

Modelling grassland responses to climate change and elevated CO₂

M. Riedo, D. Gyalistras (*), A. Grub, M. Rosset and J. Fuhrer (#)

*Swiss Federal Research Station for Agroecology and Agriculture (FAL),
Institute of Environmental Protection and Agriculture Liebefeld (IUL),
CH-3003 Bern, Switzerland.*

() Systems Ecology, Institute of Terrestrial Ecology,
Swiss Federal Institute of Technology Zurich (ETZ),
CH-8952 Zurich, Switzerland.*

(#) Corresponding author.

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Abstract

A mechanistic model for productive grassland was used to simulate the annual production of above- and belowground plant biomass in relation to fluxes of C, N, and water, and to test the sensitivity of yield, shoot/root ratio, evapotranspiration, and water use efficiency (WUE) to climate change scenarios (CC) and to elevated CO₂ (2 × CO₂) with or without consideration of photosynthetic acclimation of the plants. Validation with data from two Swiss sites revealed satisfactory agreement between simulation and measurement for yield, energy fluxes, and N-dynamics. Local weather scenarios were derived from the results of two General Circulation Models (GCM) for 2 × CO₂ by a statistical down-scaling procedure. Biomass production changed by a maximum of 8% in response to CC without 2 × CO₂ effects, by 1-17% in response to 2 × CO₂ alone, and by 6-20% in response to the combination of CC and 2 × CO₂. With plant acclimation, biomass production increased only up to 8% with elevated CO₂, as compared to a maximum increase of 20% in the absence of plant acclimation. Reduced yield with CC was obtained for sites with low soil water holding capacity. Decreased evapotranspiration and increased WUE with 2 × CO₂ were partially offset by CC. The simulations indicated that productivity of managed grassland is sensitive to different assumptions about changes in climate, CO₂ concentration, and photosynthetic acclimation, and that the effects of elevated CO₂ are modified by CC and depend on local soil conditions.

Keywords: Climate change, elevated CO₂, evapotranspiration, grassland, productivity, ecosystem model.

Résumé

Nous avons utilisé un modèle mécaniste pour les prairies productives afin de simuler la production annuelle de biomasse végétale épigée et hypogée en relation avec les flux de C, de N et hydriques et afin de tester la sensibilité du rendement, du ratio biomasse aérienne et souterraine, de l'évapotranspiration et de l'efficacité d'utilisation de l'eau (WUE) à des scénarii de changement climatique (CC) et à une élévation du CO₂ (2 × CO₂), avec ou sans considération d'une acclimatation photosynthétique des plantes. La validation avec des données provenant de deux sites suisses a fait apparaître une concordance satisfaisante entre la simulation et les mesures en ce qui concerne le rendement, les flux d'énergie et la dynamique de l'azote. Des scénarii météorologiques locaux ont été dérivés des résultats

de deux Modèles de Circulation Générale (GCM) pour un doublement du CO_2 grâce à une procédure statistique de réduction d'échelle. La production de biomasse change de 8% au maximum en réponse au changement climatique sans effets de doublement du CO_2 , de 1 à 17 % en réponse au doublement du CO_2 seul, et de 6 à 20 % en réponse à la combinaison du changement climatique et du doublement du CO_2 . Avec l'acclimatation des plantes, la production de biomasse ne s'accroît que de 8 % avec une élévation du CO_2 – à comparer avec un accroissement maximal de 20 % en l'absence d'acclimatation des plantes. Nous avons trouvé un rendement réduit avec le changement climatique sur les sites à faible capacité de rétention d'eau du sol. Une baisse de l'évapotranspiration et une augmentation de la WUE avec un doublement du CO_2 sont partiellement compensées par le CC. Les simulations indiquent que la productivité des prairies exploitées est sensible à différentes suppositions concernant les changements climatiques, la concentration en CO_2 et l'acclimatation photosynthétique et que les effets d'une élévation du CO_2 sont modifiés par le changement climatique et dépendent des conditions locales des sols.

