396	6.739	4.155	6.483	3.515	4.413	15.066	17.635
0—600		23.217	20.420	13.888	17.399	11.571	11.200	48.675	49.018

Table VII-4 The ratio of the predicted yield:observed yield for each cut and at an nitrogen application rate of 0 kg ha^{-1} at High Mowthorpe

Cut	Year	Grass	White Clover	Combined
1	78	0.98	1.10	1.00
1	79	1.75	0.92	1.45
1	80	0.71	0.24	0.56
1	81	0.97	0.33	0.67
1	78—81	1.10	0.65	0.92
2	78	1.73	1.42	1.56
2	79	1.96	1.04	1.33
2	80	1.16	0.82	0.97
2	81	1.35	0.78	0.96
2	78—81	1.55	1.02	1.20
3	78	0.77	2.80	2.01
3	79	0.25	0.85	0.59
3	80	0.29	1.35	0.93
3	81	0.16	0.64	0.42
3	78—81	0.37	1.41	0.99
Total		1.01	1.03	1.04

Table VII-5 The ratio of the predicted yield:observed yield for each cut and at an nitrogen application rate of 200 kg ha^{-1} at High Mowthorpe

Cut	Year	Grass	White Clover	Combined
1	78	0.76	2.05	0.84
1	79	1.06	1.71	1.13
1	80	0.60	0.48	0.59
1	81	0.70	0.92	0.73
1	78—81	0.78	1.29	0.82
2	78	0.71	1.61	0.78
2	79	2.62	1.90	2.46
2	80	2.04	0.41	1.22
2	81	0.86	1.29	0.92
2	78—81	1.55	1.30	1.35
3	78	1.19	3.06	1.42
3	79	0.72	1.73	0.83
3	80	0.88	0.73	0.83
3	81	0.48	1.40	0.59
3	78—81	0.82	1.73	0.92
Total		1.05	1.44	1.03

Table VII-6 The ratio of the predicted yield:observed yield for each cut and at an nitrogen application rate of 0 kg ha^{-1} at Liscombe

Cut	Year	Grass	White Clover	Combined
1	78	0.51	1.49	0.58
1	79	1.41	0.13	0.82
1	80	0.57	0.21	0.46
1	81	1.35	473.00	1.61
1	78—81	0.96	118.71	0.87
2	78	2.24	1.14	1.59
2	79	1.98	0.12	0.44
2	80	1.14	2.16	1.50
2	81	1.45	32.8	2.39
2	78—81	1.70	9.05	1.48
3	78	0.71	1.22	1.04
3	79	1.11	1.06	1.08
3	80	0.25	5.11	1.47
3	81	0.94	14.84	2.64
3	78—81	0.75	5.56	1.56
Total		1.14	44.44	1.30

Table VII-7 The ratio of the predicted yield:observed yield for each cut and at an nitrogen application rate of 200 kg ha^{-1} at Liscombe

Cut	Year	Grass	White Clover	Combined
1	78	0.45	1.38	0.49
1	79	1.01	0.25	0.87
1	80	0.85	0.32	0.73
1	81	0.92	0.00	1.04
1	78—81	0.81	0.49	0.79
2	78	1.18	0.70	1.08
2	79	1.64	0.06	0.65
2	80	1.29	0.68	1.14
2	81	0.79	16.29	0.91
2	78—81	1.23	4.43	0.94
3	78	1.03	0.72	0.95
3	79	2.20	0.14	0.96
3	80	0.93	1.73	1.02
3	81	0.97	348.00	1.14
3	78—81	1.28	85.65	1.02
Total		1.11	30.86	0.92

Table VII-8 The ratio of the predicted yield:observed yield for each cut and at an nitrogen application rate of 0 kg ha^{-1} at Rosemaund

Cut	Year	Grass	White Clover	Combined
1	78	0.81	0.15	0.43
1	79	1.10	0.40	0.78
1	80	0.86	0.22	0.53
1	81	0.65	0.53	0.61
1	78—81	0.85	0.32	0.59
2	78	0.82	0.60	0.68
2	79	1.65	0.56	0.77
2	80	1.09	0.48	0.64
2	81	0.57	1.03	0.81
2	78—81	1.03	0.67	0.72
3	78	0.36	0.61	0.57
3	79	0.35	0.69	0.60
3	80	0.40	0.83	0.69
3	81	0.44	8.76	4.86
3	78—81	0.39	2.73	1.68
Total		0.76	1.24	1.00

Table VII-9 The ratio of the predicted yield:observed yield for each cut and at an nitrogen application rate of 200/300 kg ha^{-1} at Rosemaund

Cut	Year	Grass	White Clover	Combined
1	78	0.57	0.22	0.49
1	79	1.07	0.46	0.92
1	80	1.01	0.30	0.75
1	81	0.72	0.56	0.68
1	78—81	0.84	0.39	0.71
2	78	1.11	0.12	0.70
2	79	2.47	0.12	1.02
2	80	1.19	0.19	0.65
2	81	1.09	0.57	0.88
2	78—81	1.47	0.25	0.81
3	78	0.96	0.17	0.72
3	79	1.83	0.04	0.60
3	80	1.50	0.39	0.94
3	81	6.35	4.81	5.80
3	78—81	2.66	1.35	2.02
Total		1.66	0.66	1.18

Appendix VIII

PUBLISHED PAPERS

1. Topp, C. F. E. and Doyle, C. J. (1996) Simulating the impact of global warming on milk and forage producton in Scotland: 1. The effects on dry-matter yield of grass and grass – white clover swards. *Agricultural Systems*, **52**, 213—242.

2. Topp, C. F. E. and Doyle, C. J. (1996) Simulating the impact of global warming on milk and forage producton in Scotland: 2. The effects on milk yields and grazing management of dairy herds. *Agricultural Systems*, **52**, 243—270.

3. Topp, C. F. E. and Doyle, C. J. (1996) The effect of global warming on the productivity of grass – white clover swards subjected to nitrogen and water stress. 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**, 71—78.

4. Topp, C. F. E. and Doyle, C. J. (1998) Forecasting the consequences of global warming for white clover – based systems of livestock production. *World Resource Review*, **10**, 87—99.

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Simulating the Impact of Global Warming on Milk and Forage Production in Scotland: 1. The Effects on Dry-matter Yield of Grass and Grass–White Clover Swards

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ABSTRACT

The purpose of the study was to assess the effect that global warming and changes in atmospheric CO_2 concentration would have on grassland production within Scotland. This required the development of a mathematical model of herbage production that was responsive to climatic factors and changes in CO_2 levels. A model of pure grass and grass–white clover swards is described, and this has been used to assess the effects that the predicted increases in temperature, rainfall and CO_2 might have on grass and white clover production.

It is projected that global warming will increase the length of the growing season by between 12 and 37 days for every 1°C rise in annual mean daily temperature. The indications are that global warming will have little effect on annual production of grass, either from pure grass or grass–white clover swards. On the other hand, white clover as a percentage of total herbage production is estimated to increase from 32% to 46% for a 2°C temperature rise. Nevertheless, increasing concentrations of CO_2 is predicted to increase the yields of grass and white clover under both current climatic conditions and the global warming scenario. Copyright © 1996 Published by Elsevier Science Ltd

INTRODUCTION

Man's activities have increased the concentration of CO_2 and 'greenhouse' gases in the atmosphere. By the middle of the next century the pre-industrial concentration of CO_2 is expected to have doubled (Bolin *et al.*, 1986). With the Intergovernmental Panel of Climate Change scenario

IS92a, global mean temperature is predicted to have increased by between 1·7°C and 3·8°C (Wigley & Raper, 1992). The increase in the northern hemisphere predicted by the general circulation models (GCMs) will be greater than in the southern hemisphere (Viner *et al.*, 1995). However, the prediction of regional-scale climates by the GCMs is unreliable (Schlesinger & Mitchell, 1988; Hanson *et al.*, 1993). There is thus considerable uncertainty regarding the effects that climate change will have on agriculture at a regional level (Parry & Carter, 1988; Parry *et al.*, 1989; Parry, 1990).

In a changing climate, the success of agriculture is dependent on its ability to adapt. The response of crops to increases in temperature and CO_2 levels may differ between species. Squire & Unsworth (1989) have shown that doubling CO_2 concentrations and increasing temperature by 3°C has no effect on winter wheat yields, but enhances the yield of potatoes by 50–75%. However, the crop–climate interactions are complex and for this reason Stockle *et al.* (1992) regard simulation models as having a useful and practical role for assessing the impact of global warming on agricultural production. The aim of this present study has been to develop just such 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. The model seeks to build on an earlier model by Doyle *et al.* (1989) and to incorporate some of the recent work involving modelling at the leaf level (Thornley *et al.*, 1991) into a pasture systems model.

THE MODEL

The model of the sward assumes that it is either pure grass or a grass–white clover mixture. Forage production is calculated on a daily basis, and is presumed to be dependent on herbage mass, temperature, radiation, atmospheric carbon dioxide (CO_2) concentration, available water and nutrients. There are five state variables, leaf dry matter (D_L, kg DM ha^{-1}), stem dry matter (D_S, kg DM ha^{-1}), root dry matter (D_R, kg DM ha^{-1}), dead material (D_D, kg DM ha^{-1}) and the leaf area index of the crop (L, ha leaf (ha (ground)$^{-1}$). The initial values of these variables, apart from D_R (kg DM ha^{-1}), are given in Table 1. The proportion of white clover dry matter at the start of the growing season in the mixed sward is assumed to be 10% (Orr *et al.*, 1990).

There are also five driving variables, namely the mean daily temperature (T, °C), the level of photosynthetically active radiation (I_0, MJ ha^{-1} (ground)

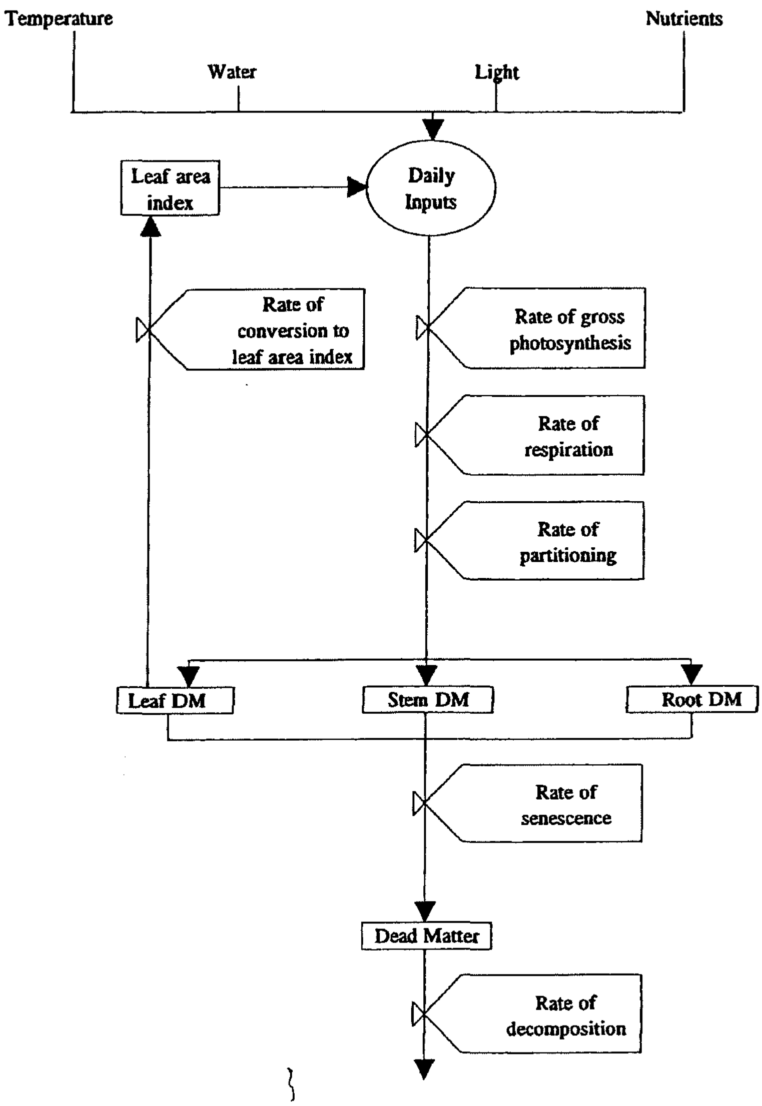

Fig. 1. A schematic diagram of the forage growth model.

Effect of temperature

Temperature is primarily seen in the model as modifying the rates of gross photosynthesis and maintenance respiration. Essentially the growing season is presumed to commence when the average daily air temperature exceeds 4·5°C for seven consecutive days for grass (Broad & Hough, 1993) and 6°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, growth is assumed to cease when the average daily temperature falls below 8°C (Broad & Hough, 1993) for three consecutive days, and does not restart before the spring.

TABLE 1
Initial Conditions For the Grass and Grass–Clover Swards

Sward	*Parameter*	*Value*	*Source[1]*
Grass	D_D	900·0	1
	D_L	1350·0	1
	D_S	450·0	1
	L	3·48	2
Grass–clover	D_D (clover)	90·0	1
	D_D (grass)	810·0	1
	D_L (clover)	135·0	1
	D_L (grass)	1215·0	1
	D_S (clover)	45·0	1
	D_S (grass)	405·0	1
	L (clover)	0·50	2
	L (grass)	3·13	2

*Source 1. Topp & Doyle (1994); 2. See equation 6.

day^{-1}); the atmospheric concentration of CO_2 (CO_2, kg CO_2 m^{-3}), the available moisture (W, mm) and the available nitrogen (N, kg ha^{-1} day^{-1}). Essentially temperature, photosynthetically active radiation and atmospheric CO_2 concentration are presumed to modify the rates of gross photosynthesis (P, kg CO_2 ha^{-1} (ground) day^{-1}). Net photosynthesis (P_n, kg CO_2 ha^{-1} (ground) day^{-1}) is then derived by deducting respiration losses (R, kg CO_2 ha^{-1} (ground) day^{-1}). The available moisture and nitrogen modify the net photosynthate, which 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.

Given the structure of the model, it is convenient to divide its description into six sub-models concerned with: (i) effect of temperature on the start and end of the growing season; (ii) photosynthesis; (iii) respiration; (iv) water and nutrient stress; (v) assimilate partitioning and senescence; and (vi) herbage accumulation under cutting. A schematic representation of the model is shown in Fig. 1. The principal variables and parameters are listed in Appendix 1, and the parameter values are listed in Appendix 2. The basic mathematical structure of the model is outlined in Appendix 3.

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, stolons and petioles are included in the 'stem' component.

Photosynthesis

The canopy gross photosynthesis (P, kg CO_2 ha^{-1} (ground) day^{-1}) for a monoculture is defined by Johnson & Thornley (1984) as:

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

where

$$Ph = \frac{\alpha * k * I_0}{(1 - m)} * e^{-k\ell} \qquad (2)$$

and I_0 is the photosynthetically active radiation in MJ ha^{-1} (ground) day^{-1}, P_{max} is the leaf photosynthetic rate in kg CO_2 ha^{-1} (leaf) day^{-1} at saturating light levels ($I_0 \rightarrow \infty$) and at atmospheric CO_2 concentration, k is the extinction coefficient, m is the leaf transmission coefficient, L is the leaf area index (ha (leaf) ha^{-1} (ground)), ℓ is the cumulative leaf area index and α is the photochemical efficiency (kg CO_2 MJ^{-1}).

P_{max} is considered to be a function of the leaf area index (Johnson *et al.*, 1989), and the mean daily temperature (Johnson & Thornley, 1983) according to:

$$P_{max} = P^0_{max}[1 - \epsilon(1 - e^{-k*L})] * \frac{T - T_0}{T_{Ref} - T_0} * H; \text{ for } T > T_0 \qquad (3)$$

where P^0_{max} is the maximum hourly rate of leaf photosynthesis (kg CO_2 ha^{-1} (leaf) h^{-1}), T (°C) is the mean daily temperature, T_0 (°C) is the temperature at which photosynthesis ceases, T_{Ref} (°C) is the temperature at which P_{max} is unconstrained by temperature, and ε is the rate of decline of P^0_{max} with irradiance. It is assumed in eqn (1) that photosynthetically active radiation and temperature do not vary throughout the day. The daily rate of photosynthesis can thus be calculated by multiplying the maximum hourly rate of leaf photosynthesis (P^0_{max}, kg CO_2 ha^{-1} (leaf) h^{-1}) by the effective day length (H, h), where H is based on nautical twilight. Following Thornley *et al.* (1991), the effect of atmospheric CO_2 on α and P^0_{max} can be described by:

$$\alpha = \alpha_{max} * \frac{1 - \varpi}{\tau * CO_2} \qquad (4)$$

$$P^0_{max} = \frac{P^{CO_2}_{max}}{1 + KP_{max}/CO_2} \qquad (5)$$

where α_{max} is the maximum value of the photochemical efficiency (kg CO_2 MJ^{-1}), CO_2 is the atmospheric concentration of CO_2 (kg CO_2 m^{-3}), τ is the CO_2 conductance parameter (m s^{-1}) and ϖ represents the photorespiration constant (kg m^{-2} s^{-1}). The maximum hourly rate of leaf photosynthesis is denoted by $P_{max}^{CO_2}$ (kg CO_2 ha (leaf) h^{-1}) and KP_{max} is the CO_2 concentration at which $P_{max}^{CO_2}$ is half its maximal value (kg CO_2 m^{-3}).

Following Johnson *et al.* (1983), the leaf area index (L, ha (leaf) ha^{-1} (ground)) is assumed to be described by:

$$L = A * D_L \tag{6}$$

where A is the specific leaf area (ha leaf (kg DM)$^{-1}$) and D_L is the leaf dry matter (kg DM ha^{-1}). It is recognized that eqn (6) represents a gross simplification in that it implies that A 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. In addition, given the way that the effects of temperature on photosynthesis were modelled (see eqn (3)), arguably the effects on the specific leaf area may already have been incorporated indirectly.

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 the grass and the white clover. The rate of canopy gross photosynthesis (P_j, kg CO_2 ha^{-1} (ground) day^{-1}) is:

$$P_j = \frac{1}{2 * \Theta} * \int_0^L Ph_j + P_{max,j} - \sqrt{(Ph_j + P_{max,j})^2 - 4 * \Theta * P_{max,j} * Ph_j}\, \frac{d\ell_j}{d\ell} * d\ell \tag{7}$$

where

$$Ph_j = \frac{\alpha_j * k_j * I_0}{(1 - m_j)} * e^{-(k_g * \ell_g + k_c * \ell_c)} \tag{8}$$

and $d\ell_j/d\ell$ describes the vertical distribution of each component through the depth of the canopy (L, ha (leaf) ha^{-1} (ground)). Subscript g refers to grass and c to white clover. In order to solve eqn (7), it is necessary to describe the vertical distribution through the depth of the canopy. In cut swards, white clover tends to predominate in the upper layers of the canopy (Woledge, 1988; Woledge *et al.*, 1992). A relationship describing the vertical distribution of the sward has been estimated from data obtained from Woledge *et al.* (1992).

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 & Thornley, 1983). The following equation describes the respiration requirements of each component (R_j, kg CO_2 ha^{-1} day^{-1}) of the sward:

$$R_j = (1 - Y_j) * P_j + r_j * Y_j * M_j * \frac{T - T_0}{T_{Ref} - T_0}; \text{ for } T > T_0 \qquad (9)$$

where Y_j is the growth conversion coefficient (kg CO_2 (kg CO_2)$^{-1}$) measuring the conversion yield of the growth process, r_j (kg CO_2 (kg DM)$^{-1}$ day^{-1}) is the maintenance respiration coefficient and M_j (kg DM ha^{-1}) is the total dry-matter weight of the particular component j (Johnson & Thornley, 1983).

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 photosynthate of each component, either by reducing the efficiency of photosynthesis or by reducing the length of the growing period. The effect of water and nutrient stress on photosynthesis has been modelled by reducing the net photosynthesis in proportion to the stress experienced by the crop.

The principal limiting nutrient for pasture in Scotland is nitrogen. The daily available nitrogen (N, kg ha^{-1} day^{-1}) is expressed as a proportion of the nitrogen at saturating level (N_{max}, kg ha^{-1} day^{-1}). The available soil water (W, mm) is expressed as a proportion of the soil water required for maximum growth (W_{max}, 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 (ϕ_g) and white clover (ϕ_c) are:

$$\phi_g = (\beta 1 * \sqrt{W/W_{max}} + \beta 2 * \sqrt{N/N_{max}})^2 \qquad (10)$$

$$\phi_c = \beta 3 + \beta 4 * W/W_{max} \qquad (11)$$

where β1–β4 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.

