

# LINGRA-CC: a sink–source model to simulate the impact of climate change and management on grassland productivity

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## SUMMARY

A simulation model for the prediction of grassland (*Lolium perenne*) productivity under conditions of climate change is described and validated for grass growing in the Wageningen Rhizolab, Wageningen, The Netherlands. In this work the model was used to study the impact of different management strategies on the productivity of grassland under present and increased atmospheric CO<sub>2</sub> concentrations. In LINGRA-CC simulated key processes are light utilization, leaf formation, leaf elongation, tillering and carbon partitioning. The daily growth rate is determined by the minimum of a sink and a source term. As in a previous model (LINGRA), the potential growth of the sink depends on the mean daily temperature, and can be modified by the effects of the availability of assimilates on tillering. The growth of roots is calculated from the amount of carbohydrates the shoot is unable to utilize when the number or activity of the sinks is small (overflow hypothesis). The main difference between LINGRA and LINGRA-CC is the way the source of assimilates for growth is calculated. Assimilate production depends on intercepted radiation, and a photosynthetic light-use efficiency (LUE) calculated as a function of CO<sub>2</sub>, temperature, light intensity and the Rubisco concentration of upper leaves. Other differences are that in LINGRA-CC, the specific shoot area for new growth depends on the level of reserves. Data from two independent experiments with *L. perenne* swards, grown in enclosures at two levels of CO<sub>2</sub> during 1994 and 1995, were used to calibrate and validate the model, respectively. The model predicted well the observed amounts of harvested biomass, and the dynamics of the leaf area index, tiller number and specific shoot area. LINGRA-CC was used to study the effects of different combinations of cutting interval and cutting height on biomass production, at ambient (350 µmol mol<sup>-1</sup> CO<sub>2</sub>) and double (700 µmol mol<sup>-1</sup> CO<sub>2</sub>) CO<sub>2</sub> conditions. Under both ambient and doubled CO<sub>2</sub>, maximum biomass was produced with cuttings of leaf area index > 1, and at cutting intervals of 20 and 17 d for ambient and increased CO<sub>2</sub> environments, respectively. Under high CO<sub>2</sub> conditions the cutting interval for maximum yield was 15% shorter than at ambient CO<sub>2</sub>. However, the gain in harvested biomass obtained by reducing the cutting interval by 3 d under high CO<sub>2</sub> conditions was negligible.

Key words: carbon dioxide, climate change, grassland productivity, *Lolium perenne*, modelling, sink–source relationships.

## INTRODUCTION

Atmospheric carbon dioxide has increased by *c.* 80 µmol mol<sup>-1</sup> since the beginning of the Industrial Revolution at the end of the eighteenth century. The current globally averaged annual value is *c.* 355 µmol mol<sup>-1</sup>, and despite some uncertainty, a doubling of

the pre-industrial value of less than 280 µmol mol<sup>-1</sup> CO<sub>2</sub> is expected at some time in the twenty-first century (Schneider, 1989). This increase in atmospheric CO<sub>2</sub> is expected to lead to substantial enhancement of growth and yield in many agricultural crops (Lawlor & Mitchell, 1991). In temperate Western Europe, ryegrasses are the main component of lowland pasture production and future climate change is expected to affect their productivity (Ferris *et al.*, 1996). Most studies where ryegrass was grown with CO<sub>2</sub> as an experimental factor focussed on the yield response of plants and canopies without

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considering the dynamics of sinks and sources in swards that are frequently cut (Saebo & Mortensen, 1995). Frequently mown grasses are maintained in a vegetative state, consisting mainly of tiller, and leaf blades that form a canopy, generally not photosynthetically light-saturated even in full sunlight (Hull, 1996). In frequently mown grasslands defoliation and thus loss of assimilatory surfaces can lead to depletion of carbohydrate reserves which may even become limiting for regrowth (Davies, 1988). Therefore the greatest responses to  $\text{CO}_2$  should be expected from frequently mown swards in which assimilates are limiting growth. Sink–source relationships of frequently mown grasses are relatively simple, but in order to understand the interactions between environmental factors and physiological processes, simulation models are generally needed.

In this work we are particularly interested in interactions between  $\text{CO}_2$  enrichment, climate and disturbance of well irrigated and well managed ryegrass swards. Consequently we intend to calibrate and validate a simulation model for the prediction of the productivity of *L. perenne* grassland under high atmospheric  $\text{CO}_2$  conditions in order to study the impact of different management strategies on grassland productivity and to test whether growth is particularly increased by  $\text{CO}_2$  when the frequency and intensity of cutting is highest.

#### MATERIALS AND METHODS

A 2-yr experiment with *Lolium perenne* L. (cv. Preference) in Wageningen, The Netherlands (lat  $51^\circ 58' \text{ N}$ , long  $5^\circ 40' \text{ E}$ ) was started in October 1993 in the Wageningen Rhizolab (Schapendonk *et al.*, 1996). Grass swards were grown from seed, under translucent polycarbonate enclosures at continuous 350 and 700  $\mu\text{mol mol}^{-1} \text{ CO}_2$ . The transmission of solar radiation by the enclosures was 0.79. Temperatures in the enclosures were controlled to correspond with the those outside the enclosures. Rates of  $\text{CO}_2$  uptake or release were calculated by multiplying the airflow rate with the difference in  $\text{CO}_2$  concentration between incoming and outgoing air of the above-ground compartments (Van de Geijn *et al.*, 1994). The rate of supply of fresh air to each above-ground compartment was 50  $\text{m}^3 \text{ h}^{-1}$  and the internal circulation rate was 800  $\text{m}^3 \text{ h}^{-1}$ . Consequently,  $\text{CO}_2$  produced in the soil compartment could not enter the above-ground enclosures because of an overpressure.  $\text{CO}_2$  treatments were replicated twice and were surrounded by grass swards to minimize border effects. Soil compartments were 1.25 m  $\times$  1.25 m  $\times$  2 m deep, and were filled with a repacked loamy-clay soil, with 4.7% organic matter and a pH of 7. Each soil compartment was kept near field capacity by drip irrigation, and 8  $\text{g m}^{-2}$  nitrogen (N) was supplied after each harvest for a total of 60

$\text{g N m}^{-2} \text{ yr}^{-1}$ . Swards were cut 10 times per year at 3 wk intervals. The grass was cut back to 5 cm; after a cutting the remaining leaf area index (LAI) was 0.8. At each harvest the number of tillers was counted, the green area of leaves and tillers measured, and the harvested above-ground dry weight determined. Leaf area was determined using a LI-3100 area meter (LI-COR, Lincoln, NE, USA). At each sampling the specific shoot area was calculated by dividing sampled leaf area by sampled above-ground biomass. For further experimental details see Schapendonk *et al.* (1996, 1997).

