

## LINGRA, a sink/source model to simulate grassland productivity in Europe

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### Abstract

A simulation model for the prediction of the productivity of *Lolium perenne* L. grasslands is described and validated. Simulated key processes are light utilization, leaf formation, leaf elongation, tillering, and carbon partitioning (storage, shoot, root). Source- and sink-limited growth are simulated independently. Sink-limited growth is characterized by temperature-dependent leaf expansion and tiller development, whereas source-limited growth is determined by photosynthetic light-use-efficiency of the canopy and the remobilization of stored carbohydrates in the stubble. At each integration step, commonly 1 day, the available amount of carbon from the source is compared with the carbon required by the sink. The actual growth is determined by the minimum value of either the sink or the source. If the source is in excess of the sink, the surplus is allocated to storage carbohydrates in the stubble. This storage carbon is available for remobilization at times that the sink requires more carbohydrates than are available from photosynthesis. In contrast to previous grassland models, LINGRA describes regrowth after defoliation in a mechanistic way, balanced by temperature-driven remobilization of stored carbohydrates. In order to validate LINGRA, an extensive set of experimental data was used, derived from measurements at 35 sites in Europe. The average error between the observed and predicted yields was 14% at the level of irrigated, and 19% at the level of non-irrigated, treatments for the whole of Europe. © 1998 Elsevier Science B.V. All rights reserved.

**Keywords:** Grass; Leaf area; *Lolium perenne* L.; Modelling; Phenology; Productivity; Sink–source

### 1. Introduction

Various models for grass growth have been described for different purposes [for a review, see Sheehy and Johnson (1988)]. The basis of most models is source-driven growth within limits determined by a statistical description of phenological processes. Such models have proven to be a valu-

able tool for optimizing grassland management (Sheehy et al., 1980; Johnson and Thornley, 1983; Johnson and Parsons, 1985). Supplementary to this approach, a more mechanistic growth model for grass leaf tissue growth (Thornley, 1991) has become the basis of a recently published version of the 'Hurley Pasture Model' (Thornley and Cannell, 1997). This model describes the interaction between the conductance of carbon and nitrogen in the plant and in the soil under changing environmental conditions. In this approach, sub-

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strate transport and chemical conversion are the processes that determine allocation of carbon. Interactions between carbon fluxes and changes in morphology, however, are not yet accounted for in the Hurley pasture model, and thus the challenge remained to implement these features in a mechanistic model. The question arises as to how detailed the description of morphological and phenological functions should be. To answer this question, a simple approach was taken as the starting point, and detailed process descriptions were supplemented stepwise.

Growth rates of field crops can be satisfactorily derived from the amount of radiation intercepted by the crop (Gaastra, 1958). Light interception, however, is related to the Leaf Area Index (LAI) and as such to morphological development with key processes such as leaf elongation rates and tillering (Schapendonk and de Vos, 1988). Models that value the importance of phenology have been successful in predicting grain yield in wheat (Porter, 1993). We have chosen to develop such a model for grasses, called LINGRA (LINTUL-GRASS), based on morphological key processes and light interception. LINGRA is based on LINTUL (Light INTERception and UtiLization simulator), which was originally developed for potato (Spitters and Schapendonk, 1990). The innovative aspects of LINGRA are the separated algorithms for source- and sink-related processes and a mechanistic, though simple, approach of grass morphological development, simulating the natural sequence of events in grasslands, including regular defoliation due to grazing or cutting. Repeated defoliation leads to temporary shortages of assimilates, alternated by periods of assimilate surplus when the leaf area index (LAI) is high and the foliage can intercept almost all of the incoming photosynthetic active radiation (PAR). The resulting alternating sequence of sink- and source-limited growth is characteristic for all grasses. New leaves can only develop when carbohydrates are remobilized from a storage pool to compensate for low photosynthetic rates after defoliation (Davies, 1988; Schnyder and Nelson, 1988). The storage pool is replenished when photosynthetic rates increase due to steadily increasing light interception. LINGRA describes this

alternating shortage and abundance of assimilates as a dual mechanism. LINGRA contains routines for light interception, light utilization efficiency, sink and source activity, tillering rate, leaf appearance rate, soil water content and evaporation by the sward.

LINGRA was designed for applications such as (regional) yield forecasting and quantitative land-use evaluation and to study the effects of climate change on grass yields. In 1996, LINGRA was included in the Crop Growth Monitoring System (CGMS, Bouman et al., 1996), which is used operationally by the Joint Research Centre of the European Commission for crop yield forecasting in the EU (Vossen and Rijks, 1995).

## 2. Model development

### 2.1. Technical information

LINGRA was developed in the Fortran Simulation Environment (FSE 2.1; van Kraalingen, 1995). FSE consists of a main program, a system for weather data input and utilities for specific tasks such as initialization, rate and state calculations and terminal calculations for output. The software runs on an IBM compatible PC-486 or higher. Uncertainty analysis and calibration of the model were performed according to Stol et al. (1992). The equations used in the model are summarized in Appendix A.

