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Empirical and dynamic approaches for modelling the yield and N content of European grasslands

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ABSTRACT

We applied two approaches to model grassland yield and nitrogen (N) content. The first was a series of regression equations; the second was the Century dynamic model. The regression model was generated from data from eighty-nine experimental sites across Europe, distinguishing between five climatic regions. The Century model was applied to six sites across these regions. Both approaches estimated mean grassland yields and N content reasonably well, though the root mean squared error tended to be lower for the dynamic model. The regression model achieved better correlations between observed and predicted values. Both models were more sensitive to uncertainties in weather than in soil properties, with precipitation often accounting for the majority of model uncertainty. The regression approach is applicable over large spatial scales but lacks precision, making it suitable for considering general trends. Century is better applied at a local level where more detailed and specific analysis is required.

1. Introduction

Effective grassland models allow researchers to evaluate different management strategies, predict how the productivity and quality of grassland will change over time, anticipate the consequences of climate change and generally gain a better understanding of grassland ecosystems. Different types of models have different ranges of applicability and effectiveness. Some are applicable over wide spatial scales while others are site-specific. Some work well in certain regions but are less useful in other areas. Our research considers two very different approaches to modelling. The first is an empirical model generated through stepwise regression on climatic, locational and managerial variables, and the second is a process-based dynamic model, namely Century, described by Parton et al. (1987).

Empirical pasture models may be site-specific or they can be applied at a larger (e.g. regional or national) scale (Armstrong et al., 1997; Hurtado-Uria et al., 2014; Trnka et al., 2006). These are simpler and therefore faster and less computationally demanding than process-based models and require less input data. Qi et al. (2017) compared the outputs of a process-based model for the productivity of several grassland sites in the UK with those of an empirical meta-model derived from the outputs of the same process-based model. While the empirical model accounted for less variation (as would be expected), it still produced 'sufficiently precise' estimations of pasture yield. There are disadvantages of empirical models. Unlike dynamic models, they are restricted to a single output (Qi et al., 2017). They are subject to issues with co-linearity between predictor variables and they assume that past relationships will hold in the future (Lobell and Burke, 2010). They are also only applicable within the confines of the experiments which contributed to their development, i.e. they cannot be used to predict grassland yield or quality under climate or management conditions different from those original experiments. Despite the drawbacks of this method, it is still useful in determining trends in grassland responses to weather and management variation.

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Dynamic models simulate the different processes in a system, looking at how the system changes over time. They can be seen as being more biologically realistic than empirical models. They are usually applied to a single site (or several homogeneous sites) and require a large number of inputs. Korhonen et al. (2018) applied several different dynamic models to timothy grass swards in northern Europe and Canada and found that the more detailed the model, the more accurate the results. However, highly detailed models require large amounts of input data, making it difficult to apply more complex models to sites where only limited data is available. The wide variety of grassland ecosystems also makes it difficult to develop a one-size-fits-all model. While models can be parametrised to individual sites, there will always be areas where they function less well (Trnka et al., 2006). A broad range of dynamic models exists for modelling grasslands, as summarised by Bellocchi et al. (2013) and Chang et al. (2013). We chose to use the Century model; this is a tool for ecosystem analysis and can be applied to croplands, forests and grasslands. It has a focus on carbon, nitrogen and water fluxes in the plant-soil system and runs on a monthly time-step; it also allows for complex agricultural management practices (Metherell et al., 1993). It was selected because the grassland part of the model is relatively simple and requires fewer inputs than many other dynamic grassland models, it can be applied to a diverse range of grasslands, and also because it has a relatively fast run-time. A daily version of Century exists (DailyDayCent), but this takes considerably longer to run and requires more input information. Having a (relatively) small number of inputs makes it easier to implement the model on a range of sites, particularly as some sites have only very limited information available. The main relevant inputs are grassland type, temperature, precipitation, grassland management and soil properties. Century has predominantly been used to model soil carbon (C) and nitrogen (N) dynamics, though Parton et al. (1993) used it to model plant production at several grassland sites around the world. They found that the predictions were within 25% of the observations 60% of the time and that Century produced slightly higher R^2 values than empirical models. Century is designed to work on a wide range of ecosystems, meaning that it can be applied throughout Europe.

Other modelling approaches, such as ensemble modelling (Sándor et al., 2017) and integrated assessment modelling (Rose, 2014), were also considered. However we wished to prioritise fast run-times in order to be able to perform a detailed sensitivity analysis. We also wanted to minimise the input information required so that we could apply the models to as many sites as possible. The other approaches considered were not compatible with these goals.

In the present study we aim to evaluate the two modelling approaches (one statistical and one dynamic) in different climatic zones across Europe for both permanent and temporary grasslands, considering both yield (dry matter) production and N content. These outputs were chosen due to their importance to grassland-based livestock systems and also because while yield has been widely modelled with these methodologies, N content has not. No attempt has been made to develop regression equations to model grassland N content over large spatial scales. Similarly, Century has not generally been used to consider plant N content and so little is known about its effectiveness. This research will address these gaps and determine if regression and/or Century are effective ways of modelling grassland N content. We will also investigate the sensitivity of each model to input uncertainties and the circumstances under which each of the models performs best. This will inform future grassland modelling work by enabling researchers to better evaluate their results when using similar models for predictive purposes, such as looking at the effects of climate change or considering alternate management practices.

2. Methods

2.1. Data

Both approaches required data from grassland experiments across Europe. To be included, these experiments had to have recorded harvested plant dry matter and/or N content over a period of at least three years. The experimental data was assembled from published literature and through contacting experts and relevant institutions. The locations of these experiments are shown in Fig. 1. The sites were divided into five geographic regions (Alpine, Atlantic, continental, northern and southern). This regional classification is consistent with the climatic zones used by the Intergovernmental Panel on Climate Change (IPCC). Sites were also divided into permanent and temporary grasslands. Permanent grasslands are dominated by one or more species of grass, though may include many different plant types. They have been used continuously as grassland for at least five years. Temporary grasslands are usually 100% grass or else a grass/legume mixture and produce high yields. They have been used as grassland for less than five years. In making these divisions by region and grassland type, we aimed to account for as much of the existing variation in grasslands as possible, while still being able to group them in a manageable way. Furthermore, more data was usually available for the temporary sites than the permanent ones (in particular data on species composition), so by separating the two types we were able to do a more detailed analysis of temporary grasslands than would otherwise have been possible. The full list of sites can be found in appendix A. Monthly temperature and precipitation data for all sites was taken from the Climatic Research Unit gridded dataset (UEA CRU et al., 2017).