INTRODUCTION

Grasslands are important ecosystems in many parts of the world, and their response to changes in atmospheric CO_2 and climatic conditions may affect global carbon and energy budgets (PARTON *et al.*, 1995). At much smaller scales, grasslands are important for agronomic reasons, or because of their role in landscape ecology, but potential effects of increasing CO_2 and climate change at the local scale have received less attention as compared to potential changes at the global scale. Detailed models working at the local scale and incorporating processes in a mechanistic manner could help to investigate the sensitivity to future conditions of specific types of grasslands in a particular region, to produce the input data necessary for socio-economic impact modelling, or to estimate the parameters of aggregated models. The aim of the present study was to develop, test and use a detailed ecosystem model to investigate the sensitivity of productive pastures in Switzerland to future climatic conditions and elevated CO_2 .

DESCRIPTION OF MODEL AND SIMULATIONS

The model is composed of sub-models for vegetation, microclimate, soil physics, and soil biology. It integrates the simultaneous dynamics of carbon (C), nitrogen (N) and water. The time step of the model is one hour, and the time scale covers one growing season. The vegetation sub-model is partly based on the Hurley pasture model developed by THORNLEY & VERBERNE (1989). Total plant dry matter is divided into structural dry matter, plant C substrate, and plant N substrate. Unlike the version of the Hurley Pasture model described by THORNLEY & VERBERNE (1989), the vegetation sub-model accounts also for the reproductive growth stage in addition to the vegetative growth stage, it allows for the dynamic change in the fractional N content of plant structural dry matter, and it simulates stomatal conductance. The developmental stage is associated with the sum of daily mean temperatures above a base temperature.

The reproductive stage has a higher light saturated leaf photosynthesis rate and an increased shoot/root allocation as compared to the vegetative stage. Fractional N content of plant structural dry matter changes dynamically through the linear dependency of the N concentration of newly produced structural dry matter on plant N substrate. Stomatal conductance is represented by a modified version of the Ball equation (BALL *et al.*, 1987), and is proportional to photosynthesis and relative air humidity, and inversely proportional to atmospheric CO_2 concentration. Leaf photosynthesis is modeled using a non-rectangular hyperbola to describe the light-dependent photosynthetic rate (THORNLEY & VERBERNE,

1989). The light-saturated rate is modified by scalars that account for the effects of CO₂, plant acclimation, temperature, total plant N concentration, developmental stage, and water. The photosynthetic quantum efficiency depends on a scalar that accounts for the effects of CO₂. Both CO₂ scalars depend on temperature (FARQUHAR & VON CAEMMERER, 1982). The plant acclimation scalar accounts for a possible reduction of the maximum rate of leaf carboxylation (*i.e.* V_{cmax} in the model of FARQUHAR & VON CAEMMERER (1982)) due to acclimation of leaf photosynthesis to elevated CO₂. Acclimation by reductions in J_{max} were not considered in the model simulations described here, because measurements in the SWISS FACE experiment at Eschikon, Zürich, did not show significant changes in this parameter (S. LONG, *pers. comm.*). Both leaf photosynthesis and stomatal conductance depend on soil water potential through a threshold function. The micro-climate sub-model is used to calculate the canopy interception of short-wave radiation, and to calculate canopy and soil energy balance. To obtain the radiation profile, the canopy is divided into n layers. A generalisation of the canopy radiation model of NORMAN (1979) is used to incorporate the ellipsoidal model for the leaf angle distribution of CAMPBELL (1986). The soil biology sub-model is used to calculate the concentrations of NO₃⁻ and NH₄⁺ in the soil. The structure follows the "soil and decomposition" and "nitrogen" sub-models of the CENTURY model (PARTON *et al.*, 1987), but soil surface and soil plant residue are not separated, and no profile of C and N pools is calculated. Prior to the application of the model for a specific site, the soil biology sub-model was brought to near steady state for the current climate condition at this site by iteratively determining the initial conditions for the state variables. This procedure was necessary to adapt the sub-model for use over only one growing season. The soil physics sub-model calculates water content and temperature in different soil layers.