#### Model description

The original version of LINGRA (Schapendonk *et al.*, 1998) was a sink–source growth model for the prediction of the productivity of *L. perenne* grasslands. Simulated key processes are light utilization, leaf formation, leaf elongation, tillering, and carbon (C) partitioning to storage, shoots and roots. In LINGRA and LINGRA-CC, the sward is assumed to remain in a vegetative stage. The main difference between LINGRA and LINGRA-CC is the way in which assimilate production is calculated. Other differences are that in LINGRA-CC the specific shoot area of the new growth depends on the balance between the sink and source terms (Thornley, 1998), and is allowed to vary between a maximum of 0.03  $\text{m}^2 \text{ g}^{-1}$  and a minimum value of 0.015  $\text{m}^2 \text{ g}^{-1}$ . Leaf area increase is derived from leaf elongation, leaf formation rate, and tillering rate. In LINGRA-CC source- and sink-related processes depend on environmental conditions in different ways and are semi-independent. We use the term semi-independent since the source term depends on radiation,  $\text{CO}_2$  and temperature, and the sink term depends on temperature. In LINGRA-CC there is a strong feedback of the source term on leaf area expansion through the effect of the level of reserves on tillering and on specific shoot area of the new growth. Tiller dynamics are determined by the rate of tiller emergence, as a function of leaf emergence and the level of reserves, and on the rate of tiller death, as a function of self-shading and temperature. The amount of C that is necessary to meet the demands of the sink should be counterbalanced by a C source, i.e. photosynthetic rates plus available reserves. Daily growth is partitioned among shoots, reserves and roots following the excess of carbohydrates hypothesis (Troughton, 1977). In LINGRA-CC root growth depends upon the quantity of carbohydrate the shoot is unable to utilize, e.g. under conditions of high photosynthetic rate or sink limitation a relatively large root system would be produced, tending to balance the metabolic activities of the root and shoot systems.

In LINGRA-CC the available source for growth ( $S$ ,  $\text{g m}^{-2} \text{ d}^{-1}$ ) results from the product of incoming

photosynthetic radiation ( $I_0$ , MJ m<sup>-2</sup> d<sup>-1</sup>), a light interception function, and light-use efficiency ( $LUE$ ) (Eqn 1) (Monteith, 1977). Existing stored reserves ( $Rvs$ , g biomass m<sup>-2</sup>) are also available to cope with the demand of the sink for assimilates. In the model the time coefficient ( $Tcoeff$ , d) for the reserves is assumed to be 2 d.

$$S = LUE \cdot I_0 \cdot (1 - e^{-k LAI}) + \frac{Rvs}{Tcoeff} \quad \text{Eqn 1}$$

In Eqn 1,  $k$  is the light extinction coefficient and  $LAI$  the leaf area index. In LINGRA-CC, a new algorithm was introduced to calculate light-use efficiency as a function of light, temperature, CO<sub>2</sub> and leaf Rubisco concentration (Eqn 2):

$$LUE = \frac{\varepsilon \cdot Pmax}{\varepsilon \cdot k \cdot \frac{I_0}{\delta} + Pmax} \cdot Y \quad \text{Eqn 2}$$

Light-use efficiency ( $LUE$ , g biomass MJ<sup>-1</sup>) is calculated from the combination of the biochemical approach of Farquhar *et al.* (1980), and the equations of Charles-Edwards (1982), (Van Oijen & Goudriaan, 1997). In Eqn 2,  $\varepsilon$  is the leaf quantum yield (g CO<sub>2</sub> MJ<sup>-1</sup>),  $\delta$  is the fraction of the daylight period (d d<sup>-1</sup>),  $Pmax$  is the photosynthesis rate of upper leaves at light saturation (g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>), and  $Y$  is the efficiency with which gross assimilation is converted into biomass (g biomass g<sup>-1</sup> CO<sub>2</sub>). The value of  $Y$  is generally independent of CO<sub>2</sub> concentration or temperature, and has a value of 0.4–0.43 (Gifford, 1995) or slightly lower (Sinclair & Horie, 1989). According to Gifford (1995), the constancy of  $Y$  avoids the need for separation of respiration into terms for growth and maintenance.

In Eqn 2,  $\varepsilon$  is derived as:

$$\varepsilon = \frac{44 \cdot \lambda}{2.1} \cdot \frac{(CO_{2i} - \Gamma)}{4.5 \cdot CO_{2i} + 10.5 \cdot \Gamma} \quad \text{Eqn 3}$$

( $\lambda$  is the conversion factor for light energy to photon density (= 4.56 mol photons MJ<sup>-1</sup> sunlight, McCree, 1972),  $CO_{2i}$  is the internal CO<sub>2</sub> mole fraction (μmol mol<sup>-1</sup>) calculated as  $0.7 \times \text{ambient CO}_2$ ,  $\Gamma$  is the compensation point for CO<sub>2</sub> (μmol mol<sup>-1</sup>), 2.1 (mol photon mol<sup>-1</sup> CO<sub>2</sub>), and 4.5 and 10.5 are constants related to the stoichiometry for electron transport and CO<sub>2</sub> fixation (Farquhar *et al.*, 1982)).