### 2.2. Experimental data

Some process descriptions in the model were derived from experimental results, and others were obtained from the literature. The parameters for leaf elongation rates, specific leaf area (SLA), and light-use efficiency were derived from a 2-year experiment with *Lolium perenne* L. (cv. Preference) that started in October 1993 in the 'Wageningen Rhizolab'. Periodically measured data on tillering were used to validate the tiller dynamics in the model. Swards were grown from seed in translucent polycarbonate enclosures in two replicates and were surrounded by swards to prevent border effects. The soil compartments were  $1.25 \times 1.25$  m and 2 m deep and were filled with a repacked

loamy clay soil, with 4.7% organic matter and a pH of 7.0. Each sward was fitted with a separate drip irrigation system, and at every 15 cm below the soil surface, sensors were installed to measure the soil moisture status, electrical conductivity and temperature. Each plot and its surrounding borders were irrigated, equivalent to 10 mm of rainfall, when the soil water status in one of the layers in the soil profile dropped below a volumetric moisture content of 27%. The temperature in the enclosures was controlled by air conditioners and followed the measured outside air temperature. The swards were cut 10 times per year to a height of 5 cm at intervals of 20–24 days, after which potassium nitrate ( $8 \text{ g N m}^{-2}$ ) was supplied. The number of tillers was then counted, and the leaf elongation rates were determined 6 days after cutting from measurements of leaf length.

### 2.3. Initialization and re-growth settings

LINGRA runs with a defined set of initial default parameter settings that are read from an external file. The initial leaf area index (LAI) in spring is fixed at 0.1, and the initial amount of carbohydrates in the stubble is fixed at  $20 \text{ g m}^{-2}$ . LAI after defoliation was obtained from a calibration procedure and fixed at a value of 0.5 (see below). The cutting dates are optional, either read from an external file or when the grass reaches a certain amount of biomass, fixed by the user. Simulated growth starts when the 10-day moving average of daily temperature exceeds a given base temperature,  $T_{B1}$ . In the evaluation runs for the regional productivity of agricultural grasslands in Europe,  $T_{B1}$  was calibrated at  $3^\circ\text{C}$  for the northern countries and  $5^\circ\text{C}$  for the southern countries. At temperatures below  $T_{B1}$ , the daily growth rate and development rate are zero.

### 2.4. Basic concept

LINGRA is based on the most simple crop growth model formulated to date, the light utilization model (Monteith, 1977). Biscoe and Gallagher (1977) showed that the light-use efficiency (LUE) of crops, when expressed per unit of intercepted light, remained fairly constant over

the growing period. This implies that when the total biomass is plotted against cumulative light interception, a linear relationship results with a slope representing the average LUE. The conservative properties of LUE combined with a high predictive value contribute much to the present notoriety of these models [see the review by Gosse et al. (1986)]. A major limitation, however, is the implicit need for calibration under diverging climatic conditions. Predictions are only valid within narrow margins of environmental conditions with a time resolution of weeks, rather than days. To improve the time resolution and to make the model more versatile, mechanistic relations can be implemented. As an alternative to Thornley and Cannell (1997), who linked fluxes of carbon and nitrogen mechanistically by evaluating their ratios, LINGRA simulates source carbon flow ( $\Delta W_{\text{source}}$ ) and sink-carbon flow ( $\Delta W_{\text{sink}}$ ) semi-independently. We intentionally use the term 'semi-independent' because, although source- and sink-limited processes are calculated independently, a strong feedback is present because each day, the growth rate ( $\Delta W$ ) equals either  $\Delta W_{\text{source}}$  or  $\Delta W_{\text{sink}}$ . We consider  $\Delta W_{\text{sink}}$  to be related to leaf appearance rate, tillering rate and leaf elongation rate (Davies and Thomas, 1983) and  $\Delta W_{\text{source}}$  to be equivalent to photosynthetic rates added to the amount of stored carbohydrates in the stubble. Thus, there are two important features to consider:

- (1) source- and sink-related processes depend on environmental conditions in different ways [for a review, see Davies (1988)], the source being radiation-dependent, whereas the sink is temperature-driven.
- (2) the imbalance between assimilate supply and assimilate requirement is caused by temporal discontinuities, such as those caused by defoliation.

The amount of stored carbohydrates ( $W_{\text{storage}}$ ) will decline when the sward is more frequently defoliated because regrowth requires more carbon, whereas periods to replenish the storage pool will be shorter.

### 2.5. Light-use efficiency (source)

The light profile within the canopy is calculated on the basis of the leaf area index (LAI) and the

extinction coefficient ( $k$ ). The efficiency conversion of absorbed light into carbon assimilation is variable in time and depends on radiation intensity, temperature and water availability. Under an optimum water- and nutrient supply, the photosynthetic response to light was simulated by a Blackman limiting response (Blackman, 1905). The initial slope and asymptote were estimated from measured LUE [ $\epsilon(t)$ ] during frequent cutting intervals over two growth seasons at the 'Wageningen Rhizolab' (Schapendonk et al., 1997). The slope of the light response curve for dry matter increase was  $2.7 \text{ g MJ}^{-1}$  at low PAR. Above  $5 \text{ MJ m}^{-2}$ ,  $\epsilon(t)$  declined to  $0.9 \text{ g MJ}^{-1}$  at  $20 \text{ MJ m}^{-2}$ .

The effect of temperature on  $\epsilon(t)$  implicitly involves effects on both respiration and photosynthesis. Maintenance respiration increases continuously with temperature, and for photosynthesis, there is an optimum temperature that shifts towards higher values with increasing radiation. Consequently, a higher temperature optimum exists at a low LAI when the incident light intensity on the leaves is, on average, higher than at high LAI. Over the seasons, the temperature optimum for net photosynthesis is rather flat (Sheehy et al., 1980). Below a certain temperature threshold ( $T_{B1}$ ), photosynthesis stops, and  $\epsilon(t)$  will become zero. As a simplified solution, the temperature effects on the canopy level were assumed to increase as a linear function of daily average temperature  $f(T)$  to a maximum value of 1 at a daily temperature,  $T_{\text{opt}}$ .  $T_{\text{opt}}$  was calibrated by an optimization routine (see below).