The amount of nitrogen 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 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 10 days after the start of growth. If this has not occurred by 1 April, 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 increases linearly with the proportion of white clover ground cover, following the observation of Cowling (1982). White clover can take up much of the available soil nitrogen (Vallis *et al.*, 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 *et al.*, 1956). It has thus been assumed that 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 recognized that this is a simplification of what happens in reality.

With regard to the availability of water, the soil is assumed to be saturated on 1 January. The change in available water on subsequent days is assumed to equal the difference between rainfall and actual evapotranspiration. The potential evapotranspiration (E, mm day^{-1}) was calculated using a Penman equation (Penman, 1948) and can be described by the following equation:

$$E = \frac{(\Delta * R_0/L_v + S * V)}{\Delta + S} \tag{12}$$

where R_0 is the radiation corrected for the soil heat flux (J m^{-2}), L_V is the latent heat of vaporization of water (J kg^{-1}) and S is the psychrometric constant (mbars °C^{-1}). The slope of the saturation vapour pressure (Δ, mbars °C^{-1}) is calculated from the average daily temperature. The evaporation component due to the wind and the vapour pressure deficit is denoted by the variable V (kg m^{-2}). The actual evapotranspiration was calculated from the potential and the available soil water.

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 & 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 & 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 (Wong *et al.*, 1979; Farquhar & Sharkey, 1982), the successful modelling of transpiration would require a more complicated form of the photosynthesis and transpiration equations. These equations would also need 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 recognized that it is a simplification, but on balance it was decided to model evapotranspiration by eqn (12).

Assimilate partitioning and senescence

The net photosynthesis is expressed as kg CO_2 ha^{-1} (ground) day^{-1}, which is converted to dry matter by multiplying the net photosynthesis by the efficiency of converting CO_2 to dry matter. Following Doyle *et al.* (1989), pasture growth occurred when there was photosynthate surplus to requirements for tissue maintenance and growth respiration. A fixed proportion of the photosynthate is assumed to be partitioned to the root (Johnson *et al.*, 1983). The remaining photosynthate is partitioned between the leaves and the stem. Losses, through senescence, offset the production of new leaf and stem material. The senescent material passes into the pool of dead material, where it remains until it decomposes.

Sheehy *et al.* (1980) observed that, for grass, the physiological stage of development affected the proportion of photosynthate partitioned to the leaves and the rate of leaf senescence. In spring, during the reproductive phase, less assimilate is partitioned to the leaves. The apparent life of the leaf 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 rates between the reproductive and vegetative phases (Spedding & Diekmahns, 1972). For white clover the proportion of photosynthate partitioned to the leaves and stem is therefore presumed to be independent of the physiological stage of the crop.

Herbage accumulation under cutting

In the grass sward, the actual quantity of grass harvested under cutting is equated with the quantity of leaf and stem material in the sward, less some predefined residual quantity of material that remains 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 has been determined from the selection coefficient ν (Ridout & Robson, 1991), which is defined as:

$$\nu = \frac{c_D}{g_D} / \frac{c_s}{g_s} \tag{13}$$

where c_D (g_D) and c_S (g_S) are the amount of white clover (grass) harvested and in the sward, respectively. Woledge *et al.* (1992) determined the selection coefficient for white clover leaf area (ν_l) and dry matter (ν_d) in a cut sward. In the model, the equation has been re-arranged so that the quantities of white clover leaf area harvested can be calculated. Once the quantity of white clover leaf area preferentially removed has been calculated, the quantity of white clover dry matter preferentially removed can be determined.

VALIDATION

The ability of the model to simulate grass production between sites and at different fertiliser nitrogen rates was investigated using data from the GM20 trial (Morrison *et al.*, 1980). The weather data was obtained from the Meteorological Office. The model was specifically run for the period 1970–1973 for Seale Hayne and High Mowthorpe, and 1970–1972 for Rosemaund. Theil's inequality coefficient (Theil, 1970), which has a value of between 0 and 1, with 0 indicating a perfect fit, was used to determine the performance of the model. The value of Theil's inequality coefficient over the four years was 0·18 for Seale Hayne and Rosemaund, and 0·22 for High Mowthorpe. The validation of grass–white clover production was investigated using GM23 data for High Mowthorpe, Liscombe and Rosemaund (J. Gilbey, personal communication). The period for which the model was specifically run was 1978–1981. At fertiliser application rates of 0 kg per hectare, Theil's inequality coefficient over the four years at the three sites had values of between 0·17 and 0·24 for grass production and 0·29 and 0·50 for white clover production.

The value of Theil's inequality coefficient was rather high at Liscombe and Rosemaund. At Liscombe, this was partly due to the observed yield of white clover being practically zero in 1981. At Rosemaund, 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. Nevertheless, the model in general proved to be reasonably valid for the grass and the combined yield, and it also gave reasonable predictions in terms of the general trends of the white clover yield.

RESULTS

The effect of global warming and increases in the atmospheric concentration of CO_2 on grass and grass–white clover production have been explored by running the model with 10 years of data for current climatic conditions and for a global warming scenario at two levels of CO_2 concentration. The expected concentration of CO_2, when all the radiative forcing effects of all the 'greenhouse' gases including CO_2 is double the pre-industrial level, is 520 ppm (Wigley & Raper, 1992). The concentrations used in the model are thus 350 ppm, representing current levels, and 520 ppm. A weather generator was used to produce realistic scenarios of daily data (Perris & McNicol, 1992). For the global warming scenario, the annual average temperature was increased by 2°C, and the rainfall on rainy days was increased according to estimates by Viner and Hulme (1994). The four scenarios used in the model were:

- scenario 1 — current climatic conditions and current CO_2 concentration of 350 ppm
- scenario 2 — current climatic conditions and increased CO_2 concentration of 520 ppm
- scenario 3 — global warming scenario and current CO_2 concentration of 350 ppm
- scenario 4 — global warming scenario and increased CO_2 concentration of 520 ppm

The model was run for four sites across Scotland; namely Kinloss, Mylnefield, Paisley and Wick. The monthly mean daily climatic conditions for the months February to September for both scenarios at each site are shown in Table 2. The quantity of fertiliser nitrogen applied to the grass sward was presumed to be 300 kg nitrogen per hectare, and 50 kg of nitrogen per hectare was applied to the grass–white clover swards. The soil type at each site determined the available soil water at field capacity (W_{max}) and the available pool of nitrogen in the soil. The significance of the effect of global warming and CO_2 concentration on grassland production was assessed using an analysis of variance (ANOVA) (Genstat, 1987) at the 5% level of significance.

TABLE 2
The Mean Daily Weather Variables for the Months February to September at Each Site for the Current Climatic (Scenarios 1 and 2) and for Global Warming Conditions (Scenarios 3 and 4)

Site	*Month*	*Radiation (MJ ha^{-1})*		*Average temperature (°C)*		*Rainfall (mm)*	
		1 & 2	*3 & 4*	*1 & 2*	*3 & 4*	*1 & 2*	*3 & 4*
Kinloss	February	27,550	30,270	3·7	5·1	1·4	2·2
	March	52,870	53,060	4·6	7·1	1·5	1·9
	April	88,480	99,410	7·7	9·8	1·3	1·5
	May	140,550	151,020	11·0	12·5	1·3	1·7
	June	172,370	192,820	13·2	14·9	2·1	1·7
	July	164,400	151,450	14·0	15·7	1·6	1·5
	August	109,890	104,390	13·5	15·9	1·5	1·4
	September	66,730	62,330	11·8	14·3	1·5	1·5
Mylnefield	February	32,450	35,280	2·9	5·2	2·3	2·9
	March	54,560	59,170	5·4	6·1	2·3	3·0
	April	96,610	103,310	6·7	9·5	1·9	2·2
	May	153,840	151,380	10·0	12·7	1·3	1·9
	June	177,980	192,180	13·7	15·7	1·6	1·7
	July	191,660	180,180	13·8	16·3	1·5	1·6
	August	125,990	107,980	14·4	16·2	1·6	1·8
	September	67,440	76,260	12·4	14·2	2·4	1·8
Paisley	February	28,240	20,910	4·0	5·8	4·3	5·1
	March	51,300	53,210	5·4	7·4	3·2	4·0
	April	86,210	97,250	8·9	9·7	2·8	2·6
	May	137,600	144,850	11·5	13·9	1·6	2·7
	June	168,830	163,070	13·6	15·6	2·6	3·2
	July	160,980	147,300	14·9	17·2	2·5	2·4
	August	103,300	100,250	14·9	17·4	2·5	2·5
	September	67,060	64,750	13·0	15·5	3·5	3·0
Wick	February	32,360	31,280	3·3	4·9	2·2	3·3
	March	54,910	49,070	4·4	6·0	2·2	3·1
	April	91,120	91,240	6·0	8·7	2·1	2·7
	May	133,620	140,120	8·8	10·7	1·7	2·4
	June	156,530	161,180	11·0	13·0	1·4	1·7
	July	154,520	145,580	12·6	14·3	1·6	1·8
	August	119,180	102,740	12·3	14·6	1·7	1·8
	September	69,600	63,400	10·5	13·3	2·3	2·2

Grass swards

Effects on the length of the growing season

With the increases in temperature predicted under global warming, grass growth at all four sites started earlier and ended later in the season than under current climatic conditions (Table 3). However, the earlier start to

TABLE 3
Ten-Year Average and Level of Significance Between Mean Start and End Dates for the Growing Season under the Current Climatic (Scenarios 1 and 2) and Global Warming Conditions (Scenarios 3 and 4) for Pure Grass Swards

	Scenarios 1 & 2	*Scenarios 3 & 4*	*Significance*
Kinloss			
start	28/4	18/4	**
end	11/10	19/11	**
Mylnefield			
start	05/5	06/4	**
end	25/10	14/11	**
Paisley			
start	14/4	07/4	ns
end	31/10	19/11	**
Wick			
start	11/5	08/4	**
end	06/10	17/11	**

**Significant at the 5% level; ns, not significant.

the growing season was not significant at Paisley. The increase in the length of the average growing season ranged from 25·2 days at Paisley to 75·5 at Wick. This was in agreement with Flohn (1985), who stated that, in high latitudes, a 1°C change in the global yearly mean air temperature would lengthen or shorten the growing season by 3–4 weeks. With the exception of Mylnefield, there was a greater increase in the number of growing days at the end of the growing season than at the start accompanying global warming.

Effects on yield

The effect of global warming on mean yield over a 10-year period varies between sites, as shown in Fig. 2. Specifically, the harvested yields are shown for a two-cut system, involving cuts on 1 June and 27 July. At all sites the increase in temperature and change in rainfall associated with global warming had no significant effect on yield. However, excluding the first cut at Wick, enhancing the CO_2 concentration under both current climatic conditions and the global warming scenario significantly increased the yield of both cuts and thus the total yield. For the first cut at Paisley and the second cut at Wick the grass yield under the global warming scenario coupled with enhanced CO_2 (scenario 4) was not significantly different from the current climate with current concentrations of CO_2 (scenario 1). Nevertheless, the seasonality of grass production was not affected by global warming or increased CO_2 concentration.

Interpreting the response

The response of grass yields to increased atmospheric CO_2 concentration are due to the increased rates of photosynthesis. The differences in the response between sites due to global warming must be interpreted in conjunction with the actual changes in the weather data. In so far as the weather data was synthetically generated (Perris & McNicol, 1992), care is needed in interpreting the differences. At Paisley, the start of the growing season was not significantly affected by global warming, (Table 3) and this would have resulted in the projected non-significant change for the first cut yield between scenarios 1 and 4 at this site (Fig. 2). The reason for the start of the growing season not being significantly affected by global warming is that the average daily temperature in April for Paisley was only increased by 0·8°C day^{-1} under the global warming scenarios, as shown in Table 2. This compares with increases of 2·1°C day^{-1}, 2·8°C

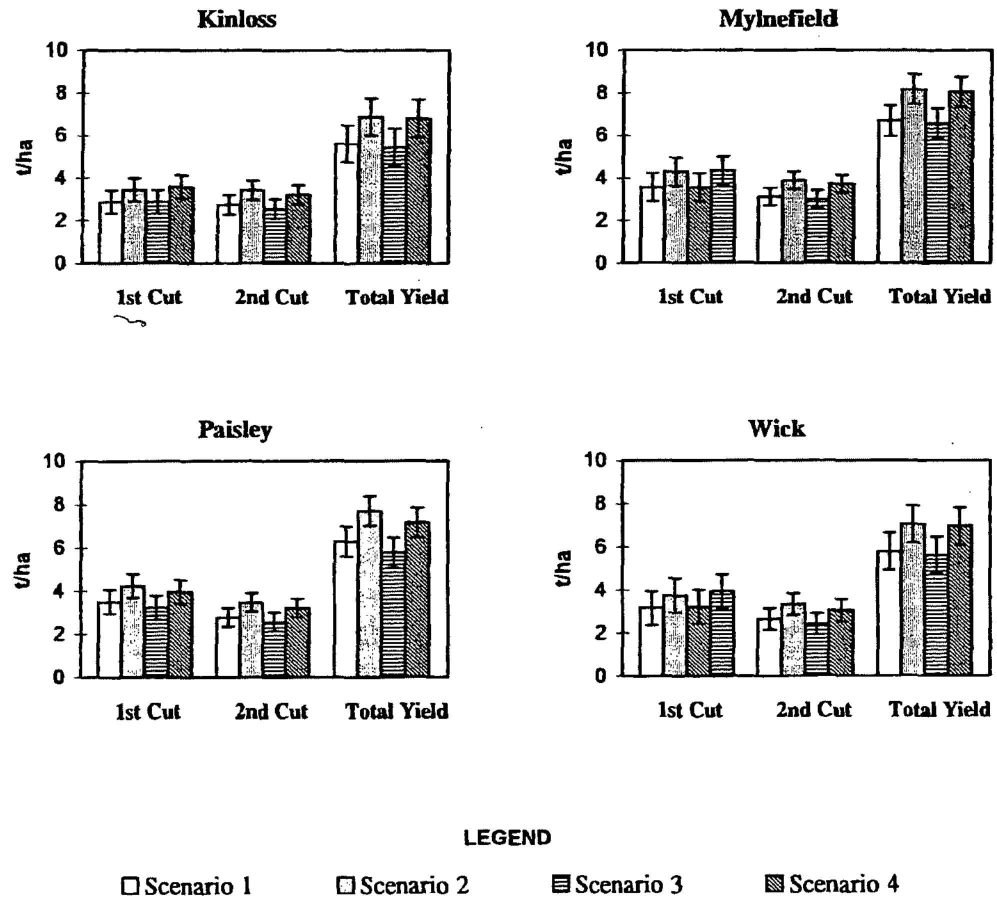

Fig. 2. Ten-year average and LSD in respect the means of the conservation yields for the current climate at 350 ppm CO_2 (scenario 1) and 520 ppm CO_2 (scenario 2), and global warming at 350 ppm CO_2 (scenario 3) and 520 ppm CO_2 (scenario 4) for pure grass swards. The error bars indicate the LSD at the 5% level of significance.

TABLE 4
Ten-Year Average, and Level of Significance for the Mean Start and End Dates for the Growing Season under the Current Climatic (Scenarios 1 and 2) and Global Warming Conditions (Scenarios 3 and 4) for Grass–Clover Swards

	Scenarios 1 & 2	*Scenarios 3 & 4*	*Significance*
Kinloss			
start clover	13/5	27/4	**
Mylnefield			
start clover	16/5	23/4	**
Paisley			
start clover	27/4	12/4	**
Wick			
start clover	26/5	29/4	**

**Significant at the 5% level; ns, not significant.

day^{-1} and 2·7°C day^{-1} for Kinloss, Mylnefield and Wick, respectively. The combined effects of the reduction in photosynthetically active radiation and the increase in the average daily temperature of 1·8°C day^{-1} for June and July at Wick (Table 2) were responsible for the non-significant change in the second cut yield for scenario 4 compared to scenario 1 (Fig. 2). The increased length of the growing season did not significantly increase the total yield at any of the sites. Within the model, it is possible that the increase in the number of growing days in the spring was not significantly increased. This is because the model measures the growing season as the period of continuous growth. However, the increase in temperature will have increased the rates of maintenance respiration and evapotranspiration, as well as the rate of photosynthesis.

Grass–white clover

Effects on the length of the growing season
At all sites the effect of global warming was to bring forward significantly the date on which white clover growth commenced, as shown in Table 4. At Kinloss and Paisley the difference in the commencement of grass and white clover growth was reduced by global warming, whereas it was increased at Mylnefield and Wick. Overall, the increase in the length of the growing season with global warming for the clover component ranged from 34 days at Paisley to 69·1 days at Wick.

Effects on the yields
As regard the impact on yields, the increased temperature, coupled with the changes in rainfall predicted with global warming, and the increased

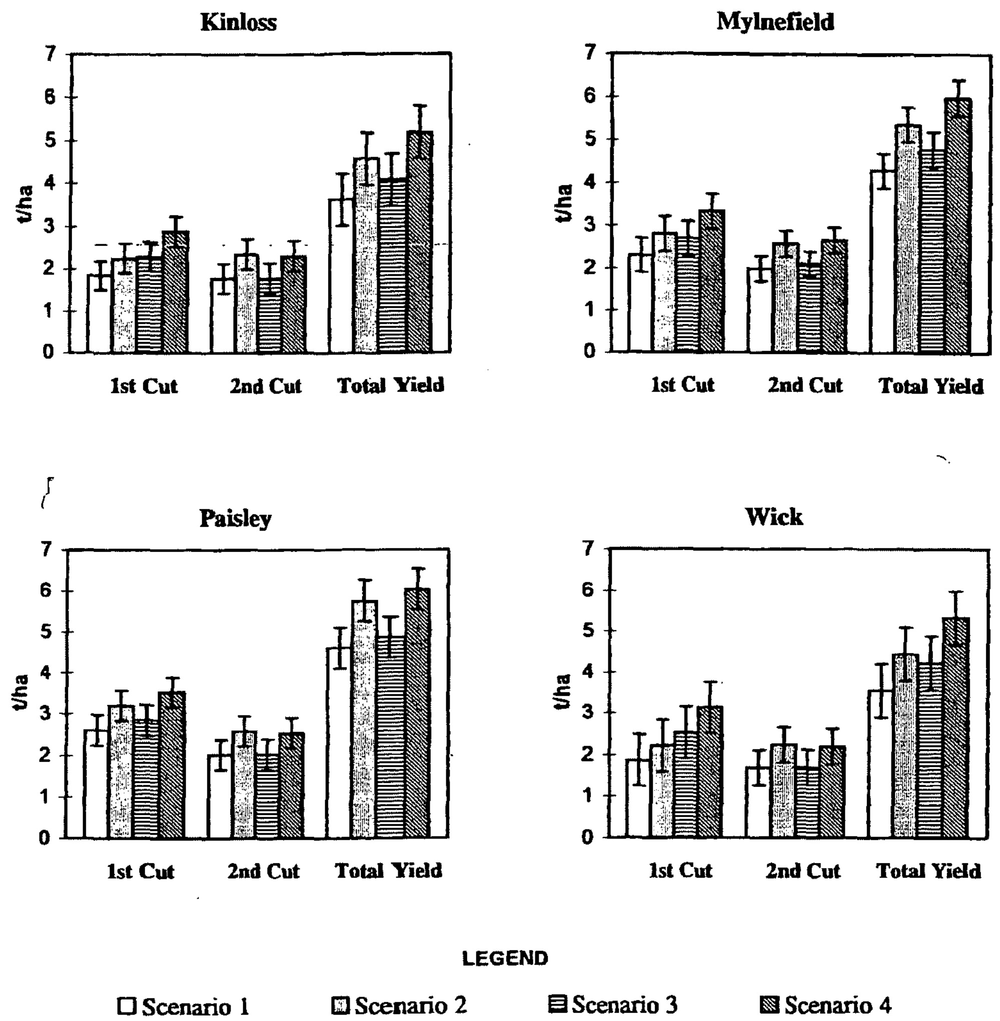

Fig. 3. Ten-year average and LSD in respect of mean yield under cutting for grass–clover swards under the current climate at 350 ppm CO_2 (scenario 1) and 520 ppm CO_2 (scenario 2), and global warming at 350 ppm CO_2 (scenario 3) and 520 ppm CO_2 (scenario 4) for grass–clover swards. The error bars indicate the LSD at the 5% level of significance.

concentrations of CO_2, significantly affected the first cut yield at all sites and the total yield at Kinloss, Mylnefield and Wick. However, for the second cut only the CO_2 concentration had a significant effect, although this occurred at all sites. At Kinloss and Wick the global warming scenario with current concentrations of CO_2 (scenario 3) significantly increased the first cut yield compared to the yield obtained from the base scenario (scenario 1), as shown in Fig. 3. This effect was also evident for the total yields at Mylnefield and Wick. Increasing the concentration of CO_2 in the atmosphere, without changing the weather conditions, significantly increased yield. The only situation in which this did not occur was for the first cut yield under current climate conditions at Wick.