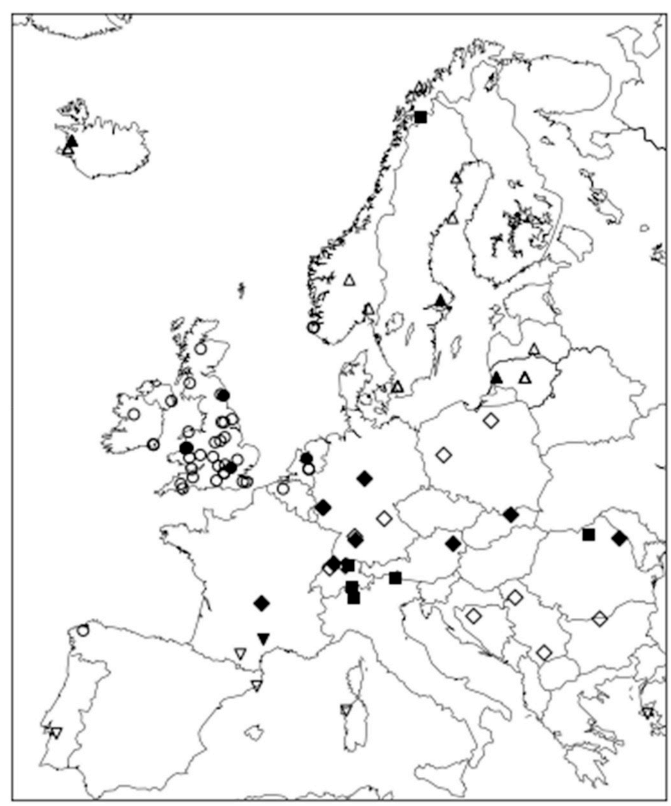

Fig. 1. Locations of sites used, by geographic region and grassland type. Regions are Alpine (■), Atlantic (●), Continental (◆), Northern (▲) and Southern (▼). Open shapes denote temporary grasslands, while solid shapes denote permanent grasslands.

2.2. Regression model

To ensure that no single site dominated the analysis, data from each experimental site was edited so that all those for a given region and grassland type contributed approximately the same number of data points. Each dataset was then divided into four quarters. Three quarters of the data from all datasets were used as input to a stepwise regression process in R (R Core Team, 2017). This was done separately for each grassland type and for both yield and N content, resulting in the following equations:

Yield, permanent grassland:

$$\text{Yield (t DM/ha)} = \alpha_0 + \alpha_{REGION} + \alpha_1 Rain_{JFM} + \alpha_2 Rain_{AMJ} + \alpha_3 Rain_{JA} + \alpha_4 Temp_{FM} + \alpha_5 Temp_{AMJ} + \alpha_6 Temp_{JA} + \alpha_7 Rain^2_{JFM} + \alpha_8 Rain^2_{AMJ} + \alpha_9 Rain^2_{JA} + \alpha_{10} Temp^2_{JA} + \alpha_{11} Altitude + \alpha_{12} Cuts + \alpha_{13} NF + \alpha_{14} Cuts^2 + \alpha_{15} NF^2 + \alpha_{16} NF{*}Rain_{JFM} + \alpha_{17} NF{*}Temp_{JA}$$

Applicable to the Alpine, Atlantic, continental and northern regions.

Yield, temporary grassland:

$$\text{Yield (tDM/ha)} = \beta_0 + \beta_{REGION} + \beta_1 Rain_{JFM} + \beta_2 Rain_{AMJ} + \beta_3 Rain_{JA} + \beta_4 Temp_{JF} + \beta_5 Temp_{MA} + \beta_6 Temp_{MJ} + \beta_7 Temp_{JA} + \beta_8 Rain^2_{JFM} + \beta_9 Rain^2_{AMJ} + \beta_{10} Rain^2_{JA} + \beta_{11} Temp^2_{MJ} + \beta_{12} Temp^2_{JA} + \beta_{13} Altitude + \beta_{14} Cuts + \beta_{15} Legume + \beta_{16} NF + \beta_{17} Altitude^2 + \beta_{18} Cuts^2 + \beta_{19} Legume^2 + \beta_{20} NF^2 + \beta_{21} NF{*}Rain_{JA} + \beta_{22} NF{*}Cuts$$

Applicable to the Atlantic, continental, northern and southern regions.

N content, permanent grassland:

$$\text{N content (kg/ha)} = \gamma_0 + \gamma_1 Rain_{March} + \gamma_2 Rain_{AM} + \gamma_3 Rain_{JJA} + \gamma_4 Temp_{January} + \gamma_5 Temp_{August} + \gamma_6 Rain^2_{March} + \gamma_7 Rain^2_{JJA} + \gamma_8 Altitude + \gamma_9 Cuts + \gamma_{10} Cuts^2 + \gamma_{11} NF + \gamma_{12} NF{*}Rain_{March} + \gamma_{13} NF{*}Temp_{January} + \gamma_{14} NF{*}Temp_{August} + \gamma_{15} NF{*}Cuts$$

Applicable to the continental region.

N content, temporary grassland:

$$\text{N content (kg/ha)} = \delta_0 + \delta_{REGION} + \delta_1 Rain_{AM} + \delta_2 Rain_{JJA} + \delta_3 Temp_{JF} + \delta_4 Temp_{MA} + \delta_5 Temp_{JJA} + \delta_6 Rain^2_{AM} + \delta_7 Rain^2_{JJA} + \delta_8 Temp^2_{JF} + \delta_9 Temp^2_{MA} + \delta_{10} Temp^2_{JJA} + \delta_{11} Altitude + \delta_{12} Cuts + \delta_{13} Legume + \delta_{14} NF + \delta_{15} Altitude^2 + \delta_{16} Cuts^2 + \delta_{17} Legume^2 + \delta_{18} NF^2 + \delta_{19} NF\ {*}TempMA + \delta 20NF{*}Cuts$$

Applicable to the Atlantic, continental and northern regions.

Coefficients for these equations are listed in appendix B.

Subscripts indicate months of the year, for example $Rain_{AM}$ is total rainfall in April and May, $Temp_{JJA}$ is average temperature in June, July and August.

Altitude is measured in metres.

'Cuts' indicates the number of harvests per year.

'Legume' is the percentage of nitrogen-fixing plants at seeding, for example 5% would be taken as 5.0 in the equation.

'NF' is the amount of nitrogen fertiliser used per year (kg N/ha).

These equations are only applicable to certain regions due to the availability of data for developing the equations.

The remaining quarter of the data was used for validation. The process was then repeated a further three times, with a different quarter being used for validation each time. This permutational approach helps to prevent over-fitting and allows standard errors of the resulting root mean squared errors (RMSEs) and correlations to be calculated.

2.3. Century model

While the Century model requires relatively little input information compared with many other dynamic ecosystem models, it still requires certain site-specific information and sufficient data for model parameterisation. Very few sites met all the necessary requirements. Six sites were eventually selected based on the availability of necessary information and also to ensure a range of sites from different regions and of different grassland types. The selected sites are listed in Table 1. The model was only applied to one temporary grassland site; this was because temporary grassland experiments tended to be of much shorter duration and there was insufficient data to parameterise the model. At the selected site (Hurley, UK), data from each of seven annual harvests was available, rather than just an annual total. Harvested yield was measured at all sites, but N content was only measured in four of the six experiments.

In order to optimally parameterise the Century model, the input parameters having the greatest effect on plant yield and N content were first identified. This was done through a review of relevant literature (Necpálová et al., 2015; Rafique et al., 2015; Wang et al., 2013; Wu et al., 2014), expert consultation and preliminary data analysis. The sensitivity of the model to each suggested parameter was tested by checking how much the predicted yield and N content changed when the parameter was varied within a reasonable range. The identified relevant parameters are shown in Table 2.