The third factor that affects  $\epsilon(t)$  is water shortage  $f(\text{wt})$ , see below.

## 2.6. Leaf and tiller dynamics (sink)

The sink strength after cutting is defined here as the temperature-driven rate of leaf area increase, which equals the product of leaf elongation rate, number of leaves and average width of elongating leaves. The relationship between the daily average temperature and the leaf elongation rate during the first 5 days after cutting was determined from a semi-field experiment in the Wageningen Rhizolab and implemented in LINGRA. Leaf

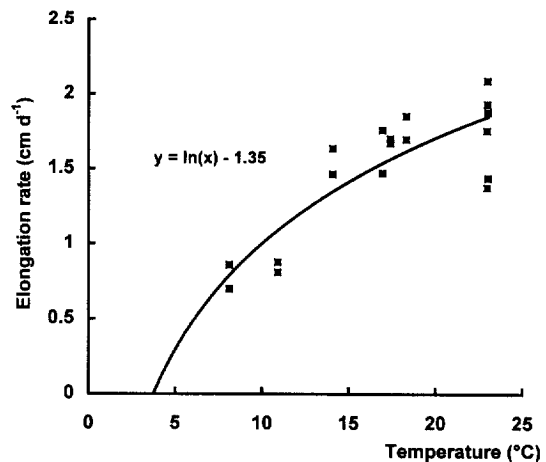


Fig. 1. Leaf elongation rates of grass leaves as a function of mean daily temperature averaged over 5 days after cutting.

elongation rates, measured after cutting, increased from  $0.3 \text{ cm day}^{-1}$  at  $5^\circ\text{C}$  to  $1.8 \text{ cm day}^{-1}$  at  $23^\circ\text{C}$  (Fig. 1). The leaf appearance rate per tiller was simulated according to a soil-temperature dependent relationship derived from the data of Davies and Thomas (1983). The tillering rate was calculated from the proportion of buds in new leaf axils that produced new tillers. This utilization of buds, called the site filling ratio, was reported to be 0.335 during the first week after defoliation and 0.69 afterwards (van Loo, 1993). In addition to this time effect, site filling decreased with increasing LAI and concomitant internal shading. This has been reported to be due to a decrease of the red-to far-red ratio of the light penetrating into the lower regions of the leaf, which causes fewer buds to emerge (Casal et al., 1990).

Leaf longevity and tiller survival are of critical importance to estimates of LAI. In LINGRA, we assume that tiller death and leaf senescence are promoted by internal shading. As LAI increases, deeper layers of the sward become shaded. The low light intensities initiate remobilization of nitrogen from the shaded leaves that then age rapidly. A faster increase in leaf area will feed forward to a higher senescence rate. Thus, relative death rates of leaves and tillers are a function of LAI. Internal shading also induces tiller death and prevents the formation of new tillers leading to a lower site-filling rate. The tillering rate was simulated as the



Fig. 2. Fluctuation in the tiller numbers measured in two experimental years in 1994 and 1995 measured in the 'Wageningen Rhizolab'. The broken lines show the simulated time courses.

ratio between the calculated amount of stored carbohydrates and an estimated maximum amount of available carbohydrates (cf. Appendix A). The maximum amount of carbohydrates ( $W_{\text{stomax}}$ ) is derived from a long-leaved genotype of *Lolium perenne* L. with a biomass of  $200 \text{ g m}^{-2}$  and a storage carbohydrate content of 20% (Davies, 1988).

A decline in stored carbohydrate implies that the tillering rate also declines because stored carbohydrates are in deficit. This condition is likely to occur in practice when the cutting frequency is high (Davies, 1988). In the 'Wageningen Rhizolab' experiment, the number of tillers fluctuated from 10 000 to 13 000  $\text{m}^{-2}$  in early spring to 5000 to 8000  $\text{m}^{-2}$  in late summer and autumn (Fig. 2). An initial increase in tiller number in spring was followed by a strong decline in summer and a small recovery in autumn. The time course of tiller dynamics agree with the experimentally observed tiller number during the 2 years except for the initial increase of tiller number observed in early spring.

## 2.7. Sink-source interaction

The rate of new leaf area formation just after cutting is crucial for the overall productivity of grass because the intercepted light at this stage determines, to a great extent, the total productivity over the year. Carbohydrate demand will be generally higher than photosynthetic supply during

the first days after defoliation (Schnyder and Nelson, 1988). At that stage, the assimilates required to attain growth rates of leaves  $\Delta W_{\text{lv}}$  and roots  $\Delta W_{\text{rt}}$  are derived from a storage pool in the stubble ( $W_{\text{storage}}$ ). This storage pool is replenished when the photosynthetic supply exceeds the demand. Under source-limiting conditions, the leaf area development is no longer determined by temperature-dependent leaf elongation rates but by the amount of assimilates partitioned to the leaves multiplied by the specific leaf area (SLA). An average figure of  $0.025 \text{ m}^2 \text{ g}^{-1}$  was found for SLA in the Rhizolab experiments. When corrected for the content of soluble carbohydrates, SLA varied from  $0.030 \text{ m}^2 \text{ g}^{-1}$  in early spring to  $0.018 \text{ m}^2 \text{ g}^{-1}$  in summer and autumn. Fluctuations of SLA over the season were not included in the model.