Most of the model parameters were derived from the literature, and some from field measurements carried out in pastures at two sites near Bern, Switzerland, located at 548 m (Ostermundigen) and 915 m above sea level (Oberbütschel). A full description of parameters and parameter values is given elsewhere (RIEDO, 1997). Calibration was performed by comparison of simulation results with data from field measurements for the ear fraction of shoot mass, net radiation above the canopy, ammonium and nitrate concentration in the soil solution, and denitrification. Hourly input data for radiation, temperature, vapour pressure, wind speed, and precipitation are used as the driving weather variables. Management options include mineral fertilisation and cutting. Atmospheric CO₂ (C_a , ppm) is used as a constant (350 ppm). Site specific model parameters include the fractional clover content, the depth of the main rooting zone, and several soil physical parameters for different soil layers, including clay and quartz fractions, saturated hydraulic conductivity, bulk density, etc. (RIEDO, 1997). These model input data and the initial conditions for the state variables to carry out simulations for validation and sensitivity analysis were derived from data collected at the two field sites. N fertilization applied was 25 kg N ha⁻¹ at the beginning of each season, and additional 20 kg N ha⁻¹ after each growth period. The cutting regime was either given by a fixed (constant) interval of six weeks at Ostermundigen and nine weeks at Oberbütschel, or by intervals of variable (flexible) length, as determined by the local farmer. Both cutting regimes resulted in the same number of growth intervals during the whole season (five or six at Ostermundigen, four at Oberbütschel). The fractional clover content of the pastures was between 7 and 18%. The main grass species at Ostermundigen, with a loamy sand soil, were *Dactylis glomerata*, *Lolium perenne*, *Poa pratensis*, and *Phleum pratense*, and at Oberbütschel, with a humus-rich loamy and soil, *Alopecurus pratensis*, *Arrhenatherum elatius*, *Dactylis glomerata*, and *Festuca pratensis*. At both sites, *Trifolium repens* and *Trifolium pratense* were the dominating clover species.

The model sensitivity to climate change scenarios and to elevated CO₂ was tested with the five hourly driving weather variables obtained from meteorological stations (*i.e.* present climate), or by a statistical down-scaling procedure using results from GCM simulations of the monthly large-scale temperature and pressure distribution over the N-Atlantic and Europe (GYALISTRAS *et al.*, 1997) (*i.e.* climate change). Model simulations for current conditions were carried out using site parameters and 14-

year weather data (1981-94) for different locations on the Swiss Plateau (reference simulation). For the simulation of climate change effects (CC), results from the two GCMs ECHAM (CUBASCH *et al.*, 1992) and CCC (McFARLANE *et al.*, 1992; BOER *et al.*, 1992) for $2 \times \text{CO}_2$ scenarios were used to derive the change in the hourly weather data. The mean changes over the period March to October were -1.6% (ECHAM) and $+5.5\%$ (CCC) for the monthly precipitation sum, $+3.1\%$ (ECHAM) and $+4.8\%$ (CCC) for daily mean global radiation, $+1.6^\circ\text{C}$ (ECHAM) and $+2.7^\circ\text{C}$ (CCC) for daily mean temperature, $+10.4\%$ (ECHAM) and $+18.6\%$ (CCC) for daily mean vapour pressure. Changes in minima, maxima, and standard deviations were also used, but are not shown here. Effects of elevated CO_2 (CO_2) were obtained by using 660 ppm (in combination with CCC) or 720 ppm (in combination with ECHAM) instead of 350 ppm (reference simulation), and by assuming either no or maximum photosynthetic acclimation. Maximum acclimation was simulated by a 30% decrease in light saturated leaf photosynthesis under elevated CO_2 compared to current CO_2 , as was approximately found in the Swiss FACE experiment at Eschikon, Zürich (S. LONG, *pers. comm.*). The combined effects of both CC and CO_2 (CC + CO_2) were determined using all combinations of weather scenarios and assumptions about CO_2 acclimation. Median and percentiles were calculated for each group using the 14-year average for each site and scenario. Because of the time scale of one growing season for model simulations, no transition from current climate to the changed climate under elevated CO_2 was simulated, and hence the simulation results for the soil biology part of the model may not reflect future conditions under climate change. The associated uncertainty about N and C cycling in the soil was probably masked by the large N fertilizer input used in the simulations.

