Net primary production and carbon stocks in differently managed grasslands: simulation of site-specific sensitivity to an increase in atmospheric CO_2 and to climate change

Marcel Riedo [a,1], Dimitrios Gyalistras [b], Jürg Fuhrer [a,*]

[a] *Swiss Federal Research Station for Agroecology and Agriculture (FAL),*
Institute of Environmental Protection and Agriculture Liebefeld (IUL), CH-3003 Bern, Switzerland
[b] *Institute of Geography, University of Bern, CH-3012 Bern, Switzerland*

Abstract

Elevated atmospheric CO_2 and climate changes are expected to influence managed grassland ecosystems. The mechanistic pasture simulation model (PaSim) was used to quantify effects on net primary productivity (NPP) and carbon (C) stocks at three locations differing in climate and soil type. An earlier model version was modified to enable long-term simulations at different altitudes, and to consider management in the form of either cutting or grazing by lactating cows. Results from simulations under current conditions agreed favourably with measured data for yield and C stocks, and model behaviour appeared to be plausible. Elevated CO_2 alone or in combination with increased temperature stimulated NPP at all sites. The stimulation was positively related to increasing precipitation at dry sites, but negatively at cool sites. Climate change scenarios in combination with elevated CO_2 led to increase C stocks. The sensitivity of C stocks to changes in temperature and precipitation was similar, and much larger than to management. Grazing led to higher C stocks compared with cutting, depending mainly on the difference in NPP between the management options. Grazing had a positive effect on C stocks under cool conditions, but the effect tended to become negative with increasing temperature. Comparing different sites revealed that local conditions affect system behaviour qualitatively. In quantitative terms, the results confirm that the combination of elevated CO_2 and climate change affects NPP and C stocks, and that the influence of management is site-specific. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Climate change; Carbon dioxide enrichment; Grasslands; Net primary production; Carbon dynamics; Simulation model

1. Introduction

Grasslands play an important role in the global carbon (C) cycle (Hall et al., 1995). They cover nearly 20% of the land surface world-wide (Lieth, 1978), and they store at least 10% of the global

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* Corresponding author. Tel.: + 41-31-3238371; fax: + 41-31-3238415.
E-mail address: juerg.fuhrer@iul.admin.ch (J. Fuhrer).
[1] Present address: Centre for Ecology and Hydrology (CEH), Bush Estate, Penicuik, Midlothian EH26 0QB, UK.

soil organic matter (SOM, Eswaran et al., 1993). It can be expected that future environmental changes, including increasing atmospheric CO_2 and climate change, will have important impacts on the C exchange between vegetation, soil, and the atmosphere (Cao and Woodward, 1998), and on the grassland soil C stocks world-wide (Parton et al., 1995). Moreover, improvements of the potential of grassland ecosystems to sequester C in the soil by changing agricultural land management could be one of the options to mitigate increases in atmospheric CO_2 concentrations (Batjes, 1998). However, the ability of soils to store additional C is highly uncertain, and it is unclear how local climate, management, and site-specific biogeochemical properties interact and influence the potential net C sink. Since the responses of terrestrial ecosystems such as grasslands to increased atmospheric CO_2 concentration and to climate change are complex, and because the response times of the resistant fractions of SOM are in the order of hundreds of years, ecosystem models are the only feasible means available to carry out sensitivity analyses and thus to investigate the effectiveness of mitigation scenarios. Ideally, models to simulate long-term changes in C stocks should link plant, soil and atmospheric processes, and account for the interaction between effects of elevated CO_2 and climatic factors. Today, a number of ecosystem models are available. The ability of some of these models to simulate the long-term changes in SOM content has been compared using sets of measured data as the reference (Smith et al., 1997). This comparison revealed important differences; for instance, models with a physiologically based plant growth submodel, such as the Hurley pasture model (e.g. Thornley and Cannell, 1997) appeared to be more specific and limited to the land uses for which they were parameterised, as compared with simple generic SOM models such as the Rothamsted C model ROTHC (Parshotam, 1996).

Simulations with the linked model carbon exchange between vegetation, soil, and atmosphere (CEVSA) revealed a strong increase in net primary production (NPP) and C stocks of terrestrial ecosystems in response to the combined effects of elevated CO_2 and climate change (Cao and Woodward, 1998). Similarly, results obtained with the multiple-element limitation model (MEL) indicate a possible long-term accumulation of organic matter in plants and soil under elevated CO_2 (Rastetter et al., 1997). In contrast, a general loss in grassland soil C was predicted by using the CENTURY model (Parton et al., 1995). Coughenour and Chen (1997) showed that the net loss of C in response to increased temperature resulted from decreased plant growth and increased decomposition, and that the effect was reversed by elevated CO_2 because of increased plant growth. These predictions may vary widely between sites because of differences in soil and vegetation properties, and in present-day climate. For example, simulations with the mechanistic pasture model PaSim (Riedo et al., 1998) driven by GCM-derived local weather scenarios showed that the magnitude and direction of the change in productivity depend on local site conditions, and that a positive effect of increased CO_2 on plant biomass production can be counteracted by climate change (Riedo et al., 1999). Hence, site-specific analyses of ecosystem responses are necessary.

C stocks of agricultural soils can be manipulated by management leading to either a net loss or a net increase in long-term C storage (Buyankovsky and Wagner, 1998). In the case of grasslands, important management options include cutting, grazing, or combinations of the two, different types of fertilisers and rates of application, and different stocking rates. In the present study, we used PaSim to assess the sensitivity of differently managed grasslands to long-term changes in CO_2 concentrations and climate. The original version of PaSim reproduced dry matter production and energy balance of cut temperate grasslands at lowland sites during one growing season (Riedo et al., 1998). One objective of this study was thus to develop an extended version which can be used to determine long-term effects of changes in CO_2 and climate on NPP and total C in the system (C_{system}). In order to increase the range of options to be tested, a new sub-model for grazing by dairy cows was added. This new model version takes into account conditions

during wintertime, in particular the presence or the absence of a snow cover. Furthermore, it considers plant acclimation to elevated CO_2 in a mechanistic way, and it accounts for a change in species characteristics with altitude.

In this paper, we present results from simulations with the extended version of PaSim. The simulations were designed to quantify long-term effects of step changes in CO_2 and climate on NPP C_{system} of either cut or grazed grasslands. Specific input data for three sites differing in altitude and in present-day climate were used in order to assess the importance of site characteristics in the ecosystem response.

2. Materials and methods

2.1. Model description

The original model version (ver 1.0) of PaSim was described in Riedo et al. (1998). For this
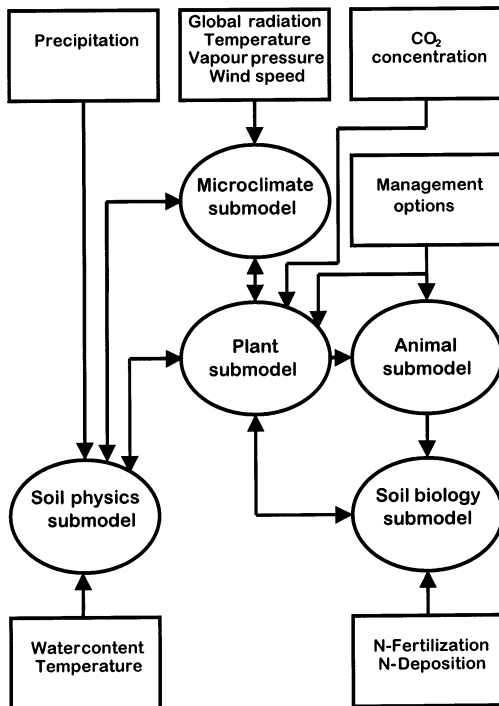

Fig. 1. PaSim. Submodels, driving variables, and internal fluxes of carbon (C), nitrogen (N), and water.

study, a modified version (ver 2.5) was used, with the main model modifications outlined below. The structure of PaSim 2.5 and the most important driving variables are shown in Fig. 1. Model input data and parameters are listed in the Section 6. PaSim was developed and run in the ACSL Graphic Modeller 4.2 environment (Aegis Research Corporation, Huntsville, AL).