In Eqn 2  $Pmax$  is calculated from the biochemistry of leaf photosynthesis of C3-plants (Farquhar *et al.*, 1980).

$$Pmax = \lim_{I \rightarrow \infty} P = \frac{Vc,max \cdot (CO_{2i} - \Gamma)}{CO_{2i} + Kmc \cdot \left( \frac{O_2}{Kmo} + 1 \right)} \quad \text{Eqn 4}$$

( $Vc,max$  is the maximum velocity of carboxylation in upper leaves (g CO<sub>2</sub> m<sup>-2</sup> d<sup>-1</sup>),  $Kmc$  is the Michaelis-

Menten constant for CO<sub>2</sub> (ml CO<sub>2</sub> m<sup>-3</sup>),  $O_2$  is the oxygen concentration (%), and  $Kmo$  is the Michaelis-Menten constant for O<sub>2</sub>.) The parameters  $Vc,max$ ,  $Kmc$ ,  $Kmo$  and  $\Gamma$  in Eqns 3 and 4 are calculated using formulae from Farquhar *et al.* (1980, 1982), with slight modification in the calculation of  $Vc,max$  to include explicitly its dependence on the concentration of Rubisco.

$$Vc,max = [Rubisco] \cdot Kc_{25} \cdot \exp \left[ \left( \frac{1}{298} - \frac{1}{T} \right) \cdot \frac{Evcmax}{8.314} \right] \quad \text{Eqn 5a}$$

$$Kmc = Kmc_{25} \cdot \exp \left[ \left( \frac{1}{298} - \frac{1}{T} \right) \cdot \frac{Ekmc}{8.314} \right] \quad \text{Eqn 5b}$$

$$Kmo = Kmo_{25} \cdot \exp \left[ \left( \frac{1}{298} - \frac{1}{T} \right) \cdot \frac{Ekmo}{8.314} \right] \quad \text{Eqn 5c}$$

$$\Gamma = 0.5 \cdot KoKc \cdot O_2 \cdot \frac{Kmc}{Kmo} \quad \text{Eqn 5d}$$

( $[Rubisco]$  is the concentration of Rubisco in the upper leaves (g m<sup>-2</sup> leaf);  $Kc_{25}$  is the CO<sub>2</sub>-turnover rate of Rubisco at 25°C (g CO<sub>2</sub> g<sup>-1</sup> Rubisco d<sup>-1</sup>),  $T$  is the average daily temperature (K), and  $Evcmax$ ,  $Ekmc$  and  $Ekmo$  are the activation energies for  $Vc,max$ ,  $Kmc$  and  $Kmo$ , respectively (J mol<sup>-1</sup>),  $Kmc_{25}$  and  $Kmo_{25}$  are  $Kmc$  and  $Kmo$  at 25°C, respectively (mol CO<sub>2</sub> m<sup>-3</sup>),  $KoKc$  is the ratio of turnover for oxygenase and carboxylase (–), and 8.314 is the universal gas constant (J K<sup>-1</sup> mol<sup>-1</sup>). The values of the parameters for these equations are those reported in the original paper, except as updated by Long (1991).

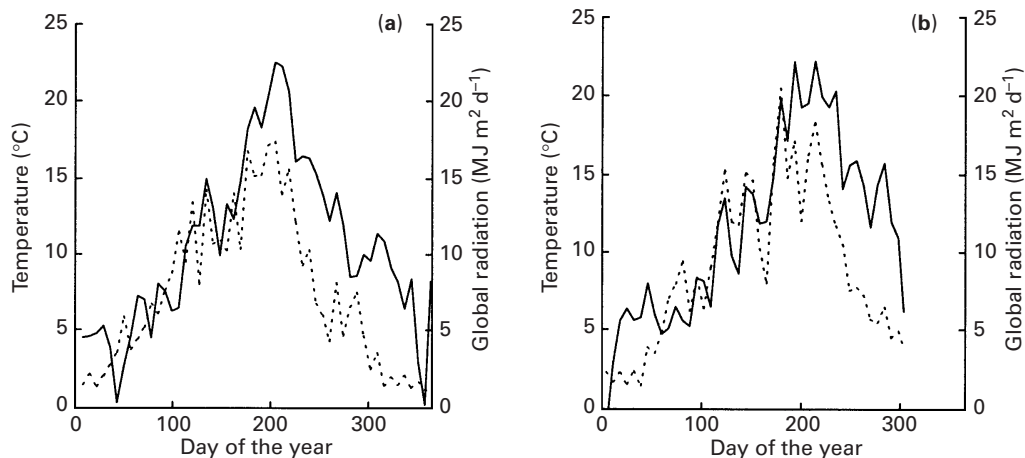
Required model inputs are daily minimum and maximum temperatures and radiation. For further details of the LINGRA model refer to Schapendonk *et al.* (1998). The model was written in FST (Rappoldt & van Kraalingen, 1996) and is available upon request to the authors.