Parameters representing the effects of temperature on growth (PPDF (1–4)) were often cited in the literature as being particularly relevant. However it was found that including them in the optimisation process often led to over-fitting and produced unrealistic predictions when the model was applied to anything other than the original experimental conditions. Instead, reasonable values for these parameters were chosen based on preliminary model runs on the available data and Century documentation.

Table 2
Century model parameters for optimisation.

Parameter	Description
PRDX(1)	Coefficient for calculating potential aboveground monthly production
PRAMN(1,1), PRAMX(1,1)	Minimum and maximum C/N ratio with zero biomass
PRAMN(1,2), PRAMX(1,2)	Minimum and maximum C/N ratio when biomass exceeds a given threshold
TEFF(1–4)	Temperature effect on soil decomposition
FWLOSS(4)	Scaling factor for interception and evaporation of precipitation by live and standing dead biomass
EPNFA(1–2)	Intercept and slope for determining the effect of annual precipitation on atmospheric N fixation
EPNFS(1–2)	Values for determining the effect of annual evapotranspiration on non-symbiotic soil N fixation
CFRTCN(1–2)	Maximum fraction of C allocated to roots under maximum and no nutrient stress
CFRTCW(1–2)	Maximum fraction of C allocated to roots under maximum and no water stress
SNFXMX(1)	Symbiotic N fixation

Table 1
Sites to which the Century model has been applied.

Site, Country	Geographic region	Grassland type	Fertiliser treatments (kg N ha^{-1} a^{-1})	Plant N content available?	Experiment duration (years)
Eschikon, Switzerland	Alpine	Permanent	140/560	Yes	10
Hurley, UK	Atlantic	Temporary	0/150	Yes	4
Rothamsted, UK	Atlantic	Permanent	0/144	No	58
Göttingen, Germany	Continental	Permanent	0/equal to that removed the previous year	Yes	40
Hvanneyri, Iceland	Northern	Permanent	0/100	Yes	25
Larzac Causse, France	Southern	Permanent	0/65	No	25

For each site, optimal values for the parameters were attained through Markov Chain Monte Carlo (MCMC) optimisation using the L-BFGS-B algorithm within the Python SciPy module (Jones et al., 2001). The optimisation routine minimised the total error X where:

$$X = SoilC + \sum_i (Y_i + N_i)$$

$$Y_i = RMSE(P_Y, O_Y) \,/\, \overline{O_Y} \text{ for fertiliser treatment } i.$$

$$N_i = RMSE(P_N, O_N) \,/\, \overline{O_N} \text{ for fertiliser treatment } i.$$

RMSE(a,b) is the root mean squared error between a and b.

P_Y and P_N are the model predictions for yield and plant N content.

O_Y and O_N are the experimental observations for yield and plant N content.

$\overline{O_Y}$ and $\overline{O_N}$ are the mean experimental observations for yield and plant N content.

$$SoilC = (100 * \text{gradient of total soil carbon at end of spin-up period})^3.$$

A Century simulation begins with a long spin-up period which allows the system to stabilise before the experimental period begins. By including the gradient of total soil carbon at the end of the spin-up period as part of the error term, we ensured that the parameter values chosen enable this stabilisation to be achieved. This precise choice of gradient term was achieved through trial-and-error and is designed not to dominate the error term (X) while still achieving a sufficiently stable state.

The optimisation procedure was run for multiple management regimes (e.g. varying fertiliser treatments, mowing frequency, grazing intensity, etc., depending on the availability of measured data) simultaneously in order to obtain a single set of optimal parameters for each site, applicable to all situations.

2.4. Model fit

To assess the goodness-of-fit of the Century model, predicted and observed values for average yield and N content were compared, and corresponding standard errors were evaluated. In addition, the RMSE and correlation between predicted and observed yields and N content were calculated for both models and the RMSE were divided into bias and variance terms.

2.5. Sensitivity analysis

We looked at the sensitivity of the model predictions to uncertainty in different input parameters. These are shown in Table 3, along with ranges for their potential uncertainty (based on Fitton et al. (2014) and Gottschalk et al. (2007)).

These parameters are prone to measurement errors, or else were estimated from other sources rather than being measured on-site, and could lead to inaccuracies. Such errors have the potential to propagate through the models and influence the results. By conducting a sensitivity analysis, we determine how uncertainties in each input affect uncertainty in our modelled estimates.

Table 3
Parameters tested as part of the sensitivity analysis and corresponding uncertainly ranges.

Parameter	Uncertainty range	Model in which the sensitivity of the parameter is tested
Precipitation	±30 mm per month	Regression and Century
Temperature	±1 °C	Regression and Century
Legume percentage	±25%	Regression
Soil pH	±1.5 pH unit	Century
Soil clay content	±30%	Century
Soil bulk density	±0.3 g/cm^3	Century

For both models, we calculated the contribution of each parameter as a percentage of the total uncertainty. To do this, we first calculated the standard deviation in the total uncertainty (σ_g) when varying all parameters simultaneously within their uncertainty ranges. This was done by running the model until σ_g converged (approximately 5000 runs), with different combinations of parameters in each run. The choice of parameter values was determined using Latin hypercube sampling for reasons of computational efficiency, which was implemented in Python. We repeated this process multiple times, now keeping one parameter at its original value while allowing the others to vary. This allowed us to calculate the standard deviation in the simulations with parameter i set to its original value (σ_i). These values were used to calculate the contribution index (c_i) for each parameter i as follows:

$$c_i = \frac{\sigma_g - \sigma_i}{\sum_{i=1}^{i_{max}} \sigma_g - \sigma_i} \times 100$$

where $i_{\max}$ is the number of input parameters varied. The higher the c_i, the greater the contribution of that parameter to the total uncertainty. This methodology is based on that of Gottschalk et al. (2007). For the regression model we performed this process twice for each regression equation and each region, once with the average fertiliser level from the experiments conducted in that region and once with no fertiliser. The weather inputs were the monthly averages from the original experiments for the given region. For Century we performed this process for each fertiliser level used in the original experiments (Table 1).

For the Century model we also investigated the linearity of the uncertainty propagation for each parameter. This was not necessary for the regression models since the linearity is obvious from the equations. For each parameter we ran the model ten times, setting the parameter to ten equally-spaced steps within the uncertainty range, while leaving the other parameters at their original values. We then found the best-fit regression (using R) between the change in yield or N content from the original prediction and the parameter value (with terms of different orders). For example, for soil pH:

$$\text{Change in model prediction} = \alpha_0 + \alpha_1 * pH + \alpha_2 * pH^2 + \alpha_3 * pH^3 + \alpha_4 * pH^4$$

By comparing the R^2 values of this regression equation with an equivalent linear equation and by seeing which of the α_i were statistically significant ($p < 0.05$), we could determine the linearity (or non-linearity) of the model's response to uncertainty in a given parameter. This was done for each of the five parameters and the analysis was performed separately for each site and fertiliser treatment. This methodology is based on that of Fitton et al. (2014) and Hastings et al. (2010).