2.1.1. Acclimation to elevated CO_2

Plants may acclimatise to elevated CO_2 via down-regulation of the photosynthetic capacity (Amthor, 1995). Earlier, the light-saturated rate of leaf photosynthesis, P_m (μmol m^{-2} s^{-1}), was multiplied by an empirical constant (Riedo et al., 1999). In PaSim 2.5, this constant is replaced by a dimensionless multiplier $P_{m,C}$ which depends on the C concentration in structural dry matter, C (kg C kg^{-1}), based on the hypothesis that down-regulation of photosynthesis is triggered by the accumulation of non-structural carbohydrates (cf. Amthor, 1995) by repressing the expression of genes transcribing for photosynthetic enzymes (Wolfe et al., 1998). $P_{m,C}$ decreases linearly when C exceeds a threshold value. $P_{m,C}$ is 1 for $C < P_{m,C1}$, and 0 for $C > P_{m,C2}$. $P_{m,C1}$ and $P_{m,C2}$ were estimated from measurements in experiments with elevated CO_2. C is given by substrate C, WC (kg C m^{-2}), divided by structural plant dry matter, WG (kg m^{-2}). The dynamics of WC is determined by carbohydrate source and sink fluxes,

$$\frac{dW_C}{dt} = P_c - f_{C,sh}G_{sh} - f_{C,r}G_r - R_{plant} - F_{C,exudation}$$

$$+ F_{C,rec} \tag{1}$$

Sources are canopy photosynthesis, P_c (kg C m^{-2} per day), and the flux of C from recycling, $F_{C,rec}$ (kg C m^{-2} per day). Sinks are the products of structural shoot and root growth rates, G_{sh} and G_r (kg m^{-2} per day), and the fractional C content of shoot and root structural dry matter, $f_{C,sh}$ (kg C kg^{-1}) and $f_{C,r}$ (kg C kg^{-1}), respectively, the respiratory fluxes associated with growth, maintenance, and root N uptake, R_{plant} (kg C m^{-2} per day), and root exudation, $F_{C,exudation}$ (kg C m^{-2} per day). P_c is the sum over all canopy layers of leaf photosynthetic rate (Riedo et al., 1998),

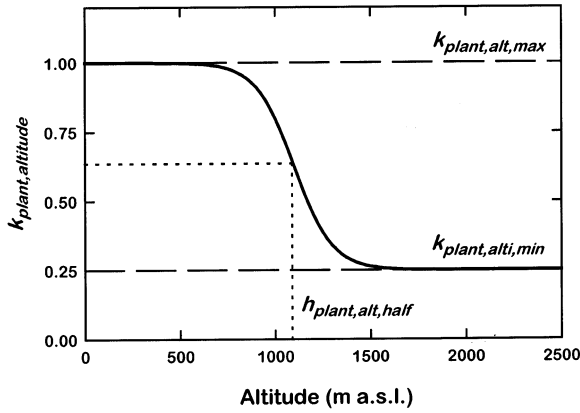Fig. 2. Influence of altitude on the growth coefficient $k_{plant,altitude}$, which determines the reduction of plant growth rate with altitude.

which in turn depends on P_m (Riedo et al., 1998) and thus on $P_{m,C}$. Because P_c depends on $P_{m,C}$, this factor maintains the balance between C source and sink activities. For example, if an increase in P_c was not balanced by sink growth, W_C would accumulate and C would increase, which would lead to down-regulation of P_m. Thus, $P_{m,C}$ reflects that the responses to elevated CO_2 of whole-plant growth and C and N partitioning alter the rate of production and utilisation of photosynthates (Wolfe et al., 1998).

2.1.2. Growth at higher altitudes

The decrease in yield with altitude is not only caused by changes in climatic and soil conditions, but also by inherited characteristics of the plant species. With increasing altitude, less demanding species with a lower yield potential and relative growth rate become more abundant (Atkin et al., 1996). This genetic change is considered by an altitude-dependent part of the growth coefficient of structural dry matter, k_{plant}, (kg^2 (kg per C) (kg per N) per day). G_{sh} and G_r are given by

$$G_{sh} = k_{plant}CN(\lambda_{sh}W_{sh} + f_G(1 - \lambda_{rep})\lambda_r W_r) \quad (2)$$

$$G_r = k_{plant}CN(1 - f_G(1 - \lambda_{rep}))\lambda_r W_r \quad (3)$$

where N is substrate N per structural dry matter (kg N kg^{-1}), λ_{sh} and λ_r are dimensionless factors controlling teleonomic partitioning between shoot and root as a function of the plant C to N balance

(Thornley and Verberne, 1989), f_G and λ_{rep} are dimensionless variables describing the influence of the developmental stage on partitioning, and W_{sh} and W_r are shoot and root structural dry matter (kg m^{-2}, Riedo et al., 1998). The factor k_{plant} is given by

$$k_{plant} = k_{plant,T}k_{plant,dev}k_{plant,altitude} \quad (4)$$

where $k_{plant,T}$ and $k_{plant,dev}$ account for temperature and developmental stage, respectively. The altitude dependent, dimensionless factor $k_{plant,altitude}$ is given by

$$k_{plant,altitude} = k_{plant,alt,min}$$
$$+ \frac{(k_{plant,alt,max} - k_{plant,alt,min})}{1 + \exp(k_{plant,alt,slope}(\text{Altitude} - h_{plant,alt,half}))} \quad (5)$$

where altitude (m) is altitude above sea level (a.s.l.), and $k_{plant,alt,min}$ (−), $k_{plant,alt,max}$ (−), $k_{plant,alt,slope}$ (m^{-1}), and $h_{plant,alt,half}$ (m) are model parameters. The plant growth coefficient k_{plant} is thus reduced from $k_{plant,alt,max}$ for highly productive lowland species to $k_{plant,alt,min}$ for alpine species (Fig. 2). The parameters in Eq. (5) were calibrated using measured yield data (Dietl, 1986).

2.1.3. Snow cover

Two state variables for the soil surface water pools were introduced in the energy balance calculations in the microclimate submodel to account for the presence of a snow cover during wintertime, i.e. the amount of snow and ice, snow (m as water equivalents), and soil surface liquid water, SSW (m). The calculation of the water balance of snow and SSW, and the soil water pools are described in Appendix B. Without snow, the procedure of PaSim 1.0 was used for the two layer energy balance calculations of the canopy and the soil surface. In the presence of a snow cover the canopy is still present, but it is assumed that it has no influence. The aerodynamic resistance between the canopy source height $d + z_0$ and the reference height z (m), r_{aa} (s m^{-1}), and between the soil surface and $d + z_0$, r_{sa} (s m^{-1}), are calculated as for bare soil,

$$r_{sa} = \frac{\ln(z/z_{0snow})\ln((d + z_0)/z_{0snow})}{k_{karman}^2 u} \quad (6)$$

$$r_{aa} = \frac{(\ln(z/z_{0snow}))^2}{k_{karman}^2 u} - r_{sa} \qquad (7)$$

where u (m s^{-1}) is wind speed at height z, k_{karman} is the von Karman constant (0.41), d (m) is zero plant displacement, z_0 (m) is the canopy roughness length, and the new parameter z_{0snow} (m) is the snow surface roughness. The calculation of the surface reflection coefficients for PAR and NIR, $REFL_{v,surface}$ and $REFL_{n,surface}$ requires the fraction of the soil surface covered by snow, A_{snow}, and snow age,

$$REFL_{v,surface} = (1 - A_{snow})REFL_{v,soil}$$
$$+ A_{snow}REFL_{v,snow} \qquad (8)$$

$$REFL_{n,surface} = (1 - A_{snow})REFL_{n,soil}$$
$$+ A_{snow}REFL_{n,snow} \qquad (9)$$

where $REFL_{v,soil}$ and $REFL_{n,soil}$ are the coefficients of the soil without snow (Riedo et al., 1998), and $REFL_{v,snow}$ and $REFL_{n,snow}$ are related to snow age. They are given by $REFL_{v,snow,fresh}$ and $REFL_{n,snow,fresh}$ for snow less than 5-days-old, and decrease linearly between 5 and 14 days to $REFL_{v,snow,old}$ and $REFL_{n,snow,old}$ (Bonan, 1991). A_{snow} is given by snow multiplied by 0.1 (Bonan, 1991) and restricted to 1, and the snow age is always set back to 0 when snowfall occurs.