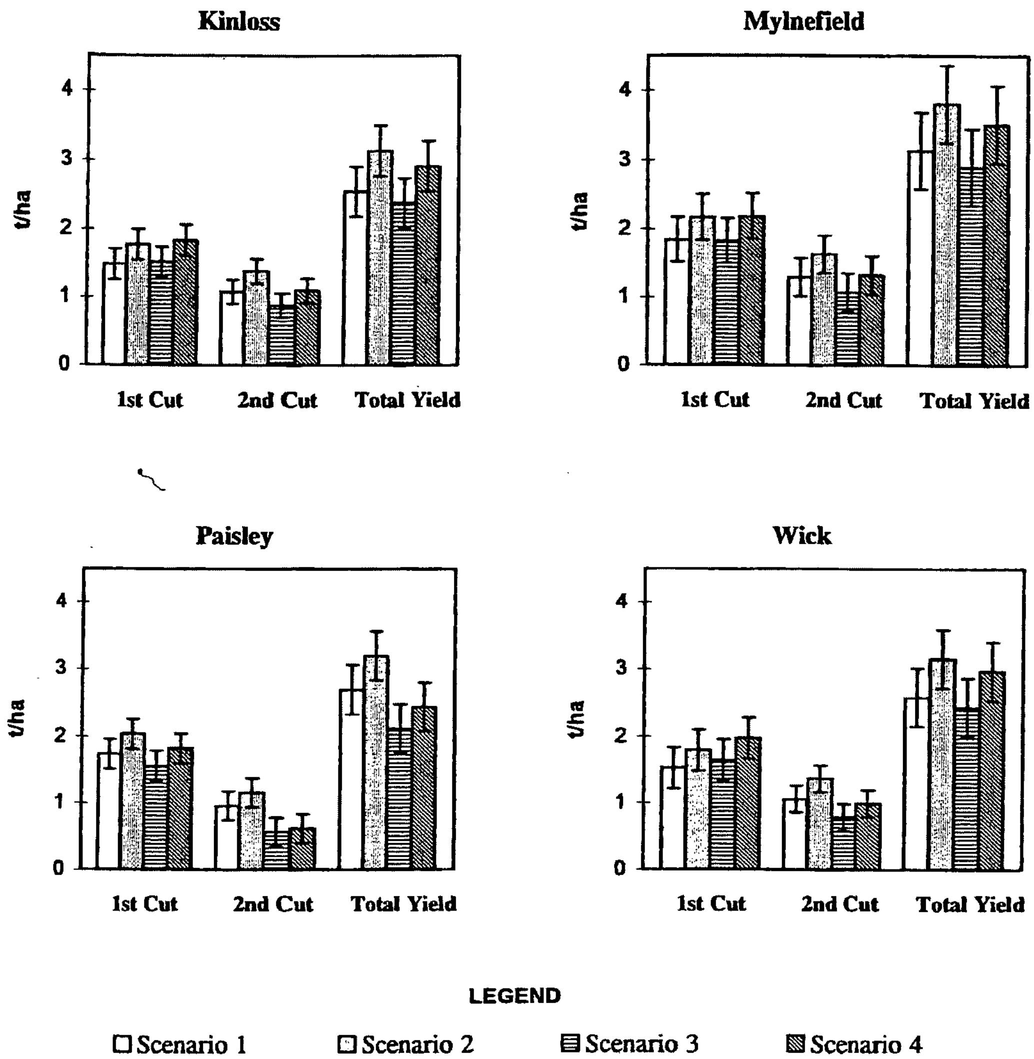

Fig. 4. Ten-year average and LSD in respect of mean yields of the grass component for grass–clover swards under the current climate at 350 ppm CO_2 (scenario 1) and 520 ppm CO_2 (scenario 2), and global warming at 350 ppm CO_2 (scenario 3) and 520 ppm CO_2 (scenario 4). The error bars indicate the LSD at the 5% level of significance.

Effects on components of yield

In respect of the yield components, global warming had a significant effect on the grass component for all cuts at Paisley and for the second cut at the other sites. At Kinloss, Paisley and Wick the yield of grass in the second cut was decreased, as was the total yield at Paisley following an increase in average daily temperature of 2°C (Fig. 4). With respect to the CO_2 concentration, this had a significant effect on all cuts at all sites, except the second cut at Paisley. Increasing the CO_2 concentration therefore resulted in increased grass yields, as shown in Fig. 4.

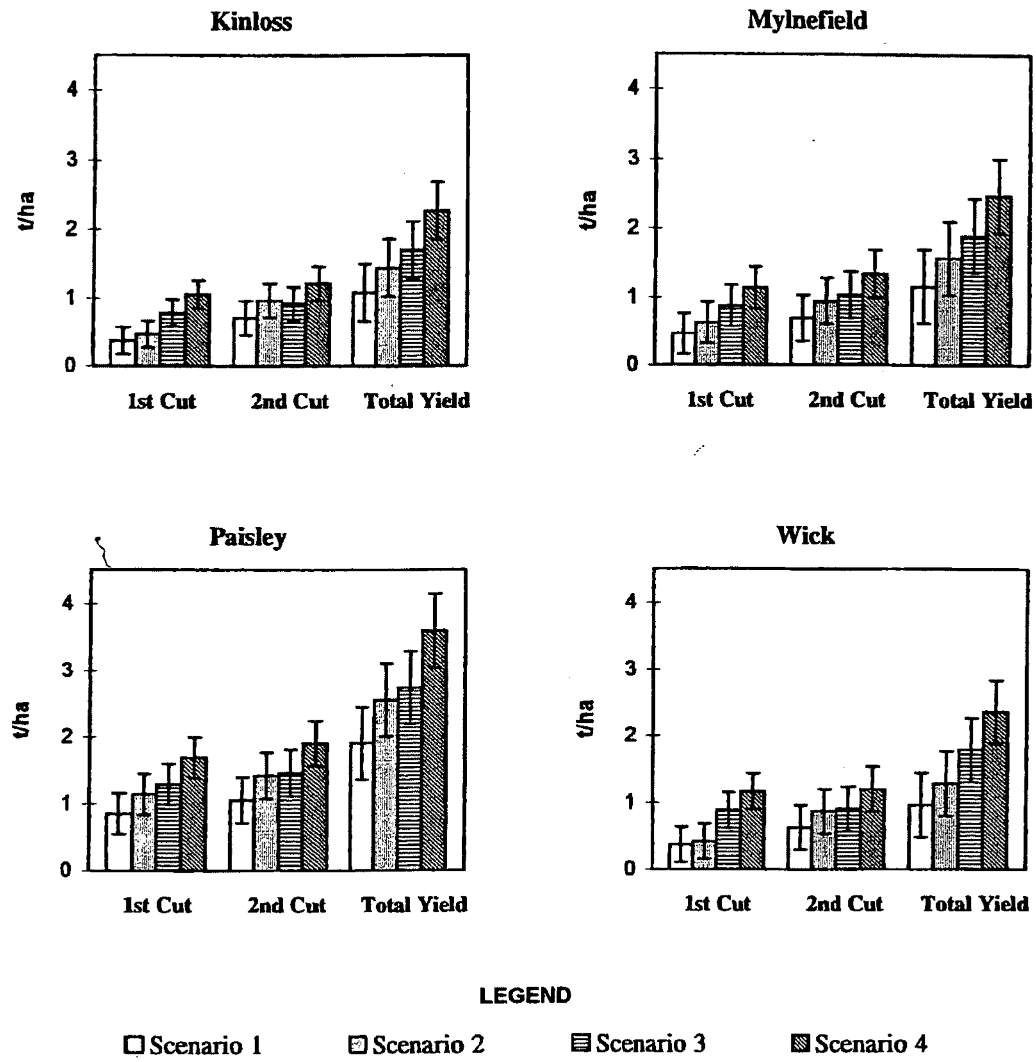

Fig. 5. Ten-year average and LSD in respect of mean yields of the clover component for grass–clover swards under the current climate at 350 ppm CO_2 (scenario 1) and 520 ppm CO_2 (scenario 2), and global warming at 350 ppm CO_2 (scenario 3) and 520 ppm CO_2 (scenario 4). The error bars indicate the LSD at the 5% level of significance.

The yield of the white clover component was significantly affected by both changes in climate and CO_2 concentration for all sites and cuts, except the first cut at Wick. White clover yields were thus significantly increased under scenario 3, relative to current climatic conditions (scenario 1), for the first cut and for total yield at all sites and for the second cut at Paisley, as shown in Fig. 5. In the case of an increased concentration of CO_2, the first cut yield of white clover was significantly increased at Kinloss, Paisley and Wick but this only occurred when enhanced CO_2 levels were associated with higher temperatures. With the second cut, the yield was projected to increase under enhanced atmospheric CO_2 concentrations for

TABLE 5
The Percentage of Total Annual Yield for each Component Obtained in the First Conservation Cut under the Current Climatic (Scenarios 1 and 2) and Global Warming Conditions (Scenarios 3 and 4) for Grass–Clover Swards

Component	*Scenario 1 mean (%)*	*Scenario 2 mean (%)*	*Scenario 3 mean (%)*	*Scenario 4 mean (%)*	*LSD (%)*
Kinloss					
grass	57·9	56·2	63·4	62·7	3·7
clover	34·1	32·3	46·1	46·4	5·0
combined	51·0	48·9	56·3	55·7	4·0
Mylnefield					
grass	58·8	57·4	63·0	62·6	3·7
clover	40·9	40·4	45·4	45·1	9·6
combined	53·7	52·1	56·0	55·3	5·4
Paisley					
grass	64·6	64·0	74·1	75·5	5·7
clover	45·4	45·0	46·7	46·9	7·1
combined	56·5	55·4	58·4	58·1	5·1
Wick					
grass	58·9	56·6	67·6	66·7	5·0
clover	36·8	34·3	49·0	48·9	11·2
combined	52·7	49·9	59·8	58·8	7·3

LSD were calculated at the 5% level of significance.

TABLE 6
The Percentage of White Clover in the Total Harvested Yield under the Current Climatic (Scenarios 1 and 2) and Global Warming Conditions (Scenarios 3 and 4) for Grass–Clover Swards

Component	*Scenario 1 mean (%)*	*Scenario 2 mean (%)*	*Scenario 3 mean (%)*	*Scenario 4 mean (%)*	*LSD (%)*
Kinloss	29·3	30·9	41·4	43·5	6·2
Mylnefield	26·9	29·1	39·4	41·2	9·5
Paisley	41·1	44·2	55·9	59·1	7·4
Wick	26·9	28·8	41·7	43·5	7·2

LSD were calculated at the 5% level of significance.

both climate scenarios (scenarios 2 and 4) at Kinloss and Paisley. Overall, the effect of an increased CO_2 concentration on total white clover yield was to increase it significantly at all sites when average daily temperatures were increased. An increase in total yield also occurred at Paisley with increased atmospheric CO_2 concentration under current climatic conditions.

Interpreting the responses

Overall, global warming was projected to increase significantly the percentage of yield obtained from the first cut for grass at all sites, as shown in Table 5. On the other hand, its effects on the seasonality of white clover production varied between sites with the percentage obtained in the first cut increasing at Kinloss and Wick and not being affected at Mylnefield and Paisley. This pattern was also repeated in respect of the combined grass–white clover production. However, the CO_2 concentration apparently had no effect on the seasonality of production. Overall, the percentage of white clover in the harvested material was significantly increased under the increased temperatures predicted under global warming (Table 6).

As the total yield of the white clover component increases at all four sites, the major difference in the response between sites for the total yield of the grass–white clover sward is due to the grass component. The increase in the first-cut white clover yield at all sites is due to the earlier start to the growing season under global warming conditions (Table 4). This is projected to increase total white clover yield at all sites (Fig. 5) and increase the combined yield at Kinloss and Wick (Fig. 3). The tendency for the second-cut white clover yield also to increase resulted in increased competition for the grass component, and thus the grass yield for this cut was reduced under global warming (Figs 4 and 5). At Paisley the result of this reduction was a decrease in the total grass yield (Fig. 3). Due to changes in the balance between grass and white clover components, the total combined yield was only increased at Mylnefield and Wick.

CONCLUSIONS

The results of the study show that grass and white clover respond differently to changes in climate and atmospheric concentration of CO_2. In a pure grass sward, yield was only influenced by the concentration of CO_2. Similarly, in the case of grass–white clover swards, at the majority of sites changes in climate had no significant effect on the annual yield of grass harvested from a mixed sward. However, at all sites the annual yield of white clover was significantly increased by increasing temperature. At all sites, the effect of increasing the atmospheric CO_2 concentration from 350 ppm to 520 ppm for each climate scenario increased the annual yields of both the grass and white clover components. However, the annual yield of grass from a mixed sward under a global warming scenario coupled with an increase in the levels of CO_2 was not significantly different from the yields obtained under current climatic conditions and at current concentrations of CO_2. Increases in temperature and changes in rainfall associated with global warming at both current and increased concentrations of CO_2 are thus projected to increase the yield of clover, while having little effect on grass production.

The composition of the total yield obtained from a grass–white clover sward was only influenced by the changes in temperature and rainfall predicted under global warming. The average percentage of white clover harvested at all four sites increased from approximately 32% for current climate (scenarios 1 and 2) to approximately 46% under the global warming scenario (scenarios 3 and 4).

In respect of the seasonality of production, grass was unaffected by global warming and enhanced CO_2 concentration. However, for grass–white clover swards, global warming increased the percentage of grass yield obtained from the first cut. There was also a tendency for global warming to increase the percentage of white clover obtained from the first cut. Nevertheless, enhanced CO_2 levels did not influence the seasonality of production.

The increase in the annual average temperature associated with global warming is projected to increase the length of the growing season for both grass and white clover swards, with the majority of sites experiencing a greater increase in the autumn than in the spring. The difference in the commencement of the grass and white clover growth varied between sites. This would influence the growth of both components throughout the growing season.

One aspect not studied in the model is the effect that higher mean temperatures under global warming may have on the digestibility and protein content of the forage harvested. Depending on how far the development and physiological stages of the grass and white clover growth are dependent on temperature; the digestibilities of the material on a given harvest date may change. Certainly, work by Gustavsson *et al.* (1995) and Fagerberg & Nyman (1994) and Fagerberg & Nyman (1995) have explored the effects of weather on nutritional value, and with time these may help to refine the output. Nevertheless, the current model has helped to bring out some interesting and relevant plant–weather interactions.

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APPENDIX 1

TABLE 7
List of Variables in the Model

Variable	*Description*	*Units*
α	Photochemical efficiency at atmospheric CO_2 concentration	kg CO_2 MJ^{-1}
ϕ_j	Effect of water and nutrient availability on the proportionate rate of dry-matter production of crop j	
ℓ	Cumulative leaf area index	ha (leaf) ha^{-1} (ground)
Δ	Slope of the saturation vapour pressure	mbar $°C^{-1}$
Atm	Atmospheric pressure	Pa
c_D	Amount of clover harvested	
c_S	Amount of clover in the sward	
CO_2	Atmospheric concentration of CO_2	kg CO_2 m^{-2}
$CO_{2,vpm}$	Atmospheric concentration of CO_2	vpm
d_G	Daily gain in above-ground dry matter	kg DM ha^{-1} day^{-1}
D_D	Dead dry matter	kg DM ha^{-1}
D_L	Leaf dry matter	kg DM ha^{-1}
D_R	Root dry matter	kg DM ha^{-1}
D_S	Stem dry matter	kg DM ha^{-1}
E	Potential evapotranspiration	mm day^{-1}
H	Effective day length	h
g_D	Amount of grass harvested	
g_S	Amount of grass in the sward	
I_0	Photosynthetically active radiation	MJ ha^{-1} (ground) day^{-1}
L	Leaf area index	ha (leaf) ha^{-1} (ground)
M_j	Total dry weight of crop component j	kg DM ha^{-1}
N	Daily available nitrogen	kg N ha^{-1} day^{-1}
P_j	Canopy gross rate of photosynthesis of crop j	kg CO_2 ha^{-1} (ground) day^{-1}
P_{max}	Leaf photosynthetic rate at saturating light levels	kg CO_2 ha^{-1} (leaf) day^{-1}
P_n	Canopy net rate of photosynthesis	kg CO_2 ha^{-1} (ground) day^{-1}
R	Growth and maintenance respiration	kg CO_2 ha^{-1} (ground) day^{-1}
R_0	Radiation corrected for the soil heat flux	J m^{-2}
T	Mean daily temperature	°C
V	Evaporation component due to the wind and the vapour pressure deficit	kg m^{-2}
W	Available soil water	mm

TABLE 7—Continued
List of Variables in the Model

Parameter	*Description*	*Units*
α_{max}	Maximum value of the photochemical efficiency	kg CO_2 MJ^{-1}
$\beta1$—$\beta4$	Constants in eqns (9) and (10)	
ε	Rate of decline of P^0_{max} with irradiance	
γ_D	Proportionate daily rate of dead matter decomposing	
γ_L	Proportionate daily senescence rate of leaf matter	
γ_S	Proportionate daily senescence rate of stem matter	
λ	Proportion of the daily gain in above ground dry matter partitioned to leaves	
ν	Selection coefficient for the preferential removal of clover	
θ	Efficiency of converting CO_2 to dry matter	kg DM (kg CO_2)$^{-1}$
Θ	Leaf photosythesis parameter	
ρ	Proportion of the assimilate partitioned to the root	
ρCO_2	Density of CO_2 at 1 atmosphere	kg CO_2 m^{-3}
τ	CO_2 conductance parameter	m s^{-1}
ϖ	Photorespiration constant	kg m^{-2} s^{-1}
A	Specific leaf area	ha leaf (kg DM)$^{-1}$
Atm_{Sea}	Atmospheric pressure at sea-level	Pa
j	Component of the crop	
k	Light extinction coefficient	
K	0°C expressed in Kelvin	K
KP_{max}	CO_2 concentration at which is half its maximal value $P^{CO_2}_{max}$	kg CO_2 m^{-3}
L_V	Latent heat of vaporization of water	J kg^{-1}
m	Leaf transmission coefficient	
N_{max}	Saturating level of nitrogen	kg N ha^{-1} day^{-1}
$P^{CO_2}_{max}$	Maximum hourly rate of leaf photosynthesis	kg CO_2 ha (leaf) h^{-1}
P^0_{max}	Maximum hourly rate of leaf photosynthesis at atmospheric CO_2 kg CO_2 ha (leaf) h^{-1}	
r	Respiration maintenance coefficient	kg CO_2 kg DM^{-1} day^{-1}
S	Psychrometric constant	mbar °C^{-1}
T_0	Temperature at which photosynthesis ceases	°C
T_{Ref}	Temperature at which photosynthesis is maximal	°C
W_{max}	Available soil water at field capacity	mm
Y_j	Respiration growth conversion efficiency of crop j	kg CO_2 (kg CO_2)$^{-1}$

APPENDIX 2

TABLE 8
Table of Parameter Values

Parameter	*Value*	*Source**	*Parameter*	*Value*	*Source**
$\alpha_{max,c}$	0·01	1	k_c	0·8	10
$\alpha_{max,g}$	0·01	1	k_g	0·5	3
$\beta 1$	0·366	2	K	273·15	7
$\beta 2$	0·664	2	KP_{max}	1·281e–3	11
$\beta 3$	0·216	2	L_V	2·465e8	12
$\beta 4$	0·789	2	m_c	0·1	3
ε	0·35	3	m_g	0·1	3
θ	0·682	4	N_{max}	4·0	2
Θ	0·95	6	r_c	0·05	4
ρCO_2	1·9636	7	r_g	0·05	13
τ	0·0015	1	$P_{max}^{CO_2}$	129·6	5
v_d	0·94	8	P_{max}^{0}	43·2	4
v_l	1·22	8	S	0·66	12
ϖ	0·3e–6	1	T_0	0·0	14
A_c	0·00258	9	T_{Ref}	20·0	14
A_g	0·00368	9	Y_c	0·63	4
Atm_{Sea}	101,325	7	Y_g	0·83	13

*Source: 1. Thornley *et al.* (1991); 2. Estimated from data from the GM23 trial (J. Gilbey personal communication); 3. Johnson *et al.* (1989); 4. Topp & Doyle (1994); 5. Calculated from eqn (4); 6. Johnson & Thornley (1985); 7. Thornley (1991); 8. Woledge *et al.* (1992); 9. Davidson & Robson (1986); 10. Brown & Blaser (1968); 11. Thornley & Cannell (1992); 12. Agriculture and Food Research Council (1991); 13. Mogensen (1977); 14. Johnson *et al.* (1983).