## 2.8. Effects of water stress

The amount of moisture available to the crop is simulated as a function of the maximum rooting depth, assumed to be 40 cm, and the volumetric soil water content (Spitters et al., 1989). The latter is derived from the difference between rainfall and water losses due to percolation out of the rooting zone, soil evaporation and transpiration. Soil evaporation and transpiration were simulated by the Makkink formula (Makkink, 1957; van Kraalingen and Stol, 1997), using incoming short-wave radiation and temperature. Transpiration rate and photosynthesis of the sward depend on soil suction on the one hand and the evaporative demand of the atmosphere on the other. When water shortage occurs, soil suction increases, and the plant closes stomata to prevent desiccation. Consequently, the uptake of  $\text{CO}_2$  from the atmosphere is reduced, and thus absorbed light is used less efficiently. This is formulated in the model by considering that the ratio of actual transpiration ( $T_a$ ) to potential transpiration without water stress ( $T_p$ ) is a measure of the reduction of stomatal conductance and light utilization efficiency (Spitters and Schapendonk, 1990). Details of the water balance used to calculate evapo-transpiration and the volumetric soil moisture content in the root zone are given elsewhere (Hijmans et al., 1994; Supit et al., 1994). As a consequence of

decreasing photosynthetic rates,  $\epsilon(t)$  declines. An additional effect of drought is expressed by the preferential distribution of assimilates to the roots.

### 2.9. Calibration procedure

To calibrate LINGRA, an extensive set of experimental data on forage production was made available by the Institute of Grassland and Environmental Research (IGER) in Aberystwyth, UK. This database was derived from the project 'Predicting production from grassland' from the FAO sub-network for lowland grassland (Corrall, 1988). It contains standardized experimental data from field experiments with *Lolium perenne* L. on 35 sites throughout Europe with different climatic and soil conditions throughout Europe (Fig. 3). Experiments were carried out over 1–5 years in the period 1982–1986, with two cultivars of *Lolium perenne* L. (perennial ryegrass) and *Phleum pratense* L. (timothy). Yields were recorded in the first year of production.

Test sites for calibration were selected on the basis of soil requirements likely to guarantee a

normal crop response to weather conditions. These site and soil-specific characteristics are: no serious drainage problems, a slope of less than 5°, ground-water table below 90 cm during the main growing season and an available water-holding capacity between 125 and 175 mm in the layer 0–100 cm below the soil surface. For water-limited production, the water balance model WATFD was used for freely draining soil types (Supit et al., 1994). Since no actual soil characteristics for the sites were available, a standard parameter set was used for a medium textured soil type with a good water-holding capacity (EC3-medium fine; Hijmans et al., 1994). Also, a standard rooting depth of 40 cm was assumed for all sites. The initial water content of the soil profile was set to the field capacity at the start of the simulation. Because of the lack of actual soil and site information, the evaluation of LINGRA at the water-limited level of production should be seen as indicative for trends only, and quite large deviations between simulations and observations can be expected.

Experiments included both irrigated and non-irrigated treatments. Irrigation was applied each week if there was a soil-water deficit exceeding 12.5 mm only, according to the Penman formula. The fertilization rate was high: 600 kg N ha<sup>-1</sup>, 70 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup>, 280 kg K<sub>2</sub>O year<sup>-1</sup>. The cutting height was 4–5 cm. Cutting started each year on 1 March, or as soon as the snow cover disappeared. The design consisted of two replicates with four plots. Each plot was cut 4-weekly with weekly intervals between the individual plots. Weekly growth was estimated from the averaged productions of the four plots (Corrall and Fenlon, 1978). Thus, each week, the average yield of 28 days' growth was recorded. When this yield fell below 0.3 t DM ha<sup>-1</sup>, harvesting was stopped (Peeters and Kopec, 1996).

The data of 15 experiments that approached unrestrained growth characterized by dry matter yields above 16 t ha<sup>-1</sup> year<sup>-1</sup> were selected for calibration of the model at the level of potential production. Three model parameters were used in the calibration process: the remaining LAI after cutting, the base temperature for the start of photosynthesis and development,  $T_{B1}$ , and the



Fig. 3. Map of Europe with the location of the sites involved in the present study. For reference, cf. Corrall (1988).

daily temperature for optimum LUE [ $\epsilon(t)$ ],  $T_{\text{opt}}$ . These parameters were calibrated according to Stol et al. (1992), using a controlled random search algorithm adapted from Price (1979) for finding the global minimum of a function with constraints on independent variables. The objective of model calibration was to minimize the sum of absolute differences between the simulated and observed DM yield within these experiments, on a weekly basis.

### 3. Model application

LINGRA was used to predict grassland productivity on a subset of the FAO database both under irrigated and non-irrigated conditions with an ample supply of nutrients. A quantitative analysis of model performance showed that the model predicts observed biomass values in time very well. The normalized error between all the observed and all the predicted dry biomass values was 13–15% at the level of potential production, and 17–21% at the level of water-limited production for the whole of Europe:

Normalized error =

$$100 \left( \sum |Y_{t,\text{sim}} - Y_{t,\text{obs}}| / n \right) Y_{\text{mean,obs}} (\%), \quad (1)$$

where  $Y_{t,\text{sim}}$  = simulated biomass at time  $t$ ;

$Y_{t,\text{obs}}$  = observed biomass at time  $t$ ;  
 $Y_{\text{mean,obs}}$  = averaged observed biomass; and  $n$  = number of (weekly) observations.

The relationship between the simulated and measured yields for all sites that were analysed are graphically presented in two scatter plots for potential or irrigated and water-limited yield (Fig. 4). The deviations from the ideal prediction lines indicate that on average, the model overestimated yields under irrigated conditions and underestimated yield under water-limited conditions. Based on these evaluation results, it was concluded that LINGRA was sufficiently accurate to simulate potential and water-limited growth and development of a reference grassland under standard management conditions in the whole of the EU, covering a broad range in climatic conditions and soil types (Bouman et al., 1996).