## RESULTS

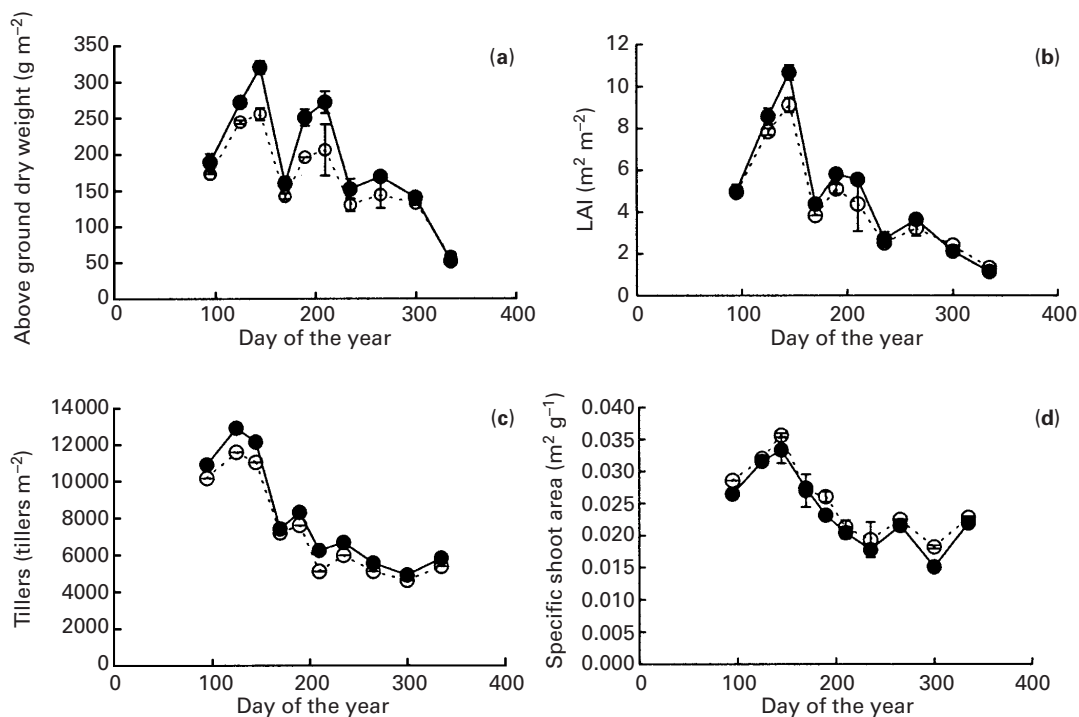
In this work the data-sets of 1994 and 1995 were considered independent and were used for model calibration and validation, respectively. Here we describe the experimental results obtained during 1994, then the simulated results obtained from the model are compared with the experimental data of 1995.

### Weather

During 1994 average daily temperature and incoming total radiation were 7.3°C and 10.6 MJ m<sup>-2</sup> d<sup>-1</sup>, respectively. During 1995 average temperatures were 1.6°C warmer, and average incident radiation was 1 MJ m<sup>-2</sup> d<sup>-1</sup> higher (Fig. 1). Air temperature inside the enclosures mimicked outside temperatures. Maximum and minimum absolute temper-



**Fig. 1.** Daily course of temperature (solid lines) and radiation (dashed lines) during experiments. (a) 1994. (b) 1995.



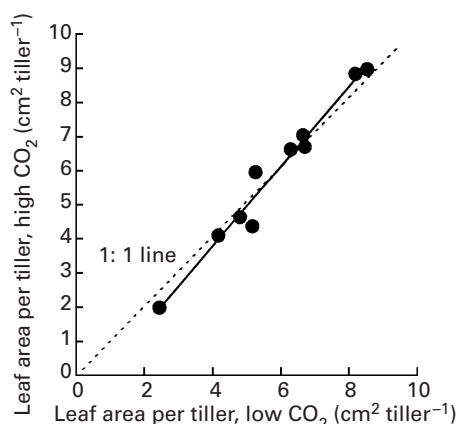
**Fig. 2.** Observed above-ground dry weight (a), leaf area index (LAI) (b), tiller number (c), specific shoot area (d) of ryegrass swards grown during the experimental season of 1994 in low (open circles) and high (closed circles) concentrations of atmospheric CO<sub>2</sub>. Bars, SE of the mean.

atures during 1994 were 33°C on 23 July and −9.6°C on 18 February, and during 1995 32.8°C on 30 July, and −9.3°C on 7 January, respectively.

#### Grass growth and production

During 1994 ambient CO<sub>2</sub> enrichment increased the annual production of above-ground dry weight by 17% (Fig. 2a) and LAI was also increased by CO<sub>2</sub> (Fig. 2b). This effect was driven by a greater number of tillers per unit of area rather than by changes in leaf area per tiller (Figs 2c, 3). In Fig. 3 the slope and the intercept of the relationship between the leaf area per tiller at high CO<sub>2</sub> with respect to the leaf area per

tiller at low CO<sub>2</sub>, were not different from 1 and 0 ( $P < 0.05$ ), respectively. On average, during the growing season of 1994, the high CO<sub>2</sub> sward had a 10% greater leaf area index, 10% more tillers, and on average, a 6% lower specific shoot area (Fig. 2d). Irrespective of year or CO<sub>2</sub> treatment, specific shoot area was related to the concentration of water-soluble carbohydrates (WSC) in the above-ground dry weight (Fig. 4a). Interestingly, tillering showed a significant negative, or nonsignificant positive relationship with WSC depending on the year (Fig. 4b). The dynamics of tiller number over the season were similar for both CO<sub>2</sub> treatments. The number of tillers per unit area fluctuated from 10000–13000 in early spring to 5000–7000 in late summer and



**Fig. 3.** Observed leaf area per tiller at high  $\text{CO}_2$  vs observed leaf area per tiller in low- $\text{CO}_2$  treatments. The 1:1 line is shown by the dashed line.

autumn (Fig. 2c). The initial increase in tiller number during spring was followed by a strong decline during summer and a small recovery in autumn.

#### Model calibration

Data from 1994 were used to calibrate the dynamics of tillering, i.e. the value of the phyllochron (thermal time interval for leaf emergence,  $100^\circ\text{Cd leaf}^{-1}$ , base temperature =  $0^\circ\text{C}$ ), and the relative rate of tiller death. The values of the maximum and minimum values for the specific shoot area were also taken from the data set of 1994. Other parameters describing leaf elongation, and site filling for tillering were taken from the original version of LINGRA (Schapendonk *et al.*, 1998). After calibration the model predicted 93% of the observed variability of the cumulated yield observed in 1994.