TABLE 9
Table of Partitioning Factors for the Grass and Clover Components

Crop	*Parameter*	*Value*	*Source**
Clover	γ_D	0·025	1
	γ_L	0·024	2
	γ_S	0·0259	3
	λ	0·33	4
	ρ	0·1	5
Grass	γ_D	0·025	1
reproductive	γ_L	0·0146	3
vegetative	γ_L	0·0311	3
	γ_S	0·0259	3
reproductive	λ	0·60	3
vegetative	λ	0·68	3
	ρ	0·1	5

*Source: 1. Doyle *et al.* (1989); 2. Chapman *et al.* (1984); 3. Sheehy *et al.* (1980); 4. Chapman *et al.* (1991); 5. Johnson *et al.* (1983).

APPENDIX 3: OUTLINE OF BASIC MATHEMATICAL STRUCTURE OF MODEL

Atmospheric carbon dioxide concentration

$$CO_2 = CO_{2,vpm} * 10^{-6} * \frac{K}{T + K} * \frac{Atm}{Atm_{Sea}} * \rho CO_2$$

Gross photosynthesis

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

where

$$Ph = \frac{\alpha * k * I_0}{(1 - m)} * e^{-k\ell}$$

$$P^0_{max,j} = \frac{P^{CO_2}_{max,j}}{1 + KP_{max,j}/CO_2}$$

$$P_{max,j} = P^0_{max,j}\left[1 - \epsilon(1 - e^{-k*L})\right] * \frac{T - T_0}{T_{Ref} - T_0} * H; \text{ for } T > T_0$$

$$\alpha_j = \alpha_{max,j} * \frac{1 - \varpi}{\tau * CO_2}$$

$$L = A * D_L$$

Net photosynthesis

$$P_n = P - R_j$$

where

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

Dry-matter production

$$d_{Gj}(1 - \rho_j) * P_{n,j} * \phi_j * \tau$$

$$\phi_g = (\beta 1 * \sqrt{W/W_{max}} + \beta 2 * \sqrt{N/N_{max}})^2$$

$$\phi_c = \beta 3 + \beta 4 * W/W_{max}$$

Assimilate partitioning

$$D_{Lj} = D_{Lj} + \lambda_j * d_{Gj} - \gamma_{Lj} * D_{Lj}$$

$$D_{Sj} = D_{Sj} + (1 - \lambda_j) * d_{Gj} - \gamma_{Sj} * D_{Sj}$$

$$D_{Dj} = D_{Dj} + \gamma_{Lj} * D_{Lj} + \gamma_{Sj} * D_{Sj} - \gamma_{Dj} * D_{Dj}$$

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Simulating the Impact of Global Warming on Milk and Forage Production in Scotland: 2. The Effects on Milk Yields and Grazing Management of Dairy Herds

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ABSTRACT

The potential impact of global warming and the enhanced atmospheric CO_2 concentration on grassland management on dairy farms within the UK requires assessment. This has led to the development of a mathematical model of the grazing dairy cow. The model, that embraces grass and grass–white clover swards, has been used to assess the effects that the projected increases in temperature and rainfall under global warming and the increased levels of CO_2 might have on milk production and on silage conservation for a typical dairy farm. The results suggest that the impact on milk production for grass-based systems will vary depending on the locality. On the other hand, for herds grazed on grass–white clover swards milk output might increase regardless of site, when the concentration of CO_2 is enhanced. As regards silage production from grass–white clover swards, under global warming and at current levels of CO_2 there is an apparent tendency to increase the percentage of total silage yield obtained from the first cut, although this does not occur for grass swards. At the same time, there are also indications that global warming will increase the percentage of clover in the herbage cut for conservation. Copyright © 1996 Published by Elsevier Science Ltd

INTRODUCTION

The concentration of carbon dioxide (CO_2) and 'greenhouse' gases in the atmosphere have increased, with the concentration of CO_2 being expected to double by the middle of next century from pre-industrial levels (Bolin *et al.*, 1986), and this is expected to increase annual rainfall and the annual average daily temperature by 2°C (Viner & Hulme, 1994). This will have consequences for forage production (Topp & Doyle, 1996) and in turn ruminant livestock output. The expected concentration of CO_2 at the middle of the next century is 520 ppm (Wigley & Raper, 1992).

Although climatic change is likely to affect metabolic processes within animals, the primary effect of global warming on dairy production will probably operate through the effects on forage production. Topp & Doyle (1996) have described the effect of these climatic changes on the production of herbage from pure grass and grass–white clover swards. The aim of the current work has been to develop a model capable of simulating the effect of the projected changes in forage production under global warming and enhanced CO_2 levels on dairy production within the UK generally and Scotland in particular.

THE MODEL

A schematic representation of the basic model is provided in Fig. 1. Within the model, the leaf area index of the crop is altered as the dairy cows 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 ratio of leaf-to-stem further regulate the digestibility of the herbage on offer and so influences the intake of the cows. 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. Although there may be direct effects of climatic change on the nutritive value of the forage crop (Gustavsson *et al.*, 1995; Fagerberg & Nyman, 1994, 1995), these have been ignored, because they are likely to be dwarfed by those due to changes in botanical composition.

A model, that describes the effect of temperature, radiation, atmospheric CO_2 concentration, and nitrogen and water availability on daily herbage accumulation in grass and grass–white clover swards, has been described in detail in Topp & Doyle (1996). This was used to assess the effect of climate change on dry-matter yields of harvested material under cutting. The present model seeks to extend the previous work by looking at how interactions between the grazing animal and the sward modifies leaf area, rates of photosynthesis, sward structure and herbage accumulation rates for a grazing dairy herd. Within the model, account is taken of how changes in sward structure and mass affect intake, digestibility of the diet and consequent animal performance.

Basically, a spring-calving dairy herd, rotationally grazed during the summer period on a pure grass or a grass–white clover sward, is simulated. The pasture is divided into 12 equal-sized paddocks. Herbage

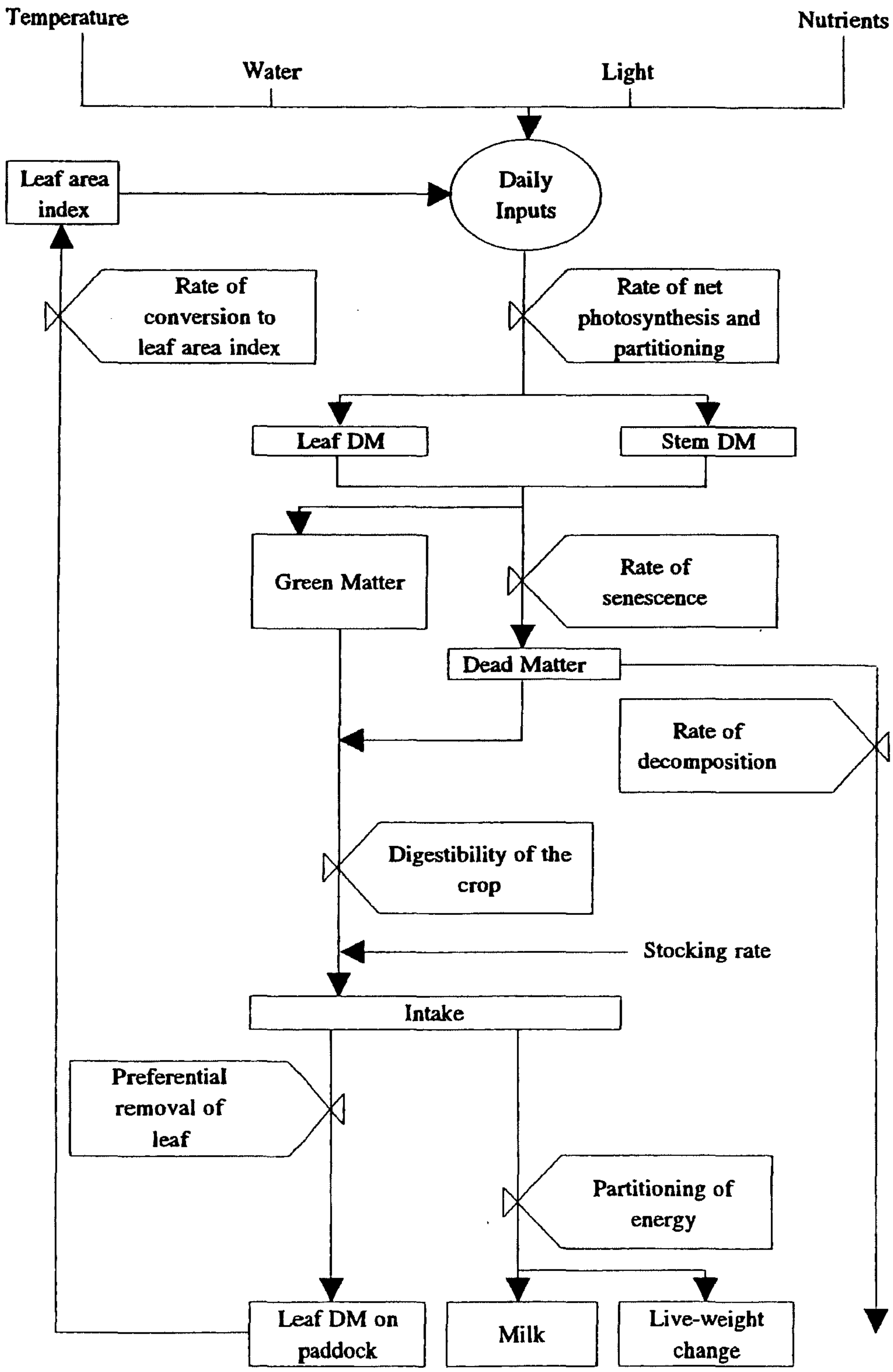

Fig. 1. A schematic diagram of the grazing model.

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 CO_2 concentration (Topp & Doyle, 1996). The herd is represented in the model by the 'average dairy cow' weighing 525 kg at the start of lactation. It is assumed to comprise 25% first-year heifers, 25% second lactation cows and 50% cows in later lactations. Therefore, each year 25% of the cows are presumed to be culled and replaced.

The overall model of herbage production and utilization outlined in Fig. 1 comprises eight state variables, namely leaf dry matter (D_L, kg DM ha^{-1}), stem dry matter (D_S, kg DM ha^{-1}), root dry matter (D_R, kg DM ha^{-1}), dead matter (D_D, kg DM ha^{-1}), the leaf area index of the crop (L, ha leaf (ha (ground)$^{-1}$), digestibility of the herbage mass (d_g), intake of the cow (I, kg DM head^{-1} day^{-1}) and milk yield (Y, kg day^{-1}). The driving variables include climatic (temperature, radiation, rainfall and atmospheric CO_2 concentration) and management (nitrogen level and grazing rates) factors. The mathematical structure of the herbage growth sub-model is described in detail in Topp & Doyle (1996), so this paper confines itself to outlining the grazing model. Basically, this starts with a given herbage mass on a paddock on a given day, and a decision is taken regarding which paddock should be grazed. Given the selected paddock, herbage intake is calculated and from this milk yield is estimated.

The principle variables and parameters within this model are listed in Appendix 1, whereas the parameter values can be found in Appendix 2. In addition, an outline of the basic mathematical structure of the sub-model is given in Appendix 3. For convenience the model may be divided into four sub-models concerned with: (i) rules for conservation; (ii) grazing rules; (iii) herbage intake; and (iv) dairy cow production. Each sub-model is described briefly below. All dates within the model are measured from 1 January and time is measured in days. The initial values of the state variables are derived from the crop growth model and depend on the start date of grazing, whereas the initial daily milk yield (Y, kg day^{-1}) is presumed to be zero on day one.

Rules for conservation

Within the model, it is assumed that half the area will 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. Details regarding the cutting of grass and the preferential removal of white clover have been described in Topp & Doyle (1996).

Grazing rules

Combellas & 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 *et al.*, 1979). In the model, it has thus been assumed that the cows will not graze below a herbage mass of 900 kg DM ha^{-1} (Ministry of Agriculture & Fisheries, 1985). Under ideal conditions, the herbage mass available for grazing permits the cows to consume the maximum daily intake of dry matter, and therefore their level of production is not constrained by the daily herbage allowance. The maximum daily intake is assumed to be a function of the metabolic live-weight. The dairy cows are also fed 0·1545 kg of concentrates per kg of milk throughout the grazing season (Hollinshead, 1995).

In the model, the start of the grazing season is presumed to occur when there is sufficient herbage mass on the paddocks for the cows to graze following calving and the biomass on the paddock has increased by 2·5% from that at the start of the growing season. It is assumed that the cows 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: (i) the metabolizable energy available from the dry-matter intake does not meet the metabolizable energy requirements for maintenance and pregnancy; (ii) the predicted dry-matter intake falls to less than 20% of the potential level; (iii) the available soil moisture has been greater than or equal to the available water capacity for five consecutive days and thus poaching is likely to occur; or (iv) the growing season has ended. The rotation of the livestock around the paddocks on a day-to-day basis is determined solely by the quantity of herbage mass on each paddock. When there is an ample supply of herbage, the cows are 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 is greater than the specified minimum (900 kg DM ha^{-1}).

Should the herbage mass on that paddock be less than the absolute minimum required, the paddocks set aside for silage production will he used for grazing.

Herbage intake

The intake of dry matter by grazing ruminant animals was assumed to be regulated by three factors: (i) the feed availability; (ii) the physiological

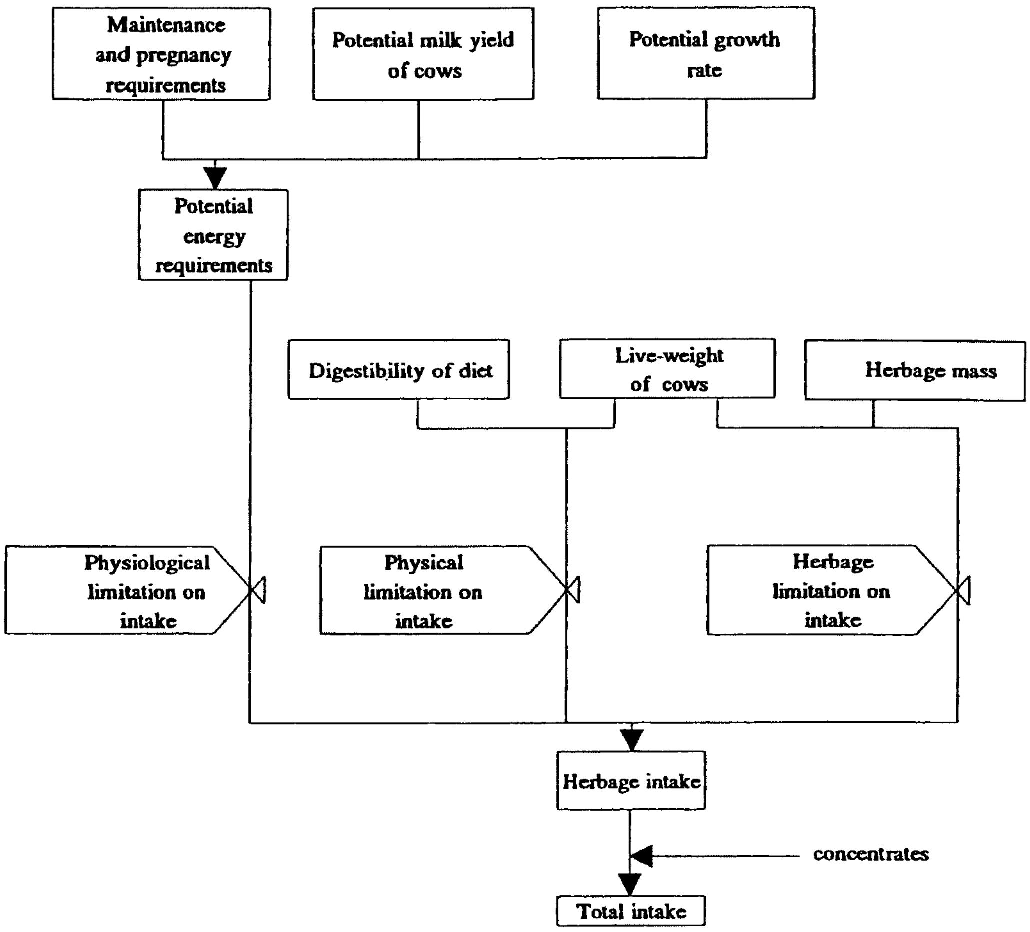

Fig. 2. A schematic diagram of the factors controlling intake.

limit on intake; and (iii) the physical ability of the animal to consume feed (Loewer *et al.*, 1983). The actual intake on any given day was determined by the most limiting factor as schematically represented in Fig. 2.

Feed availability

When the quantity of herbage available for consumption was less than that required for 95% of maximum daily intake, the daily allowance of green herbage regulated intake. The green herbage allowance is taken to be the green herbage mass above the minimum herbage mass of 900 kg DM ha^{-1} required for grazing. Zemmelink (1980) described the relationship for tropical grasses between herbage intake (I_f, kg DM head^{-1}) and the daily allowance of green herbage (H, kg DM head^{-1}) as:

$$I_f = I_{max} * \left(1 - \exp(-H/I_{max})^{a(1)}\right)^{1/a(1)} \quad (1)$$

where I_{max} was the maximum daily intake in kg DM per head per day and a(1) was a constant. In the absence of any established relationships for temperate grasses, eqn (1) has been adopted and the model calibrated using the assumption that the maximum daily intake of herbage is related to the metabolic live-weight of the cow and is presumed to increase by 136 g DM for every kg of metabolic weight.

Physiological limit to intake

The physiological limit to intake is considered to be regulated by the daily metabolizable energy (ME, MJ head^{-1} day^{-1}) requirements of the animal. Energy requirements by the dairy cow are divided into those for maintenance (E_m, MJ day^{-1}), pregnancy (E_p, MJ day^{-1}), milk production (E_l, MJ day^{-1}), and growth and fattening (E_f, MJ day^{-1}). Hulme *et al.* (1986) described the maintenance requirements of the dairy cow by the following relationship:

$$E_m = \frac{1.4 * (0.28 * W^{0.75} * \exp(-0.03 * A))}{k_m} + 0.1 * E_{prod} \tag{2}$$

where $W^{0.75}$ (kg) is the metabolic weight of the cow, A is the age in years and E_{prod} (MJ head^{-1} day^{-1}) is the energy required for production. The net utilization efficiency of ME for maintenance (k_m) is related to the metabolizability of the feed, whereas the mean age of the 'average dairy cow' is assumed to be four. Daily energy requirements for pregnancy (E_p) have been derived using relationships specified in Agricultural Research Council (1980).The potential energy requirements for lactation (E_l) have been derived from estimates of the potential milk yield (Y, kg day^{-1}) based on a Wood's lactation curve (Wood *et al.*, 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. The energy requirements for milk production (E_l) have then been derived as follows:

$$E_l = \frac{Y * M_E}{k_l} \tag{3}$$

where M_E, (MJ kg^{-1}) is the energy value of 1 kg of milk containing 4% fat and k_l is the proportionate efficiency with which ME is assumed to be utilized for milk production and is related to the metabolizability of the feed.

Finally, the estimates of the daily energy requirements for growth and fattening (E_f) assume that the potential growth of an animal can be described by a Gompertz equation (Taylor, 1968). Thus E_f can be described by:

$$E_f = \frac{\Delta_W * N_W}{k_{fl}} \tag{4}$$

where Δ_W (kg head^{-1} day^{-1}) is the potential gain in live-weight and N_W (MJ kg^{-1}) is the net energy requirement for 1 kg of live-weight gain. The proportionate efficiency of ME utilization for growth and fattening for a lactating cow is denoted by k_{fl} and is considered to be a function of the metabolizability of the feed. The physiological energy requirements (E_{Ph} MJ head^{-1} day^{-1}) of the 'average dairy cow' are then obtained in the model by summing the four elements (E_m, E_p, E_l and E_f). As the energy retention of the cow is not linearly related to intake (Schiemann *et al.*, 1971; van Es, 1976), the physiological intake has been corrected for feeding level (C_{Ph}, MJ head^{-1} day^{-1}) (Agricultural Research Council, 1980). The physiological limit to herbage intake (I_{Ph} kg DM head^{-1} day^{-1}) is then given by:

$$I_{Ph} = \frac{C_{Ph} - M_{Conc}}{M_{Fod}} \tag{5}$$

where M_{Conc} (MJ day^{-1}) represents the daily metabolizable energy intake of concentrates and M_{Fod} (MJ (kg DM)$^{-1}$) is the metabolizable energy value of ingested herbage per kg of dry matter.

