

Using an ecosystem model linked to GCM-derived local weather scenarios to analyse effects of climate change and elevated CO₂ on dry matter production and partitioning, and water use in temperate managed grasslands

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Abstract

Local effects of climate change (CC) and elevated CO₂ (2 × CO₂, 660 μmol mol⁻¹) on managed temperate grasslands were assessed by forcing a dynamic ecosystem model with weather scenarios. The aims of the study were to compare the relative importance of individual and combined effects of CC, 2 × CO₂, and photosynthetic acclimation, and to assess the importance of local site conditions. The model was driven by hourly means for temperature (*T*), precipitation (*P*), global radiation (*G*), vapour pressure (*VP*), and wind speed (*U*). Local climate scenarios were derived by statistical downscaling techniques from a 2 × CO₂ simulation with the General Circulation Model of the Canadian Climate Centre (CCC-GCMII). Simulations over 14 growing seasons to account for year-to-year variability of climate were carried out for a low, relatively dry site, and a high, more humid site.

At both sites, shoot dry matter responded positively to 2 × CO₂ with the site at low elevation being more sensitive than the higher site. The effect of assumed changes in climate was negative at the lower, but positive at the higher site. Shoot dry matter was more sensitive to the effects of 2 × CO₂ than to CC. Both effects combined increased shoot dry matter by up to 20%. This was attributed to direct effects of 2 × CO₂ and increased *T*, and indirect stimulation via increased soil N availability. Biomass partitioning to roots increased with 2 × CO₂ but decreased with CC, while an intermediate response resulted from the combination. Leaf area index (*LAI*) increased under 2 × CO₂, but not enough to compensate fully for a decrease in leaf conductance. Under the 2 × CO₂ scenario evapotranspiration (*ET*) decreased, but increased under CC. Photosynthetic acclimation reduced the effect of 2 × CO₂ on shoot growth, but had little effect on *ET*. The seasonal water use efficiency (*WUE*) was improved under 2 × CO₂, and reduced under CC. With the combination of both factors, the change was small but still positive, especially at the high elevation site with more favourable soil water conditions. This reflects the stronger positive yield response in combination with a smaller increase in *ET* under cooler, more humid conditions.

The results for the combination of factors suggest that except for shoot growth, effects of 2 × CO₂ and CC tend to offset each other. While CC determines the sign of the *ET* response, the sign of the biomass response is determined by 2 × CO₂. The results highlight the importance of a site-specific analysis of ecosystem responses by using a flexible approach based on a combination of state-of-the-art downscaling, spatially resolved data sets, and a mechanistic model to obtain quantitative and reproducible assessments of climate change impacts at the ecosystem level.

Keywords: climate change, downscaling, elevated CO₂, grassland model, productivity, water use

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Introduction

Grasslands occupy a large portion of the nonforested land in pre-Alpine and Alpine regions of Europe. Climate change (CC) and increasing atmospheric CO₂ concentrations may affect their structure and functioning. For instance, changes in water use, biomass allocation, and productivity may have implications for regional water balances (Field *et al.* 1995), storage of carbon (C) below-ground (Parton *et al.* 1995), or economic aspects of grassland management (Campbell *et al.* 1997). Such effects result from complex plant-dominated ecophysiological responses to climatic and edaphic factors in combination with the direct effects of an elevated ambient CO₂ concentration.

Based on experimental evidence, elevated CO₂ is expected to generally increase dry matter production in intensively managed grassland (Hebeisen *et al.* 1997), depending on the level of photosynthetic acclimation. On the other hand, the effect of CC is more difficult to project. At temperate sites, an increase in temperature (*T*) has been found to affect grass growth positively (Nijs *et al.* 1996), but a decrease in soil moisture due to higher evapotranspiration (*ET*) may cause drought stress and reduced soil nitrogen (N) availability, two important factors determining grassland productivity. A change in *ET* not only results from changed *T*, but also depends on associated shifts in precipitation (*P*), radiation (*G*), vapour pressure (*VP*), and wind speed (*U*), and is strongly modified by soil texture. Therefore, effects of CC are likely to show considerable spatial variation (Pan *et al.* 1996), in particular within climatically and topographically complex regions, such as the European Alps. Effects of *ET* on soil moisture and N availability may affect the balance between shoot and root growth, which may lead to a change in the shoot:root ratio (*S:R*). This would interact with the direct effect of elevated CO₂ which by itself tends to decrease *S:R* (Rogers *et al.* 1996). While individual effects of CC and 2 × CO₂ on growth, biomass partitioning and water use may qualitatively be known, the changes resulting from the combination of factors are highly uncertain, and the assessment of the balance between them must consider local site conditions.