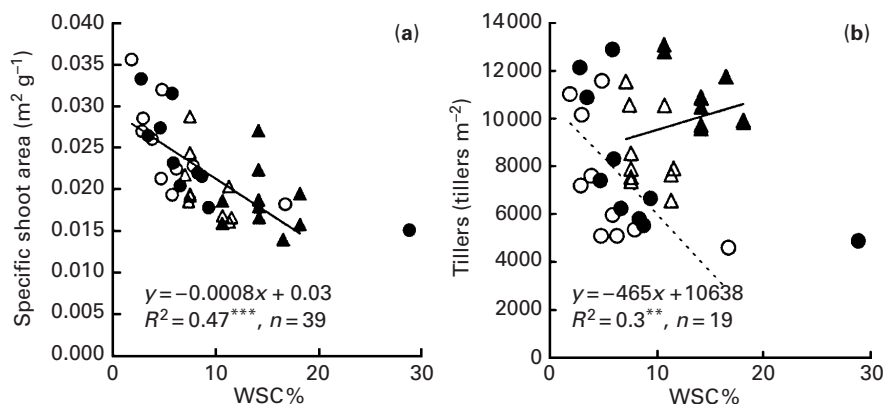
#### Model validation

The simulations (Fig. 5a) predicted effectively the cumulative yield production in both ambient and

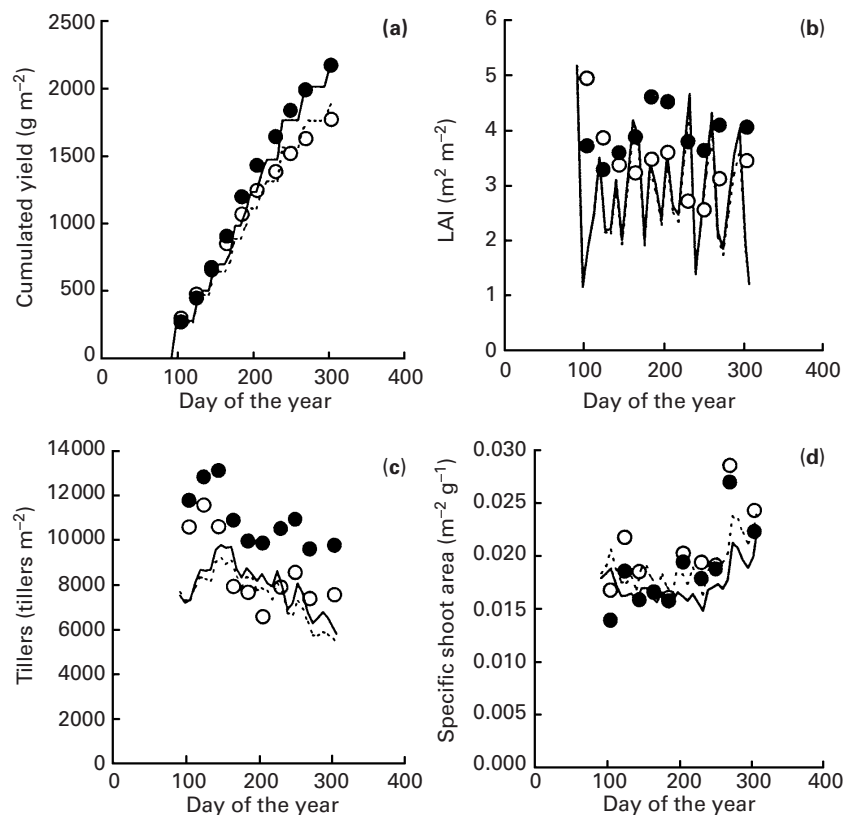
increased  $\text{CO}_2$  environments. Observed and simulated cumulative yields were linearly related, for high and low  $\text{CO}_2$   $P < 0.01$ ,  $R^2 > 0.98$ ,  $n = 8$ . The root mean squared prediction errors for cumulative yield were 78.6 and 91.4 for low and high  $\text{CO}_2$ , and the relative errors 4.1 and 4.2%, respectively. The model tended to underestimate the relative effect of  $\text{CO}_2$  on LAI and tiller number. Fig. 6 shows the observed and simulated effects of  $\text{CO}_2$  on yield, LAI, tiller number and specific shoot area. The model predicted the positive effects of  $\text{CO}_2$  on yield, LAI and tiller number, and a negative effect on specific shoot area, but the trend of the responses was not well predicted. During spring the model failed to predict a negative effect of  $\text{CO}_2$  on yield and LAI, and during summer the model failed to predict peak relative effects of  $\text{CO}_2$  of about 1.5 in yield, 1.4 in LAI and 1.5 in tiller number. Fig. 7 shows the simulated time course of the sink and source terms during 1995. The simulations indicated that the sward grown at ambient  $\text{CO}_2$  (Fig. 7a) was sink-limited during most of the growing season; only during part of the winter and for short periods after each harvest did the model predict a source-limited growth. At high  $\text{CO}_2$  (Fig. 7b) assimilates limited the growth of the sward less frequently. In the model, tillering depends on the level of cumulated reserves and high  $\text{CO}_2$  increases the level of reserves; therefore, the simulated sink term was indirectly enhanced under high  $\text{CO}_2$  (Fig. 8). The slope of the regression line between the strength of the sink at high  $\text{CO}_2$  and the strength of the sink at low  $\text{CO}_2$  was different from 1 ( $P < 0.001$ ).