Physical limit to intake

With feeds having a low digestibility, the actual intake may be lower then 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 *et al.*, 1964). Following Kahn & Spedding (1984) the physical limit (I_a, kg DM head^{-1} day^{-1}) on daily intake was accordingly assumed to be given by:

$$I_a = \frac{d_{max} * W}{(1 - D_{diet})} \tag{6}$$

where d_{max} (kg DM (kg live-weight)$^{-1}$ day^{-1}) represented the ability of the digestive tract to process and void undigested feed residues and d_{diet} represented the average digestibility of the feed in terms of the proportion of digestible organic matter in the dry matter. The stage of lactation was considered to have an influence on the capacity of the cow's digestive tract. Following Kahn & Spedding (1984), d_{max} was 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 the lactation. At the same time, following the recommendations of the Agricultural Research Council (1980), the physical limit to herbage intake was 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).

Components of intake

The actual daily intake (I, kg DM head^{-1} day^{-1}) can be derived from eqns (1), (5) and (6) on the basis of the most restrictive factor such that:

$$I = \text{minimum}(I_f, I_{Ph}, I_a) \tag{7}$$

However, this provides no information on the composition of the diet in terms of leaf and stem or grass and white clover. Observations by Jamieson & Hodgson (1979) have shown that grazing lambs and calves preferentially select green material. The same has been assumed for dairy cows. The proportions of leaf, stem and dead material in the sward are also known to differ from the proportions in the diet (Rattray & Clark, 1984). Accordingly, following Doyle *et al.* (1989) the mean daily intakes of leaf (I_L, kg DM head^{-1} day^{-1}), stem (I_S, kg DM head^{-1} day^{-1}) and dead material (I_D kg DM head^{-1} day^{-1}) have been assumed to be given by:

$$I_L = 1 - \exp(-a(2) * (\xi_L + \xi_S)) * \frac{\xi_L}{(\xi_L + \xi_S)} * I \tag{8}$$

$$I_S = 1 - \exp(-a(2) * (\xi_L + \xi_S)) * \frac{\xi_S}{(\xi_L + \xi_S)} * I \tag{9}$$

$$I_D = I - I_L - I_S \tag{10}$$

where ξ_L and ξ_S represent the proportions of green herbage accounted for by leaves and stems, respectively. On the other hand, the preferential removal of clover from grass–white clover swards, and thus the method for determining the quantities of grass and white clover in the diet, are described by Topp & Doyle (1996). The ME value of 1 kg of ingested herbage (M_{Fod}, MJ (kg DM)$^{-1}$) is presumed to be given by (McDonald *et al.*, 1988):

$$M_{Fod} = 16 * d_g \tag{11}$$

where d_g represents the digestibility of the herbage, which is calculated from the digestibility and level of intake of each component. Details of the assumed digestibilities for the different components of the grass and white clover crops can be found in Appendix 2, Table 12. In the model, the proportionate digestibilities have been assumed to decrease as the season progresses (Osbourn, 1980). Following the Agricultural Research Council (1980), the intake of ME was corrected for the level of feeding.

Dairy cow production

Within the model, the energy intake is partitioned between maintenance, pregnancy, live-weight gain and milk production. 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 and growth are reduced by an equal amount (Bruce *et al.*, 1984). Accordingly, the energy available for actual milk production (E_{Al} MJ head^{-1} day^{-1}) is described by:

$$E_{Al} = E_{I} - E_{f} + \Delta_{E} \qquad (12)$$

where E_{l}, (MJ head^{-1} day^{-1}) and E_{f}, (MJ head^{-1} day^{-1}) represent the daily potential energy requirements for milk production, and growth and fattening, respectively. The actual energy available for growth is denoted by Δ_{E}, (MJ head^{-1} day^{-1}). In the event of the maternal body being catabolized to meet maintenance and pregnancy requirements, the energy available for milk production may become less than zero. If this occurs, no milk is produced and the quantity of maternal body catabolized is restricted to the shortfall in energy requirements for maintenance and pregnancy.

VALIDATION

The ability of the model to simulate the pattern of milk production for a spring-calving herd has been investigated using data comprising daily milk yields recorded for herds grazed on grass and grass–white clover swards over 4 years at Johnstown Castle in Ireland (M. Ryan, personal communication). The model was specifically run for the period 1985–1987 with both high and low stocking densities for each forage system. Theil's inequality coefficient (Theil, 1970), which has a value of between 0 and 1, with 0 indicating a perfect fit, was used to determine the performance of the model. The value of Theil's inequality coefficient for the grass-based system over the 3 years was 0·054 and 0·061 for low and high stocking densities, respectively, and for the grass–white clover-based system was 0·063 for the low stocking rate and 0·059 for the high stocking density, indicating a good fit.

RESULTS

For grass and grass–white clover-based systems, the likely effect of global warming on milk production and silage yields has been explored by running the model with 10 years of weather data for two sets of climatic conditions (current and global warming) and two levels of atmospheric CO_2 concentrations (350 ppm and 520 ppm):

- scenario 1 — current climatic conditions and 350 ppm CO_2
- scenario 2 — current climatic conditions and 520 ppm CO_2
- scenario 3 — global warming scenario and 350 ppm CO_2
- scenario 4 — global warming scenario and 520 ppm CO_2

The significance of the effects has been assessed using an analysis of variance (ANOVA) (Genstat, 1987) at the 5% level of significance. A weather generator was used to produce realistic daily scenarios (Perris & McNicol, 1992). For the global warming scenario, the annual average temperature was increased by 2°C and the rainfall on rainy days was increased according to estimates by Viner & Hulme (1994). The model was run for four sites across Scotland; namely Kinloss, Mylnefield, Paisley and Wick.

The mean date of calving was assumed to be 15 February, whereas stocking rates were based on observations. The stocking rates were thus taken to be 2·25 cows per forage hectare for grass swards and 1·89 per hectare for grass–white clover-based systems (Ryan, 1988). The grazing area itself was assumed to be divided into 12 paddocks which were fertilised at one of two rates. Pure grass swards received 300 kg of nitrogen per hectare applied throughout the grazing season, whereas 50 kg of nitrogen per hectare were applied to grass–white clover paddocks. Whatever the management system adopted, silage cuts were taken on 1 June and 27 July.

Milk production and silage yields from grass swards

Length of grazing season

The only site at which global warming significantly affected the date of turnout was Mylnefield, as shown in Table 1. This resulted in an earlier start to the grazing season under scenario 4 than under scenario 1. However, both enhanced temperature under global warming and a higher CO_2 concentration significantly affected the date of yarding, although the only case for which the date of yarding was significantly different from the base scenario was for scenario 3 at Wick.

Milk yield

The total milk yield per cow, during the grazing season, was significantly influenced by both climatic changes and alterations in the atmospheric concentration of CO_2 at Kinloss, Paisley and Wick, as shown in Table 2.

TABLE 1

Ten-Year Averages and Level of Significance in Respect of the Means of Dates of Turn-Out and Yarding Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and under Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Grass-Based System at Four Scottish Sites

Site	*Scenario 1*	*Scenario 2*	*Scenario 3 (days)*	*Scenario 4*	*LSD*
Kinloss					
Turn-out date	14/4	13/4	14/4	10/4	8·0
Yarding date	25/9	03/10	18/9	25/9	8·5
Mylnefield					
Turn-out date	10/4	09/4	04/4	30/3	10·9
Yarding date	30/9	08/10	25/9	04/10	8·7
Paisley					
Turn-out date	09/4	07/4	12/4	08/4	9·0
Yarding date	29/9	08/10	21/9	29/9	10·9
Wick					
Turn-out date	19/4	14/4	19/4	14/4	12·6
Yarding date	03/10	09/10	20/9	28/9	9·2

LSD were calculated at the 5% level of significance.

TABLE 2

Ten-Year Averages and Level of Significance in Respect of the Mean Annual Milk Yield for the Months of March to October Under the Current Climate at 350 ppm CO_2 (Scenario 1) and 520 ppm CO_2 (Scenario 2), and Global Warming at 350 ppm CO_2 (Scenario 3) and 520 ppm CO_2 (Scenario 4) for Grass-Based System at Kinloss, Mylnefield, Paisley and Wick

Month	*Scenario 1 mean yield (kg cow^{-1})*	*Scenario 2 mean yield (kg cow^{-1})*	*Scenario 3 mean yield (kg cow^{-1})*	*Scenario 4 mean yield (kg cow^{-1})*	*LSD (kg cow^{-1})*
Kinloss	2670	2817	2447	2710	192·5
Mylnefield	2812	2971	2846	3111	218·8
Paisley	2771	2978	2580	2835	231·0
Wick	2659	2862	2422	2688	244·0

LSD were calculated at the 5% level of significance.

However, compared to scenario 1, the only significant effect was for the yield to be reduced at Kinloss under the global warming scenario at current CO_2 concentrations. At Mylnefield, CO_2 concentration had an observable effect on total milk yield, but only that for scenario 4 was significantly different from the base scenario.

TABLE 3
Ten-Year Averages and Level of Significance in Respect of the Mean Live-Weight at the End of the Grazing Season Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and under Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Grass-Based System at Four Scottish Sites

Site	*Scenario 1* *(kg cow^{-1})*	*Scenario 2* *(kg cow^{-1})*	*Scenario 3* *(kg cow^{-1})*	*Scenario 4* *(kg cow^{-1})*	*LSD* *(kg cow^{-1})*
Kinloss	547	554	525	543	11·3
Mylnefield	551	558	546	554	4·6
Paisley	544	555	535	548	10·2
Wick	552	557	532	547	8·2

LSD were calculated at the 5% level of significance.

Live-weight change

At all sites, both climatic conditions and the concentration of CO_2 had significant effects on the live-weight of the cow at the end of the grazing season, as is shown in Table 3. This resulted in the live-weight being significantly lower for scenario 3 at Kinloss, Mylnefield and Wick. On the other hand, the increased levels of CO_2 at current climatic conditions (scenario 2), increased live-weight of the dairy cows at Mylnefield and Paisley.

Silage areas and yields

With the increases in temperature and rainfall predicted by global warming, the percentage of paddocks harvested for the first conservation cut was significantly increased at Mylnefield and Wick, as shown in Table 4. For both sites scenarios 3 and 4 therefore had significantly more paddocks harvested at the first cut than under the base scenario. On the other hand, a higher concentration of CO_2 significantly increased the mean percentage of paddocks harvested for the second conservation cut at all sites, and at Wick, global warming was also projected to have a significant effect. Under current climatic conditions with increased CO_2 (scenario 2) the percentage of paddocks harvested increased at all sites, and it also increased for scenario 4 at Mylnefield and Paisley. However, at Wick the effect of climatic changes at current concentrations of CO_2 (scenario 3) was to decrease the paddocks harvested for the second cut.

The effect of global warming on the yield of herbage cut for silage, expressed per cow, varied between sites. The significant factor at Kinloss, Mylnefield and Paisley in determining the yield of the first cut was the CO_2 concentration, whereas at Wick the significant factor was climatic conditions. The silage yield obtained from the first cut was significantly increased at Kinloss, Mylnefield and Paisley for scenario 2 and at Mylnefield and Wick for scenario 4. With the exception of Kinloss, both CO_2 levels and

TABLE 4

Ten-Year Averages and Level of Significance in Respect of the Percentage of Paddocks Cut for Conservation Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and Under Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Grass-Based Dairy System at Four Scottish Sites

Site	*Scenario 1 mean (%)*	*Scenario 2 mean (%)*	*Scenario 3 mean (%)*	*Scenario 4 mean (%)*	*LSD(%)*
Kinloss					
1st cut	37·5	41·7	45·0	48·3	12·5
2nd cut	35·8	52·5	32·5	43·3	11·2
Mylnefield					
1st cut	42·5	47·5	49·2	50·0	4·3
2nd cut	43·3	58·5	35·0	55·0	9·0
Paisley					
1st cut	46·7	49·2	46·7	47·5	8·2
2nd cut	36·7	52·5	32·5	47·5	8·7
Wick					
1st cut	31·7	31·7	47·5	50·0	6·8
2nd cut	40·0	55·8	26·7	39·2	11·8

LSD were calculated at the 5% level of significance.

climatic conditions were significant factors in determining the second-cut yield. Only CO_2 concentrations had an effect at Kinloss. At all sites scenario 2 significantly increased the second-cut silage yield (Fig. 3). In contrast, at current CO_2 concentrations, the global warming scenario significantly reduced the second-cut yield harvested at Wick. At all sites, the total yield harvested per cow was increased by enhanced CO_2 with both current and global warming climatic conditions (scenarios 2 and 4). With respect to the percentage of total herbage yield obtained from the first cut, both CO_2 levels and climate had significant effects at Mylnefield, as shown in Table 5. In contrast at Kinloss and Wick only changes in temperature and rainfall had a significant effect. At all three sites therefore where there was a significant effect, global warming (scenario 3) resulted in an increase in the percentage of total harvested material accounted for by the first cut. This also occurred for scenario 4 at Wick.

Interpretation of the results

The difference in response of the swards and the herds at the different sites to global warming must be interpreted in conjunction with actual changes in weather data. As the weather data was synthetically generated, care is needed in interpreting the differences. The average weather data for each month is given in Topp & Doyle (1996). The significantly earlier finish to the grazing season for scenario 2 at Wick, shown in Table 1, was due to

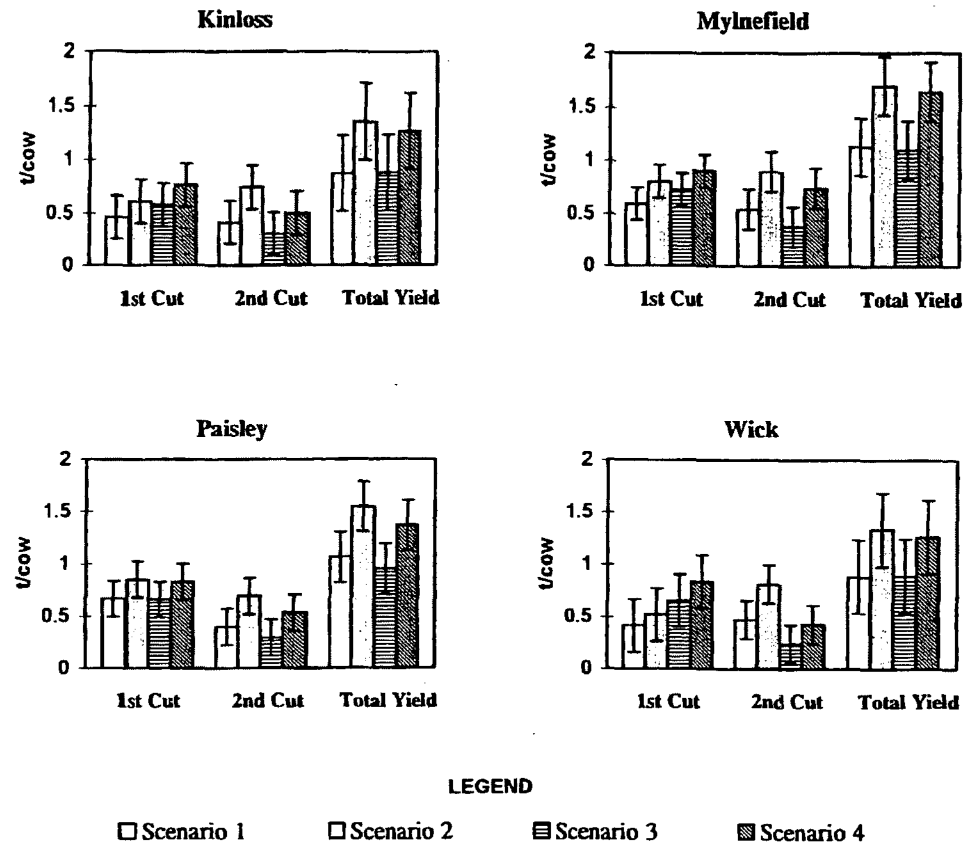

Fig. 3. Ten-year averages and LSD in respect of the mean conservation yields per cow under the current climate at 350 ppm CO_2 (scenario 1) and at 520 ppm CO_2 (scenario 2), and under global warming at 350 ppm CO_2 (scenario 3) and at 520 ppm CO_2 (scenario 4) for grass-based system at four Scottish sites. The error bars indicate the LSD at the 5% level of significance.

TABLE 5

The Percentage of Total Yield Obtained in the First Conservation Cut Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and Under Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Pure Grass Swards

Site	*Scenario 1 mean (%)*	*Scenario 2 mean (%)*	*Scenario 3 mean (%)*	*Scenario 4 mean (%)*	*LSD(%)*
Kinloss	47·5	43·0	66·9	62·1	14·9
Mylnefield	52·2	47·1	66·6	55·7	8·4
Paisley	62·2	56·1	67·9	60·7	10·9
Wick	40·1	33·0	75·4	67·6	17·7

LSD were calculated at the 5% level of significance.

the photosynthetically active radiation being 6200 MJ ha^{-1} day^{-1} lower for the month of September in the global warming scenario, compared to the base conditions. This would have reduced the rate of photosynthesis and therefore net herbage accumulation. The significant decrease in the total milk yield at Kinloss for scenario 3 (Table 2), was the result of decreased daily milk yields during the months of July to September, which was due to the decreased photosynthetically active radiation for this scenario, compared with current climatic conditions. At Mylnefield, the increase in yield under scenario 4 was primarily due to higher CO_2 levels stimulating photosynthesis in March and May, although the earlier, but non-significant, start to the grazing season would also have been a factor.

The increase in the number of paddocks harvested under scenarios 2 and 4 was essentially due to the stimulation of photosynthesis, which was the result of increased CO_2 concentrations (Table 4). Together the increased number of paddocks harvested and the increased rate of herbage accumulation due to the increased CO_2 level, increased herbage yield under scenarios 2 and 4 (Fig. 3). At current concentrations of CO_2, global warming (scenario 3) tended to decrease the grass yield per cow obtained from the second cut, although this, as well as the reduction in the paddocks harvested at the second cut, was only significant at Wick. The main reason for this was the reduction in photosynthetically active radiation that occurred for all sites and the increase in the rate of respiration due to the increased daily temperature.

Milk production and silage yields from grass–white clover swards

Length of the grazing season

Parallel simulations for the dairy system, based on grass–white clover swards indicated some important differences. As with the grass-based system, at all four sites the date of turn-out was not significantly affected either by changes in the climate or the density of CO_2 in the atmosphere, Table 6. However, at all sites the CO_2 concentration had a significant effect on the date of yarding; with the date being later under current climatic conditions at elevated levels of CO_2 (scenario 2) for all sites, and for the global warming scenario with elevated CO_2 (scenario 4) at Mylnefield. Specifically for scenario 2, increasing the CO_2 concentration resulted in yarding being between 11 and 14 days later.

Milk yield and live weight changes

Much more so than in the case of the grass-based system, milk yield per cow during the grazing season was significantly increased at all four sites for both climate scenarios at the higher concentrations of CO_2 (scenarios 2 and 4)

TABLE 6

Ten-Year Averages and Level of Significance in Respect of the Mean Dates of Turn-Out and Yarding Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Grass Clover-Based System at Four Scottish Sites

Site	*Scenario 1*	*Scenario 2*	*Scenario 3*	*Scenario 4*	*LSD* (*days*)
Kinloss					
Turn-out date	14/4	12/4	13/4	08/4	8·8
Yarding date	21/9	03/10	21/9	29/9	8·6
Mylnefield					
Turn-out date	09/4	06/4	03/4	30/3	11·4
Yarding date	26/9	09/10	27/9	08/10	8·8
Paisley					
Turn-out date	09/4	08/4	10/4	07/4	9·1
Yarding date	03/10	17/10	28/9	07/10	11·5
Wick					
Turn-out date	14/4	14/4	18/4	15/4	11·6
Yarding date	27/9	09/10	24/9	06/10	8·5

LSD were calculated at the 5% level of significance.