To study the relevance of individual climatic factors and 2 × CO₂, elaborate multifactorial field experiments could be conducted. However, due to constraints in resources and measuring techniques, alternative

approaches are needed. One such approach is to calibrate mechanistic models with experimental data from carefully designed experiments, and then to analyse in extensive simulation studies the effects of individual factors plus some factor combinations on variables of major interest. Such an approach would also foster the formulation of new testable hypotheses. To our knowledge, few grassland ecosystem models which explicitly include direct CO₂ fertilization effects have been used to study impacts of future climatic changes. Furthermore, potential changes at the local and regional scale have received less attention in comparison to changes at larger scales (IPCC 1996). At the global scale, simulations with the Global Terrestrial Ecosystem Model (TEM) have revealed that under temperate moist conditions, both elevated CO₂ and CC stimulate net primary production of grasslands (Mellilo *et al.* 1993). According to this global study the positive direct effects of elevated CO₂ are smaller than the effects of CC. Contrasting results were obtained at the local scale. For instance, by using a model consisting of submodels simulating water balance, grass growth, *ET*, and soil nitrate, a site-specific decrease in the productivity of farmed grassland in the U.K. has been obtained, which was caused by reductions in soil water content (Eatherall 1997). Further developments of this local approach to quantitatively estimate the overall effect of CC and 2 × CO₂ under realistic site conditions seems most promising.

A well-tested, mechanistic grassland ecosystem model is necessary to elucidate the nature of interactive effects of different factors, given that it is capable of simulating realistically at local scale the annual course of the fluxes of carbon (C), nitrogen (N), energy, and water, in relationship to above- and below-ground plant biomass production. For this purpose, a model was developed for managed (i.e. fertilized and cut) grasslands and compared with data for above- and below-ground plant biomass production, *ET*, soil moisture and substrate N and C concentrations collected during two years at several grassland sites differing in altitudes and soil characteristics (Riedo *et al.* 1998). It was concluded that under present climatic conditions the model can realistically reproduce the dry matter production and energy balance in the course of a growing season. Thus it seemed feasible to use this model to analyse individual and combined effects of altered climatic conditions and 2 × CO₂.

In view of the complexity of the issue, we adopted a case study approach, and several measures were taken

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to enhance the generality of the results. First, in order to account for the spatial variability of ecosystem responses we considered two distinct sites, both representative of climatic conditions in the northern foothills of the Alps. A low elevation site characterized by a relatively warm and dry climate was compared with a cooler and more humid site at a higher elevation. Secondly, the analysis of CC responses was based upon self-consistent and robust climatic scenarios, as derived from the application of statistical down-scaling techniques (Gyalistras *et al.* 1994, 1997) to the output of a global climate model. Finally, we considered a range of climatic conditions by taking into account the year-to-year variability of climate, such that the results are indicative of possible changes also in other regions.

The main aims of this paper are,

- 1 to quantify the shifts in biomass production and related changes in biomass partitioning and water use caused by individual and combined effects of CC scenarios and $2 \times \text{CO}_2$, and to assess the relative importance of the factors;
- 2 to compare the projected shifts between sites differing in altitude and soil characteristics.

Materials and methods

Study sites

Two locations at the northern foothills of the European Alps were selected: Payerne (6.9°E, 46.8°N) at 489 m above sea level on the Swiss Plateau and La Chaux-de-Fonds (6.8°E, 47.0°N) at 1018 m in the Jura mountains. These sites are representative in terms of climatic conditions found at the respective altitudes near the Alps (Gyalistras *et al.* 1997). Site-specific vegetation, soil parameters, and initial conditions were obtained from field measurements in 1993 and 1994 in plots of cut perennial swards. Table 1 contains the main characteristics of the two measuring sites; a more detailed description is given by Rosset *et al.* (1997).

Model description

The grassland ecosystem model simulates above- and below-ground dry matter production of a cut and fertilized perennial sward relative to fluxes of C, N, water, and energy. The model which was described in detail by Riedo *et al.* (1997, 1998), consists of four submodels: (i) The plant submodel, which was developed on the basis of the Hurley Pasture model (Thornley & Verberne 1989), is used to simulate shoot and root growth in relationship to C and N uptake, energy fluxes, and soil moisture conditions; (ii) the microclimate submodel calculates canopy radiation interception and the energy

balances of canopy and soil surface; (iii) the soil biology submodel calculates plant available soil C and N; (iv) soil profiles of water and temperature are calculated by a submodel for soil physics. The driving weather variables are hourly temperature (T), precipitation (P), vapour pressure (VP), radiation (G), and wind speed (U). The cutting days are determined by an algorithm which maximizes the seasonal dry matter production.

In the model, the atmospheric CO₂ concentration has direct effects on leaf photosynthesis and stomatal conductance. Leaf photosynthesis is calculated as a nonrectangular hyperbola for the light response curve, with two parameters depending on CO₂, i.e. the light-saturated rate of leaf photosynthesis and the photosynthetic quantum efficiency. Light-saturated leaf photosynthesis is modulated according to stage of canopy development, leaf temperature, and plant nitrogen (N), by a factor describing CO₂-temperature interactions, $P_{m,\text{CO}_2,T}$, and by an acclimation scalar, $V_{\text{cmax,acclim}}$. $P_{m,\text{CO}_2,T}$ is given by the light saturated rate according to the Farquhar & von Caemmerer (1982) leaf photosynthesis model, as parameterized by Long (1991), divided by the same term calculated for current CO₂ of 350 $\mu\text{mol mol}^{-1}$. Thus, at current CO₂ this factor is 1 for all temperatures (Fig. 1). $V_{\text{cmax,acclim}}$ is used to account for a reduction in the ribulose biphosphate saturated rate of the carboxylation reaction of Rubisco reflecting the effect of acclimation of leaf photosynthesis to elevated CO₂. Values of 1 or 0.7 were used for simulation without or with acclimation, respectively. Similar to the CO₂- T interaction factor of the light saturated photosynthesis rate, the photosynthetic quantum efficiency used in the nonrectangular hyperbola for the leaf photosynthesis light response curve also depends on a CO₂- T interaction factor, which was calculated from the Farquhar & von Caemmerer model, as parameterized according to Long (1991). Again, this factor is normalized to 1 for ambient CO₂ at all temperatures. Calculation of the CO₂-dependent stomatal conductance is based on the equation of Ball *et al.* (1987) (see Riedo *et al.* 1998).