Precipitation P_a (m per day) occurs as rainfall for air temperature $T_a > 0°C$ and as snowfall for $T_a < 0°C$. In the calculation of the energy balance with a snow cover neutral conditions are assumed. With or without rainfall, it is assumed that the soil surface and the snow cover have the same temperature, T_{ss}, and that T_{ss} is $\leq$ the freezing temperature T_{fr}. With a snow cover and no rainfall, the procedure for neutral conditions from PaSim 1.0 was used to calculate T_{ss}. If $T_{ss} < T_{fr}$ then soil evaporation, LE_s (W m^{-2}), sensible soil heat flux, H_s (W m^{-2}), and soil heat flux, G_s (W m^{-2}), are calculated according to PaSim 1.0. However, if $T_{ss} > T_{fr}$ then $T_{ss} = T_{fr}$. In this case, LE_s is proportional to the difference between saturated air vapour pressure at T_{fr} and vapour pressure e_a at height z, H_s is set proportional to the difference between T_{fr} and T_a at height z, and G_s is set equal to the net radiation at the soil surface, $I_{net,s}$ (W m^{-2}) minus LE_s minus H_s. With

a snow cover and rainfall, the change in energy stored in the snow pack during the simulation time step, ΔU_{snow} (W m^{-2}), and the latent heat of phase change between snow or ice and water, ε(W m^{-2}), are considered. When rain falls onto snow both change their temperature to T_{fr}, and subsequently a phase change takes place. ΔU_{snow} is thus given by

$$\Delta U_{snow}$$
$$= \frac{C_w((T_{fr} - T_{ss,t-\Delta t})snow/\Delta t + (T_{fr} - T_a)P_a)}{86\,400} \qquad (10)$$

where Δt is the model time step (0.02 day), $T_{ss,t-\Delta t}$ is the value of T_{ss} from the previous time step, C_w is the volumetric specific heat capacity of water, and 86 400 converts days to seconds. By calculating LE_s, H_s, and G_s using T_{fr} for T_{ss} it is possible to obtain ε through the energy balance of the soil surface,

$$\varepsilon = LE_s + H_s + G_s + \Delta U_{snow} - I_{net,s} \qquad (11)$$

Depending on the sign of ε, either snow melt ($\varepsilon < 0$), snowmelt (m per day), or freezing ($\varepsilon > 0$), Freezing (m per day), occurs. The fluxes are obtained by dividing ε by the latent heat of fusion and the density of water. The associated changes in snow and SSW are described in Appendix B. The new submodel for snow cover is essential for multi-year simulations at higher altitudes where a snow cover typically exists for several months. Different levels of complexities in dealing with snow cover in the model were investigated for their ability to reproduce the end of the period with snow cover in spring. The comparison with historical data for the high altitude site Davos showed that over 24 years the average deviation between simulated and measured first day in spring without snow cover was 30 days.

2.1.4. Grazing

The animal submodel considers grazing by lactating cows. The daily amount of grazed plant dry matter, Intake (kg per animal per day), depends on the leaf area index L (m^2 m^{-2}, Thornley, 1998), and is given by

$$\text{Intake} = \frac{\text{Intake}_{\text{max}}}{1 + (1/(L/K_{\text{intake}})^{q_{\text{intake}}})} \quad (12)$$

L is calculated in the plant submodel, K_{intake} (m² m⁻²) and q_{intake} (−) are as given by Thornley (1998), and $\text{Intake}_{\text{max}}$ (kg per animal per day) is the potential intake rate per lactating cow. Grazed plant dry matter, grazing (kg m⁻² per day), is given by intake multiplied by the stocking density, n_{animal} (animal m⁻²). Grazing_C (kg C m⁻² per day) and grazing_N (kg N m⁻² per day) are associated fluxes of C and N. The distribution of grazing among the different shoot compartments is described in Appendix A. One part of C and N in grazing is used for milk production. The associated fluxes, milk_C (kg C m⁻² per day) and milk_N (kg N m⁻² per day), are fractions of 0.0588 for C (RAC, 1994) and 0.00517 for N (RAC, 1994) of milk production, milk (kg m⁻² per day), which is given by

$$\text{Milk} = \frac{n_{\text{animal}}(\text{NEL} \cdot \text{Intake} - \text{NEL}_{\text{maintenance}})}{3.14} \quad (13)$$

where NEL (MJ kg⁻¹) is the net energy content of the forage, $\text{NEL}_{\text{maintenance}}$ (MJ per animal per day) is the required daily maintenance energy, and 3.14 is the energy content of milk (MJ kg⁻¹, RAC, 1994). Maintenance energy is calculated according to RAC (1994) as

$$\text{NEL}_{\text{maintenance}} = \frac{W_{\text{animal}}}{20 + 5} \quad (14)$$

where W_{animal} (kg) is animal life weight. The calculation of NEL is given in Appendix C. From grazing_C the fraction $f_{\text{R,animal}}$ is respired, R_{animal} (kg C m⁻² per day), and the fraction f_{methane} is lost as methane, methane (kg C m⁻² per day, Minonzio et al., 1998). No fluxes of N are associated with these gaseous C fluxes. The total N excreta, excreta_N (kg N m⁻² per day), is given by the difference between grazing_N, and N converted into milk, milk_N. The fraction $f_{\text{vol,animal}}$ of excreta_N is volatilised as ammonia (Menzi et al., 1997), and the rest is divided among urine, urine_N (kg N m⁻² per day) and faeces, faeces_N (kg N m⁻² per day), according to the parameter f_{Nurine} (Menzi et al., 1997). With the assumption that all urine is in the form of urea, the urine C flux,

urine_C (kg C m⁻² per day), is given by the product of excreta_N and f_{Nurine}, and the urea C:N ratio of 12:28. C in faeces, faeces_C (kg C m⁻² per day), is then given by the difference between grazing_C and the sum of all the other output C fluxes. Incorporation of C and N in urine and faeces into the soil biology submodel is described in Appendix A. The mass of the animals is kept constant and no C and N is retained. Accordingly, there are no state variables for C and N in the animal mass, and C and N of the animal mass are not accounted for in the C- and N-balances of the system.

2.1.5. System and submodel balances of C

C fluxes (in kg C m⁻² per day) considered in the model are shown in Fig. 3. NPP is the difference between P_c and R_{plant}. C is exported from the plant submodel via cutting, yield_C, grazing, grazing_C, litter, $F_{\text{C,residue}}$, and root exudation, $F_{\text{C,exudation}}$. The amount of C in the forage is divided into excreta, faeces_C and urine_C, and methane, R_{animal}, and milk_C. C losses from SOM are associated with mineralisation plus root exudation, R_{som}, and with urea hydrolysis, R_{urine}. The total amount of C in the system, C_{system} (kg C m⁻²), is divided among plant C substrate, W_C, C in shoot and root structural dry matter, $f_{\text{C,shWsh}}$ and $f_{\text{C,rWr}}$, C in plant residue, $W_{\text{C,metabolic}}$ and $W_{\text{C,struct}}$, and C in the SOM pools $W_{\text{C,active}}$, $W_{\text{C,slow}}$, and $W_{\text{C,passive}}$.

2.2. Simulations for different scenarios of climatic change and different management options

Simulations were carried out for three Swiss sites. Bern on the Swiss Plateau represents conditions suitable for high productivity, Sion in the Valais represents very dry conditions at roughly the same altitude as Bern, and Davos was chosen as a high altitude site in the Alps. The main site characteristics are given in Table 1. Soil type was used together with soil bulk density, $\rho_b(h)$ (kg m⁻³), and approximate estimates of SOM content to calculate soil physical parameters, including saturated water content $\theta_{\text{s,sat}}$ (m³ m⁻³). These were used to relate soil matric potential to water content, and to calculate soil hydraulic conductiv-

ity (AG Boden, 1994). As a simplification, these parameters were kept constant, and the water content of the lower soil boundary layer, $\theta_{s,b}$, was kept constant at field capacity.

Two management options were considered, cutting or grazing. With cutting, an algorithm was used to determine cutting days so as to optimise annual dry matter yield. After each cut, an application of mineral N fertiliser occurred (Table 1). For grazing, the stocking density of lactating cows was varied each day in such a way that L remained near a pre-set input value (Table 1). Two other model input parameters related to management was animal life weight, W_{animal}, and potential intake rate of lactating cows, intake$_{max}$ (Table 1).

Scenarios of hourly T_a, P_a, global radiation, vapour pressure, and u were obtained by stochastic simulation of hourly weather sequences from 22 monthly inputs (Gyalistras et al., 1997; Riedo et al., 1999). The monthly inputs were derived from measurements by the Swiss Meteorological Institute (Bantle, 1989, 1993) for a period of 24 years at Bern and Davos (1971–1994), and of 20 years at Sion (1978–1997).
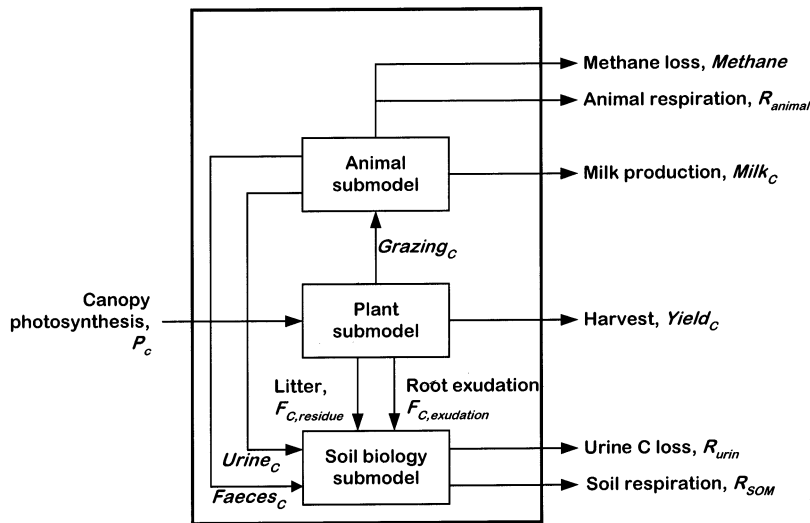

Fig. 3. Pasim: C fluxes considered in the system C balance.