MODEL VALIDATION

Weekly data for harvestable plant biomass and leaf area index from plots with flexible or fixed growth periods, continuous records of microclimatic variables, energy fluxes, and soil water content and temperature, periodic measurements of root biomass, and C- and N-contents of plant dry matter were used to validate the model. These data were obtained from field measurements carried out at the same two sites at which the data for the model parametrization were also collected. In general, the agreement between measured and simulated annual dry matter yield was satisfactory (table I); largest deviations ($> 10\%$) were caused by single growth periods during which extreme weather conditions occurred, such as strong drought or very cold

TABLE I. – Two-year comparison between measured and simulated annual dry matter yield for two Swiss sites at different altitudes. Yield was measured in plots with a fixed or flexible length of individual growth periods (GP).

	Measured (kg m^{-2})	Simulated (kg m^{-2})	Difference (%)	Measured (kg m^{-2})	Simulated (kg m^{-2})	Difference (%)
	1993			1994		
Ostermundigen, 548 m a.s.l.						
Fixed GP	1.39	1.42	2.6	1.30	1.47	13.0
Flexible GP	1.36	1.32	-3.1	1.39	1.58	13.8
Oberbütschel, 918 m a.s.l.						
Fixed GP	0.98	1.12	14.9	1.08	1.17	8.3
Flexible GP	1.15	1.13	-1.7	1.09	1.31	20.4

temperatures with snowfall. Correlation between measured and simulated data for latent heat flux yielded values for R^2 between 0.789 and 0.896. Lower R^2 was obtained for sensible heat flux and soil heat flux (not shown). The relative difference in N-yield ranged between -17.3% and 5.7%. Overall, the validation procedure suggested that the model could acceptably reproduce plant growth, energy fluxes, and N-dynamics.

SENSITIVITY ANALYSIS

The sensitivity of the model to parameters and initial conditions was tested by (i) analysing the extent of change in annual yield caused by a $\pm 25\%$ change in the parameter value (parameter sensitivity), and (ii) by determining the contribution of the uncertainty associated with the parameter value of the 20 most sensitive parameters to the uncertainty of the simulation results (parameter importance) using random Monte Carlo sampling of parameters and rank transformation (HAMBY, 1994). The most important parameters were (the values used in the simulations are given in parenthesis) (a) reference value for dependency of the N concentration of newly produced structural dry matter on plant N substrate (0.022 kg N kg⁻¹ for a value of 0.004 kg N kg⁻¹ for plant N substrate), (b) light-saturated rate of photosynthesis (22.6 and 15.0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for reproductive and vegetative grass, respectively), and (c) rate of plant ageing (0.05 and 0.03 d⁻¹ for shoots and roots, respectively).

RESULTS AND DISCUSSION

Biomass production increased in response to most scenarios, with the largest increase in response to the combination of CC and CO₂ (CC + CO₂) (fig. 1). The median increase of about 10% in response to elevated CO₂ is comparable to the relatively modest increase in herbage accumulation measured in pasture turves (NEWTON *et al.*, 1994), and to the weak response of *Lolium perenne* grown in mixture with *Trifolium repens* in the Swiss FACE experiment (HEBEISEN *et al.*, 1996). Decreased yield with only CC was obtained for soils with low water holding capacity, resulting from the occurrence of soil water limitation. Relative allocation of dry matter to shoots (S/R) increased with CC and decreased with CO₂, whereas both magnitude and direction of the change in response to CC + CO₂ were uncertain. The relatively stronger simulation of root biomass as compared to shoot biomass with elevated CO₂ agreed with results from experiments with pasture turves (NEWTON *et al.*, 1994) and *Lolium perenne* (SCHENK *et al.*, 1995), but the extent of the change obtained in the simulations tended to be smaller. With CC, mainly characterised by an increase in temperature, vapour pressure and wind speed, evapotranspiration (ET) increased substantially. In contrast, with elevated CO₂ water was conserved due to decreased stomatal conductance. The extent of the CO₂-induced decrease in ET of 10-20% was similar to the change in cumulative ET measured at elevated CO₂ over 24 h d⁻¹ from a prairie ecosystem (HAM *et al.*, 1995) and from fertilized plots of alpine grassland during daytime (DIEMER, 1994). The increase in WUE resulting from reduced ET and increased yield with elevated CO₂ of 20-30% corresponded to the change observed in the prairie ecosystem (HAM *et al.*, 1995), whereas changes in instantaneous WUE observed in experiments may be much larger (cf. EAMUS, 1991). WUE obtained in the simulations may be less sensitive to elevated CO₂ than WUE determined over shorter