The following model outputs were considered: (i) total seasonal above-ground dry matter production, W_{shoot} , total root dry matter at the end of the season, W_{root} , and shoot/root ratio, $S:R = W_{\text{shoot}}/W_{\text{root}}$, (ii) cumulative harvested leaf area index, LAI , and (iii) seasonal evapotranspiration as a measure for system water use, ET , and water use efficiency, $WUE = W_{\text{shoot}}/ET$.

Scenarios of climatic change

Scenarios of hourly weather under present and changed climatic conditions were obtained by a two-step procedure (Gyalistras *et al.* 1997): (i) Construction of site-specific climatic scenarios based on statistical down-

Table 1 Site characteristics¹

	Payerne	La-Chaux-de-Fonds
Soil type	Sandy loam	Loam
Sand:Silt:Clay (%)	63:23:14	45:34:21
Soil organic matter content (%)	4.8	9.7
Number of plant species	19	27
Dominant species	<i>Dactylis glomerata</i> L. <i>Lolium perenne</i> L. <i>Poa pratensis</i> L. <i>Phleum pratense</i> L. <i>Trifolium pratense</i> L. <i>Trifolium repens</i> L.	<i>Alopecurus pratensis</i> L. <i>Arrhenatherum elatius</i> L. <i>Dactylis glomerata</i> L. <i>Festuca pratensis</i> L. <i>Trifolium pratense</i> L. <i>Trifolium repens</i> L.
Number of cuts	5	4
Mineral N fertilization (kg ha ⁻¹)		
at start of growing season	25	25
after each harvest	20	20

¹For a more detailed description of the field measuring sites see Rosset *et al.* (1997)

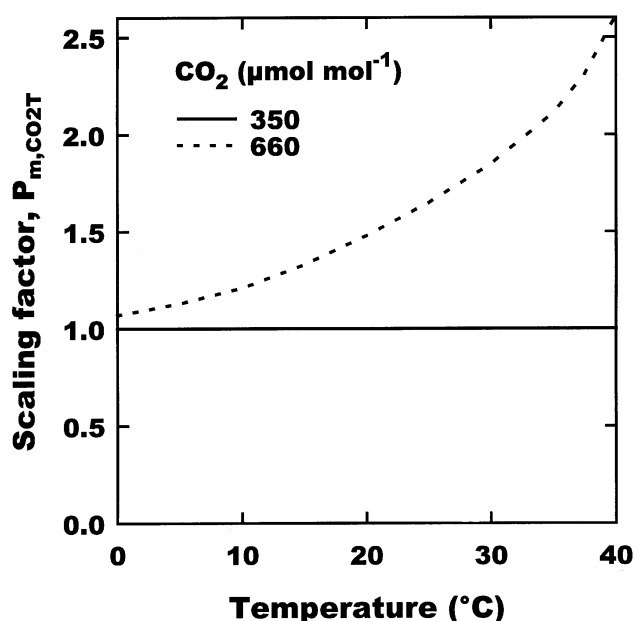


Fig. 1 CO₂-temperature interaction factor for the light-saturated rate of leaf photosynthesis. The relationship is shown for two CO₂ concentrations.

scaling of global climate model output; (ii) Stochastic simulation of hourly weather sequences. All necessary local measurements were obtained from the Swiss Meteorological Institute (Bantle 1989, 1993).

The first step uses month- and site-specific, multivariate regression models to predict interannual variations of monthly weather variables from large-scale (40°W–40°E and 30°N–70°N), gridded anomaly fields of monthly mean sea-level pressure and near-surface temperature (Gyalistras *et al.* 1994; Fischlin & Gyalistras 1997). 22 monthly weather variables related to *P*, *T*, *G*, *VP*, and

U were considered (see Table 2). The regression models were applied to five years of anomaly fields, as simulated by the Canadian Climate Centre CCC-GCMII climate model (McFarlane *et al.* 1992; Boer *et al.* 1992) under 2 × CO₂ conditions relative to the mean from a 5-yr control (1 × CO₂) simulation. Changes in expected values relative to the 1901–80 baseline were estimated by averaging the five downscaled anomalies for each month. This procedure yielded the reference CC scenario (RefCC).

Table 2 lists the expected values of the weather variables under current climatic conditions and their shifts under the RefCC scenario. The changes showed distinct seasonal cycles which are not reported here (for details see Gyalistras *et al.* 1997). Since downscaling is associated with large uncertainties for *P* and *U* (Gyalistras *et al.* 1994) two modifications of the RefCC scenario were considered: modification P– with changes of – 20% and – 10% for monthly precipitation totals and precipitation probabilities throughout the year, respectively – and modification U0 with no change in variables related to *U*.