3. Results

3.1. Regression model

Looking at the coefficients of the regression equations (Appendix B), some trends become apparent. For both yield and N content, rainfall usually has a positive effect, but when these terms are squared they are usually negative, suggesting that exceptionally high rainfall decreases yield and N content. Higher spring temperatures lead to higher yields, while higher winter temperatures lead to reduced N content and higher summer temperatures increase it. More cuts per year implies high yields and N content, but only up to a certain point, with the $cuts^2$ term always being negative, indicating that excessive harvests reduce yield and N content. A similar effect was seen for legume percentage in temporary grasslands, with both yield and N content increasing up to a certain threshold, beyond which they begin to decrease.

The goodness-of-fit of the equations is evaluated in Table 4. In all cases, the fit was reasonably good, with high correlations but also relatively high RMSEs, though the latter were due entirely to variation

Table 4
Goodness-of-fit of regression model equations.

	Grassland type	R^2 *(SE)*	Correlation *(SE)*	Root mean squared error as a percentage of mean observed value *(percentage of which is due to bias)*
Yield	Permanent	0.59 *(0.00)*	0.76 *(0.01)*	40.5 *(0.0)*
	Temporary	0.59 *(0.00)*	0.76 *(0.01)*	34.6 *(0.0)*
N content	Permanent	0.72 *(0.04)*	0.80 *(0.03)*	37.6 *(0.2)*
	Temporary	0.80 *(0.00)*	*1.89 (0.00)*	28.1 *(0.0)*

rather than bias. The equations for N content had better fit than those for yield, having higher R^2 values and correlations. The models were usually similarly good for permanent and temporary grasslands, though the RMSEs for permanent grasslands were slightly higher than those for temporary.

3.2. Century model

The goodness-of-fit of the parameterised models is shown in Table 5. The observed and predicted means were usually very close to one another, as such the RMSE tended to be dominated by variance rather than bias. The correlations between predictions and observations showed more variation, ranging from no correlation (Iceland) to quite high correlation (Hurley). It should also be noted that the standard errors of the predicted means were always less than those of the observed means (for both yield and N content). The predictions showed considerably less inter-annual variation than there was in reality.

For yield, the greatest discrepancies between observed and predicted means were in the Atlantic region when fertiliser was used. This region also had some of the highest RMSEs (for permanent grasslands), though many of the RMSEs were quite high. Two sites exhibited no correlation between observed and predicted yields, these being the Alpine site with fertiliser and the northern site without fertiliser. For N content, the model performed very well for the Atlantic site, though it is not clear if this is due to the region or due to it being the only temporary grassland in the analysis. The model also performed well for the Alpine site under the low fertiliser treatment. The model was less successful at predicting N content in the continental and northern regions and was particularly poor in the northern region when no fertiliser was used, where there was a large discrepancy between the predicted and observed means, a high RMSE and no correlation.

Overall the dynamic model performed best in the Atlantic region (especially for the temporary grassland site) and particularly poorly in the Alpine region with high fertiliser use and the northern region with no fertiliser use.

3.3. Sensitivity analysis

3.3.1. Regression model

The sensitivity analysis results for the regression model are shown in Table 6. There was no apparent difference in the variation of yield and N content between the fertiliser treatments when the input parameters were varied. There was a much higher level of variation for southern temporary grasslands than in other regions. While it appears that temporary grasslands exhibit more variation than permanent ones, these are not comparable as the regression equations for permanent grasslands do not account for legume percentage and so this could not be varied.

Uncertainty associated with precipitation measurements was by far the largest contributor to total uncertainty, often accounting for more than 80%. The exception was for yields of permanent grasslands in the continental region, where temperature uncertainties had much more of an influence. The contribution indices show that there was generally very little difference between the distribution of uncertainty in the fertilised and unfertilised cases, though there were large differences in these distributions for yields of permanent grasslands in the Atlantic and continental regions.

3.3.2. Century model

The standard deviations of the total uncertainty (σ_g) for each site are shown in Fig. 2. There was considerably more variation at the Atlantic permanent site than at any of the others, while for the Atlantic temporary site the variation was very small. The contribution indices for each site are shown in Fig. 3. Overall, the weather parameters made the greatest contribution to the total uncertainty, with the soil parameters often contributing a negligible amount. Uncertainty in the yield results was usually due to the same input parameters as uncertainty in the N

Table 5
Goodness-of-fit of the Century model, parameterised for different sites. O_Y and P_Y are observed and predicted yields, O_N and P_N and observed and predicted plant N content, $\bar{O}_Y$ and $\bar{O}_N$ are mean observed yield and N content. All results are based on total annual harvested dry weight, except for the root mean square error and correlation for Hurley, which were calculated from individual harvests.

Site	Fertiliser treatment (kg N ha^{-1} a^{-1})	Mean *(SE)* observed yield (t DM ha^{-1} a^{-1})	Mean *(SE)* predicted yield (t DM ha^{-1} a^{-1})	Root mean squared error between O_Y and P_Y as percentage of $\bar{O}_Y$ *(Percentage of which is due to bias)*	Correlation between O_Y and P_Y	Mean *(SE)* observed N content (kg ha^{-1} a^{-1})	Mean *(SE)* predicted N content (kg ha^{-1} a^{-1})	Root mean squared error between O_N and P_N as percentage of $\bar{O}_N$ *(Percentage of which is due to bias)*	Correlation between O_N and P_N
Eschikon,	140	6.85 *(0.38)*	6.93 *(0.10)*	14.8 *(0.6)*	0.53	141.2 *(8.9)*	148.0 *(2.9)*	18.9 *(6.6)*	0.28
Switzerland	560	12.16 *(0.95)*	12.15 *(0.13)*	23.5 *(0.0)*	0.06	381.4 *(41.5)*	346.9 *(9.3)*	33.2 *(7.5)*	0.21
Hurley, UK	0	1.82 *(0.56)*	1.62 *(0.39)*	13.8 *(1.4)*	0.74	34.6 *(9.1)*	28.1 *(6.5)*	13.6 *(5.9)*	0.77
	150	4.76 *(0.88)*	6.37 *(0.29)*	14.8 *(10.7)*	0.57	99.7 *(18.0)*	81.3 *(5.1)*	15.1 *(4.6)*	0.54
Rothamsted,	0	2.72 *(0.16)*	2.93 *(0.04)*	41.7 *(3.5)*	0.36	NA	42.7 *(0.8)*	NA	NA
UK	144	6.86 *(0.25)*	5.76 *(0.07)*	30.6 *(27.2)*	0.33	NA	155.3 *(1.8)*	NA	NA
Göttingen,	0	3.56 *(0.21)*	3.53 *(0.03)*	35.0 *(0.1)*	0.20	34.1 *(2.3)*	35.1 *(0.5)*	41.7 *(0.58)*	0.12
Germany	Equal to previous year's N removal	6.33 *(0.31)*	6.37 *(0.10)*	25.5 *(0.1)*	0.61	135.0 *(6.7)*	107.6 *(3.4)*	31.1 *(42.7)*	0.68
Hvanneyri,	0	5.73 *(0.40)*	6.29 *(0.06)*	35.9 *(7.2)*	−0.04	82.5 *(6.8)*	66.4 *(1.3)*	45.3 *(18.7)*	0.04
Iceland	100	7.64 *(0.23)*	7.30 *(0.04)*	14.8 *(9.3)*	0.23	126.3 *(4.5)*	124.2 *(1.3)*	19.2 *(0.8)*	−0.23
Larzac	0	1.57 *(0.11)*	1.55 *(0.04)*	21.6 *(0.2)*	0.63	NA	10.0 *(0.4)*	NA	NA
Causse, France	65	5.25 *(0.29)*	5.31 *(0.07)*	25.7 *(0.2)*	0.36	NA	47.1 *(0.8)*	NA	NA

Table 6
Standard deviation of the total uncertainty (σ_g, units are t/ha for yield and kg/ha for N content) and contribution indices (c_i) for temperature, precipitation and legume percentage, indicating the contribution of each parameter to the total uncertainty in the regression equations.