Table 1
Characteristics of the test sites

	Bern, lowland, warm, humid	Sion, lowland, warm, dry	Davos, alpine, cool, humid
Location	E7° 25′ 17″, N46° 55′ 47″	E7° 20′ 19″, N46° 13′ 13″	E9° 50′ 44″, N46° 48′ 52″
Altitude above sea level (m)	565	482	1590
Soil type	Sandy loam	Sandy loam	Loam
Mean air temperature (°C)	8.7	9.6	3.3
Average annual precipitation (mm)	1033	625	995
Mineral N fertilisation after each cut (kg N ha^{-1})	20	20	20
Leaf area index (L) with grazing (m^2 m^{-2})	2.0	2.0	2.0
Animal life weight (kg)	600	600	600
Potential intake rate of lactating cows (kg per animal per day)	15.0	15.0	14.0

Table 2
Annual net primary production (NPP), C stocks (C_{system}), annual yield and net energy lactation (NEL) for reference simulations with current climate and ambient atmospheric CO_2 concentration

	Bern		Sion		Davos	
	Cutting	Grazing	Cutting	Grazing	Cutting	Grazing
NPP (kg C m^{-2} per year)	0.78	0.67	0.58	0.55	0.38	0.46
C_{system} (kg C m^{-2})	5.05	5.15	5.25	6.30	5.86	9.89
Yield (forage or milk, kg m^{-2} per year)	1.07	1.08	0.77	0.87	0.47	0.66
NEL (MJ m^{-2} per year)	6.42	5.44	4.60	4.39	2.81	3.33

For the reference simulations, periodically the 24 year (20 for Sion) simulation cycle of hourly weather data was used, and the CO_2 concentration was 350 μmol mol^{-1}. Simulations were determined when the equilibrium was reached, i.e. when the relative differences between the mean values of both C_{system} and the total amount of N in the system, N_{system} (kg N m^{-2}), for two consecutive cycles were less than 0.1%.

Simulations with seven different climate scenarios were carried out with a step change in CO_2 concentration from 350 to 700 μmol mol^{-1}. The first scenario (T0P0) was used with the same weather data as for the reference simulations. The other scenarios were generated by applying to the monthly input data an increase in temperature by 2 (T2) or 4°C (T4), combined with three scenarios for P_a, (i) a 20% decrease in the amount and a 10% decrease in probability (Pm); (ii) no change (P0); or (iii) an increase in the amount by 20% and an increase in probability by 10% (Pp). Initial values for the SOM state variables were given by the equilibrium values at the end of the reference simulations. Simulations were terminated when the new equilibrium was reached.

The model outputs represent annual means for the last 20- or 24-year simulation cycle prior to equilibrium. NPP and other C fluxes represent the cumulative flux over 1 year, C_{system} the value at the end of a year, yield is the cumulative annual amount of cut dry matter, and milk production is given as annual sum.

According to sensitivity analyses, the differences between the three locations in terms of soil type and intake$_{max}$ had only a minor influence on the simulation results, as compared with climate and management (data not shown).

3. Results

The reference simulations revealed that NPP and yield in the form of dry matter or milk was highest at Bern, lowest at the high altitude site Davos, and intermediate at the warm and dry site Sion (Table 2). No uniform influence of management was obtained, with NPP at Bern and Sion being higher with cutting, but higher with grazing at Davos. C_{system} was consistently higher with grazing than with cutting at all sites. The fraction of system C output directly related to management, i.e. yield (yield$_C$) for cut swards, or the sum of milk$_C$, R_{animal}, R_{urine} and methane for grazed systems, was higher for cut swards at all three sites (Fig. 4).

The effect of elevated CO_2 on NPP under current climatic conditions was positive, and it was related to the local temperature (T0P0, Fig. 5).
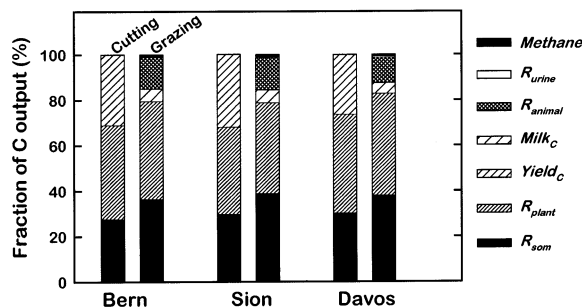

Fig. 4. Partitioning of C output among the different fluxes. Data for the reference simulations are shown as % of total system C output.
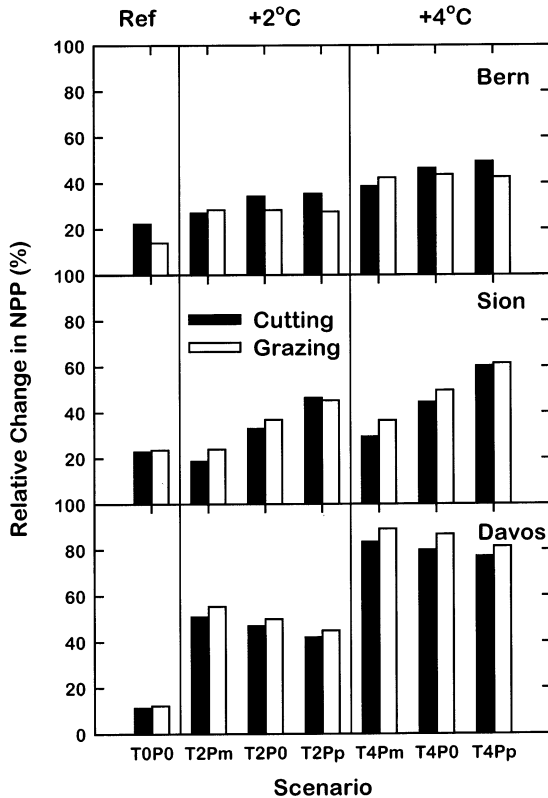
Fig. 5. Relative changes in NPP for different climate scenarios, as compared with reference simulations. For abbreviations, see text.

ship was observed for cut swards, while no relationship was found with grazing.

The relative CO_2-stimulation of C_{system} was not consistent across the different sites and management options (T0P0 in Fig. 6). While the increase with grazing was lowest at Bern and highest at Davos, the opposite trend was obtained for cut swards. For both managements, the increase in C_{system} at Bern and Sion was clearly reduced in combination with increased temperature, in contrast to the result for Davos (T2P0, and T4P0 in Fig. 6). The increase in C_{system} under grazing at Davos was similar for T0P0, T2P0, and T4P0, and increased with temperature in the case of cutting. At Bern, grazing led to a significantly lower increase in C_{system} than cutting, while at Sion the sensitivity to the management was small. For both management options, the changes in
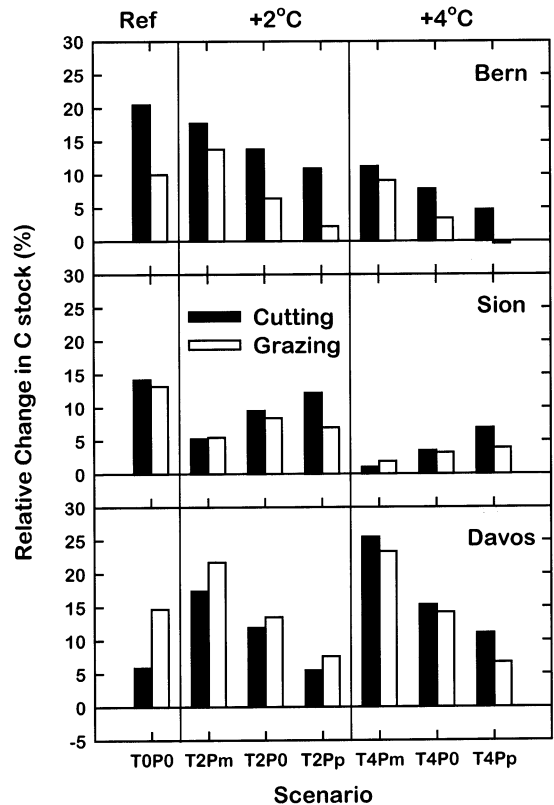
Fig. 6. Relative changes in C_{system} for different climate scenarios, as compared with reference simulations. For abbreviations, see text.

The average for both management options was highest at Sion, and lowest at Davos. Management had no effect on the CO_2 response at Sion and Davos, but at Bern CO_2-stimulation with grazing was less than with cutting. Scenarios with increased T_a (T2P0, T4P0) positively affected the CO_2-stimulation of NPP (Fig. 5). For all sites and both managements, the increase in NPP was higher for T4P0 than for T2P0, and higher for T2P0 than for T0P0. The sensitivity to temperature was comparable at Bern and Sion, but much higher at Davos. Grazing led to a slightly larger increase in NPP than cutting at Sion and Davos, but not at Bern. Independent of management, precipitation was positively related to the extent of the increase in NPP at Sion, but negatively at Davos (T2Pm, T2P0, and T2Pp, T4Pm, T4P0, and T4Pp in Fig. 5). At Bern, a positive relation-

C_{system} were negatively correlated with precipitation at Bern and Davos (T2Pm, T2P0, and T2Pp, T4Pm, T4P0, and T4Pp); with increasing precipitation a reduction in the relative change in C stocks occurred. In contrast, for cut swards a positive correlation was obtained for Sion, i.e. more C was stored with increasing precipitation, whereas no trend was found for grazing.