A graphical and quantitative analysis of model performance shows the results for three sites with weather conditions that cover a large part of the climatic diversity in Western Europe (Fig. 5). The actual defoliation dates at the different sites were used as the input. For the sites Wageningen and La Coruna, data were available for both irrigated and non-irrigated field plots. The weather conditions in 1984 were relatively wet for La Coruna, normal for Wageningen and relatively sunny in summer, followed by a wet autumn in Saerheim (Table 1, Fig. 6). The predictions for both

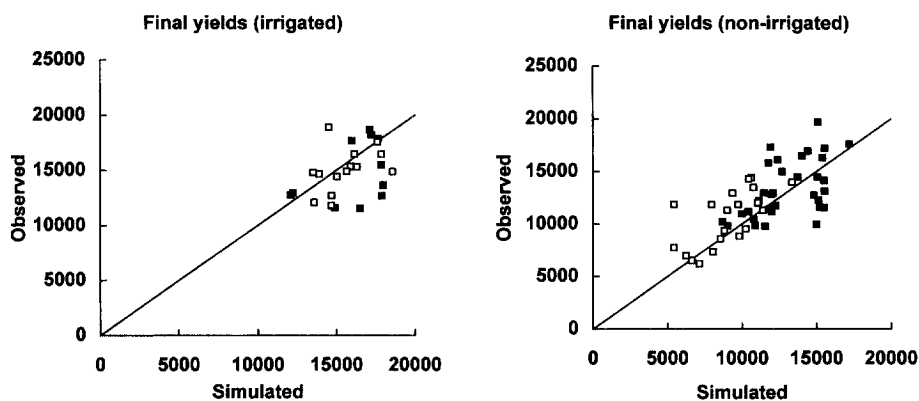


Fig. 4. Measured total above ground biomass of *Lolium perenne* L. for irrigated and non-irrigated conditions plotted against the simulated results. Open symbols represent data from Southern Europe and closed symbols represent data from Northern Europe.

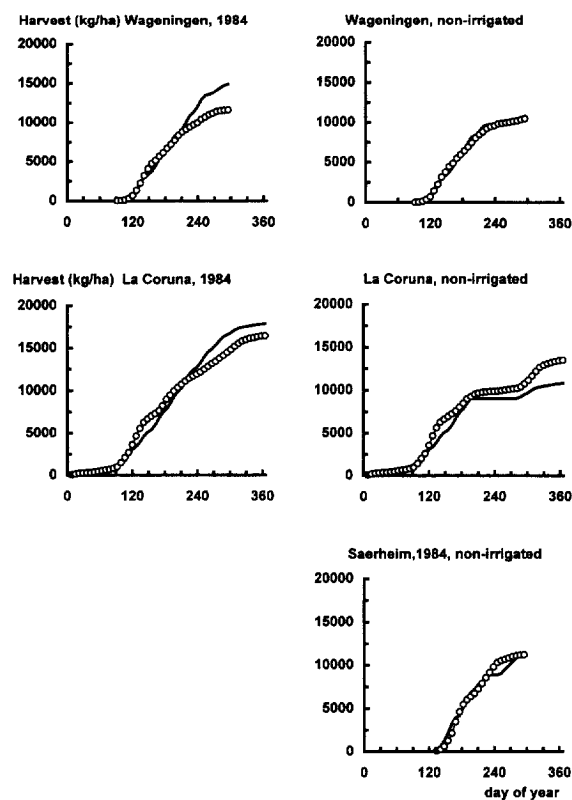


Fig. 5. Observed (°) and predicted (—) total above-ground biomass of irrigated and non-irrigated treatments in Wageningen, La Coruna and Saerheim in 1984.

potential- and water-limited treatments agree well with the experimental data. This is reflected in the timing of initial growth, the production rates and the consistency in the observed decline in productivity in response to drought periods. Instead of

Table 1  
Incoming shortwave radiation, total precipitation and average daily temperatures in 1984

	Average daily radiation (MJ m <sup>-2</sup> day <sup>-1</sup> )	Temperature (°C)	Precipitation (mm year <sup>-1</sup> )
La Coruna	11.1	12.6	1303
Wageningen	8.3	9.2	826
Saerheim	10.3	7.3	1356