		Average fertiliser				No fertiliser			
Grassland type	Region	σ_g	c_{Temp}	c_{Prec}	c_{Leg}	σ_g	c_{Temp}	c_{Prec}	c_{Leg}
Yield									
Temporary	Atlantic	0.70	3%	96%	1%	0.38	10%	89%	1%
	Continental	0.48	1%	89%	10%	0.41	0%	85%	15%
	Northern	0.83	0%	97%	3%	0.74	1%	94%	4%
	Southern	1.25	1%	98%	1%	1.19	0%	99%	1%
Permanent	Alpine	0.34	7%	93%	*NA*	0.18	1%	99%	*NA*
	Atlantic	0.24	36%	64%	*NA*	0.36	2%	98%	*NA*
	Continental	0.21	97%	3%	*NA*	0.18	51%	49%	*NA*
	Northern	0.37	0%	100%	*NA*	0.49	1%	99%	*NA*
N content									
Temporary	Atlantic	27.6	0%	100%	0%	29.9	11%	88%	0%
	Continental	19.9	5%	84%	11%	20.8	11%	78%	11%
	Northern	32.5	0%	98%	1%	32.6	0%	98%	2%
Permanent	Continental	7.9	1%	99%	*NA*	7.0	6%	94%	*NA*

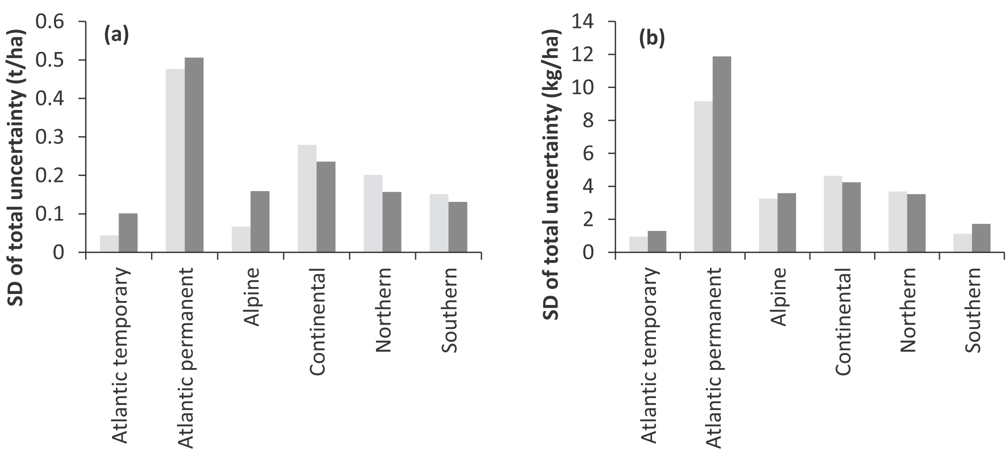

Fig. 2. Standard deviations of the total uncertainty in (a) yield and (b) N content predictions in the Century model when precipitation, temperature, soil pH, soil clay content and soil bulk density are allowed to vary. Light grey bars denote the no/low fertiliser treatment, dark grey bars denote the with/high fertiliser treatment.

content results, though the Alpine site was a notable exception to this. Here the yield uncertainty was almost exclusively due to temperature variations (93–98%), while for N content it was almost exclusively due to uncertainties in the precipitation amount (94–96%). For the Atlantic permanent and continental sites, most of the uncertainty was due to potential precipitation errors (66–99%), while for the northern region it was primarily due to potential temperature errors (51–88%). Results for the Atlantic temporary and southern sites were more mixed, with no one parameter dominating the uncertainty and with very different combinations of parameters making up the uncertainty for yield and N content and for the different fertiliser treatments, though neither site was sensitive to variations in soil pH.

When each parameter was varied individually, the results for yield and N content were very similar. Changing soil pH generally had very little effect on either yield or N content, except at the Atlantic permanent site where reducing soil pH led to large increases in both yield and N content (+26% and +44% respectively). Varying the soil clay content also had little influence, except at the southern European site where it did have an effect, particularly for yield when no fertiliser was used (ranging from a 7% increase with decreasing clay content to an 8% decrease with increasing clay content). Here the uncertainty propagation was linear when fertiliser was used, but non-linear without fertiliser. Varying soil bulk density led to some small changes in plant yield and N content, again this was most noticeable at the southern site with no fertiliser (9% yield increase and 12% N content increase when bulk density is increased). Plant responses to uncertainty in bulk density were usually linear. Changing precipitation amounts had an effect at all sites and the uncertainty propagation was always non-linear (except for N content at the Alpine site). Reductions in precipitation nearly always led to decreases in both yield and N content, while increasing precipitation generally led to either increasing yields and N content or else very little change. The strongest responses were at the Atlantic permanent, continental and southern sites (the largest being a 42% decrease in N content at the Atlantic permanent site with decreasing precipitation). For temperature, the results were very mixed. There tended to be a greater response to changes in temperature under the no/low fertiliser treatments, though the direction of the response varied between the sites. The uncertainty propagation was always linear at the northern site and always non-linear at the continental and Atlantic temporary sites, but varied for the other locations. Full results can be found in the supplementary materials.

4. Discussion

The present study set out to model the yield and N content of European grasslands using both a statistical (regression) and a dynamic model approach. The models' goodness of fit and sensitivity to input uncertainties were considered. The results presented above address these objectives.