With both management options, the response of NPP to a step change in CO_2 alone, or in combination with climate change, was characterised by a steady increase during the simulation period, but most of this increase occurred during the first simulation cycle (not shown). For Bern, NPP for cut swards during the first simulation cycle was 32.8% higher than for the reference simulation, as compared with 34.2% at equilibrium. For Sion, the corresponding values were 31.8 and 33.0%, and for Davos 44.1 and 46.8%.

The pattern of the transient response of C_{system} to a step change in CO_2 and/or climate with both management options revealed that C_{system} was composed of two components, C_{fast} and C_{slow} (kg C m^{-2}), separated by different response times. C_{fast} and C_{slow} were obtained by fitting the function

$$C_{system} = C_{fast} + C_{slow}$$
$$= C_{fast,end} - (C_{fast,end} - C_{fast,start})e^{-k_{fast}t}$$
$$+ C_{slow,end} - (C_{slow,end} - C_{slow,start})e^{-k_{slow}t}$$
(15)

to the simulated transient values of C_{system}. The fitted values for k_{fast} and k_{slow} differed between sites. For the scenario T2P0 with cutting, values for k_{fast} were 0.0511 per year for Bern, 0.0438 per year for Sion, and 0.0292 per year for Davos, and for Kslow 0.00263 per year, 0.00255 per year, 0.00095 per year for the three sites, respectively.

4. Discussion

The simulations with PaSim 2.5 confirm that an increase in CO_2 concentration, in combination with changes in temperature and precipitation, may have important implications for NPP and for C and N cycling in grasslands. In general, the effect of elevated CO_2 and higher mean temperature on NPP and C stocks appears to be positive (Figs. 5 and 6). In the past, different ecosystem models have been used to study the question of climate change effects on grasslands. With the Hurley pasture model, it was shown that the net effect of increased CO_2 and temperature on humid, temperate grasslands is likely to be a carbon sink (Thornley and Cannell, 1997), in agreement with the prediction obtained with the CEVSA model for terrestrial ecosystems (Cao and Woodward, 1998). Simulations with the grassland ecosystem model (GEM) predicted increased productivity and C storage in plant residue and SOM for temperate grasslands in response to doubled CO_2 (Hunt et al., 1991). Simulations with the CENTURY model produced a net loss of C caused by the combination of increased temperature and CO_2 (Parton et al., 1995). However, Thornley and Cannell (1997) concluded that the response of grasslands is drastically altered by sheep grazing and is highly site-specific. By introducing a simple animal submodel it was possible to simulate grazing and milk production, and to assess interactions between management and climate change effects. Thus, PaSim 2.5 is comparable to other models developed for managed grasslands, such as the simulation of production and utilisation of rangelands (SPUR, Carlson and Thurow, 1996) which integrates FORAGE, a model of forage intake in beef cattle (Baker et al., 1992). The results with PaSim show that the influence of management on NPP and C stocks depends on the combination of environmental factors involved, and differs between sites. The high specificity of PaSim for site conditions confirms that models with a detailed plant growth submodel are highly ecosystem specific, much more than simple SOM models (Smith et al., 1997).

4.1. Model behaviour under current climatic conditions and ambient CO_2

Under current conditions NPP at the dry site Sion was much lower as compared with the more humid Bern site, in spite of the 1°C higher mean temperature. As expected, NPP was lowest at the

cool Davos site. Direct validation of simulated NPP was not carried out for these study sites, but the data for simulated annual dry matter yield, which is largely determined by NPP, could be compared with measurements. Mean simulated dry matter yield of 1.1 kg m^{-2} for Bern and 0.6 kg m^{-2} for Davos agreed reasonably well with measurements, i.e. 1.3 kg m^{-2} at Bern, and about 0.65 kg m^{-2} at Davos (Dietl, 1986). The analysis of the first simulation cycle revealed a net loss of N for the assumed initial conditions. On the way towards a long-term equilibrium, this N loss is decreased. Therefore, the values for the simulated yield at equilibrium (after some hundreds years of simulation) for the reference scenario (Table 2) were lower than those obtained for the first cycle.

Simulated equilibrium C stocks under current conditions were higher at the alpine site Davos than at the two lowland sites. The simulated values (Table 2) agreed well with data from soil surveys (NABO, 1993). The amount of C removed from the system through cutting was approximately the same as the amount grazed (data not shown). But only part of the grazed C was lost, because C in animal excrements stayed in the system. Consequently, the loss of C is smaller with grazing than with cutting (Fig. 4), and grazing leads to higher C pools compared with cutting, because the reduction in C loss through management must be compensated through larger losses via respiration under equilibrium conditions. Apparently, this is in contrast to the results reported by Thornley and Cannell (1997), but the reason for higher C pools without grazing as compared with grazing in their simulations is the lack of a C loss through cutting.

The site-specific difference in NPP between the management options determines the extent to which the potential of increased C sequestration under grazing as compared with cutting is actually reached. At Bern, NPP with cutting was 17% higher than with grazing and led to a value for C_{system}, which was only 2% higher. At Sion, NPP was 5% and C_{system} 20% higher with grazing than with cutting. At Davos, the increase in C_{system} with grazing as compared with cutting was most pronounced (69%) because NPP with cutting was even smaller than with grazing (-17%).

4.2. Equilibrium effects of increased temperature and elevated CO_2

The effect of elevated CO_2 on photosynthesis increases with temperature (e.g. Long, 1991), as described for PaSim elsewhere (Riedo et al., 1999). Accordingly, the CO_2-stimulation of NPP under current climatic conditions was stronger at Bern and Sion than at Davos, but the relative stimulation of NPP with increased temperature but no change in precipitation was much stronger at Davos. This is due to the fact that current temperatures at Bern and Sion are closer to the temperature optimum of the plant processes, and a further increase in temperature is less effective. The positive influence of increased temperature on the CO_2-stimulation of NPP found here agrees with other predictions for grasslands (Parton et al., 1995; Thornley and Cannell, 1997; Rodriguez et al., 1999).

The effect of increased NPP on C_{system} depends on the balance between NPP, C loss related to management, and R_{som} (Fig. 3). For the temperature conditions at Bern and Sion, the increase in NPP with temperature was smaller than the increase in C outputs, especially R_{som} (data not shown). Consequently, C_{system} at equilibrium was smaller than at current temperature. At the cooler Davos site, NPP increased more relative to the rate of decomposition, thus leading to a stronger increase in C_{system} with increasing temperature. The system behaviour at Bern and Sion, i.e. a reduction in soil C stocks at elevated CO_2 with increased temperature, agrees with results from other simulation experiments using similar models for soil C dynamics (Parton et al., 1995; Coughenour and Chen, 1997; Thornley and Cannell, 1997). But also the stimulation of C sequestration with increased temperature, as found for Davos, is in agreement with long-term predictions from other studies (Cao and Woodward, 1998). It should be noted that differences between results obtained with different models may be caused by differences in the functions to describe the effects of temperature and water content on microbial processes (Rodrigo et al., 1997). The differences between sites found here underline the need for site-specific studies of ecosystem behaviour in re-

sponse to climate change and elevated CO_2, and the results can help to formulate hypotheses which are useful for the design of experimental field work. However, these results must be viewed with some caution. In models such as PaSim the amount of C returned to the soil is calculated with a detailed plant growth module, and the coupling with the soil biology submodel may introduce additional uncertainty (Smith et al., 1997).

4.3. Equilibrium effects of changes in precipitation and elevated CO_2

For the same increment in temperature, increasing precipitation generally led to a decrease in plant and soil temperature, because a higher fraction of the net energy available to the system was used for evapotranspiration and a lower fraction for sensible heat flux, and vice versa for decreasing precipitation. The balance between the two counteracting effects of increased precipitation, i.e. stimulation of biological processes through increased water availability, and a decrease of process rates through decreased temperature, determined the overall effect of an increase in precipitation on NPP. At the cool Davos site with no soil water limitation, decreased leaf temperature, in combination with a minor effect of increased plant water availability on P_c, led to a decrease in P_c which exceeded the decrease in R_{plant} (data not shown), and the increase in NPP was negatively related to precipitation. In contrast, at the warmer and water-limited site Sion the stimulating effect of increased water availability on P_c led to a smaller decrease in P_c relative to the decrease in R_{plant}, and thus NPP was stimulated with increased precipitation. Except for Davos, the scenarios with decreased precipitation caused a reduction in NPP which was most pronounced at currently dry sites. The data underline the importance of the interrelationship between changing climate and effects of elevated CO_2. From a comparison of different ecosystem models it was concluded that NPP responses along climatic gradients are controlled by changes in soil processes associated with increased soil moisture that results from reduced evapotranspiration (Pan et al., 1998).