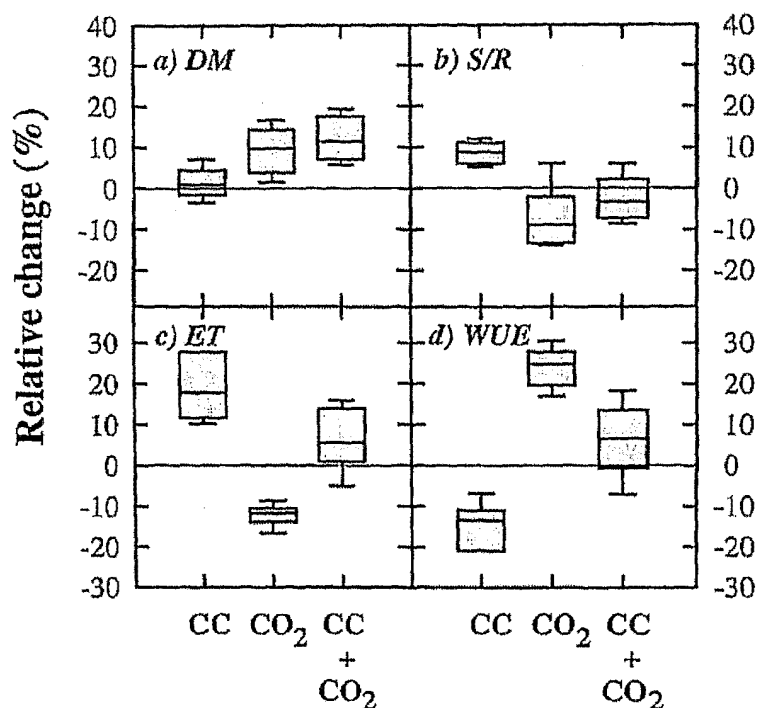


FIG. 1. – Changes in harvestable dry matter yield, DM (a), shoot: root ratio, S/R (b), evapotranspiration, ET (c), and water use efficiency, WUE (d) of productive grassland at different Swiss sites relative to 1981-1994 in response to different climate change scenarios (CC), elevated CO₂ with or without plant acclimation (CO₂), or combinations of CC and CO₂ (CC + CO₂). The median is shown inside the box indicating the 25th and 75th percentiles, capped bars indicate the 10th and the 90th percentiles.

experimental periods because it is based on accumulated biomass production and ET per unit ground area over the whole season, and it is influenced by soil evaporation during periods with little standing biomass present. The increase in WUE with elevated CO₂ was partially offset by CC because of the proportionally stronger increase in ET as compared to biomass production.

Biomass production was found to be strongly influenced by the assumption about photosynthetic acclimation. With elevated CO₂ and with or without CC an increase between 1 and 8% was obtained with acclimation, as compared to changes between 13 and 20% in the absence of acclimation. In contrast, ET was less sensitive to acclimation; changes of -17% to 14% in response to elevated CO₂ with acclimation and with or without CC were similar to those obtained without acclimation (-14 and 17%).

In conclusion, these preliminary results suggest that productive managed grassland with site conditions representative of the Swiss Central Plateau is sensitive to different assumptions about climate change, elevated CO₂, and photosynthetic acclimation. The simulations reveal improved resource efficiencies and enhanced grassland productivity in response to elevated CO₂ or to the combination of elevated CO₂ and climate change, except for sites with unfavourable soil water conditions.

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