4.1. Regression model

Looking at the R^2 values and the correlations for the regression equations, there was a very good fit with the observed data. Also the

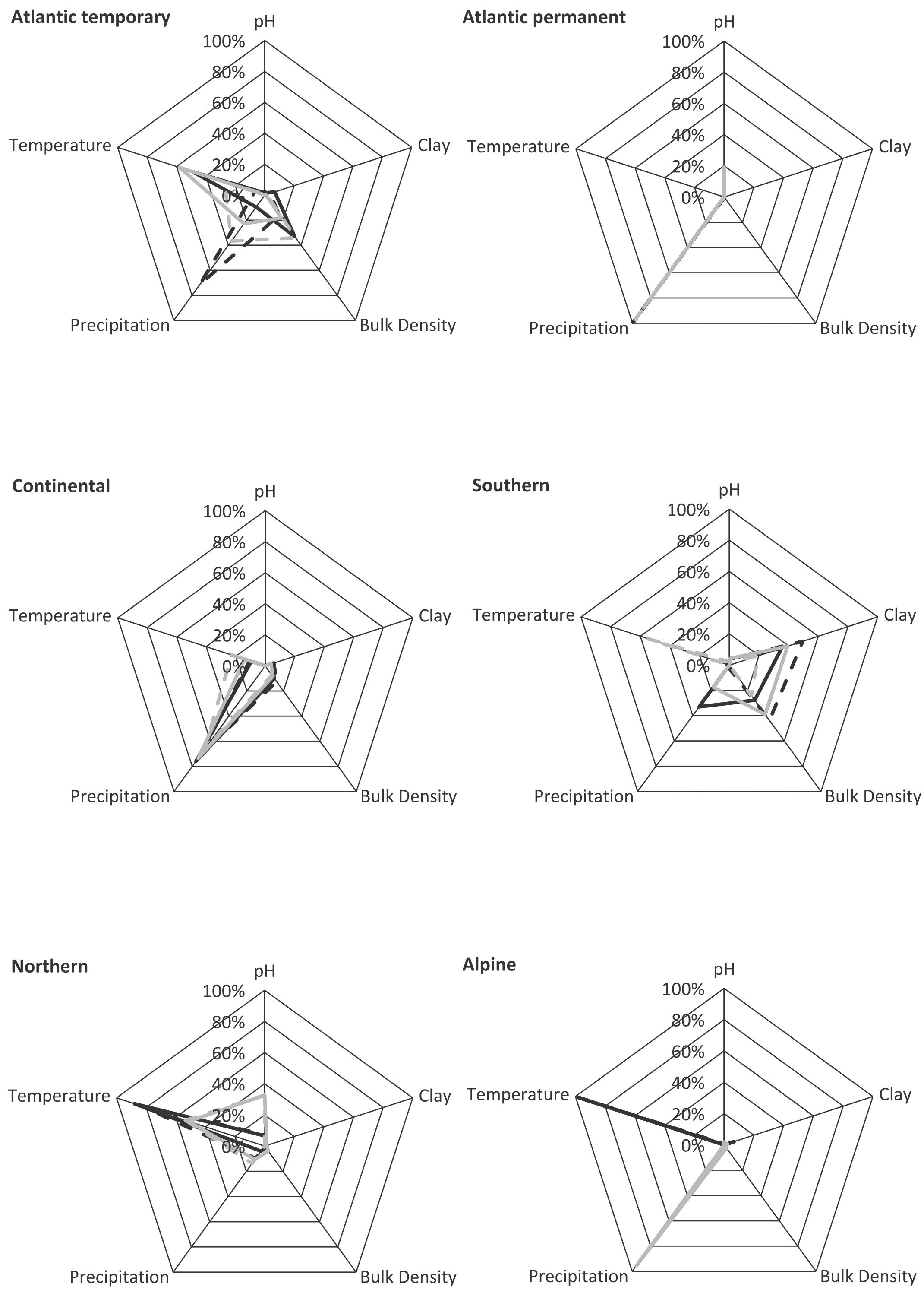

Fig. 3. Contribution indices, representing the contribution of each parameter to the total uncertainty, for the six sites to which the Century model has been applied. Black lines indicate results for yield and grey lines results for N content. Solid lines indicate the no/low fertiliser treatment and dashed lines indicate the with/high fertiliser treatment.

standard errors of these measures were very low, suggesting that the models were not over-fitted. However the RMSEs were relatively high, likely due to the considerable amount of variation amongst the experimental sites and the large geographical regions involved. It is not surprising that the equations for permanent grasslands produce higher RMSEs than those for temporary grasslands, since permanent grasslands tend to be more variable and have a higher degree of plant species diversity and are therefore less predictable. Several previous studies have found difficulties with using a linear regression methodology to relate plant yields with weather conditions, such as low signal-to-noise ratios (Lobell and Burke, 2010), large numbers of relevant variables and interactions of variables, many of which were correlated with one another or were non-linear, and extreme climatic events having an influence lasting multiple years (Jenkinson et al., 1994). These factors may also partly explain the high RMSEs, though it is encouraging that there was no evidence of bias in the results, suggesting that these regression equations can be a useful predictive tool, albeit one which produces relatively large confidence intervals.

4.2. Century model

For the Century model, there was more variance in the correlation coefficients than the error terms, as the optimisation process minimised the RMSE but did not look at correlation. The Hurley site had the largest discrepancies between predicted and observed annual totals. This is likely because this experiment took place over a much shorter duration than the others, so there were only four years of data to use for model parameterisation. It is also the only temporary grassland site, though without more temporary sites for comparison it is not clear if this has an influence on the fit of the model. It is encouraging that the observed and predicted means were usually quite similar, suggesting that while the model may struggle to capture inter-annual variation, it is producing the right value on average. The instances where there was little to no correlation between predictions and observations (sites in Iceland, Switzerland with high fertiliser and Germany with no fertiliser) are more concerning. While it is expected that the modelled results will not display the full range of inter-annual variation, because the model used monthly weather data rather than daily values, it is hoped that they should pick up the general trends. An absence of any correlation suggests that the model is not sufficiently capturing the effects of temperature and precipitation and these results should be treated with caution. For the Swiss site, the high fertiliser treatment is very high (560 kg N $ha^{-1}a^{-1}$) and it may be that this is causing the model to allow grass growth to reach its maximum potential every year, meaning it becomes relatively insensitive to weather. Parton et al. (1993) found a similar result (i.e. a lack of inter-annual variation) for some sites in Ukraine and Russia when using Century to model grassland live biomass, though for other sites the model was more effective. The use of a model with a monthly time-step rather than daily also means that the effect of rainfall distribution is not captured. A plant will respond differently to exceptionally heavy rain on one day than it will to the same amount of rain over a longer period. The use of a daily model would account for this and it would likely have a better fit than Century, though it would have a considerably longer run-time. While we considered using DailyDayCent (the daily version of Century) for this study, the time it takes to run would have meant that such in-depth parameterisation and sensitivity analysis would not have been possible.

The effectiveness of the Century model varied considerably between the sites, grassland types and fertiliser levels. There are indications that it performed less well in the Alpine and northern sites (two of the more climatically extreme locations) and better in the Atlantic region (where it is more temperate), but it is difficult to draw a firm conclusion from such a small number of sites. There is some evidence that dynamic crop models perform less well in mountainous areas or under stress conditions (Timsina and Humphreys, 2003; Xiong et al., 2008), so it may be that such models are generally more reliable in temperate regions.

4.3. Sensitivity analysis

Some general trends were apparent across the different sensitivity tests. The level and distribution of the uncertainty was usually about the same for different fertiliser treatments. This is consistent with the findings of Fitton et al. (2014) and suggests that there is no significant interaction between fertiliser use and the sensitivity of yield and N content to measurement uncertainties.

In terms of the linearity of the models' responses, the main causes of variation were uncertainties in precipitation and temperature measurements. For both models, the responses to these uncertainties were usually non-linear (for the regression model this is apparent from the equations). This is logical since plants' response to precipitation and temperature is non-linear in general, there being optimal values for growth beyond which plant performance will decrease.