TABLE 7

Ten-Year Averages and Level of Significance in Respect of the Mean Annual Milk Yield for the Months of March to October Under the Current Climate at 350 ppm CO_2 (Scenario 1) and 520 ppm CO_2 (Scenario 2), and Global Warming at 350 ppm CO_2 (Scenario 3) and 520 ppm CO_2 (Scenario 4) for Grass Clover-Based System at Kinloss, Mylnefield, Paisley and Wick

Month	*Scenario 1 mean yield (kg cow^{-1})*	*Scenario 2 mean yield (kg cow^{-1})*	*Scenario 3 mean yield (kg cow^{-1})*	*Scenario 4 mean yield (kg cow^{-1})*	*LSD (kg cow^{-1})*
Kinloss	2647	2947	2708	3057	191·2
Mylnefield	2872	3178	3074	3364	238·7
Paisley	3014	3294	3009	3263	237·5
Wick	2729	2991	2686	2983	234·8

relative to the base scenario, as shown in Table 7. Global warming was also projected to have an effect on milk yield per cow at Mylnefield, but this was not significant compared to scenario 1. Furthermore, the increased milk yields per cow during the grazing season were not achieved at the expense of lower cow body weights at the end of the season or lower total silage yields. The live-weight of the dairy cows were therefore significantly increased at all sites with increasing CO_2 concentrations as reported for the grass-based systems.

TABLE 8

Ten-Year Averages and Level of Significance in Respect of the Percentage of Paddocks Cut for Conservation Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and Under Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Grass Clover-Based Dairy System at Four Scottish Sites

Month	*Scenario 1 mean (%)*	*Scenario 2 mean (%)*	*Scenario 3 mean (%)*	*Scenario 4 mean (%)*	*LSD(%)*
Kinloss					
1st cut	25·8	27·5	32·5	35·0	8·9
2nd cut	30·8	39·2	36·7	49·2	12·2
Mylnefield					
1st cut	29·2	31·7	34·2	40·0	7·0
2nd cut	33·3	50·0	42·5	60·8	9·2
Paisley					
1st cut	30·8	40·8	33·3	47·5	9·4
2nd cut	42·5	55·0	49·2	61·7	11·0
Wick					
1st cut	19·2	21·7	34·2	42·5	11·2
2nd cut	27·5	37·5	32·5	50·0	11·5

LSD were calculated at the 5% level of significance.

Silage areas and yields

The percentage of paddocks available for conservation at the first cut date were significantly changed by global warming at all sites, except Paisley where CO_2 concentration had a significant effect (Table 8). In contrast, both global warming and CO_2 concentration influenced the percentage of paddocks harvested at the second cut at Mylnefield and Wick, and at the remaining two sites significant changes were associated with elevated CO_2. This resulted in a greater proportion of paddocks being harvested for all cuts at all sites under scenario 4, whereas under scenario 2 the number of paddocks harvested increased at Paisley for both cuts, as well as at Mylnefield for the second cut. A greater percentage was also harvested for the second cut at Mylnefield and the first cut at Wick, when only the climate was changed.

With respect to the combined grass–white clover yield obtained from the first-cut, both CO_2 concentration and climatic conditions were significant factors in determining the yield obtained at Kinloss, Mylnefield and Wick. At Paisley only the CO_2 concentration was significant. At all sites scenario 4 resulted in significantly higher silage yields as shown in Fig. 4. Current climatic conditions at enhanced CO_2 concentrations also significantly increased the first-cut yield at Paisley. At Wick, the yield was also significantly increased by global warming at current CO_2 concentrations. The second-cut yield at all sites was significantly increased by scenarios 2 and

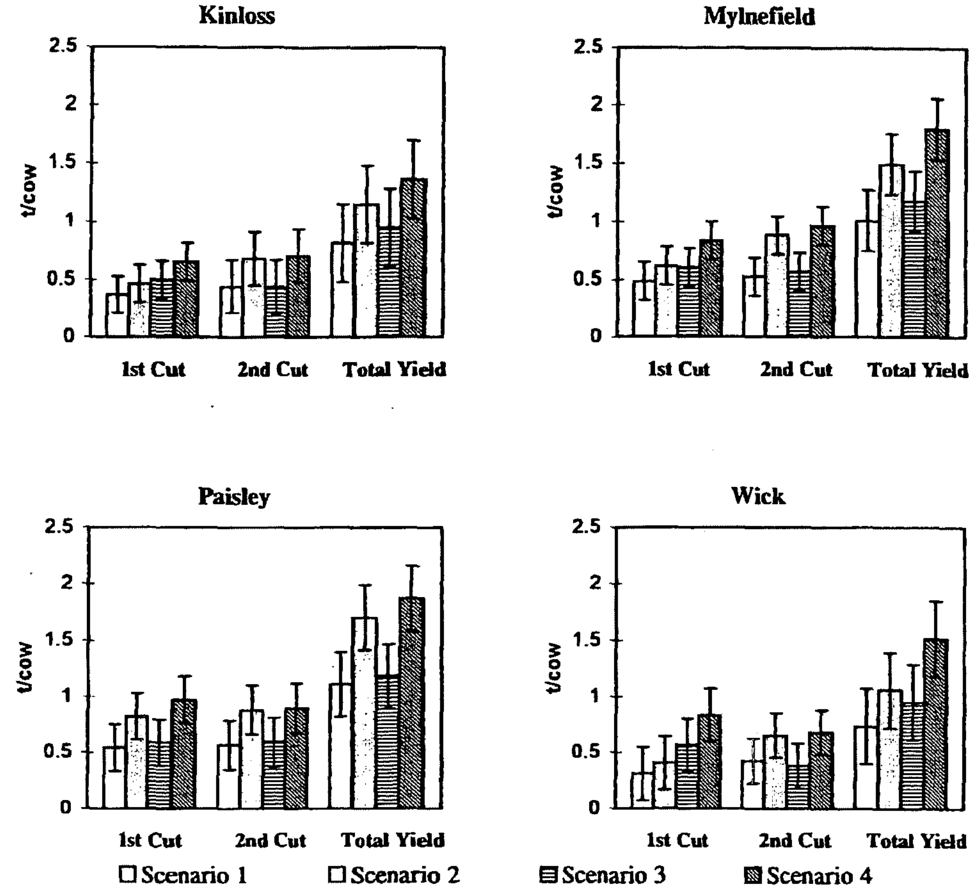

Fig. 4. Ten-year averages and LSD in respect of the mean combined conservation yields per cow under the current climate at 350 ppm CO_2 (scenario 1) and at 520 ppm CO_2 (scenario 2), and under global warming at 350 ppm CO_2 (scenario 3) and at 520 ppm CO_2 (scenario 4) for grass–clover-based dairy systems at four Scottish sites. The error bars indicate the LSD at the 5% level of significance.

4. Global warming conditions with enhanced CO_2 also increased the total yield at all sites (Fig. 4). Increasing the CO_2 concentrations for current climatic conditions also increased the yield at Mylnefield and Paisley. The criterion that influenced the percentage of white clover in the harvested material for all cuts at all sites was the climatic conditions, with scenarios 3 and 4 always exhibiting an increase in the white clover content of the cut material, as shown in Table 9. Only in the case of the second cut at Mylnefield did CO_2 concentration have a significant impact on clover percentage, although increasing the CO_2 levels under current climatic conditions had no effect. The proportion of the total conserved yield coming from the first cut, compared to the base scenario, only increased for scenarios 3 and 4 at Wick; this was primarily due to the significant increase in the percentage of grass harvested at the first cut. Global warming without elevated CO_2 levels (scenario 3) also increased the percentage of grass harvested at the first cut at Kinloss.

TABLE 9

Ten-Year Average and Level of Significance in Respect of the Percentage of Clover in the Conserved Yield Under the Current Climate at 350 ppm CO_2 (Scenario 1) and at 520 ppm CO_2 (Scenario 2), and Under Global Warming at 350 ppm CO_2 (Scenario 3) and at 520 ppm CO_2 (Scenario 4) for Grass–Clover Swards

Month	*Scenario 1 mean (%)*	*Scenario 2 mean (%)*	*Scenario 3 mean (%)*	*Scenario 4 mean (%)*	*LSD (%)*
Kinloss					
1st cut	11·0	12·0	20·8	22·6	4·3
2nd cut	9·9	11·3	19·0	23·1	5·8
Total	11·6	12·5	20·2	23·1	4·2
Mylnefield					
1st cut	12·5	12·7	19·9	21·8	6·7
2nd cut	8·5	14·1	18·3	25·5	8·3
Total	10·8	13·6	19·4	24·0	7·6
Paisley					
1st cut	19·8	22·6	31·2	35·5	6·5
2nd cut	19·4	25·4	40·7	47·9	11·7
Total	20·2	25·3	36·6	42·0	8·3
Wick					
1st cut	8·4	9·9	21·9	24·1	6·1
2nd cut	8·2	10·1	17·3	25·0	7·7
Total	9·8	11·2	21·0	25·3	5·7

LSD were calculated at the 5% level of significance.

Interpretation of results

There was no variation between sites in the response of the total milk yield (Table 7) and the live-weight of the dairy cow at the end of the grazing season, with atmospheric CO_2 levels in all cases being the significant factor. With respect to total yield, CO_2 concentrations again had the major influence (Fig. 3). However, the increase in the first-cut yield for scenario 3 at Wick was due to the start of the growing season for white clover being almost 1 month earlier than occurred for scenario 1 (Topp & Doyle, 1996). Against this, climatic conditions had a major impact on the percentage of white clover harvested in the sward, as shown in Table 9.

CONCLUSIONS

The results of the study show that grazing management based on pure grass sward will respond differently to changes in climate and atmospheric levels of CO_2, compared to those based on a grass–white clover sward. In general the length of the grazing season for a grass-based system is anticipated to be unaffected either by global warming or CO_2

concentrations. However, the yarding date on white clover-based systems is delayed under global warming (Table 6), so that it moves closer to that of grass-based systems. As regards the milk yield per cow from the grass swards, this changed at two sites; with global warming reducing yield at Kinloss and increasing it at Mylnefield when CO_2 levels are elevated (Table 2). For the grass-based system, global warming also associated with a decrease in the live weight of the dairy cow at the end of the grazing season at three sites (Kinloss, Mylnefield and Wick), as shown in Table 3. In contrast the milk yield per cow from herds grazing on a grass–white clover mixture increased at all sites under both climatic scenarios when coupled with increasing atmospheric levels of CO_2 (Table 7). Interestingly, Hanson *et al.* (1993) predicted that animal production from a cow/calf system grazing on a rangeland (grass-based) ecosystem generally decrease with the rise in temperature and rainfall predicted under global warming. However, in the current model this only occurred for the milk yield at Kinloss and for the live weight at the end of the season at all sites, except Paisley. In contrast, animal production from a grass–white clover system was largely unaffected by climatic change.

In respect of the quantities of conserved material, there was a tendency for CO_2 concentration to be the only significant factor influencing both the grass and the grass–white clover-based systems (Fig. 3). However, global warming increased the proportion of white clover in the conserved material for the grass–white clover-based herds as shown in Table 9. As white clover has a higher nutritive value than grass and tends to stimulate intake (Thomson, 1984); this would be expected to increase the milk production during the winter period. However, the model simulations have not been extended to cover the winter period, so that the effects of global warming on overall lactation yields remain a matter of inference.

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APPENDIX 1: VARIABLES AND PARAMETERS IN THE GRAZING MODEL

TABLE 10

Variables and Parameters in the Grazing Model

Variable	*Description*	*Units*
Δ_E	Actual energy available for growth and fattening	MJ head^{-1} day^{-1}
Δ_W	Potential gain in live-weight	kg head^{-1} day^{-1}
ξ_L	Proportion of the total pasture by weight accounted for by leaf material	
ξ_S	Proportion of the total pasture by weight accounted for by stem material	
C_{Ph}	Physiological limit to energy intake corrected for feeding level	MJ head^{-1} day^{-1}
D_D	Dead dry matter	kg DM ha^{-1}
D_L	Leaf dry matter	kg DM ha^{-1}
d_{diet}	Proportion of digestible organic matter in the dietary dry matter	
d_g	Proportion of digestible organic matter in the forage dry matter	
D_R	Root dry matter	kg DM ha^{-1}
D_S	Stem dry matter	kg DM ha^{-1}
E_{Al}	Daily metabolizable energy requirements for actual milk yield	MJ head^{-1} day^{-1}
E_f	Daily metabolizable energy requirements for potential growth	MJ head^{-1} day^{-1}
E_l	Daily metabolizable energy requirements for potential milk yield	MJ head^{-1} day^{-1}
E_{Loss}	Metabolizable energy deficit for potential growth and fattening, and milk production	MJ head^{-1} day^{-1}
E_m	Daily energy requirements for maintenance	MJ head^{-1} day^{-1}
E_p	Daily energy requirements for pregnancy	MJ head^{-1} day^{-1}
E_{Ph}	Daily physiological energy requirements	MJ head^{-1} day^{-1}
E_{Prod}	Metabolizable energy required for production	MJ head^{-1} day^{-1}
H	Mean daily herbage allowance	kg DM head^{-1} day^{-1}
I	Actual daily feed intake	kg DM head^{-1} day^{-1}
I_a	Physical limit to intake	kg DM head^{-1} day^{-1}
I_D	Daily intake of dead matter	kg DM head^{-1} day^{-1}
I_f	Intake limit imposed by herbage availability	kg DM head^{-1} day^{-1}
I_L	Daily intake of leaf dry matter	kg DM head^{-1} day^{-1}
I_{max}	Maximum daily intake of herbage	kg DM head^{-1} day^{-1}
I_{Ph}	Physiological limit to herbage intake	kg DM head^{-1} day^{-1}
I_S	Daily intake of stem dry matter	kg DM head^{-1} day^{-1}
k_l	Proportionate utilization efficiency of energy for lactation	
k_m	Proportionate utilization efficiency of energy for maintenance	
L	Leaf area index	ha (leaf) ha^{-1} (ground)
M_{Fod}	Metabolizable energy value of the herbage in the diet	MJ (kg DM)$^{-1}$
M_{Diet}	Metabolizable energy value of the feed	MJ (kg DM)$^{-1}$

TABLE 10—*contd*
Variables and Parameters in the Grazing Model

Variable	*Description*	*Units*
$W^{0.75}$	Metabolic weight of the 'average dairy cow'	kg
Y	Potential milk yield	kg day^{-1}
a(1)–a(2)	Constants	
A	Age of the 'average dairy cow'	years
d_{max}	Limit of the digestive tract's ability to process feed	kg DM (kg live-weight)$^{-1}$
k_{bl}	Proportionate utilization efficiency of maternal body for milk production	
k_{fl}	Proportionate utilization efficiency of energy for growth and fattening for a lactating cow	
M_{Conc}	Metabolizable energy intake of concentrates	MJ $head^{-1}$ day^{-1}
M_E	Net energy value of 1 kg of milk containing 4% fat	MJ kg^{-1}
N_W	Net energy requirement for 1 kg of live-weight gain	MJ kg^{-1}

APPENDIX 2: PARAMETER VALUES

TABLE 11
Parameter Values

Parameter	*Value*	*Source*
a(1)	1·23	1
a(2)	4·662	2
A	4	3
d_{max}	0·0086	4
k_{bl}	0·84	5
M_e	3·1	5
M_{Conc}	6·875	3
N_e	27·36	5

Source: 1. Doyle *et al.* (1989); 2. Lantinga (1985); 3. Topp & Doyle (1994); 4. Kahn & Spedding (1984); 5. Agricultural Research Council (1980).

PRESUMED DIGESTIBILITIES OF THE DIFFERENT COMPONENTS OF THE GRASS AND CLOVER CROPS, TOGETHER WITH THAT FOR CONÇENTRATES

TABLE 12
Presumed Digestibilities of the Different Components of the Grass and Clover Crops, Together with that for Concentrates

Feed	*Component*	*Proportionate digestibilities*	*Source*
Clover	Leaf	0·85	1
	Stem	0·8	1
	Dead material	0·5	1
Grass	Leaf	0·75	3
	Stem	0·65	2
	Dead material	0·5	2
Concentrates		0·86	4

Source: 1. Topp & Doyle (1994); 2. Wilman *et al.* (1976); 3. Wilman & Altimimi (1982); 4. Holmes *et al.* (1980).

APPENDIX 3: OUTLINE OF BASIC MATHEMATICAL STRUCTURE OF GRAZING SUB-MODEL

Total intake

$$I = \text{minimum}(I_f, I_{Ph}, I_a)$$

where

$$I_f = I_{max} * \left(1 - \exp(-H/I_{max})^{a(1)}\right)^{1/a(1)}$$

$$I_{Ph} = \frac{C_{Ph} - M_{Conc}}{M_{Fod}}$$

$$I_a = \frac{d_{max} * W}{(1 - d_{diet})}$$

Components of intake

$$I_L = 1 - \exp(-a(2) * (\xi_L + \xi_S)) * \frac{\xi_S}{(\xi_L + \xi_S)} * I$$

$$I_S = 1 - \exp(-a(2) * (\xi_L + \xi_S)) * \frac{\xi_S}{(\xi_L + \xi_S)} * I$$

$$I_D = I - I_L - I_S$$

Energy intake

$$M_{Diet} = 16 * d_g * I + M_{Conc}$$

Milk production

$$E_{Loss} = -(M_{Diet} - C_{Ph})$$

Assuming the energy intake will meet the energy requirements for pregnancy and maintenance.

If $\Delta_E = E_f - E_{Loss}/2 > 0$ then

$$Y = k_l * \left(E_l - \frac{E_{Loss}}{2}\right) / M_E$$

else $\Delta_E = (E_f - E_{Loss}/2 > 0$

$$Y = k_l * \left(E_l - \frac{E_{Loss}}{2}\right) - \Delta_E * k_{bl}/M_E$$

The effect of global warming on the productivity of grass-white clover swards subjected to nitrogen and water stress

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Summary

The potential impact of global warming and the associated increases in the concentration of atmospheric CO_2 on grass-white clover production within the UK requires assessment, if the consequences for livestock farming of climatic change are to be understood. Accordingly, a mechanistic model of herbage production, that is responsive to climatic factors, CO_2 concentrations and the availability of water and nutrients, was developed for a mixed sward. This model has been used to assess the effects of increasing temperature, rainfall and CO_2 concentrations on production from a grass/white clover sward. The length of the growing season was projected to increase for both grass and white clover. However, while global warming apparently had little effect on the production of grass, that of white clover was predicted to increase. Finally, increases in the concentration of atmospheric CO_2 increased the projected yield of both grass and clover.

Key words: Forage production, grass-white clover swards, water stress, nutrient stress, carbon dioxide

Introduction

The activities of man have increased the concentration of the greenhouse gases in the atmosphere. By the middle of the next century the concentration of all greenhouse gases, including CO_2, in the atmosphere is expected to be double the 1990 levels. With this increase in the greenhouse gases, Viner & Hulme (1994) predicted that in the UK the annual average temperature will increase by 2°C and annual rainfall would also increase. However, the response of different crops to changes in climate will differ. Increasing the annual average temperature by 3°C and doubling the concentration of CO_2 in the atmosphere has been shown to increase the yield of potatoes by between 50 and 75%, but wheat yields have shown no response (Squire & Unsworth, 1989). As crop-climate interactions are complex, simulation models can be useful in assessing the impact of climate change on agricultural production. The aim of the present study has been to develop a simulation model that can predict the likely effect of climate change on the productivity of grass-white clover swards. The knowledge gained is an important step in understanding how ruminant livestock farming in the UK may be affected by the projected climatic change.

Materials and Methods

The model describes a grass-white clover sward where forage production is calculated on a daily basis and is assumed to be dependent on herbage mass, temperature, radiation, atmospheric CO_2 concentration and the availability of water and nutrients. Within the model the grass and white clover components are separately distinguished. For each component there are five state variables; leaf dry matter, stem dry material, root dry matter, dead material and the leaf area index. A schematic diagram of the model is shown in Fig. 1. Given the structure of the model it is convenient to divide it into five sub-models concerned with i) temperature, ii) photosynthesis and respiration, iii) water and nutrient stress iv) assimilate partitioning and senescence and v) herbage accumulation under cutting.

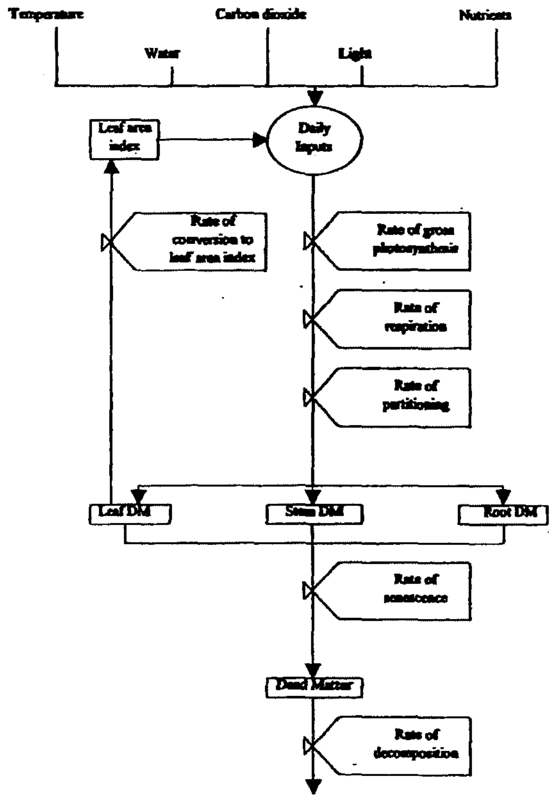

Fig. 1. A schematic diagram of the forage growth model.