#### Sensitivity analysis

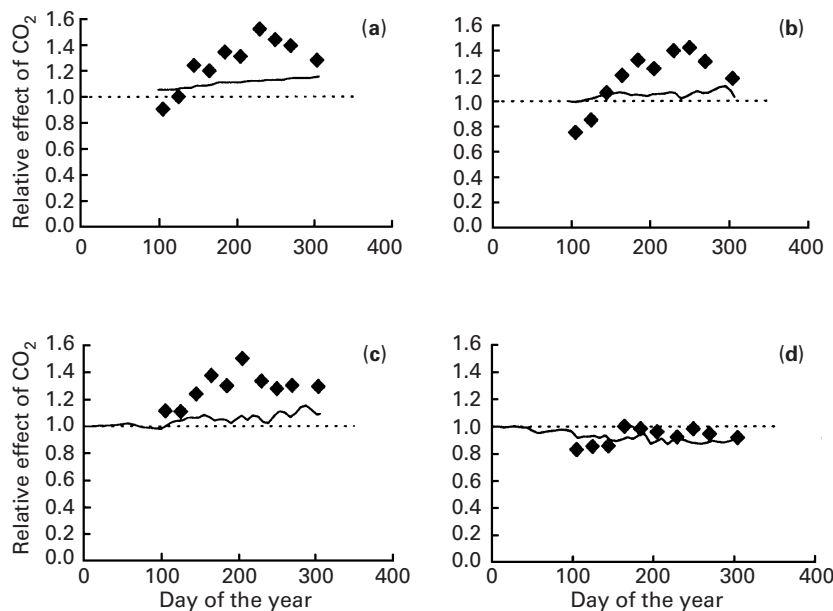
An analysis of sensitivity of cumulated yield to  $\pm 10\%$  changes in some model parameters (i.e. phyllochron, aerial concentration of Rubisco of upper leaves, Michaelis-Menten constant for  $\text{CO}_2$  at



**Fig. 4.** Specific shoot area vs the concentration of water-soluble carbohydrates (WSC%) (a), and tiller number vs WSC% (b), of ryegrass swards grown during 1994 (circles) and 1995 (triangles) at low (dashed lines and open symbols) and high (continuous lines and closed symbols) concentrations of atmospheric  $\text{CO}_2$ .



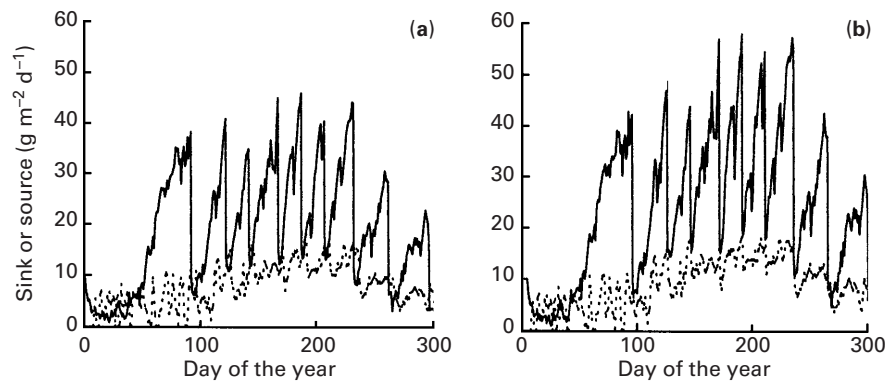
**Fig. 5.** Observed and simulated-cumulated yield (a), leaf area index (LAI) (b), tiller number (c) and specific shoot area (d), of ryegrass swards grown during 1995 in low (open circles) and high (closed circles) concentrations of atmospheric  $\text{CO}_2$ . Lines and symbols as in Fig. 4.



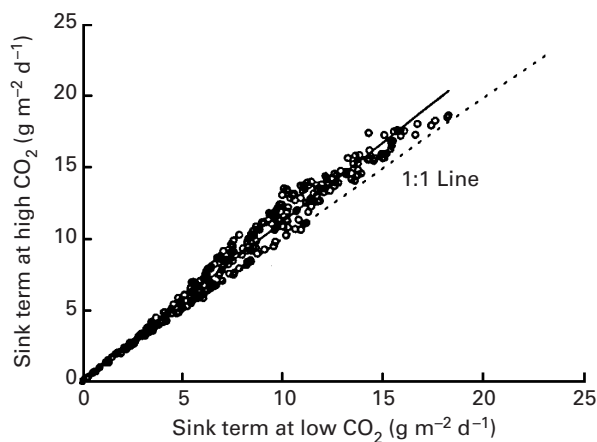
**Fig. 6.** Observed and simulated effects of increased atmospheric  $\text{CO}_2$  on yield (a), leaf area index (LAI) (b), tiller number (c) and specific shoot area (d), of ryegrass swards grown during 1995. Dashed line indicates no effect of  $\text{CO}_2$ .

25°C, Michaelis-Menten constant for  $\text{O}_2$  at 25°C, ratio turnover for oxygenase and carboxylase activities) was performed in different environments: high incident radiation and high air temperature,

low radiation and low temperature, high radiation and low temperature and low radiation and high temperature (Table 1). A sensitivity coefficient (SC) was calculated as  $|SC| = (\Delta V/V)/(\Delta P/P)$  (Thornley



**Fig. 7.** Trends of the sink (dashed lines) and source (solid lines) terms calculated by the simulation model at (a) low CO<sub>2</sub> (350 μmol mol<sup>-1</sup>) and (b) high concentrations of atmospheric CO<sub>2</sub> (700 μmol mol<sup>-1</sup>).



**Fig. 8.** Simulated sink terms in high- vs simulated sink term in low atmospheric CO<sub>2</sub>.

& Johnson, 1990), where  $V$  and  $P$  are model variables (i.e. the predicted cumulated yield) and model parameters, respectively. Annual yield production proved particularly sensitive (values of sensitivity coefficient  $>|0.5|$ ), to a negative change in the concentration of Rubisco under low ambient CO<sub>2</sub> in a low radiation and low temperature environment. Variations in the phyllochron or in the kinetic parameters of Rubisco had no or minor effects on yield.

#### Sward management

The validated model was used to study the impact of differences in management such as cutting interval

**Table 1.** Sensitivity coefficients<sup>a</sup> of calculated annual yield to a 10% positive and negative change in different model parameters, at low (350 μmol mol<sup>-1</sup>), high (700 μmol mol<sup>-1</sup>) ambient CO<sub>2</sub>, high<sup>b</sup> radiation and high air temperature (hrhT), low<sup>c</sup> radiation and low air temperature (lrlT), high radiation and low air temperature (hrlT), and low radiation and high air temperature (lrhT).