The large effect of uncertainty in precipitation measurements is likely because errors in precipitation are cumulative. If the measurements are wrong by 1 mm a day then they can be wrong by up to 30 mm a month. For the regression equations, multiple months are grouped together, further multiplying the error. This is not the case for errors in temperature measurements, where an error of 1 °C in daily measurements will lead to the same error in average monthly measurements.

For the regression model, yield predictions for the southern region displayed a particularly high amount of variability when the inputs were varied and this was due almost exclusively to variations in the amount of precipitation. This region had by far the lowest amount of rainfall, suggesting that drier regions are more sensitive to uncertainties in rainfall measurements than wetter regions. This is likely because soil water reserves are lower in such areas and thus a reduction in rainfall has more effect on plant growth than it would in wetter regions. Southern Europe is predicted to become drier as a result of climate change (IPCC, 2013), suggesting that irrigation may become increasing necessary as these results suggest that water-limitation is already an issue.

For the Century model, when looking at the parameters individually the largest changes occurred when precipitation was varied and precipitation also often dominated the total uncertainty when the parameters were allowed to fluctuate simultaneously, the other major contributor to the uncertainty being temperature. When we identified the parameters having the greatest influence on plant yield and N content for the purposes of model parameterisation (Table 2), many of these related to temperature and precipitation effects. It is therefore consistent that the sensitivity analysis has shown that the model is more sensitive to weather parameters than soil properties. Plant production in the Century model is constrained by temperature and moisture (Metherell et al., 1993), which is likely why grass yields were so sensitive to variations in these parameters. Necpálová et al. (2015) found a similar sensitivity of crop productivity to temperature and soil moisture when applying DailyDayCent to a corn-soybean cropping system. This fits with areas where growth is typically limited by short growing seasons due to low temperatures, i.e. Alpine and northern regions, having most of their sensitivity being due to uncertainties in temperature measurements, while areas where growth is not temperature limited, e.g. Atlantic and continental regions, were more affected by uncertainties in precipitation measures. It is not clear why the Atlantic permanent site exhibited such a large degree of uncertainty compared with the other sites, though it is consistent with this site also having the largest RMSEs in its yield predictions (Table 5). This site does not experience such extreme climatic conditions as some of the others, suggesting that this uncertainty may be due to some local property, possibly relating to soil characteristics, management practices or species composition. It is possible that legumes in the plot are generating cyclical dynamics for which the model is not accounting.

A possible reason for the Century model's lack of sensitivity to soil properties is that the soil pools are stabilised during the spin-up period. A shorter spin-up time may lead to more uncertainty. In contrast, Fitton et al. (2014) found that crop yields are mostly sensitive to soil pH and not at all to uncertainties in precipitation or temperature. However they use a variation on the contribution index formula which will tend to give opposite results, suggesting that our findings are in agreement.

The results emphasise the need to ensure that weather measurements are as precise as possible, especially for precipitation. If at all possible, data from on-site weather stations should be used, rather than larger-scale estimates. On the other hand, estimations of soil parameters rather than direct measurements are acceptable, as small errors have little effect on the results.

4.4. Model comparison

Overall, there was a greater amount of uncertainty in the regression model predictions than those from the Century model (i.e. the standard deviation when the inputs were varied was higher for the regression model). This is likely because the Century model applies to a single site, whereas the regression models are valid over a large geographic region, meaning that they are considerably less precise. Similarly the RMSEs from the regression model were at the high end of the range of those produced by Century. On the other hand, the correlations between observed and predicted values from the regression results were higher than those from Century. This suggests that the regression approach is better at modelling trends in the annual response of grassland yields and N content to temperature and precipitation (since the correlations are so high), but it is less precise at predicting absolute values (due to the high sensitivity and large RMSEs).

In terms of the models' utility, the regression model is applicable over very large spatial scales, making it particularly useful for considering general trends, for example the impacts of climate change. However, because this model is purely statistical it cannot be used to extrapolate beyond the bounds of the experiments which were used in its development. Century is usually applied to a single site (or multiple homogeneous sites), which makes it more useful for local considerations, such as alterations to management practices. Because it is process-based, extrapolation to consider alternative scenarios is possible (to some extent). Applying the regression model to a single site would be problematic due to its imprecision, while applying Century to large spatial scales would require a huge amount of input data. Century and DailyDayCent have been applied over large scales using a gridded approach (e.g. Del Grosso et al. (2009)), but this leads to very approximate results and requires considerable effort to determine suitable input parameters.

The relative performance of the two models suggests that they each have their benefits and limitations and that users should carefully consider which approach is more appropriate for their needs.

Author contributions

M.D., C.T., A.d.P., G.P., G.B. and E.W. designed the research; M.D. performed the research and analysed the results; G.P. and N.F. advised on Century parameterisation, M.D. and D.H. wrote code for the models; M.D. wrote the paper; all other authors provided feedback on the paper.

Declaration of competing interest

None.

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Appendix C. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envsoft.2019.104562.

Appendix A. Sites used for regression modelling

Dataset/Location	Climatic region	Data available	Source
Permanent grasslands			
South Tyrol, Italy	Alpine	Yield	Peratoner et al. (2010)
Pojorata - Suceava County, Romania	Alpine	Yield	Samuil et al. (2011)
Kärkevagge valley, Sweden	Alpine	Yield	Olofsson and Shams (2007)
Negrentino and Pree, Switzerland	Alpine	Yield	Stampfli (2001)
Eschikon, Switzerland	Alpine	Yield	Schneider et al. (2004)
Rothamsted, England	Atlantic	Yield	*Private communication*
Cockle Park, England	Atlantic	Yield	Kidd et al. (2017)
Lelystad, the Netherlands	Atlantic	Yield	Schils and Snijders (2004)
Aberystwyth, Wales	Atlantic	Yield	Williams et al. (2003)
Vienna, Austria	Continental	Yield	Karrer (2011)
Auvergne, France	Continental	Yield	Klumpp et al. (2011)
Göttingen, Germany	Continental	Yield, N	*Private communication*
Stuttgart, Germany	Continental	Yield	Thumm and Tonn (2010)
Eifel Mountains, Germany	Continental	Yield	Schellberg et al. (1999)
Eifel Mountains, Germany	Continental	Yield	Hejcman et al. (2010)
Czarny Potok, Poland	Continental	Yield, N	Kopeć and Gondek (2014)
Iasi County, Romania	Continental	Yield	Samuil et al. (2009)
North-western Switzerland	Continental	Yield	Niklaus et al. (2001)
Hvanneyri, Iceland	Northern	Yield	Brynjólfsson (2008)
Vėžaičiai, Lithuania	Northern	Yield	Butkutė and Daugėlienė (2008)
Nåntuna, Sweden	Northern	Yield	Marissink et al. (2002)
Temporary grasslands			
The Agrodiversity Experiment, 24 sites used	Atlantic, Continental, Northern, Southern	Yield, N	Kirwan et al. (2014)
BIODEPTH, 5 sites used	Continental, Northern, Southern	Yield	Hector et al. (1999)

(*continued on next page*)

(*continued*)