Temperature

The average daily temperature determines when growth starts and ceases. The requirement for growth in the spring is that the average daily temperature has exceeded 4.5°C for seven consecutive days for grass (Broad & Hough, 1993) and 6°C for white clover (Peel, 1988). However, if there is a cold spell in the spring, growth ceases until the temperature requirement has been re-attained. Growth ceases in the autumn for both components when the average daily temperature has fallen below 8°C (Broad & Hough, 1993) for three consecutive days. Temperature also modifies the rates of gross photosynthesis and maintenance respiration.

Canopy photosynthesis is described by a non-rectangular hyperbola and the function is integrated through the depth of the canopy. For a grass-white clover mixture, the rate of photosynthesis can be derived by summing the rates for the individual components (Johnson, Parsons & Ludlow, 1989). The irradiance incident on the leaves for either component depends upon the leaf area of both the grass and white clover. The rate of canopy gross photosynthesis (P_j, kg CO_2 ha^{-1} (ground) day^{-1}) for component j is given by:

$$P_j = \frac{1}{2*\Theta} * \int_0^L Ph_j + P_{max,j} - \sqrt{\left(Ph_j + P_{max,j}\right)^2 - 4*\Theta*P_{max,j}*Ph_j} \frac{dl_j}{dl} * dl$$

$$\text{where } Ph_j = \frac{\alpha_j * k_j * I_0}{\left(1-m_j\right)} * e^{-\left(k_g*l_g + k_c*l_c\right)}$$

and I_0 is the photosynthetically active radiation in MJ ha^{-1} (ground) day^{-1}, P_{max} is the leaf photosynthetic rate in kg CO_2 ha^{-1} (leaf) day^{-1} at saturating light levels ($I_0 \rightarrow \infty$) and at the atmospheric CO_2 concentration experienced by the crop, k is the extinction coefficient, m is the leaf transmission coefficient, L is the leaf area index (ha (leaf) ha^{-1} (ground)), l is the cumulative leaf area index, α is the photochemical efficiency (kg CO_2 MJ^{-1}) and Θ is a dimensionless parameter. Subscript g refers to grass and c to clover. The vertical distribution of each component through the depth of the canopy is described by dl_j/dl (ha (leaf) ha^{-1} (ground)).

The maximum rate of leaf photosynthesis (P_{max}, kg CO_2 ha^{-1} (leaf) day^{-1}) is modified by the leaf area index of the crop (Johnson *et al.*, 1989), the mean daily temperature (Johnson & Thornley, 1983) and the concentration of CO_2 in the atmosphere (Thornley, Fowler & Cannell, 1991). The photochemical efficiency (α, kg CO_2 MJ^{-1}) is also a function of the concentration of CO_2 (Thornley *et al.*, 1991).

In order to calculate the gross photosynthesis, the vertical distribution of the grass and white clover components through the depth of the canopy is required. In grass-white clover swards, the white clover tends to predominate in the upper layers of the canopy (Woledge, 1988; Woledge, Reyneri, Tewson & Parsons, 1992). The vertical distribution has been estimated from data obtained from Woledge *et al.* (1992).

The respiration requirement is deducted from gross photosynthesis to give net photosynthesis. Respiration has been divided into growth and respiration components with growth respiration being related to gross photosynthate and maintenance respiration being a function of the mass of the plant and the growth conversion efficiency (Thornley, 1976). Following Johnson & Thornley (1983), temperature modifies the rate of the maintenance respiration.

Water and Nutrient Stress

The rate of net photosynthesis is presumed to be reduced by a lack of water or plant nutrients. This will either occur by reducing the efficiency of photosynthesis or by reducing the length of the growing period. Within the model the effect of water and nutrient stress has been incorporated by reducing the net photosynthesis in proportion to the stress experienced by the crop. The water and nutrients available to the crop are expressed as a proportion of the saturating levels. The relationships have been estimated from part of the GM23 data (J. Gilbey, *personal communication*). On 1 January the soil is assumed to be saturated. The change in water is calculated on a daily basis and is presumed to equal the difference between rainfall and actual evapotranspiration. In the UK the principal limiting nutrient is nitrogen. The pool of nitrogen available to the crop is dependent on the quantity of available nitrogen in the soil, the applied fertiliser nitrogen and the quantity of nitrogen biologically fixed by the white clover.

Assimilate Partitioning and Senescence

After modifying for water and nitrogen stress, the net photosynthesis is converted to dry matter. Following the procedure of Johnson, Ameziane & Thornley (1983), a fixed proportion of the photosynthate is partitioned to the root. The remaining photosynthate is partitioned between the leaves and stem. The production of the new leaf and stem material is offset by losses through senescence to the dead pool, where it remains until it decomposes. For the grass component, the physiological stage of development determines the proportion of photosynthate partitioned to the leaves and the rate of leaf senescence (Sheehy, Cobby & Ryle, 1980). As there is less difference in the growth and senescence rates for white clover (Spedding & Diekmahns, 1972), the partitioning factors are presumed to be independent of physiological stage of this crop.

Herbage Accumulation Under Cutting

The quantities of leaf and stem material of each component removed under cutting must be determined. Robson & Ridout (1991) defined the selection coefficient (ν) as:

$$\nu = \frac{c_D}{g_D} \bigg/ \frac{c_S}{g_S}$$

where c_D (g_D) and c_S (g_S) are the amount of white clover (grass) harvested and in the sward respectively. Woledge *et al.* (1992) calculated the selection coefficient for leaf area and the total dry matter for the white clover component in a mixed sward. From the equation and the selection coefficient value the quantities of each component harvested have been calculated.

Validation

The ability of the model to simulate the production from grass white clover swards was investigated using GM23 data for High Mowthorpe, Liscombe and Rosemaund (J. Gilbey, *personal communication*). The performance of the model was evaluated using Theil's inequality coefficient (Pindyck & Rubinfeld, 1981), which has a value of between zero and one, with zero indicating a perfect fit. Daily weather data for the sites were obtained from the Meteorological Office. The model was run for the period 1978—1981, and no fertiliser nitrogen was applied to the swards. Over the four years at the three sites, Theil's inequality coefficient had values of between 0.17 and 0.24 for grass production and 0.29 and 0.50 for white clover production.

Results

The effect of global warming and increasing CO_2 concentrations has been investigated by running the model for current climatic conditions and a global warming scenario at two levels of CO_2 concentrations as shown in Table 1. By the middle of the next century the expected level of CO_2 in the atmosphere is 520 μl litre^{-1} (Wigley & Raper, 1992). Based on estimates by Viner & Hulme (1994), the average annual temperature has been increased by 2°C and the rainfall on rainy days has also been increased for the global warming scenario. Realistic daily weather data was obtained from the weather generator developed by Perris & McNicol, 1992. The model was run for four sites across Scotland; namely Kinloss, Mylnefield, Paisley and Wick. In the spring, 50 kg ha⁻¹ of nitrogen was applied to the mixed sward and the swards were cut on 1 June and 27 July. The significance of the effect of global warming and CO_2 concentrations was assessed using an ANOVA at the 5% level of significance.

Table 1. *The climate change scenarios*

	Scenario 1	Scenario 2	Scenario 3	Scenario 4
Weather	current	current	global warming	global warming
CO_2 (μl litre^{-1})	350	520	350	520

The global warming climate change scenario increased the length of the growing season for both the grass and white clover components at all sites. For the grass component the increase in the length of the growing season ranged from 25.2 days at Paisley to 75.5 days at Wick. The corresponding increase for the white clover component ranged from 34 days to 69.1 days. The difference in the dates of the start of grass and white clover growth was reduced at Kinloss and Paisley, but at Mylnefield and Wick it was increased.

The effect of scenario 3 on the yield of the grass component was to reduce the second-cut yield at Kinloss, Paisley and Wick, and also the total yield at Paisley (Fig. 2). Compared to the same scenario with current CO_2 concentrations, increasing the concentration of CO_2 resulted in increased yields for all cuts at all sites except the second cut at Paisley. However, in the case of scenario 4 yield was only significantly increased, compared to scenario 1, for the first cut at Kinloss, Mylnefield and Wick, and for the total yield at Kinloss (Fig. 2).

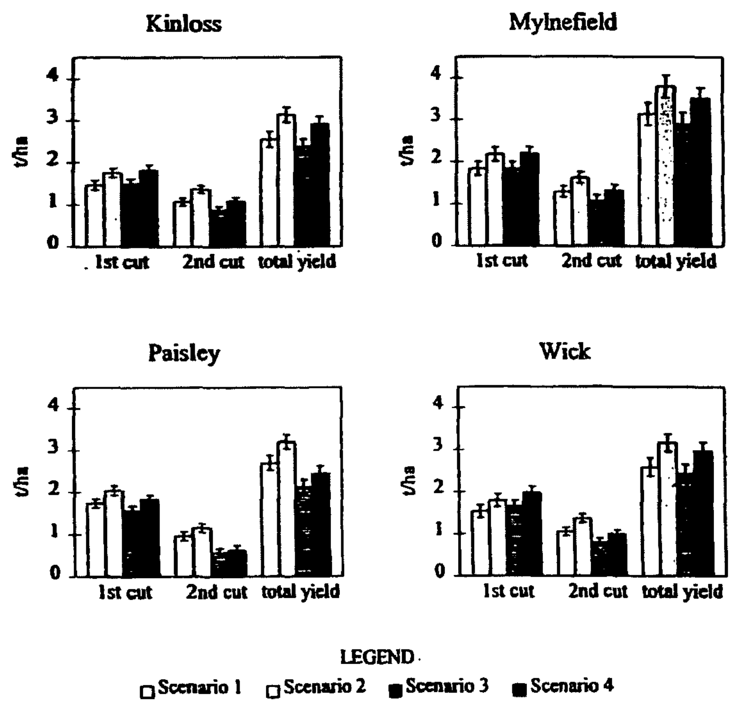

Fig. 2. Ten-year average and standard errors in respect of mean yields of the grass component for grass – clover swards for scenarios 1-4. Mean ± sed.

75

As regards the clover component yields were significantly increased at all sites in scenario 3 for the first cut and in total, but only for the second cut at Paisley (Fig. 3). The effect of increasing the concentration of CO_2 in the atmosphere for current climate conditions was to increase the second-cut yield at both Kinloss and Paisley, and the total clover yield at Paisley. The effect of scenario 4 was to increase the yield at all sites for all cuts.

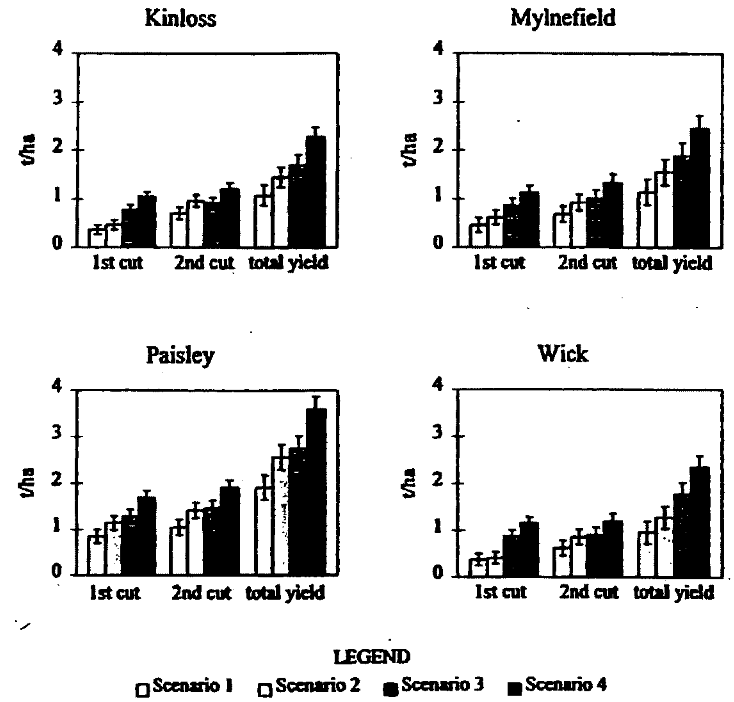

Fig. 3. Ten-year average and standard errors in respect of mean yields of the clover component for grass – clover swards for scenarios 1-4. Mean ± sed.

With respect to the combined yield of grass and white clover, the effect of scenario 3 was to increase significantly the first-cut yield at Kinloss and Wick and the total yield at Mylnefield and Wick. Increasing the CO_2 concentrations for both climate scenarios increased the yield of all cuts, except the first cut at Wick under current climatic conditions.

The effect of global warming on the seasonality of production, as represented by the percentage of the combined yield obtained from the first cut, varied between sites. The percentage of total yield obtained from the first cut increased at Kinloss and Wick, whereas it was not affected by global warming at Mylnefield and Paisley. This pattern was repeated for the white clover component, but the percentage of total grass yield obtained from the first cut increased at all sites under global warming. On the other hand, the seasonality of production of both components was unaffected by CO_2 concentrations.

Discussion

At all sites increasing the annual average temperature by 2°C significantly increased the combined yield of grass and white clover, and the yield of the clover component. However, at the majority of sites global warming had no significant effect on the grass yield. Thus, the grass and white clover components are not projected to respond equally to the changes in climate. The contribution of the white clover component to total yield increased on average from 32% under current climatic conditions to 46% under scenarios 3 and 4. On the other hand, the concentration of CO_2 had no effect on the balance of grass and white clover in the harvested material. For each climate scenario increasing the concentration of CO_2 in the atmosphere increased the yield of both components. However, increased CO_2 levels coupled with global warming (scenario 4) did not significantly affect the yield of grass harvested compared to current climatic conditions coupled with current concentrations of CO_2.

Global warming at both current and increased concentrations of CO_2 is expected to lengthen the growing season and increase the yield of white clover, but to have no effect on grass yield. If however, the climate remains unchanged and CO_2 levels increase; the yields of both components are projected to increase.

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FORECASTING THE CONSEQUENCES OF GLOBAL WARMING FOR WHITE CLOVER-BASED SYSTEMS OF LIVESTOCK PRODUCTION

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Keywords: White clover, photosynthesis, global warming

SUMMARY

Although swards containing white clover have possible benefits both for the environment and for livestock production, their potential has never been fully exploited in Western Europe. Under a global warming scenario, the contribution made by white clover to a mixed sward is predicted to increase and hence the benefits of switching from all grass to grass-legume swards. Currently these predictions rest on assumptions about the functional form of the photosynthesis equation. As there are a number of possible mathematical functions for describing the effect of diurnal variation in radiation and temperature on photosynthesis, there is a concern that past simulations may have overstated the benefits of grass-white clover systems. However, the examination of four different functional forms has revealed similar trends in the predictions of both the total and the components of yield of grass-white clover swards, although there are significant differences in the actual yields predicted. Nevertheless, the percentage of white clover in the total yield varied from 19.6% to 21.2% with the different photosynthesis models. Equally, any differences in the predictions from the models were not associated with the site or the ambient concentration of carbon dioxide, albeit the climate change scenarios did affect the actual level of the predictions of the photosynthesis models. Accordingly the results suggest that earlier conclusions reached by the authors on the increased value of grass-white clover swards with global warming are fairly robust and suggest that continued research into the breeding and management of white clover-based systems should remain a priority.

INTRODUCTION

Climate change will impact on agricultural production. However, the majority of simulation models so far constructed to examine the effects of global warming on food production have concentrated on the four main cereals, namely wheat (*Triticum aestivum*) (e.g., Godwin et al., 1990; Groot, 1993; Porter, 1993; Nonhebel, 1996), maize (*Zea mays*) (e.g., Stockle and

Campbell, 1985; Sharpley and Williams, 1990; Kenny and Harrison, 1992; Moen et al., 1994; Williams, 1995), soybean (*Glycine max*) (e.g., Sharpley and Williams, 1990; Williams, 1995) and rice (*Oryza sativa*) (e.g., Alocilja and Ritchie, 1988; Bachelet and Gay, 1993). In comparison work on the effects of global warming on forage production is limited and has either been concerned with only one phase of growth, namely the vegetative stage (Thornley et al., 1991; Sheehy et al., 1996), or has been developed for sward types typically found in the United States (Hanson et al., 1988; Hunt et al., 1991).

In Western Europe livestock production from grass-based systems is an important economic activity. Perennial ryegrass (*Lolium perenne*) is an important component of these grass-based systems, although the use of mixed grass-legume swards, such as perennial ryegrass-white clover (*Trifolium repens*), could play a more significant role. However, the area under from clover-based swards is currently limited, even though white clover has a higher nutritive value than grass and stimulates intake (Thomson, 1984). Another potential benefit of grass-white clover swards is the ability of the legume to biologically fix nitrogen and thus permit a reduction in fertilizer nitrogen applications, with possible associated environmental gains. Indeed the forage yield from a mixed sward containing approximately 30 per cent white clover is similar to the yield from a pure grass sward receiving 200 kg fertilizer nitrogen per hectare (Morrison, 1981). Nevertheless, farmers perceive that the annual yield of forage from grass-white clover swards is much more variable than that from grass swards receiving high levels of nitrogen (Haggar, 1989). However, this perception may be exaggerated, as Haggar et al. (1987) have reported that the variability in animal production was only slightly higher on mixed than on all-grass swards.

Recently, a mechanistic model of a mixed sward developed by Topp and Doyle (1996a) has predicted that, under a climate change scenario involving a 2°C increase in the annual average temperature and associated monthly changes in rainfall (Viner and Hulme, 1994), the yield of white clover is raised and its percentage contribution to total yield is also increased (Topp and Doyle, 1996a). They have also observed that both effects are increased when the carbon dioxide concentration (CO_2) is raised from 350 ppm to 520 ppm. This is the expected CO_2 concentration when the combined radiative forcing effects of all the 'greenhouse' gases is double the pre-industrial level (Wigley and Raper, 1992). Furthermore the implications of these increases in forage yields for animal production have been simulated for a spring-calving dairy herd (Topp and Doyle, 1996b). Lactation yields are forecasted to increase by 4 per cent and 12 per cent respectively for herds grazing all-grass and grass-white clover swards under the global warming scenario (Topp and Doyle, 1996b). As such, the increased use of white clover is more attractive under global warming than under present climatic conditions, with implications for future forage research and pasture management in Western Europe.

However, these predictions can be shown to be sensitive to the mathematical representation of the photosynthesis process. There are currently a number of functional forms that have been used to represent the diurnal variation in radiation and temperature in the photosynthesis sub-model, with possible consequences for the predicted photosynthate available to the crop. The differences are potentially sufficient to affect the balance of the forage components harvested, as well as the yields from mixed swards. In turn, the projected changes could have implications for the forecasted gains in lactation yields. Accordingly, this paper aims to study how far the conclusions of Topp and Doyle (1996a, 1996b), regarding the effects of global warming on the production of forage from perennial ryegrass-white clover swards, are critically affected by the functional form of the gross photosynthesis process. This has clear implications for the perceived benefits of future research into clover-based systems (Hopkins et al., 1995; Doyle and Bevan, 1996).

PHOTOSYNTHESIS SUB-MODELS

One of the most commonly used functional forms to describe both leaf and crop photosynthesis is the non-rectangular hyperbola. According to Johnson et al. (1989), this is one of the most versatile curves, which, while being empirical, its parameters have biological meaning. This form of equation has been used by several workers (e.g., Marshall and Biscoe, 1980a, 1980b; Johnson and Thornley, 1984; Johnson et al., 1989), and all the sub-models investigated are based it. The four different mathematical representations of the process of photosynthesis are outlined below and the mathematical structures of the models are described in the Appendix.

■ Sub-Model 1

The canopy photosynthesis is determined by integrating the function through the depth of the canopy. For a mixed sward, the rate of photosynthesis can be derived by summing the rates for the individual components (Johnson et al., 1989). The irradiance incident on the leaves for either component depends upon the leaf area of both the grass and white clover and thus the vertical distribution of each component through the depth of the canopy must be described. According to Woledge (1988) and Woledge et al. (1992) white clover tends to predominate in the upper layers of the canopy in grass-white clover swards.