CO <sub>2</sub>	Positive change					Negative change				
	Phy	Rub	Km <sub>C25</sub>	Km <sub>O25</sub>	K <sub>O</sub> K <sub>C</sub>	Phy	Rub	Km <sub>C25</sub>	Km <sub>O25</sub>	K <sub>O</sub> K <sub>C</sub>
350 <sub>hrhT</sub>	0.3	0.4	0.3	0.2	0.1	0.3	0.5	0.3	0.2	0.1
700 <sub>hrhT</sub>	0.3	0.2	0.1	0.05	0.02	0.4	0.2	0.1	0.06	0.02
350 <sub>lrlT</sub>	0.2	0.6	0.4	0.2	0.1	0.1	0.7	0.3	0.2	0.1
700 <sub>lrlT</sub>	0.2	0.3	0.1	0.1	0.02	0.2	0.4	0.2	0.1	0.02
350 <sub>hrlT</sub>	0.2	0.5	0.3	0.1	0.04	0.2	0.6	0.3	0.1	0.04
700 <sub>hrlT</sub>	0.3	0.3	0.1	0.04	0.01	0.3	0.3	0.1	0.05	0.01
350 <sub>lrhT</sub>	0.2	0.5	0.5	0.3	0.2	0.2	0.6	0.5	0.3	0.2
700 <sub>lrhT</sub>	0.3	0.2	0.1	0.1	0.04	0.3	0.3	0.1	0.1	0.04

<sup>a</sup>Sensitivity coefficients are calculated as  $|SC| = (\Delta V/V)/(\Delta P/P)$ , where  $V$  and  $P$  are model variables and parameters, respectively.

<sup>b,c</sup>25% increase or decrease on incoming radiation and air temperature.

Phy = phyllochron (100 degree days per leaf).

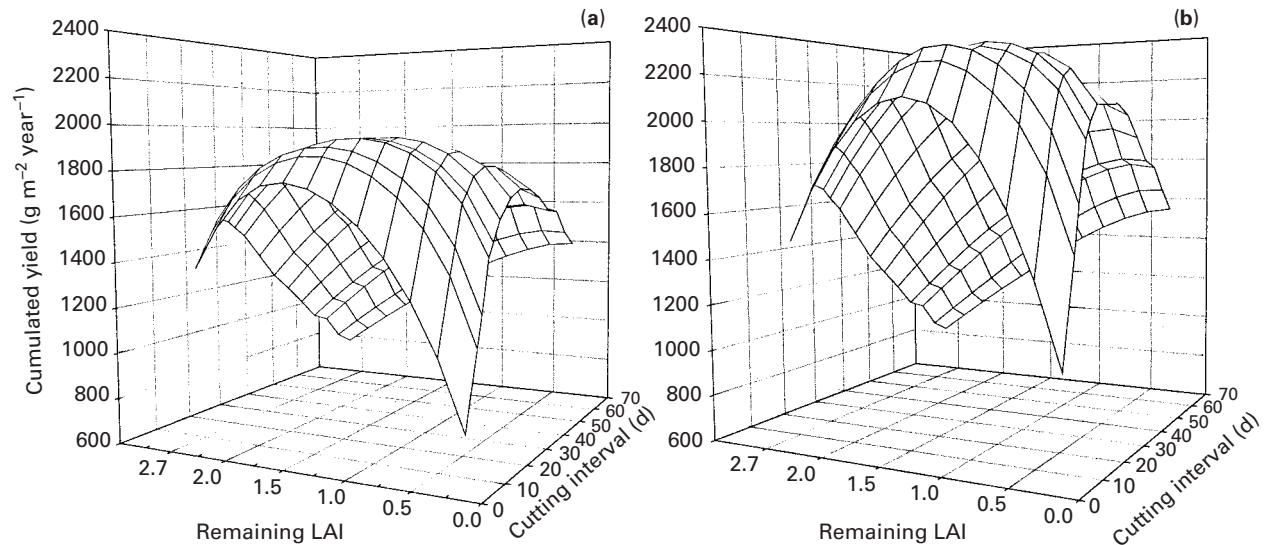
Rub = concentration of Rubisco of upper leaves (2.7 g Rubisco m<sup>-2</sup> leaf).

Km<sub>C25</sub> = Michaelis-Menten constant for CO<sub>2</sub> at 25°C (460 ml CO<sub>2</sub> m<sup>-3</sup>).

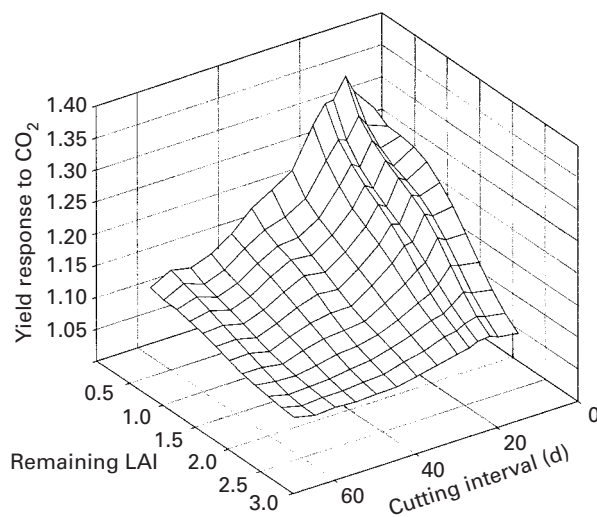
Km<sub>O25</sub> = Michaelis-Menten constant for O<sub>2</sub> at 25°C (33 ml O<sub>2</sub> m<sup>-3</sup>).

K<sub>O</sub>K<sub>C</sub> = Ratio of turnover for oxygenase and carboxylase (0.21).





**Fig. 9.** Simulated annual yield as a function of cutting interval and remaining leaf area index for a ryegrass sward grown in (a) low and (b) high concentrations of atmospheric  $\text{CO}_2$ .