The second step uses the stochastic weather generator *WeathGen* to simulate local weather (Gyalistras *et al.* 1997). *WeathGen* generates from 22 monthly inputs 11 daily weather variables, which in turn are used to simulate the five hourly driving variables for the ecosystem model. Both these transitions are based upon month- and site-specific first-order Markov chain-exponential models to simulate *P*, and first-order auto-regressive models to simulate all other variables conditional on the occurrence of *P* (cf. Richardson 1981). For each individual month or day, parameters of the stochastic processes are adjusted conditional on the monthly or daily inputs (cf. Wilks 1989; Katz & Parlange 1996). Furthermore, to ensure consistency among temporal aggregation levels, *WeathGen* repeatedly simulates daily and hourly weather

Table 2 Site-specific current climate and local climate change scenarios

Variable	Current climate ¹ (RefClim)		Climate Change ² (RefCC)	
	Payerne	La Chaux-de-Fonds	Payerne	La Chaux-de-Fonds
P_{prob}	0.45	0.52	-2.4	-4.5
P (mm)	81.2	123.4	5.7	3.2
T_{mean} (°C)	11.9	8.7	2.8	2.6
T_{min} (°C)	7.58	4.4	2.9	2.3
T_{max} (°C)	16.6	13.1	3.0	2.9
G_{mean} (W m ⁻²)	160.9	155.2	6.3	2.1
VP_{mean} (kPa)	1.10	0.91	17.9	19.7
VP_{min} (kPa)	0.95	0.76	17.7	19.0
VP_{max} (kPa)	1.25	1.05	16.0	20.8
U_{mean} (m s ⁻¹)	2.03	2.38	50.3	32.5
U_{min} (m s ⁻¹)	0.61	0.60	57.1	4.1
U_{max} (m s ⁻¹)	3.94	4.60	35.4	20.2

P_{prob} , precipitation probability; P , precipitation amount; T , temperature; G , global radiation; VP , vapour pressure; U , wind speed.

¹Current climate: Means (March–November) of monthly values for the period 1981–94.

²Climate Change: Changes (in percentage or °C) obtained by downscaling (Gyalistras *et al.* 1994, 1997) from the CCC-GCMII (Boer *et al.* 1992; McFarlane *et al.* 1992).

sequences until the statistics of a weather sequence for a given month (day) are sufficiently close to the prescribed monthly (daily) inputs. For the simulation of present-day weather *WeathGen* was driven with measured monthly time series from the interval 1981–94. For the simulation of future weather scenarios climatic change was defined as the changes in the annual cycles of the expected values of the 22 input variables. Accordingly, depending on the climatic scenario, each element of a measured monthly time series was shifted by the same, variable-, month- and site-specific amount. Inter-annual standard deviations and further higher-order moments of the monthly variables, as well as all parameters of the daily and hourly stochastic models, were left unchanged.

Simulations

Simulations with a time step of one hour were carried out for a 14 individual growing seasons (1981–94, March to November). For each simulation we used the same initial conditions. Initial conditions for the soil biology submodel were determined iteratively by bringing the model to near steady-state (Riedo *et al.* 1998).

At ambient CO₂ (RefCO₂, 350 µmol mol⁻¹), simulations were carried out for four different climates: (i) baseline simulations with the current climate (RefClim), (ii) The reference CC scenario (RefCC), (iii) RefCC with modification P-, and (iv) RefCC with modification U0. At elevated CO₂ (660 µmol mol⁻¹), simulations were performed for both RefClim and RefCC with acclimation (2 × CO_{2a}) or without acclimation (2 × CO₂). For each growing season, starting from the monthly inputs, three realizations of the daily weather, and for each day three realizations of

Table 3 Results from baseline simulation of seasonal biomass production of shoots (W_{shoot}) and roots (W_{root}), shoot/root ratio (S:R), leaf area index (LAI), evapotranspiration (ET), and seasonal water use efficiency (WUE)¹

Variable	Payerne	La Chaux-de-Fonds
W_{shoot} (kg m ⁻²)	1.26	1.18
W_{root} (kg m ⁻²)	0.56	0.75
S:R (kg kg ⁻¹)	2.33	1.59
LAI ² (m ² m ⁻²)	20.32	17.76
ET (mm)	574.4	547.5
WUE (g kg ⁻¹)	2.20	2.16

¹Calculated with current climate (RefClim) and current CO₂ concentration (RefCO₂) of $C_a = 350 \mu\text{mol mol}^{-1}$ ($n = 126$).

²Seasonal total of the values simulated for each cutting day.

hourly weather were used. For each variable and scenario considered, means were calculated from 14 simulated growing seasons and compared with the corresponding means from the baseline simulation, i.e. the simulation conducted with RefClim and RefCO₂. The significance of the difference was tested with a *t*-test ($n = 14$).