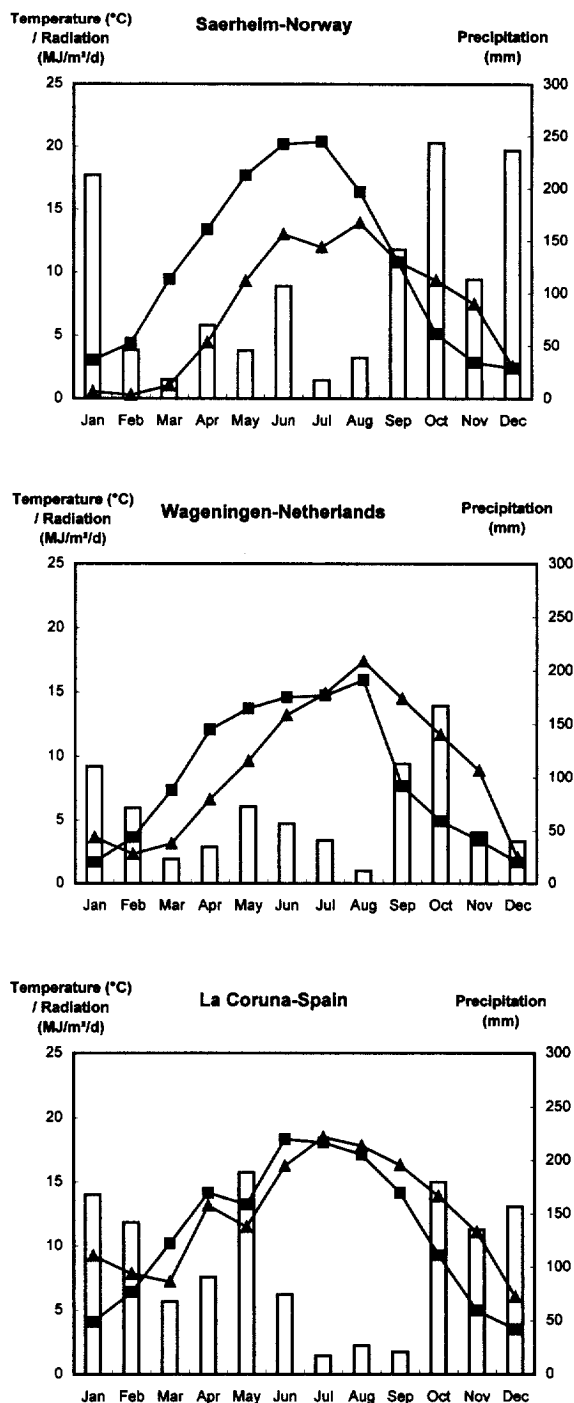


Fig. 6. Time courses of daily radiation sums (■), temperature (▲) and precipitation (bars) in La Coruna, Wageningen and Saerheim in 1984.



Table 2

The simulated effects of a 3°C temperature shift and a 10% difference in precipitation on grass yield at three selected sites in Western Europe, compared with simulated productivity for the year 1984

A Precipitation (percentage of control)	Change in yield (percentage of control)			
	Site	−3°C	Control	+3°C
−10	La Coruna	−21	−4	+6
0	La Coruna	−18	0	+10
+10	La Coruna	−15	+3	+14
−10	Wageningen	−15	−3	+9
0	Wageningen	−12	0	+15
+10	Wageningen	−9	+3	+18
−10	Saerheim	−11	−2	+1
0	Saerheim	−9	0	+4
+10	Saerheim	−6	+3	+7

initiating growth at a certain temperature sum (Spitters et al., 1989), a temperature offset ( $T_{B1}$ ) was used to restrict sink limited growth rates to favourable conditions.  $T_{B1}$  was also used as offset for the LUE [ $\epsilon(t)$ ]. Source activity was a function of temperature with a lower limit at  $T_{B1}$  and a optimum at  $T_{opt}$ . This resulted in a more realistic simulation procedure and much better prediction of the onset of the growth in early spring than by simulating the start of growth at a given temperature sum.

An example to illustrate how the impact of a change in temperature or a shift in precipitation can be anticipated is presented in Table 2. A temperature shift of 3°C and a 10% difference in precipitation in both positive and negative directions were used in simulations for the year 1984 in Saerheim, Wageningen and La Coruna. In each case, a temperature increase had a positive effect on yield, which could be attributed mainly to a more rapid start of spring growth. A rapid start of growth compensated for faster senescence and negative effects of higher water consumption and water shortage, especially in Wageningen. Incoming short-wave radiation did not differ much between the sites (Fig. 6). The total precipitation was high for all sites (Table 1), and the temporal variation was considerable. The observed differences in yield were mainly attributed to differences

in temperature and temporal variation in precipitation. A decrease in temperature had the most negative effect at southern latitudes. The reason for this rather unexpected outcome is the importance of temperature on the onset of grass production in spring. A lower spring temperature in La Coruna induced a delay in the onset of growth because temperatures then often stayed below the base temperature  $T_{B1}$ . In contrast, an increase of 3°C in Saerheim appeared to be insufficient for a more rapid start of grass growth because  $T_{B1}$  was still not attained frequently. Wageningen appeared to be the most sensitive site to temperature because spring growth benefits most. On the whole, and provided that the water supply is not limiting grass growth, the yield in 1984 was increased by 4–15% when the temperature was raised by 3°C. When this was accompanied by a decrease in precipitation, the benefit of an increased temperature dropped to 1–7%.

Water shortage occurred mainly from June until September. Drought in that period was most severe in La Coruna and less in Saerheim and Wageningen. The effect of manipulating precipitation is therefore most clearly reflected in the yields for La Coruna and least for Saerheim where water supply was almost non-limiting. For this particular year, the effects on yield, due to a 20% difference in precipitation, were only small and ranged from

6% at the low temperature to 9% in the high-temperature scenarios.

#### 4. Discussion

LINGRA provides a solid basis for the prediction of grassland productivity in temperate climates. Because the model is partly based on general physiological principles, it is applicable for different environmental conditions. However, there are certain restrictions, for instance, the fact that calibration of the model was needed with respect to the base temperature for development and the optimum temperature for photosynthesis. This concession was made to the requirement that the model should be generic, but also predictive. This meant that some groups of processes were simplified or treated statistically, and thus some calibration of parameters was needed. In this respect, it was also obvious that the model behaviour was slightly different under irrigated and non-irrigated conditions. The yield was overestimated in the irrigated treatments but underestimated in the non-irrigated treatments (Fig. 5). Calibration would have been an obvious tool, but we considered the deviations to be too small in comparison with the random variation to make this an option worth considering.