**Fig. 10.** Yield response to  $\text{CO}_2$  and remaining leaf area index of a ryegrass sward at different cutting intervals.

and cutting height (remaining LAI after each cutting), on the annual yield of a sward growing at ambient and double  $\text{CO}_2$  concentrations. The combinations of cutting interval and height that maximize yield at low and high  $\text{CO}_2$  concentrations were similar (Fig. 9). At ambient  $\text{CO}_2$  a maximum yield of  $1931 \text{ g m}^{-2} \text{ yr}^{-1}$  and a remaining leaf area index of 1 were obtained by cuttings at 20-d intervals. In a double- $\text{CO}_2$  environment, a maximum yield of  $2308 \text{ g m}^{-2} \text{ yr}^{-1}$  and a remaining LAI of 1 were obtained at cutting intervals of 17 d. Although in high- $\text{CO}_2$  conditions the optimum cutting interval for maximum yield was 15% shorter than in ambient  $\text{CO}_2$ , the gain in harvested biomass obtained by reducing the cutting interval by 3 d in high- $\text{CO}_2$  conditions was unimportant (2%). The response of annual yield production to  $\text{CO}_2$  (Fig. 10) for different combinations of cutting interval and cutting height

indicates that the maximum response to  $\text{CO}_2$  is obtained when the sward is maintained in a source-limited condition by frequent cutting, with low remaining LAI.

#### DISCUSSION

The test of model capacity to predict annual yield of a grass sward under frequent cutting, showed that LINGRA-CC is capable of handling seasonal variations in temperature and radiation, as well as different levels of ambient  $\text{CO}_2$  (Fig. 5). The evaluations presented in this paper show that the model captured the main features of the seasonal dynamics of crop LAI, tiller number and specific shoot area. Model formulation and testing have also served to pinpoint areas where more work is needed to increase knowledge and the domain of applicability of the model. We believe that these particularly include information on the acclimation of photosynthesis to  $\text{CO}_2$  and its interaction with the sink and source terms. During periods of relatively low temperature and high radiation (spring) the model was not able to simulate null or even negative effects of increased ambient  $\text{CO}_2$  on LAI and yield. There are surprisingly few experiments where the stimulation of growth by  $\text{CO}_2$  was studied in the range of  $0\text{--}10^\circ\text{C}$  of ambient temperature. Zero (Newton *et al.*, 1994; Saebo & Mortensen, 1995; Oechel & Vourlitis, 1996) and even inhibitory (Idso & Kimball, 1989; Nijs & Impens, 1996) effects of  $\text{CO}_2$  on growth are not new. The carbon dioxide sensitivity of photosynthesis is known to be lowest at low temperatures (Long, 1991; Kirschbaum, 1994). Lack of response of a tundra ecosystem after 3 yr of growth in high  $\text{CO}_2$  was attributed to both the low availability of nutrients and low temperatures limiting sink formation and assimilate demand (Oechel &



Vourlitis, 1996). Photosynthetic acclimation as a consequence of sink limitation has been recognized as a major controlling factor of the response of plants and crops to CO<sub>2</sub> (Stitt, 1991; Rogers *et al.*, 1998). In our work nutrients were supplied in nonlimiting amounts and did not limit sink strength. During spring the swards had the lowest values of specific shoot area (Fig. 2c), in great part explained by an accumulation of WSC (Fig. 4a). Low temperatures and high radiation levels during spring probably impaired sink development and increased the concentration of sugars in leaves, which might have induced acclimation of photosynthesis (Azcón-Bieto, 1983).

Zero effects of CO<sub>2</sub> on sward growth could also occur even when assimilation increases because of a high CO<sub>2</sub> environment, as we do not know for certain how these assimilates are partitioned. Assimilates produced by plants grown in high CO<sub>2</sub>, have been reported to be partitioned into root structure (McKee & Woodward, 1994) or storage (Smart *et al.*, 1994), exuded into the soil by the roots (Schapendonk, *et al.*, 1997), and even respired (Drake *et al.*, 1996).

Simulations (Figs 7a,b) suggest that the sward was source limited only after each cutting and for a few days. This effect was observed at both CO<sub>2</sub> levels, even when increased CO<sub>2</sub> promoted sink strength through tillering (Figs 2, 8). Clear indications exist that CO<sub>2</sub> enrichment increases the maximum as well as the final number of shoots (Rogers *et al.*, 1996), even at contrasting temperatures and levels of N supply (Mitchell *et al.*, 1993).

The sensitivity analysis reported here (Table 1), serves to establish the general consistency of model behaviour. The model had a low sensitivity to positive or negative changes in the parameters for the kinetics of photosynthesis. The highest sensitivity of annual yield production was to changes in the concentration of Rubisco, particularly at ambient CO<sub>2</sub> and in low radiation and temperature environments. This indicates that despite the fact that the model predicted a sink limitation during most of the growing season, increase in the rate of photosynthesis through increased concentration of photosynthetic components, i.e. Rubisco, still increased growth at ambient CO<sub>2</sub>.

The model was sensitive to sward-management practices. Those practices that reduced the size of the source of assimilates, i.e. reduction of remaining LAI and cutting interval (Fig. 9), drastically reduced annual yield and increased yield response to CO<sub>2</sub> (Fig. 10). Consequently, growth was particularly promoted by CO<sub>2</sub> when the frequency and intensity of the disturbance was highest.

Annual yields were maximized, for both low and high CO<sub>2</sub> environments, at similar cutting intervals and cutting heights, that do not differ much from those obtained experimentally in cultivated grass-

lands (Bell & Ritchie, 1989) and in controlled conditions (Hume, 1991).

LINGRA-CC can be used to simulate yield production of a well irrigated and managed sward of *L. perenne* in ambient- and increased-CO<sub>2</sub> environments. The model provides a good simulation of the seasonal dynamics of LAI, tiller number and specific shoot area. Future work will focus on including the effects of drought and N supply.

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