Results

Baseline simulations

The results of the baseline simulations for RefClim and RefCO₂ reflected the differences in climatic conditions between the two sites (Table 3). At the low-elevation site Payerne with a high mean T (Table 2), both W_{shoot} and ET were higher than at the more elevated site La Chaux-

de-Fonds. Because of similar differences between sites in W_{shoot} and ET , WUE based on W_{shoot} was not affected by the difference between sites. On the other hand, WUE calculated for total plant biomass ($W_{\text{shoot}} + W_{\text{root}}$) increased from 3.17 at the low to 3.52 at the high site, because of a higher proportion of biomass allocated to roots, as indicated by the higher value for $S:R$.

Effects of climate change

Under RefCC, W_{shoot} was slightly reduced at the lower but increased at the higher site, whereas W_{root} was reduced in both cases (Fig. 2a). This led to an increase in $S:R$. Independently of site, RefCC led to a strong increase in ET by about 20%. Because of the relatively smaller change in W_{shoot} , WUE declined.

At Payerne, P- led to more pronounced changes in dry matter production (W_{shoot} and W_{root}) (Fig. 2b) when compared with RefCC (Fig. 2a), indicating stronger sensitivity to shifts in P at this site. The reduction in the proportion of biomass allocated to roots was clearly more pronounced with P- than with RefCC at both sites. These changes were accompanied by a reduction of the effect on ET , especially at Payerne, but the change in WUE was similar for RefCC and P-.

The most pronounced differences between RefCC and U0 occurred in ET and WUE with a smaller increase in ET and a smaller decrease in WUE with U0 (Fig. 2c). For all other variables differences between RefCC and U0 were small.

Effects of elevated CO_2

The effect of elevated CO_2 alone ($2 \times CO_2$) on W_{shoot} and ET depended on the site and on the assumption about CO_2 acclimation (Fig. 2d,e). Relative to current CO_2 (Ref CO_2) W_{shoot} increased by 12% and 17% without acclimation, with the larger change occurring at Payerne. In comparison, W_{root} increased even more in response to $2 \times CO_2$. This caused a decrease in $S:R$ at both sites. Compared to W_{shoot} , changes in LAI were smaller. Elevated CO_2 reduced ET by 6 and 11% at the two sites. In contrast to W_{shoot} , sensitivity of ET to elevated CO_2 was larger at the site La Chaux-de-Fonds. The opposing trends in W_{shoot} and in ET led to nearly equal changes in WUE at both sites.

With the assumption of maximum photosynthetic acclimation, i.e. $V_{\text{cmax,acclim}} = 0.7$, the changes in the various variables in response to elevated CO_2 ($2 \times CO_2a$) did not differ qualitatively from the changes obtained without acclimation, but were generally smaller (Fig. 2e). The differences between the effect of $2 \times CO_2$ and $2 \times CO_2a$ were smallest for ET for which practically no effect of acclimation was observed. For shoot and root

biomass, and LAI , changes in response to $2 \times CO_2a$ relative to Ref CO_2 were generally not significant.

Combined effects of climate change and elevated CO_2

Figure 2(f) shows the results from simulations with the combination of elevated CO_2 ($2 \times CO_2$) and CC (RefCC). Shoot biomass was increased by 16% and 20% at Payerne and La Chaux-de-Fonds, respectively. At Payerne, the effect was almost the same as with $2 \times CO_2$ alone, whereas at La Chaux-de-Fonds, the combined effect was larger. The two factors had a nearly additive effect on W_{shoot} and LAI . Accordingly, the effect of $2 \times CO_2$ with U0 was larger than with RefCC, and with P0 it was similar at the cooler site, but strongly reduced at the warmer site (data not shown). On the other hand, changes in W_{root} were smaller as compared to $2 \times CO_2$ alone. With the combination of $2 \times CO_2$ and RefCC, the positive effect of RefCC and the negative effect of $2 \times CO_2$ were almost balanced and no change in $S:R$ was found. Thus, the increase in LAI was proportional to the increase in W_{shoot} . ET was significantly increased at both sites.

Photosynthetic acclimation reduced the change in W_{shoot} in response to RefCC, and even more effectively in W_{root} , as compared to RefCC plus $2 \times CO_2$, while the changes in LAI , ET and WUE were not significantly affected by acclimation (Fig. 2g).

Discussion

With the approach used in this study, it was found for temperate conditions that (a) the relative importance of effects of CC and $2 \times CO_2$ on biomass production and water use differs, and (b) that both magnitude and direction of ecosystem responses vary between sites. It becomes evident that for the accurate analysis of local effects, the use of detailed weather scenarios to drive the ecosystem model is highly important.