Other simplifications were, for instance, the assumption of a constant SLA in LINGRA, estimated as the average value from experiments in the 'Wageningen rhizolab'. In the presented model, we have not yet implemented a mechanism by which SLA varies over the season. Part of the observed discrepancies between observed and simulated productivity may have arisen from this simplification (Fig. 4). A more realistic perspective would be to make SLA dependent on the source/sink interaction to explain the commonly observed thicker leaves under conditions of a relative assimilate surplus. The differences in leaf thickness between cultivars and experimental treatments were found to be highly correlated with differences in water soluble carbohydrates (van Loo, 1993). This could also apply to the partitioning between leaf- and root growth, which, in the present model, is simulated as a function of water

availability only. In a more generic approach, it is likely to be coupled to relative assimilate abundance and preferential partitioning of carbon to the roots. These refinements have not yet been made. Still, we conclude that the concept of the model provides a sound basis to predict the regional differences in grass productivity, interacting with environmental conditions. Tailor-made subroutines such as those mentioned above can be easily implemented by the user.

For all attributes genetic variation is expected, and if enough information was available, the impact of genotypical variation would be accounted for on the process level in the model. However, this was not the case in the present study. Therefore, it is to be expected that part of the variation around the regression between simulated data and experimental data must be attributed to genetic differences (Fig. 4).

Having a validated grass model available within the CGMS—ready to monitor potential and water-limited forage production on a European scale—new opportunities and alternative applications of this module arise, such as the evaluation of nutrient deficiency, (Sheehy et al., 1996). Environmental problems on grassland, mainly related to the low recovery of nutrients from organic manure but also partially to sub-optimal recovery of inorganic nitrogen fertilizer, are important issues in grassland research and a continuous topic for debate in the EU. It has been well established that the nitrogen content in the leaves often affects basic processes related to the sink differently from those related to source activity (Soussana et al., 1996; Casella and Soussana, 1997). An extension of LINGRA for forage production under sub-optimal nutrient availability would be a logical step to take. The extended LINGRA model could then serve as a tool for the diagnosis of environmentally sound nitrogen management on grassland in the EU, adapted to regional agro-climatic conditions.

The assessment of the impact of climate change on forage production in the EU is also a topic that can be effectively studied with LINGRA. New relations between atmospheric CO<sub>2</sub> concentration and photosynthesis (as a function of radiation and temperature, obtained from experimental research) could then be introduced.

## 5. Conclusions

LINGRA provides the basic algorithms for the simulation of grass growth, under irrigated and non-irrigated conditions. Though simple, it contains the most important features of grass growth, not only related to photosynthesis but also with respect to leaf morphology and tillering. Only small adaptations are required to add functions or replace constants by rate variables. This makes the structure of LINGRA especially useful for both the assessment of agronomic questions and for sensitivity analyses at the level of single physiological processes.

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## Appendix A

A sink/source model to simulate grassland productivity in Europe; LINGRA (v. 1.0)

### Basic constants and rate equations for grass growth

Constants	Description	Units	Value
$k$	Light extinction coefficient	(m <sup>2</sup> ground m <sup>-2</sup> leaf)	0.6
$\epsilon_p$	Potential light use efficiency	(g MJ <sup>-1</sup> )	2.7
$LAI_{cr}$	Critical leaf area for internal shading effect	(m <sup>2</sup> leaf m <sup>-2</sup> ground)	4.0
$SLA$	Specific leaf area	(m <sup>2</sup> g <sup>-1</sup> )	0.025
$L_w$	Leaf width	(m 10 <sup>-2</sup> )	0.3
$I_{til}$	Initial tiller number	(tiller m <sup>-2</sup> )	7000
$FS_{max}$	Maximum site filling	(tiller leaf <sup>-1</sup> )	0.693
$W_{stmax}$	Maximum storage capacity	(g m <sup>-2</sup> )	40
$T_{B1}$	Base temperature for light utilization and development (daily average)	(°C)	3 or 5
$T_{opt}$	Optimum of daily temperature for photosynthesis (daily average)	(°C)	10

### Input variables

Equations	Description	Units
$T(t)$	Average daily air temperature at time $t$	(°C)
$PAR(t)$	Daily photosynthetic radiation at time $t$	(MJ m <sup>-2</sup> day <sup>-1</sup> )
$\Delta W = \min(\Delta W_{sink}, \Delta W_{source})$	Growth rate of crop dry matter	(g m <sup>-2</sup> d <sup>-1</sup> )
$\Delta W_{source} = \Delta W_{phot} + \Delta W_{storage}$	Source determined growth rate	(g m <sup>-2</sup> d <sup>-1</sup> )
$\Delta W_{phot} = (1 - e^{-kLAI}) PAR(t) \epsilon(t)$	Photosynthesis determined growth rate	(g m <sup>-2</sup> d <sup>-1</sup> )
$\Delta W_{sink} = \Delta LAI_s / SLA \times 1/f(lv)$ ; if $T < T_{B1}$ , then $\Delta W_{tsink} = 0$	Sink-determined growth rate	(g m <sup>-2</sup> d <sup>-1</sup> )
$\Delta W_{storage} = \Delta W_{phot} - \Delta W$	Fluctuation storage carbohydrates	(g m <sup>-2</sup> d <sup>-1</sup> )
$\Delta W_{lv} = \Delta W \times f(lv)$	Growth rate of leaves	(g m <sup>-2</sup> d <sup>-1</sup> )
$\Delta W_{rt} = \Delta W \times \{1 - f(lv)\}$	Growth rate of roots	(g m <sup>-2</sup> d <sup>-1</sup> )
$f(lv) = 0.735 + 0.1 f(wt)$	Fraction of dry matter to leaves	(—)
$DVS = \Sigma(T - T_{B1})/600$	Developmental stage	(—)