Soil organic C content is controlled by many factors, including precipitation (Burke et al., 1989).

Here, the effect of increased precipitation on C_{system} depended, on the one hand, on the balance between the influences of decreasing leaf and soil temperature and increasing water availability on NPP (as discussed above), but on the other hand on the C loss by decomposition, R_{som}. A reduction in NPP with increased precipitation at Davos, accompanied by only a small effect of increased soil water availability on decomposition, caused a reduction in C_{system}. Similar to NPP, C_{system} at Sion showed the opposite behaviour, as the increase in P_c due to increased soil water availability was strong enough to cause an increase in C_{system} despite increased decomposition, similar to the results obtained with the CENTURY model for other types of grasslands (Coughenour and Chen, 1997). At Bern, increased soil water availability also stimulated NPP with increased precipitation, but not enough to compensate for the increase in decomposition; in turn, C_{system} decreased with increased precipitation.

4.4. Transient responses under step change of temperature and CO_2

The response of NPP to a step change in CO_2 and temperature (scenario T2P0) occurred mainly within the first 20–25 simulation years. In contrast, C_{system} showed a much larger response time, in agreement with findings by others (Thornley and Cannell, 1997). C_{system} is composed of two fractions differing in decay rates, similar to other SOM models (Parshotam, 1996). The response times of the two components of C_{system}, i.e. C_{fast} and C_{slow}, were mainly determined by the decomposition rates of the slow and resistant SOM pools (Riedo et al., 1998). Values for k_{fast} between 0.029 and 0.051 per year obtained for the scenario T2P0 are similar to the value determined by Cao and Woodward (1998) for tall grasslands (0.040 per year).

4.5. Influence of management on the response to climate change and elevated CO_2

The difference in NPP between cut and grazed swards was small, relative to the changes caused

Table 3
C stocks (C_{system}, kg C m^{-2}) for current conditions (reference), elevated CO_2 concentration (T0P0), or a combination of elevated CO_2 and different climate change scenarios

	Scenario[a]	Bern		Sion		Davos	
		Cutting	Grazing	Cutting	Grazing	Cutting	Grazing
Reference		5.05	5.15	5.25	6.30	5.86	9.89
Elevated CO_2	T0P0	6.08	5.67	5.99	7.13	6.21	11.34
Climate change	T2Pm	5.94	5.87	5.52	6.65	6.88	12.04
	T2P0	5.75	5.49	5.75	6.83	6.56	11.22
	T2Pp	5.60	5.27	5.89	6.74	6.18	10.64
	T4Pm	5.62	5.62	5.30	6.42	7.36	12.19
	T4P0	5.45	5.33	5.43	6.50	6.76	11.29
	T4Pp	5.29	5.13	5.61	6.54	6.51	10.55

[a] See text for explanations.

by elevated CO_2 or climate change (Fig. 5). However, the influence of management on the response of C stocks to changes in atmospheric conditions can be pronounced (Fig. 6). The gain in C with elevated CO_2 at the productive site Bern was strongly reduced by grazing, relative to cutting. In the extreme case, for a 4°C increase in temperature and increased precipitation, C is lost from grazed swards. A significant reduction in C storage by grazing as compared with cutting also occurred at the warmest site, but only if precipitation was increased. For the coolest site, C storage for a 2°C increase in temperature is higher, but lower for a 4°C increase. Therefore, with the larger temperature increase, grasslands at higher elevations tend to behave like those at lower altitudes. Compared with the scenario with no climate change, increased temperature reduces the positive effect of grazing on C storage, and the results from all sites indicate that with increasing temperature, the effect of grazing on C storage may change from positive to negative. Overall, highest C stocks generally occurred under grazing at the mountain site Davos (Table 3).

5. Conclusions

PaSim 2.5 can be used to assess long-term changes in grasslands under a broad range of environmental and management options, ranging from intensively managed meadows under temperate conditions to grazed or cut swards at cool high altitude sites. Thus, it is possible to use a single model to explore the interactions between the influence of management and environmental factors with processes such as NPP and the dynamics of N and C. The consideration of three different sites clearly showed that the local site conditions can even qualitatively lead to different system behaviour; for instance, the increase in C stocks with elevated CO_2 declines with increasing temperature at the lowland sites, but not at the alpine site. However, a major limitation of PaSim is that it does not consider changes in species composition, and hence most of the plant-specific parameters are constant. It was suggested by Jørgensen (1992) that adaptation and species replacement should be considered to make ecosystem models more realistic. With PaSim, dynamic adaptation is only considered in terms of the response of photosynthesis to elevated CO_2.

From the simulation results we may propose that,

- with current conditions the potential for C sequestration is highest in grazed swards at high elevation sites;
- NPP increases with elevated CO_2 and increased temperature at all sites, increases with enhanced precipitation at dry sites, but decreases with increased precipitation at cool sites;

- in most scenarios with elevated CO_2, C stocks increase and are equally sensitive to changes in temperature and precipitation, but much less to management;
- grazing has a positive effect on C stocks under cool conditions, but the effect tends to become negative as the temperature increases.

These results are based on simulations with a highly complex ecosystem model for temperate grasslands. Clearly, further model validation using data from field measurements, and comparisons with results from simulations with other ecosystem models will be necessary before drawing firm conclusions related to the question of how management could positively influence both productivity and C sequestration in the soil.

6. Nomenclature

Input data
Plant

Altitude	altitude of site	m a.s.l.
C_a	atmospheric CO_2 concentration	$\mu mol\ mol^{-1}$

Microclimate

e_a	vapour pressure at reference height	kpa
$I_{ATM,tot}$	global radiation	$W\ m^{-2}$
P_a	precipitation	m per day
T_a	air temperature at reference height	K
u	wind speed at reference height	$m\ s^{-1}$

Soil physics

$\theta_{s,b}$	volumetric water content in lower soil boundary layer	$m^3\ m^{-3}$
$\theta_{s,sat,b}$	volumetric water content at saturation in lower soil boundary layer	$m^3\ m^{-3}$
$\theta_{s,sat}(h)$	volumetric water content at saturation in layer h	$m^3\ m^{-3}$
$\rho_b(h)$	bulk density in layer h	$kg\ m^{-3}$

Animal

$Intake_{max}$	potential intake rate of lactating cow	kg per animal per day
W_{animal}	animal life weight	kg

Parameters
Plant

Devear	plant developmental stage at which ear emergence starts	0.52	Riedo et al. (1998)
$f_{C,r}$	fractional C content of root structural dry matter	0.50 kg C kg^{-1}	Riedo et al. (1998)
$f_{C,sh}$	fractional C content of shoot structural dry matter	0.39 kg C kg^{-1}	Riedo et al. (1998)
g_0, g_1, g_{D0}	stomatal conductance parameters	0.08 mol m^{-2} s^{-1}, 9.5, 1.5 kPa	estimate
$k_{exu,20}$	$k_{exu,T}$ at 20°C	0.02 per day	Thornley (1998)

$h_{plant,alt,half}$	altitude at which $k_{plant,altitude}$ is the mean between $k_{plant,alt,max}$ and $k_{plant,alt,min}$	1100 m a.s.l.	calibration
$K_{C,un}$	root activity parameter	0.05 kg C kg^{-1}	Thornley and Verberne (1989)
K_{Neff}	root activity parameter	0.005 kg N m^{-2}	Thornley and Cannell (1992)
$K_{N,un}$	root activity parameter	0.005 kg N kg^{-1}	Thornley and Verberne (1989)
$k_{plant,alt,max}$, $k_{plant,alt,min}$	maximum and minimum values of $k_{plant,altitude}$	1.0, 0.25	calibration
$k_{plant,alt,slope}$	slope parameter for dependence of $k_{plant,altitude}$ on altitude	0.01 m^{-1}	calibration
$k_{W,un}$	root activity parameter	1.0 kg m^{-2}	Thornley (1998)
N_{crit}	parameter in $P_{m,N}$	0.035 kg N kg^{-1}	Woledge and Pearse (1985)
OS	organic substance content	0.9 kg kg^{-1}	estimate
$P_{m,C1}$, $P_{m,C2}$	parameters in $P_{m,C}$	0.05, 0.1	estimate
RF1, RF3, RF7	value of RF at specific developmental stages for A2 mixture	0.17, 0.22, 0.36 kg kg^{-1}	RAC (1994)
α_{350}	photosynthetic quantum efficiency at $C_a = 350$ μmol mol^{-1}	0.145 μmol J^{-1}	Thornley (1998)
v_1, v_2, v_3, v_4	root activity weighting parameters	1.0, 0.5, 0.25, 0.1	Thornley and Verberne (1989)
Microclimate			
$REFL_{v,snow,fresh}$, $REFL_{n,snow,fresh}$	reflection coefficient in visible (v) and NIR (n) for fresh snow	0.8, 0.4	Bonan (1991)
$REFL_{v,snow,old}$, $REFL_{n,snow,old}$	reflection coefficient in visible (v) and NIR (n) for old snow	0.4, 0.2	Bonan (1991)
$Z_{0,snow}$	snow surface roughness	0.0005 m	Grant (1992)
Soil biology			
$f_{R,exudation}$	fraction of $F_{C,exudation}$ respired	0.75	estimate
k_{decomp}	factor for decomposition of SOM	2.0	calibration
$k_{denitrif,20}$	denitrification rate constant for 20°C	3500 kg (kg per C) per day	calibration
$k_{nitrif,20}$	nitrification rate constant for 20°C	0.5 per day	calibration
$k_{volatil,soil,20}$	soil volatilisation rate constant for 20°C	0.005 per day	Whitehead and Lockyer (1989)
Animal			
$f_{methane}$	fraction of grazing$_C$ converted to methane	0.03	Minonzio et al. (1998)
f_{Nurine}	fraction of N in excreta not volatilised, that is in urine$_N$	0.6	Menzi et al. (1997)
$f_{R,animal}$	fraction of grazing$_C$ respired	0.5	Minonzio et al. (1998)
$f_{vol,animal}$	fraction of excreta$_N$ volatilised	0.05	Menzi et al. (1997)