Climate change scenarios

By using appropriate statistical procedures for the construction of CC scenarios, an attempt was made to reduce the number of weather inputs necessary to assess ecosystem responses. When testing the weather generation approach by driving the ecosystem model for the period 1981–94 with measured and stochastically simulated hourly weather inputs, good agreements were found for W_{shoot} and ET , with mean relative deviations of $< \pm 3\%$, and $r \geq 0.83$ for the year-to-year variability (Gyalistras *et al.* 1997). A maximum of 22 monthly inputs thus seems sufficient to estimate first-order effects of CC. A second aim was to choose sensible working points for the relevant climatic/meteorological factors. This require-

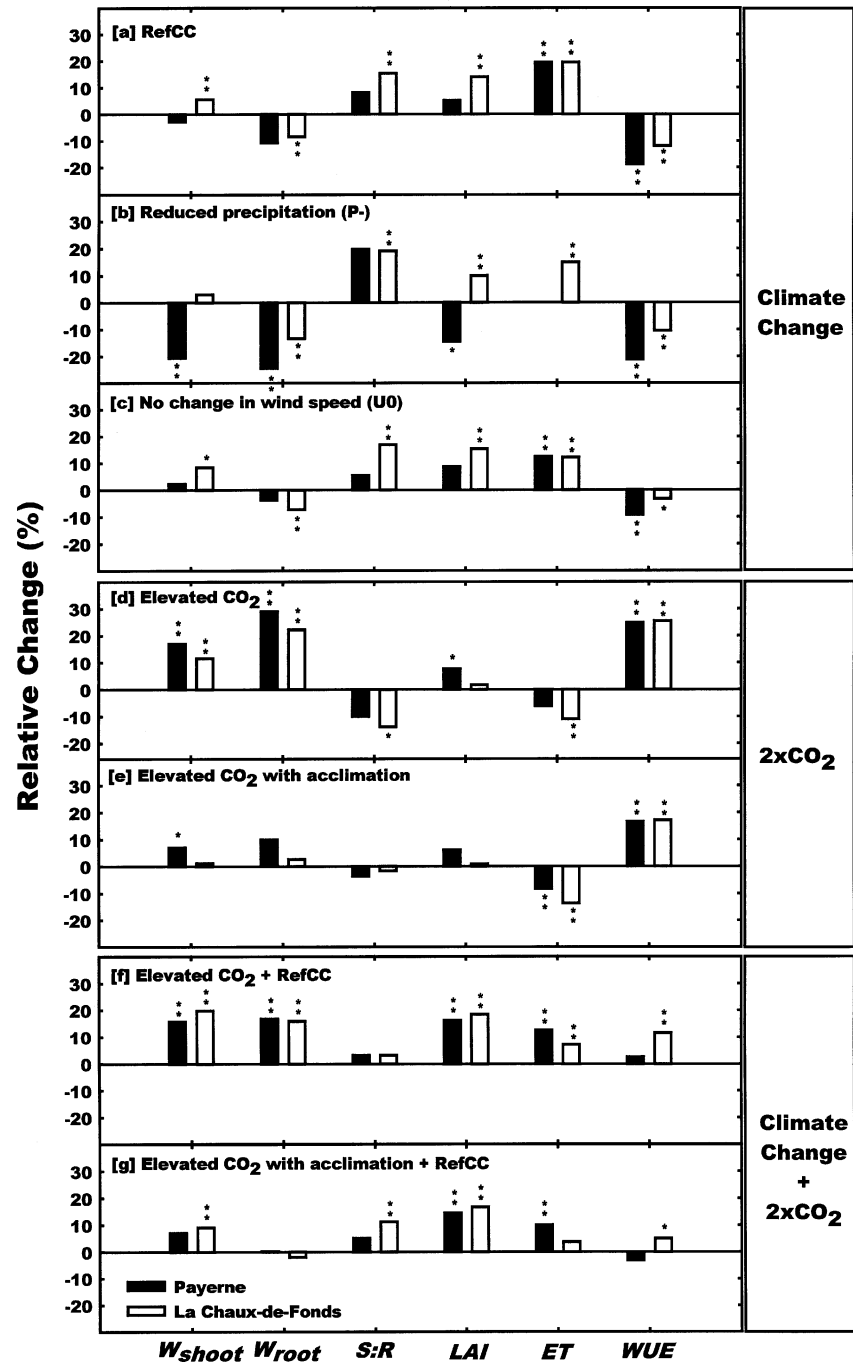


Fig. 2 Effects of different scenarios for climate change (a–c), elevated CO₂ without (d) or with photosynthetic acclimation (e), and combinations of climate change (RefCC) and elevated CO₂ (f–g) on shoot biomass production (W_{shoot}), root biomass at the end of the season (W_{root}), shoot/root ratio ($S:R$), leaf area index (LAI), evapotranspiration (ET), and seasonal water use efficiency (WUE) of managed grasslands at two sites. Level of significance * $P < 0.05$, ** $P < 0.01$.

ment seems satisfied because the downscaled scenarios depend plausibly on large-scale CC simulated by the CCC-GCMII, they are consistent both spatially and among weather variables, and they appear realistic in view of the current understanding of the physical processes involved (e.g. Gyalistras *et al.* 1994, 1997; Fischlin & Gyalistras 1997; Gyalistras *et al.* 1998). In terms of the projected change in T_{mean} (+ 2.5 °C) the RefCC scenario was close to the middle of the range (1.2–4.4 °C) estimated from a comparison of different scenarios for the Alpine

region (Gyalistras *et al.* 1998). Main uncertainties relate to the choice of the global forcing scenario and climate model (e.g. Gyalistras & Fischlin 1995), and to the downscaling procedure (e.g. Winkler *et al.* 1997). Additional sources of error are inhomogeneous weather data used to fit the statistical models, which may have contributed to the projected increase in U (Gyalistras *et al.* 1997). Hence, the scenario U0 might present the most realistic variant (see also Schiesser *et al.* 1997). In spite of these uncertainties, we believe that the scenarios presented

here have enabled more realistic simulations than could have been obtained with arbitrarily specified changes in climate. For instance, the use of scenarios which neglect changes in *VP* would have yielded significantly different ecosystem responses (Riedo 1997).