The maximum rate of leaf photosynthesis is modified by the leaf area index of the crop (Johnson et al., 1989), the mean daily temperature (Johnson and Thornley, 1983) and the concentration of CO_2 in the atmosphere (Thornley et al., 1991). The photochemical efficiency is also a function of the concentration of CO_2 (Thornley et al., 1991). In this representation of the photosynthesis process it is assumed that radiation and temperature are constant throughout the day.

■ **Sub-Model 2**

The rate of photosynthesis of the grass and white clover sward is described by the same functions as in the previous sub-model. However, the integral is calculated at 20-minute intervals throughout the day and thus the daily canopy gross photosynthate is the summation of the rate for each of the 20-minute period. The radiation and temperature for each time period is approximated by a sinusoidal time function (Thornley and Johnson, 1990). The maximum rate of photosynthesis for each 20-minute period is modified by the temperature for that period.

■ **Sub-Model 3**

While the rate of photosynthesis of the grass and white clover sward is based on the functions described in sub-model 1, account is taken of the diurnal variability of radiation and temperature. This requires expanding the function describing canopy photosynthesis as a Taylor series about the mean value of the radiation and temperature (Thornley and Johnson, 1990). The diurnal variations in the environmental variables are incorporated in this sub-model by defining the coefficients of variations of radiation and temperature, and the correlation coefficient between radiation and temperature.

■ **Sub-Model 4**

This model is a development of the daily canopy photosynthesis model described by Sands (1995), which permits the photosynthesis of a mixed sward to be determined. It is assumed that photosynthetically active radiation (PAR) incident on a leaf surface can be described by Beer's law and the light saturated photosynthetic rate is proportional to the photosynthetically active radiation at each point in the canopy. In deriving the model Sands (1995) assumed that the above-canopy PAR varied sinusoidally. This functional form of the canopy photosynthesis equation can be solved analytically for the rectangular hyperbola (Charles-Edwards, 1982) and the Blackman response curve (Sands, 1995). Using empirical relationships, a non-rectangular functional form has been derived by Sands (1995). The diurnal variation in the temperature is incorporated in the model by calculating the function for the average morning and afternoon temperatures, where the temperature for each time period is approximated by a sinusoidal time function (Thornley and Johnson, 1990).

VALIDATION

The model of the grass-white sward incorporating the first of these sub-models (sub-model 1) has been validated using GM23 data for three sites in the United Kingdom, namely High Mowthorpe, Liscombe and Rosemaund (J. Gilbey, personal communication). Theil's inequality coefficient (Theil, 1970), which has a value of between 0 and 1, with 0 indicating a perfect fit was used to determine the performance of the model. At nitrogen fertiliser application rates of 0 kg per hectare, Theil's inequality coefficient over a four-year period and at the three sites had a value of between 0.17 and 0.24 for grass production and 0.29 and 0.50 for white clover production. The value of Theil's inequality coefficient was rather high at Liscombe and Rosemaund. At Liscombe, this was partly due to the observed yield of white clover being practically zero in 1981. At Rosemaund, the reason for the failure of the model to predict the yield of white clover adequately was that the total yield tended to be composed predominately of white clover, whereas the yield at the other two sites was dominated by grass. Nevertheless, the model of the grass-white clover sward described by Topp and Doyle (1996a) incorporating photosynthesis sub-model 1 in general proved to be reasonably valid for the grass and the combined yield, and it gave reasonable predictions in terms of the general trends of white clover yield.

RESULTS

The effect of the four different representations of photosynthesis were evaluated by: running the grass-white clover model under the following four climate change scenarios:

- scenario 1 current climatic conditions at a CO_2 concentration of 350 ppm;
- scenario 2 current climatic conditions at a CO_2 concentration of 520 ppm;
- scenario 3 global warming climatic conditions at a CO_2 concentration of 350 ppm; and
- scenario 4 global warming climatic conditions at a CO_2 concentration of 520 ppm.

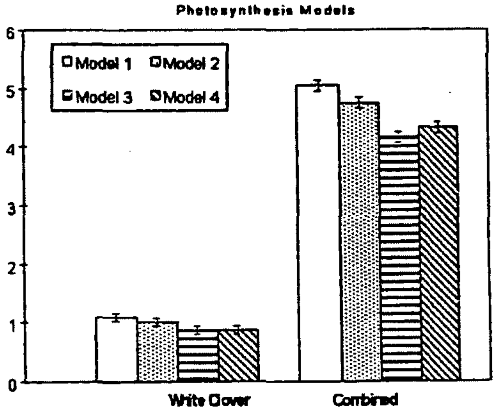

Figure 1 Ten-year average and lsd in respect of the mean total yield of white clover and combined componts for the four sub-models

For the global warming scenario the annual average temperature was increased by 2°C and the rainfall on rainy days was increased according to the estimates by Viner and Hulme (1994). In order to remove site-specific effects from the analysis the sward model was run for five sites, namely Auchincruive, Blyth Bridge, Craibstone, Drummond and Wick. The sites are situated across Scotland and the weather data was obtained from Biotechnology and Biological Sciences Research Council's ARCMET database. In the spring, 50 kg per hectare of nitrogen was applied to the mixed swards which were cut on 1 June and 27 July. All the models were run at the parameter values which have been validated for sub-model 1. The significance of the effect of incorporating the different sub-models was assessed using an ANOVA at the 5% level of significance.

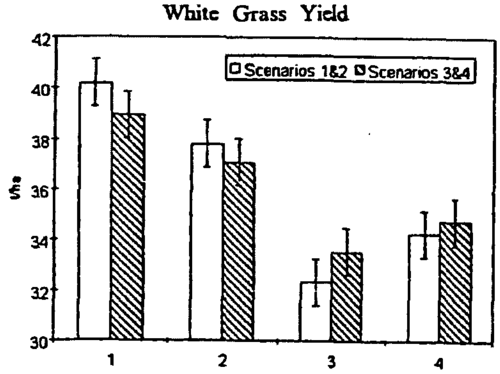

Figure 2 Ten-year average and lsd in respect of the mean total yield of grass for the four sub-models by climatic conditions

■ **Effect on yield**

There was no interaction effect between photosynthesis sub-models and either site or level of CO_2 for all components of yield. Nevertheless, there was a significant interaction between climatic conditions and sub-models for the total grass yield as well as the first-cut white clover yield and the second-cut grass yield. Where the interaction between sub-models and climate conditions was not significant the yields have been averaged across the sites, climatic scenario and CO_2 level. The results from the grass-white clover model indicated that, in terms of the total yield of white clover and the combined yield, photosynthesis sub-model 1 gave the highest production, followed by sub-models 2, 4 and 3 in that order, as shown in Figure 1. The differences between sub-models 3 and 4 were not significant. However, sub-model 1 resulted in significantly higher yields than sub-model 2, which was significantly higher than sub-models 3 and 4. With regards to the total grass yield, a similar trend was observed, see Figure 2. However, the differences between the sub-models were greater under ambient climatic conditions

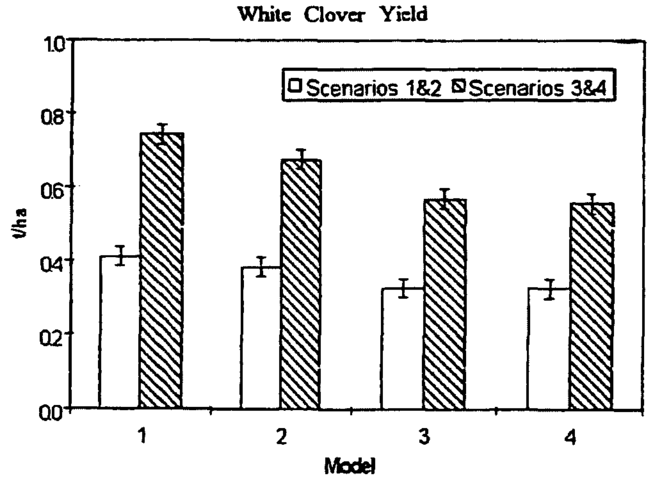

Figure 3 Ten-year average and lsd in respect of the mean first cut white glover for the four sub-models by climatic conditions

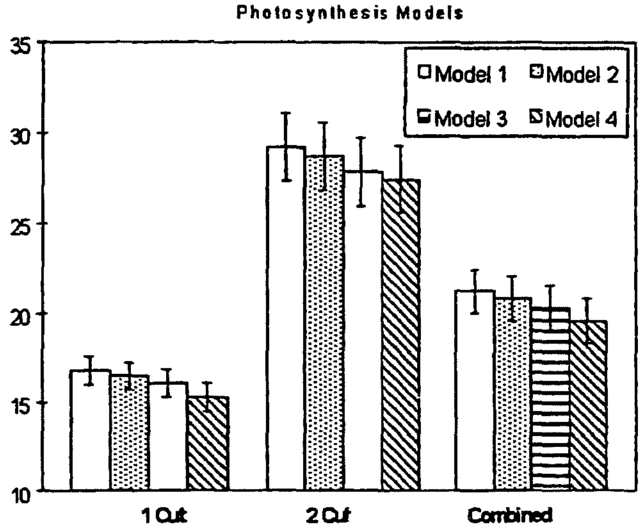

Figure 4 Ten-year average and lsd in respect of the mean percentage of white clover in the sward for the four sub-models

(scenarios 1 and 2) than under global warming (scenarios 3 and 4). A comparable trend was observed for the yields from the individual cuts. The interaction between sub-model and climatic conditions for the second grass yield showed a similar trend to the total grass yield. Nonetheless, for the first-cut white clover yield, the differences between the sub-models increased with global warming, as shown in Figure 3.

■ **Effect on Sward Composition**

The effect of the different photosynthesis sub-models on the proportion of clover harvested at each cut was also assessed. As there were no interaction effects between the photosynthesis sub-model and site, climatic conditions or level of CO_2, the proportions were averaged across the sites, climatic scenario and CO_2 level. These results indicate that the percentage of white clover in the sward is highest for sub-model 1, followed by sub-models 2, 3 and 4 in that order, as shown in Figure 4. However, with regard to the combined yield, sub-model 1 resulted in a significantly higher percentage of white clover than sub-model 4. In the case of the first and second cuts, a similar trend was observed with the difference between sub-models 1 and 4 being significant.

DISCUSSION

Of the four sub-models, conceptually the representation of gross photosynthesis that most accurately described the process was sub-model 2. In this model, the gross photosynthesis was calculated at 20-minute intervals, with radiation and temperature being described by sinusoidal functions. Using sub-model 1, the projected combined (grass-white clover) and total grass yields were increased by 6% and 5% under current and global warming conditions respectively, while the total white clover yield was increased by

Table 1 Percentage difference for the components of yield for each sub-model compared to sub-model 2

		Photosynthesis Sub-Model					
		1		3		4	
Scenario		1 & 2	3 & 4	1 & 2	3 & 4	1 & 2	3 & 4
Combined Yield	1st Cut	+7	+7	-16	-12	-10	-9
	2nd Cut	+6	+5	-12	-8	-7	-6
	Total	+6	+6	-14	-11	-9	-8
Grass	1st Cut	+7	+6	-16	-11	-10	-7
	2nd Cut	+5	+3	-12	-5	-6	-3
	Total	+6	+5	-14	-10	-9	-6
White Clover	1st Cut	+7	+10	-15	-16	-15	-17
	2nd Cut	+6	+8	-14	-13	-11	-12
	Total	+7	+9	-14	-14	-13	-14

between 7 and 9% (see Table 1). In contrast, the yields of grass, white clover and the combined yields were 14% lower under current climatic conditions (scenarios 1 and 2) using sub-model 3. Analogously, the yields from sub-model 4 were approximately 9%, 13% and 9% lower for grass, white clover and total yield than forecasted under sub-model 2. Similar reductions in yield were observed under global warming scenarios for sub-models 3 and 4.

Nevertheless, in spite of these differences all the sub-models exhibited a similar distribution in the percentage of white clover in the harvested material. Thus, the results from all four sub-models indicated that white clover production would increase under global warming and enhanced CO_2, although the actual predictions for the levels of production and the composition of the herbage differed. Nevertheless, the results do raise some concerns as the yield differences between the sub-models decrease in respect of grass yields under global warming, while they increase for white clover (see Figures 2 and 3), although it does not significantly affect the percentage of white clover in the sward.

Overall, the results of this analysis suggest that the choice of functional form representing photosynthesis does not significantly affect the conclusions reached by Topp and Doyle (1996a, 1996b) that under global warming the expectation is that grass-legume swards and specifically grass-white clover swards will perform better than currently. Accordingly, more research effort into the breeding and management of legume swards is justified. With expected changes in climate and a rise in CO_2 concentrations over the next 20 to 40 years, forage legumes, like white clover, should show increased yield and reliability. As a result the perceived potential of grass-white clover swards may be more fully realized, with livestock farmers in Western Europe emulating those in New Zealand and Australia, where grass-legume swards are central to forage management.

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APPENDIX

▪ Sub-Model 1

The rate of canopy gross photosynthesis (P_j, kg CO_2 ha^{-1} (ground) day^{-1}) for component j is given by:

$$P_j = \frac{1}{2*\theta} * \int_0^L \left(Ph_j + P_{max,j} - \sqrt{(Ph_j + P_{max,j})^2 - 4*\theta*P_{max,j}*Ph_j}\right) \frac{dl_j}{dl} * dl \qquad (1)$$

where

$$Ph_j = \frac{\alpha_j * k_j * I_0}{1 - m_j} * e^{-(k_g * l_g + k_c * l_c)} \qquad (2)$$

and I_0 is the photosynthetically active radiation in MJ ha^{-1} (ground) day^{-1}, P_{max} is the leaf photosynthetic rate in kg CO_2 ha^{-1} (leaf) day^{-1} at saturating light levels ($I_0 \rightarrow \infty$) and at the atmospheric CO_2 concentration experienced by the crop, k is the extinction coefficient, m is the leaf transmission coefficient, L is the leaf area index (ha (leaf) ha^{-1} (ground)), l is the cumulative leaf area index, α is the photochemical efficiency (kg

CO_2 MJ^{-1}) and θ is a dimensionless parameter. Subscript g refers to grass and c to clover. The vertical distribution of each component through the depth of the canopy is described by dl_j/dl (ha (leaf) ha^{-1} (ground)).

Following the procedure of Thornley et al. (1991), the photochemical efficiency (α, kg CO_2 MJ^{-1}) and the maximum rate of leaf photosynthesis (PCO_{max}, kg CO_2 ha^{-1} (leaf) day^{-1}) are modified by the atmospheric concentration of CO_2, and are described by:

$$\alpha = \alpha_{max} * \frac{1-\varpi}{\xi * CO_2} \quad (3)$$

$$P_{max} = \frac{PCO_{max}}{1+KP_{max}/CO_2} \quad (4)$$

where CO_2 is the atmospheric concentration of CO_2 (kg CO_2 m^{-3}), ξ is the CO_2 conductance parameter (m^{-2} s^{-1}), ω represents the photorespiration constant (kg m^{-2} s^{-1}), α_{max} represents the maximum value of the photochemical efficiency (kg CO_2 MJ^{-1}) and PCO_{max} (kg CO_2 ha^{-1} (leaf) day^{-1}) is the maximum rate of leaf photosynthesis. The CO_2 concentration at which PCO_{max} is half its maximal value is denoted by KP_{max} (kg CO_2 m^{-3}).

■Sub-Model 2

The radiation for each time period (I_0, MJ ha^{-1} (ground) 20 min^{-1}) is approximated by a sinusoidal time function given by:

$$I_0 = \bar{I}_0 * \frac{\pi}{2} * \sin(\pi * t/h) \quad (5)$$

where $\bar{I}_0$ (MJ ha^{-1} (ground) 20 min^{-1}) is the mean value for a 20-minute period, t is the number of seconds that has elapsed since sunrise and h (s) is the day length. The maximum rate of photosynthesis for each 20-minute period (P_{max}, kg CO_2 ha^{-1} (leaf) 20 min^{-1}) is modified by the temperature for that period. Following Thornley and Johnson (1990), the average temperature for the time period is given by:

$$T = \tau_1 + \tau_2 * \sin\left[\frac{\pi}{h} * (t-\Phi)\right] \quad (6)$$

where

$$\tau_1 = \frac{\bar{T} - (2T_m/\pi) * \cos(\pi * \Phi/h)}{1-(2/\pi) * \cos(\pi * \phi/h)} \quad (7)$$

and

$$\tau_2 = \frac{T_m - \bar{T}}{1-(2/\pi) * \cos(\pi * \phi/h)} \quad (8)$$

where $\bar{T}$ (°C) is the average daily temperature and T_m (°C) is the maximum daily temperature which occurs at Φ seconds after midday. This is typically 10800 seconds.

■ **Sub-Model 3**

Following Thornley and Johnson (1990), the daily gross photosynthesis ($P_{d,j}$, kg CO_2 ha^{-1} (ground) day^{-1}) in the presence of variable radiation and temperature can be described by:

$$P_d = hP + \frac{h}{2}\bar{I}_0^2 v_{I0}^2 \frac{\partial^2 P}{\partial I_0^2} + h\rho \bar{I}_0 \bar{T} v_{I0} v_T \frac{\partial^2 P}{\partial I_0 \partial T} + \frac{h}{2}\bar{T}^2 v_T^2 \frac{\partial^2 P}{\partial T^2} \tag{9}$$

where P (kg CO_2 ha^{-1} (ground) s^{-1}) is calculated from equation 1 for a 1-second period. Thus, the photosynthetically active radiation (I_0, MJ ha^{-1} (ground) s^{-1}) and the leaf photosynthetic rate (P_{max}, kg CO_2 ha^{-1} (leaf) s^{-1}) are expressed on a per second basis. The variable h (s) represents the day length, and $\bar{I}_0$ (MJ ha^{-1} (ground) s^{-1}) and $\bar{T}$ (°C) are the average photosynthetically active radiation and the average daily temperature respectively. The coefficients of variation for radiation (v_{I0}) and temperature (v_T), where radiation and temperature for each time period are defined by equations 2 and 3, are described by:

$$v_{I0} = \left(\frac{\Pi^2}{8} - 1\right)^{1/2} \tag{10}$$

$$v_T = \frac{(T_m/\bar{T} - 1)[\pi^2/8 - \cos^2(\pi * \Phi/h)]^{1/2}}{\pi/2 - \cos(\pi * \Phi/h)} \tag{11}$$

The variable ρ is the correlation coefficient between radiation and temperature and is described by:

$$\rho = \left[\frac{\pi^2/8 - 1}{\pi^2/8 - \cos^2(\pi\Phi/h)}\right]^{1/2} * \cos(\pi * \Phi/h) \tag{12}$$

■ **Sub-Model 4**

Following Sands (1995), daily canopy photosynthesis (P_d, kg CO_2 ha^{-1} (ground) day^{-1}) can be described by:

$$P_d = \int^{L} e^{-kl} * P_x * h * g(q,\theta) \tag{13}$$

where k is the extinction coefficient, L is the leaf area index (ha (leaf) ha^{-1} (ground)), h (s) is the day length, P_x is the leaf photosynthetic rate in kg CO_2 ha^{-1} (leaf) day^{-1}) at the top of the canopy and the function g(q,θ) is described by:

$$g(q,\theta) = \frac{g_R(q)f_1(\theta)}{1 + [g_R(q)/g_B(q) - 1]f_2(\theta)} \tag{14}$$

where

$$q = \frac{I_0 \pi k \alpha}{2h(1-m)P_x} \tag{15}$$

where I_0 is the photosynthetically active radiation in MJ ha^{-1} (ground) day^{-1}, k is the extinction coefficient and m is the leaf transmission coefficient and

$$f_1 = 1 + 0.22*\theta(1-\theta) + 0.74*\theta^2(1-\theta)^2 \tag{16}$$

and

$$f_2 = -0.18*\theta + 0.50*\theta^2 + (1+0.18-0.50)*\theta^3$$

$$
\begin{aligned}
q<1 \quad & g_R(q) = 1 - \frac{4}{\pi\sqrt{1-q^2}} \\
q=1 \quad & g_R(q) = 1 - \frac{2}{\pi} \\
q>1 \quad & g_R(q) = 1 - \frac{2}{\pi\sqrt{q^2-1}} \ln\left[\frac{1+\sqrt{\frac{q-1}{q+1}}}{1-\sqrt{\frac{q-1}{q+1}}}\right]
\end{aligned} \tag{17}
$$

and

$$
\begin{aligned}
q<1 \quad & g_B(q) = \frac{2}{\pi}q \\
q\geq 1 \quad & g_B(q) = 1 + \frac{2}{\pi}\left(q - \sqrt{q^2-1} - \arcsin(1/q)\right)
\end{aligned} \tag{18}
$$