| K_{intake} | intake parameter | 1 m^2 m^{-2} | Thornley (1998) |
| q_{intake} | intake parameter | 3 | Thornley (1998) |

Appendix A

In PaSim 2.5, the temperature response of the various processes in all submodels is represented according to Thornley (1998),

$$f(T) = \frac{(T - T_0)^{qft}(T'_0 - T)}{(T_{ref} - T_0)^{qft}(T'_0 - T_{ref})}$$

and for most processes the values 0°C for T_0, 45°C for T'_0, 20°C for T_{ref}, and 2 for qft, are used. For P_m the value of 50°C is used for T'_0, and the value 1.5 for qft, and for plant maintenance respiration the value 2.5 for qft is used. The parameter values related to plant photosynthesis and maintenance respiration reflect their different temperature responses.

A.1. Plant submodel

The development stage Devstage of the plant canopy during the growing season with cutting is calculated as in PaSim 1.0. In PaSim 2.5, during the period of the year before the growing season, the plant canopy is in the vegetative stage until the condition for the start of the new growing season is reached (mean air temperature of 7 day period above given threshold). At this point, with cutting the canopy changes to the reproductive stage and then back to vegetative growth at the latest after the second cut, as in PaSim 1.0, or with grazing it is assumed that the canopy is in the vegetative stage during the entire growing season. After the growing season, with both cutting and grazing the canopy remains in the vegetative state.

C exudation, $F_{C,exudation}$ (kg C m^{-2} per day), was added as a new output flux of C to the dynamics of plant substrate carbon, W_C, (Eq. (1)), given by

$$F_{C,exudation} = k_{exu,T}W_rC$$

where $k_{exu,T}$ (per day) is temperature-dependent (Thornley, 1998).

The dimensionless factor $P_{m,N}$ controls the dependency of P_m on total N content of plant dry matter, N_{tot} (kg N kg^{-1}). It is linearly related to N_{tot}, as in PaSim 1.0, but only up to N_{crit}. For $N_{tot} > N_{crit}$, $P_{m,N}$ is assumed to be constant, reflecting the observation that photosynthesis is only reduced when the organic N concentration of leaves is less than about 3% (Woledge and Pearse, 1985).

N uptake rate of roots, U_N (kg N m^{-2} per day), is

$$U_N = \sigma_N \sum_{i=1}^{4} v_i W_{r,i} \frac{N_{amm} + N_{nit}}{N_{amm} + N_{nit} + K_{Neff}}$$

$$\frac{1}{[1 + K_{C,un}/C(1 + N/K_{N,un})](1 + W_r/K_{w,un})}$$

where the term with the parameter $K_{w,un}$ (kg m^{-2}) ensures that uptake does not simply scale with root mass (Thornley, 1998). $W_{r,i}$ (kg m^{-2}) are the root structural dry matter components, Namm (kg N m^{-2}) and N_{nit} (kg N m^{-2}) are soil ammonium and nitrate, and v_i, K_{Neff} (kg N m^{-2}), $K_{C,un}$ (kg C kg^{-1}), and $K_{N,un}$ (kg N kg^{-1}) are model parameters. The root activity parameter σ_N (kg N kg^{-1} per day) now depends not only on temperature through $\sigma_{N,T}$ (kg N kg^{-1} per day), but also on soil water,

$$\sigma_N = \sigma_{N,T}\sigma_{N,\theta}$$

where $\sigma_{N,\theta}$ is given by the normalised mean value of the plant available water over the different soil layers.

The photosynthetic quantum efficiency, α(μmol J^{-1}), used in the nonrectangular hyperbola for the leaf photosynthesis light response curve (Riedo et al., 1998), is calculated by its value at

350 μmol CO_2 mol^{-1}, α_{350} (μmol J^{-1}, Thornley, 1998), multiplied by a CO_2–temperature interaction factor (Riedo et al., 1999).

Fluxes representing plant internal C and N recycling from plant litter fluxes to plant C and N substrate pools are calculated according to Thornley (1998).

The calculation of leaf stomatal conductance is now a simplified derivation from Leuning (1995), and the stomatal conductance of the canopy, G_c (mol m^{-2} s^{-1}), is given by

$$G_c = f_{watpc} g_0 L + \frac{g_1 (P_c / P_{c,conv})}{C_a (1 + D_a / g_{D0})}$$

where f_{watpc} accounts for the influence of soil water, L is leaf area index (m^2 m^{-2}), C_a (μmol mol^{-1}) is CO_2 concentration, D_a (kPa) is air vapour pressure deficit at reference height z, and $P_{c,conv}$ is a factor converting the units of P_m to the units of P_c. The values for g_0, g_1, and g_{D0} were estimated from measurements (Leuning, 1995; Nijs et al., 1997). The use of a simplification of the Leuning equation instead of the Ball equation (Ball et al., 1987), as in PaSim 1.0, is based on experimental evidence that leaf stomatal conductance is more related to vapour pressure deficit than to relative humidity (Aphalo and Jarvis, 1991; Körner, 1994).

The distribution of the amount of plant dry matter grazed by animals, grazing, among the different shoot compartments is calculated according to Thornley (1998), with a value of 1 for the parameter which determines the partitioning among lamina and sheath + stem.

A.2. Soil biology submodel

As a simplification, the partitioning of C in Faeces$_C$ among two of the soil organic C pools, $W_{C,struct}$ (kg C m^{-2}) and $W_{C,metabolic}$ (kg C m^{-2}), is determined in the same way as the distribution of C in the plant residue flux, $F_{C,residue}$ (Riedo et al., 1998). Faeces$_N$ is input to $W_{N,metabolic}$ (kg N m^{-2}). Urine is assumed to be hydrolysed instantly by urease, so that urine$_N$ is input to the soil ammonium pool, N_{amm}, and all C in urine$_C$ is lost from the system by respiration, R_{urine} (kg C m^{-2} per day).

The fraction $f_{R,exudation}$ of the C exudation output flux from the plant submodel, $F_{C,exudation}$, is assumed to be lost by respiration, and the remaining part is input to the active soil organic C pool, $W_{C,active}$ (kg C m^{-2}). Associated with exudation is N immobilisation, $F_{N,imm,exu}$ (kg N m^{-2} per day), a flux derived in equal parts from N_{amm} and N_{nit} to the active soil organic N pool, $W_{N,active}$ (kg N m^{-2}). $F_{N,imm,exu}$ is given by the C:N ratio of newly formed active SOM (Riedo et al., 1998) multiplied by the fraction of exudation which is input to $W_{C,active}$.

In addition to N volatilisation related to mineral N fertilisation, soil N volatilisation, $F_{N,volatil,soil}$ (kg N m^{-2} per day), is considered as

$$F_{N,volatil,soil} = k_{volatil,soil,T} N_{amm}$$

where the value of $k_{volatil,soil,T}$ (per day) at 20°C, $k_{volatil,soil,20}$, was set in such a way that the annual volatilisation is about 1 kg N m^{-2} ha^{-1} (Whitehead and Lockyer, 1989).

The parameters k_{decomp}, $k_{nitrif,20}$, and $k_{denitrif,20}$ were recalibrated based on experimental data (Rudaz et al., 1997).