Effects of climate change

Shoot biomass (W_{shoot}) was increased under RefCC at the higher but decreased at the lower site (Fig. 2a). The warmer conditions at Payerne are closer to the optimum for grass growth, and the increase in *T* pushes the system beyond the optimum range at the lower, but not at the higher site. A decline in annual biomass production in *L. perenne* due to increased *T* has also been measured experimentally at a corresponding low elevation site on the Swiss Plateau (Nijs *et al.* 1996), whereas an increase was found at a cooler site in Wales (UK) (Jones & Jongen 1996). In addition to the difference in current *T*, less precipitation and a lower groundwater table at Payerne contributed to the difference in the response of W_{shoot} between the sites. These conditions led to more rapid soil drying which reduced both plant growth and *ET*. Consequently, the change in *ET* was similar at the two sites, in spite of a larger increase in *U* and warmer conditions at Payerne, which would stimulate *ET* more strongly under well-watered conditions. The results from the scenario P- further underline the sensitivity of W_{shoot} at Payerne to reductions in soil moisture (Fig. 2b). However, the difference was unrelated to differences in soil physical characteristics, as shown by results obtained with simulations in which the soil parameters were exchanged between sites (data not shown). The different relative responses between sites highlight the importance of the current climatic and soil conditions in determining the magnitude and direction of ecosystem responses to CC scenarios.

Plant growth is not only influenced directly by climatic changes, but also via changed plant available soil N from increased mineralization at higher *T* (Mellilo *et al.* 1993; Parton *et al.* 1995). Our simulations show that the increase in plant available soil N leads to an increase in *S:R*. The model uses a partitioning function that regulates shoot/root partitioning in such a way that the ratio between plant internal C and N substrate concentrations is kept in balance with plant demand to obtain a maximum relative growth rate (Johnson & Thornley 1987). Thus, increased N uptake caused by increased soil N leads to a higher *S:R* to balance shoot C assimilation and root N uptake. The results for RefCC and P- showed that increased *T* led to a higher *S:R* even at reduced soil moisture, which is in conflict with experimental data (Hamblin *et al.* 1991). Such data must be further studied and eventually incorporated into the model. The model

considers soil moisture effects on C assimilation and stomatal conductance, but not on root N uptake and partitioning. Consideration of a reduction of root N uptake at decreased soil water content due to decreased root water uptake in the model would lead indirectly to a decrease in *S:R*, and an explicit dependency of partitioning on soil water content would lead to a direct effect of drought on *S:R*.

Effects of elevated CO₂

Elevated CO₂ was found to strongly increase W_{shoot} in the absence of acclimation (Fig. 2d), which agrees with results from a Free Air CO₂ Enrichment (FACE) experiment with a balanced mixture of *L. perenne* and *T. repens* under comparable climatic conditions on the Swiss Plateau (Hebeisen *et al.* 1997). At the higher and cooler site, the simulated effect of CO₂ was less pronounced than at the lower warmer site, mainly because the sensitivity of photosynthesis to CO₂ declines with decreasing *T* (Fig. 1). This can be attributed to the increase in the competitive inhibition of RubP carboxylation by oxygenation (Long 1991; Kirschbaum 1994). This reduction of the effect of CO₂ under cool climatic conditions may at least partly explain the modest response to elevated CO₂ of high-altitude alpine grassland (Schäppi & Körner 1996), and of grasses in a cool maritime climate (Saebø & Mortensen 1995).

With acclimation, the CO₂ stimulation of W_{shoot} was about 10% less ($2 \times \text{CO}_2\text{a}$, Fig. 2e). Measurements in the Swiss FACE experiment confirm photosynthetic reductions in *L. perenne* near the end of a growth period by about 30% (S. Long, pers. comm.) to 40% (Nijs *et al.* 1996). The agreement between the magnitude of the simulated change in W_{shoot} under $2 \times \text{CO}_2\text{a}$ and the observed change in the yield of a *L. perenne* monoculture (Hebeisen *et al.* 1997) suggests that *L. perenne* cannot compensate for the increased C assimilation, and thus the simulations are representative for the response of grasses. In a mixture with a large clover fraction, increased N demand to compensate for higher C assimilation under elevated CO₂ could be delivered through increased N₂ fixation (Zanetti *et al.* 1996), leading to a reduction in the overall degree of acclimation. However, the amount of this acclimation in the FACE plant mixture cannot be assessed from the simulation results, as the model was developed for mixtures with a low clover fraction, and thus neglects effects of CO₂ on biological N₂ fixation.

In contrast to the effect of RefCC, soil water conditions were improved under $2 \times \text{CO}_2$ due to decreased *ET*. The increase in *LAI* with $2 \times \text{CO}_2$ was not enough to completely compensate for decreased stomatal conductance. The effect of $2 \times \text{CO}_2$ on *ET* and soil moisture is

in agreement with field data (Ham *et al.* 1995; Field *et al.* 1997; Schapendonk *et al.* 1997).