## Source determinants

Equations	Description	Units
$\epsilon(t) = \epsilon_p f(\text{PAR}) f(T) f(\text{wt})$	Light-use efficiency	(g MJ <sup>-1</sup> )
$f(\text{PAR}) = \min[1, 1 - 0.0445 (\text{PAR}(t) - 5)]$	Reduction factor at high daily radiation	(—)
$f(T) = \max[0, \min[1, (T - T_{B1})/(T_{opt} - T_{B1})]]$	Factor for temperature	(—)
$f(\text{wt}) = T_a/T_p = \min[1, (V_{act} - V_{wp})/(V_{cr} - V_{wp})]$	Reduction factor for water deficit	(—)
$V_{act}$ = simulated volumetric water content in the rooting zone		(—)
$V_{wp}$ = volumetric soil water content at wilting point		(—)
$V_{cr}$ = volumetric soil water content below which transpiration decreases		(—)

## Sink determinants

Equations	Description	Units
$\Delta L_v(t) = \max[0, 0.01 T_{soil}]$	Leaf formation rate	(leaves tiller <sup>-1</sup> day <sup>-1</sup> )
$T_{soil} = 0.1 T \sum_{i=1}^{10} (t-i)$	Moving average of daily air temperature (10 days)	(°C)
$\Delta L_{lv} = \max[0, \ln(T) - 1.35]$	Leaf elongation rate	(cm day <sup>-1</sup> )
$\Delta LAI_s = L_v(t) \Delta L_{lv} L_w 0.0001$	Sink-limited leaf area index increase when $T > T_{B1}$ ; otherwise $\Delta LAI_s = 0$	(m <sup>2</sup> day <sup>-1</sup> )
$L_v(t) = 1.3 \text{ Til}(t)$	Number of expanding leaves	(leaves m <sup>-2</sup> )
$\text{Til}(t) = I_{til} + \sum_{i=0}^1 \Delta \text{Til}_i$	Tiller number	(tiller m <sup>-2</sup> )
$R_{T1} = \max[0, 0.335 - 0.067 \text{ LAI}] f(T)$ ; for $0 < t_m < 8$ ( $t_m$ : days after mowing)	Site filling	(tiller leaf <sup>-1</sup> )
$R_{T1} = \max[0, \min[F_{s_{max}}, 0.867 - 0.183 \text{ LAI}] f(T)]$ ; for $t_m > 8$		(tiller leaf <sup>-1</sup> )
$R_{Td} = \max[0.01 (1 + \text{DVS}), 0.03 [\text{LAI}(t) - \text{LAI}_{cr}]/\text{LAI}_{cr}]$	Tillering death rate	(tiller leaf <sup>-1</sup> )
$\Delta \text{Til}(t) = \Delta L_v(t) \text{ Til}_{(t-1)} (R_{T1} - R_{Td}) \min[1, W_{storage}/W_{stormax}]$	Tiller number increase	(tiller m <sup>-2</sup> day <sup>-1</sup> )

## Leaf area increase

Equations	Description	Units
$\Delta \text{LAI} = \text{SLA } f(lv) \Delta W - \Delta \text{LAI}_d$	Leaf area index increase	(m <sup>2</sup> day <sup>-1</sup> )
$\Delta \text{LAI}_d = \text{LAI}(t) (1 - e^{-\text{RDL } t_m})$	Death rate of leaf area	(m <sup>2</sup> day <sup>-1</sup> )
$t_m$ = days after defoliation		(day)
$\text{RDL} = \max[\text{Rd}_{sh}, \text{Rd}_{wt}]$	Relative death rate of leaf area	(day <sup>-1</sup> )
$\text{Rd}_{sh} = 0.01 + \min[0.03, 0.03 [\text{LAI}(t) - \text{LAI}_{cr}]/\text{LAI}_{cr}]$	Relative death rate due to shading	(day <sup>-1</sup> )
$\text{Rd}_{wt} = 0.01 + 0.05 [1 - f(\text{wt})]$	Relative death rate due to water shortage	(day <sup>-1</sup> )

## Water balance

Equations	Description	Units
$\Delta S = \text{Rain} - \text{Evap} - T_a - \text{Perc}$	Daily change in soil moisture content	(mm day <sup>-1</sup> )
Rain	Daily precipitation	(mm day <sup>-1</sup> )
Evap	Soil evaporation	(mm day <sup>-1</sup> )
$T_a$	Actual transpiration by the sward	(mm day <sup>-1</sup> )
Perc	Percolation out of the rooting zone	(mm day <sup>-1</sup> )
$E_{\text{mak}} = \text{Rad } 0.63s / (\lambda s + \lambda \gamma)$	Makkink formula for evapotranspiration of grass	(mm day <sup>-1</sup> )
Rad	Downward flux of shortwave radiation	(MJ m <sup>-2</sup> day <sup>-1</sup> )
$s$	Slope of saturated vapour pressure against temperature	(kPa °C <sup>-1</sup> )
$\gamma$	Psychrometric constant	(kPa °C <sup>-1</sup> )
$\lambda$	Latent heat of water evaporation	(MJ kg <sup>-1</sup> )
$T_p = Kc E_{\text{mak}} [1 - e^{(0.75K \text{ LAI})}]$	Potential transpiration; $Kc = 1$	(mm day <sup>-1</sup> )

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