Appendix B. Soil water module

The soil water module in PaSim 1.0 was replaced by a simplified module, which still uses Darcy's law in the calculation of drainage and capillary rise. The reduced level of detail is in agreement with the objectives of the CERES crop–soil models (Gabrielle et al., 1995) with a similar level of detail and time scales. The water pools are SSW, snow, and the water contents of the different soil layers, $\theta_s(h)$ (m^3 m^{-3}), with layer 1 ranging from the soil surface to depth $z_s(1)$ (m), and soil layer h ($1 < h \leq N_{soil}$) ranging from $z_s(h-1)$ to $z_s(h)$ (m). N_{soil} is the number of soil layers considered in the model. The calculation of the changes in the water pools for each time step Δt occurs in the following order. First, the amount of soil evaporation, LE$_s$, integrated over the time step Δt and converted to the unit of metres, LE$_{s,step}$ (m), is subtracted from SSW, then for LE$_{s,step}$ > SSW the remaining amount is subtracted from snow, and for LE$_{s,step}$ > SSW +

snow, the rest is subtracted from soil layer $h = 1$. The amount of transpiration from soil layer h, $LE_{c,s}(h)$, integrated over the time step Δt, $LE_{c,s,step}(h)$ (m), is subtracted from the respective soil layer. In the next step, precipitation P_a is either added to SSW as rain for $T_a > 0°C$, or else as snow-to-snow. Then, snowmelt and freezing are added or subtracted to SSW and snow:

$$SSW = SSW + MIN(snow, \Delta t\, snowmelt)$$
$$- MIN(SSW, \Delta t\, freezing)$$
$$snow = snow + MIN(SSW, \Delta t\, freezing)$$
$$- MIN(snow, \Delta t\, snowmelt)$$

Water fluxes between soil layers h, i.e. infiltration, drainage, and capillary rise, depend on soil water content (SWC), $\theta_s(h)$, soil matric potential $\Psi(h)$ (m), and soil hydraulic conductivity $k_s(h)$ (m per day). $\Psi(h)$ is related to $\theta_s(h)$, and $k_s(h)$ is calculated from $\Psi(h)$. Infiltration into soil layer $h = 1$, I_s (m per day), is given by

$$I_s = MIN\, \frac{SSW}{\Delta t}, MIN$$
$$\left[\left(\frac{(\theta_{s,sat}(1) - \theta_s(1))z_s(1)}{\Delta t}, \frac{k_{s,mean}(-\Psi(1) + z_s(1)/2)}{z_s(h)/2}\right)\right]$$

where $k_{s,mean}$ (m per day) is the soil hydraulic conductivity calculated from the matric potential derived from the mean value of $\theta_s(1)$ and the saturated SWC of layer 1, $\theta_{s,sat}(1)$. If both snow and SSW are greater than 0 after subtraction of infiltration from SSW, all soil surface liquid water of SSW is assumed to be lost as runoff. Starting with layer $h = 1$, and with $z_s(0)$ equal 0, drainage from layer h to layer $h + 1$, drainage$_{h,h+1}$ (m per day), is calculated as

$$Drainage_{h,h+1,pot}$$
$$= MIN\left(k_s(h)\right.$$
$$\left., MAX\left(0, \frac{(\theta_s(h) - \theta_{s,fc}(h))(z_s(h) - z_s(h-1))}{\Delta t}\right)\right)$$
$$Drainage_{h,h+1} = MIN\left(Drainage_{h,h+1,pot}, \right.$$
$$\left.\frac{(\theta_s(h+1) - \theta_{s,sat}(h+1))(z_s(h+1) - z_s(h))}{\Delta t}\right)$$

where $\theta_{s,fc}(h)$ is the SWC of soil layer h at field capacity, and $\theta_{s,sat}(h)$ is the saturated SWC of soil layer h. The drainage flow is instantly transferred from layer h to layer $h + 1$, which in turn loses water via drainage. Drainage from soil layer N_{soil} to the lower boundary layer is given by

$$Drainage_{N_{soil},b} = MIN\left(Drainage_{N_{soil}, N_{soil}+1, pot}, \right.$$
$$\left.\frac{(\theta_{s,b} - \theta_{s,sat,b})(z_{s,b} - z_s(N_{soil}))}{\Delta t}\right)$$

where $\theta_{s,b}$ is the SWC of the lower boundary layer, $\theta_{s,b,sat}$ is the saturated SWC of the lower boundary layer. The lower boundary layer ranges from $z_s(N_{soil})$ to $z_{s,b}$ (m). While drainage is calculated starting with layer $h = 1$ and ending with layer $h = N_{soil}$, capillary rise is subsequently calculated bottom up. First, capillary rise from the lower boundary layer, CapRise$_{b,N_{soil}}$ (m per day), into soil layer N_{soil} is given by

$$CapRise_{b,N_{soil},pot} = MAX\left(0, \right.$$
$$\left.\frac{k_{s,mean}(\Psi_b - \Psi(N_{soil}) - (z_{s,b} - z_s(N_{soil} - 1))/2)}{2(z_{s,b} - z_s(N_{soil} - 1))}\right)$$
$$CapRise_{b,N_{soil},max}$$
$$= \frac{(\theta_{s,sat}(N_{soil}) - \theta_s(N_{soil}))(z_s(N_{soil}) - z_s(N_{soil} - 1))}{\Delta t}$$
$$CapRise_{b,N_{soil}}$$
$$= MIN(CapRise_{b,N_{soil},pot}, CapRise_{b,N_{soil},max})$$

where $k_{s,mean}$ is calculated from the matric potential, which is calculated from the mean value of $\theta_s(N_{soil})$ and $\theta_{s,b}$. Ψ_b (m) is the matric potential of the lower boundary layer calculated from $\theta_{s,b}$. This capillary rise is instantly transferred to layer N_{soil}, which in turn loses water from capillary rise. Starting with layer $h = N_{soil}$, capillary rise from layer h to layer $h - 1$ is given by

$$CapRise_{h,h-1,pot} = MAX\left(0, \right.$$
$$\left.\frac{k_{s,mean}(\Psi(h) - \Psi(h-1) - (z_s(h) - z_s(h-2))/2)}{2(z_s(h) - z_s(h-2))}\right)$$

$$\text{CapRise}_{h,h-1,\text{max}}$$

$$= \frac{(\theta_{s,\text{sat}}(h-1) - \theta_s(h-1))(z_s(h-1) - z_s(h-2))}{\Delta t}$$

$$\text{CapRise}_{h,h-1}$$

$$= \text{MIN}(\text{CapRise}_{h,h-1,\text{pot}}, \text{CapRise}_{h,h-1,\text{max}})$$

where $k_{s,\text{mean}}$ is calculated from the matric potential calculated from the mean value of $\theta_s(h)$ and $\theta_s(h-1)$. This capillary rise is instantly transferred from layer h to layer $h-1$, which in turn loses water from capillary rise. When SWC in one of the soil layers $h-1$ is below field capacity, then the gravimetric water potential terms are not considered for the calculation of capillary rise from soil layer h.

Appendix C. Calculation of net energy lactation (NEL) in the plant submodel

Available energy in forage, NEL (MJ kg^{-1}), is a function of organic matter, OS (kg kg^{-1}), protein, RP (kg kg^{-1}), and fibre, RF (kg kg^{-1}, RAC, 1994). OS is constant (0.9 kg kg^{-1}) and RP is $6.25 \times N_{\text{tot}}$. With cutting, RF depends on Devstage during reproductive growth,

$$\text{RF} = \text{MIN}\left(\frac{\text{RF7, RF1} + (\text{RF3} - \text{RF1})\text{Devstage}}{\text{Devear}}\right)$$

where Devear represents the stage at which ear emergence starts (Riedo et al., 1998), and during the vegetative stage on t_{growth} (day), the number of days since the last cut,

$$\text{RF} = \text{MIN}\left(\frac{\text{RF7, RF1} + (\text{RF3} - \text{RF1})t_{\text{growth}}}{49}\right)$$

With grazing, RF is set equal to RF1. The empirical parameters RF1, RF3, and RF7 define the value of RF at specific phenological stages. OS, RP and RF determine the digestible organic substance, VOS (kg kg^{-1}),

$$\text{VOS} = \left(\frac{0.835 + 0.114\text{RP}}{\text{OS} - 1.45(\text{RF/OS})^2}\right)\text{OS}$$

the digestible crude protein, VP (kg kg^{-1}),

$$\text{VP} = \text{RP}\left(\frac{0.33 + 3.3\text{RP}}{\text{OS}}\right) - 6.1\left(\frac{\text{RP}}{\text{OS}}\right)^2$$

and the gross energy in forage, BE (MJ kg^{-1})

$$\text{BE} = 18.8\text{OS} + 7.8\text{RP}$$

VOS and VP determine the convertible energy, UE (MJ kg^{-1}). For VOS/VP < 7, UE $= 14.2$ VOS $+ 5.9$ VP, and for VOS/VP > 7, UE $= 15.1$ VOS.

Finally, NEL (MJ kg^{-1}) is given by.

$$\text{NEL} = 0.9752\left(\frac{0.463 + 0.24 \text{ UE}}{\text{BE}}\right)\text{UE}$$

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