Effects of the combination of climate change and elevated CO₂

Simulations with the combination of RefCC and $2 \times \text{CO}_2$ (Fig. 2f) showed for both sites that the effects of both factors on W_{shoot} are additive. Accordingly, the effect of $2 \times \text{CO}_2$ was much smaller when combined with P-, and more positive when combined with U0 (not shown). While this additive behaviour seems plausible under well-watered conditions, it remains to be examined whether after incorporation of direct soil water effects on partitioning and root N uptake in the model under less favourable water conditions, $2 \times \text{CO}_2$ would reduce the negative effect of P- on W_{shoot} in a more-than-additive way. In this case, improved water conditions under $2 \times \text{CO}_2$ could lead to larger relative CO₂ effects in dry than in wet years. This would lead to substantial interannual variations in CO₂ effects on biomass, as observed in multiyear field experiments (Owensby *et al.* 1997). Similarly to W_{shoot} , effects of CO₂ and RefCC on *ET* were almost additive, even for P- and U0 (not shown). The reduction in *ET* under $2 \times \text{CO}_2$ was antagonized by the effect of RefCC, and *ET* was increased at both sites. In other words, in a warmer and much windier climate with increased *ET* the positive effect of CO₂ on water use is reduced.

The difference between sites in the response of W_{shoot} to the combination of RefCC and $2 \times \text{CO}_2$ was smaller than the difference obtained with single factors. This is because the larger CO₂ response at the lower site was offset by the negative impact of RefCC. The large response of W_{shoot} at both sites seems to be robust under a broad range of cool temperate conditions. For individual years, the increase in W_{shoot} ranged between 5 and 27% for *P* ranging from 56 to 163 mm, and for T_{mean} from 8 to 13 °C (not shown). While under RefCC increased plant available soil N favoured shoot growth over root growth, increased leaf C assimilation under $2 \times \text{CO}_2$ had the opposite effect (Fig. 2d), in agreement with experimental data (Jongen *et al.* 1995; Nijs & Impens 1997; Owensby *et al.* 1997). Under RefCC plus $2 \times \text{CO}_2$ the effects of the two factors offset each other resulting in no significant change in *S:R*, and there was no difference between sites (Fig. 2f) because the stronger increase with RefCC at La Chau-de-Fonds was counteracted by the stronger decrease with $2 \times \text{CO}_2$ at this site as compared to Payerne. This suggests that the magnitude of changes in *S:R*, as observed in CO₂ enrichment experiments, may be overestimated when the interaction with increased *T* and other climatic factors is not considered. The CO₂-climate interaction could explain the variability in the CO₂

response of *S:R* across different experimental conditions (Rogers *et al.* 1996), and it should also be considered when examining at the ecosystem level the long-term input of C to soils under elevated CO₂ (Hunt *et al.* 1991; Parton *et al.* 1995; Schapendonk *et al.* 1997).

Conclusions

This work demonstrates the potential of using mechanistic grassland models consisting of linked submodels for plant growth, microclimate, soil physics and soil biology to analyse effects of CC, $2 \times \text{CO}_2$, and photosynthetic acclimation on temperate grassland ecosystems. This appears to be particularly important for the assessment of net changes caused by combinations of factors which potentially off-set each other. Moreover, by combining the ecosystem model with statistically downscaled CC scenarios spatially differentiated response patterns across a given region can be analysed.

The simulation results for the selected sites appear to be plausible and generally agree with experimental findings. Several uncertainties remain, however, with respect to the assumed changes in local climate, as well as the projected changes in biomass partitioning in response to reduced soil moisture, and the importance of CO₂ effects on biological N₂ fixation. Furthermore, the model was not used for long-term simulations; consequently, the results represent sensitivity estimates around a working point, as given by present ecosystem conditions, rather than transient responses.

The simulations show that the positive direct effect of $2 \times \text{CO}_2$ on shoot biomass exceeds that of RefCC alone. Effects of both factors appear to be additive and larger at the cooler site with the more favourable soil water conditions. The increase in *LAI* with $2 \times \text{CO}_2$ was not enough to completely compensate for decreased stomatal conductance, and *ET* decreased with $2 \times \text{CO}_2$, but increased when RefCC is added. This change in the sign of the response was independent of site, thus illustrating the importance of climate in determining ecosystem responses. *S:R* increases with RefCC and decreases with $2 \times \text{CO}_2$, and an intermediate response results from the combination of both. The balance between the effects of the two factors depends on photosynthetic acclimation and site. Acclimation reduced the biomass response to $2 \times \text{CO}_2$ with or without RefCC, but had only a small effect on *ET*. Overall, the simulations suggest a significant increase in dry matter production and *ET*, but only small changes in dry matter partitioning and *WUE* in response to the combination of RefCC and $2 \times \text{CO}_2$. While CC determines the sign of the *ET* response, $2 \times \text{CO}_2$ determines the sign of the biomass response.

These results highlight the importance of a site-specific analysis of ecosystem responses, and underline the need

for interdisciplinary research which aims at combining downscaling with spatial data sets and mechanistic models. Such interdisciplinary efforts enable quantitative, consistent, and reproducible assessments of climate change impacts at the ecosystem level.

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