Permanent grasslands			
Dataset/Location	Climatic region	Data available	Source
FAO sub-network for lowland grasslands, 10 sites used	Atlantic	Yield	*Private communication*
GM20, 21 sites across England and Wales	Atlantic	Yield, N	Morrison et al. (1980)
Novi Sad, Serbia Banja Luka, Bosnia & Hercegovina Pristina, Kosovo	Continental	Yield, N	Ćupina et al. (2017)
Pleven, Bulgaria	Continental	Yield	Vasilev (2012)
Tomaszkowo, Poland	Continental	N	Bałuch-Małecka and Olszewska (2007)
Central Latvia	Northern	Yield	Rancane et al. (2016)
Vėžaičiai, Lithuania	Northern	Yield	Skuodienė and Repšienė (2008)

Appendix B. Coefficients of regression equations

i	α_i	β_i	γ_i	δ_i
0	15.1128199	−19.9492871	−171.2297218	−379.6930803
REGION	Alpine:0 Atlantic: 3.2947027 Continental: 2.0093908 Northern: 2.8885051	Atlantic:0 Continental: 1.0002833 Northern: 2.3116753 Southern: 1.2554504	NA	Atlantic:0 Continental:5.2174092 Northern: 70.2426315
1	−0.0067281	0.0160201	0.2110533	0.5719420
2	0.0069159	0.0131461	0.1571394	1.2061140
3	0.0169409	0.0245117	0.5471275	−0.7157295
4	0.3917243	−0.2989545	−2.7136310	4.2274162
5	0.1889399	0.3006537	6.2716467	22.1656249
6	−1.3063298	−1.0667277	−0.0039319	−0.0021845
7	0.0000187	2.2108232	−0.0008956	−0.0017167
8	−0.0000175	−0.0000149	−0.0983881	0.6348516
9	−0.0000347	−0.0000487	16.5380800	1.2036786
10	0.0262419	−0.0000639	−1.2203143	−0.8367894
11	−0.0042733	0.0340660	1.4488548	0.0309453
12	1.3375788	−0.0556828	0.0010329	79.2531653
13	−0.0014676	−0.0133913	0.0217244	5.0620701
14	−0.1259848	3.7554609	−0.0436554	−0.0260712
15	−0.0000182	0.1696452	−0.0481049	0.0001132
16	−0.0000355	0.0075429		−11.4084793
17	0.0017150	0.0000353		−0.0657122
18		−0.4353109		−0.0004892
19		−0.0026230		−0.0538573
20		−0.0000339		0.1806854
21		0.0000369		
22		0.0033288		

References

Armstrong, H.M., Gordon, I.J., Grant, S.A., Hutchings, N.J., Milne, J.A., Sibbald, A.R., 1997. A model of the grazing of hill vegetation by the sheep in the UK. I. The prediction of vegetation biomass. J. Appl. Ecol. 34, 166–185. https://doi.org/10.2307/2404857.

Bałuch-Małecka, A., Olszewska, M., 2007. Efficiency of mineral fertilization of legume-grass mixtures under climatic conditions of the Olsztyn Lakeland. In: De Vliegher, A., Carlier, L. (Eds.), EGF 2007: Permanent and Temporary Grassland: Plant, Environment and Economy. EGF2007, pp. 150–153. Ghent, Belgium.

Bellocchi, G., Shaoxiu, M., Köchy, M., Braunmiller, K., 2013. Identified Grassland-Livestock Production Systems and Related Models (D-L2.1.1).

Brynjólfsson, R., 2008. Two long-term experiments in Hvanneyri, Iceland. In: Christensen, B.T., Petersen, J., Schacht, M. (Eds.), Long-Term Field Experiments-A Unique Research Platform. Proceedings of NJF Seminar 407. University of Aarhus, Askov Experimental Station and Sandbjerg Estate, pp. 44–47.

Butkutė, R., Daugėlienė, N., 2008. Study on long-term meadow productivity and botanical composition in response to different liming and fertilization. In: Hopkins, A., Gustafsson, T., Bertilsson, J., Dalin, G., Nilsdotter-Linde, N., Spörndly, E. (Eds.), EGF 2008: Biodiversity and Animal Feed - Future Challenges for Grassland Production. Organising Committee of the 22nd General Meeting of the European Grassland Federation. Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden, pp. 224–226.

Chang, J.F., Viovy, N., Vuichard, N., Ciais, P., Wang, T., Cozic, A., Lardy, R., Graux, A.-I., Klumpp, K., Martin, R., Soussana, J.-F., 2013. Incorporating grassland management in ORCHIDEE: model description and evaluation at 11 eddy-covariance sites in Europe. Geosci. Model Dev. (GMD) 6, 2165–2181. https://doi.org/10.5194/gmd-6-2165-2013.

Ćupina, B., Vujić, S., Krstić, D., Djurić, B., Aliu, S., Manojlović, M., Čabilovski, R., Lombnaes, P., 2017. Performance of legume–grass mixtures in the West Balkan region. Acta Agric. Scand. Sect. B Soil Plant Sci 67, 1–11. https://doi.org/10.1080/09064710.2016.1208268.

Del Grosso, S.J., Ojima, D.S., Parton, W.J., Stehfest, E., Heistemann, M., DeAngelo, B., Rose, S., 2009. Global scale DAYCENT model analysis of greenhouse gas emissions and mitigation strategies for cropped soils. Glob. Planet. Chang. 67, 44–50. https://doi.org/10.1016/J.GLOPLACHA.2008.12.006.

Fitton, N., Datta, A., Smith, K., Williams, J.R., Hastings, A., Kuhnert, M., Topp, C.F.E., Smith, P., 2014. Assessing the sensitivity of modelled estimates of N2O emissions and yield to input uncertainty at a UK cropland experimental site using the DailyDayCent model. Nutrient Cycl. Agroecosyst. 99, 119–133. https://doi.org/10.1007/s10705-014-9622-0.

Gottschalk, P., Wattenbach, M., Neftel, A., Fuhrer, J., Jones, M., Lanigan, G., Davis, P., Campbell, C., Sousanna, J.-F., Smith, P., 2007. The role of measurement uncertainties for the simulation of grassland net ecosystem exchange (NEE) in Europe. Agric. Ecosyst. Environ. 121, 175–185. https://doi.org/10.1016/j.agee.2006.12.026.

Hastings, A., Wattenbach, M., Eugster, W., Li, C., Buchmann, N., Smith, P., 2010. Uncertainty propagation in soil greenhouse gas emission models: an experiment using the DNDC model and at the Oensingen cropland site. Agric. Ecosyst. Environ. 136, 97–110. https://doi.org/10.1016/j.agee.2009.11.016.

Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Högberg, P., Huss-Danell, K., Joshi, J., Jumpponen, A., Körner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J., Scherer-Lorenzen, M., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S., Lawton, J.H., 1999. Plant diversity and productivity experiments in European grasslands. Science 80 (286), 1123–1127.

Hejcman, M., Schellberg, J., Pavlů, V., 2010. Long-term effects of cutting frequency and liming on soil chemical properties, biomass production and plant species composition of Lolio-Cynosuretum grassland after the cessation of fertilizer application. Source: Appl. Veg. Sci. 13 (3), 257–269.

Hurtado-Uria, C., Hennessy, D., Shalloo, L., O'Connor, D., Delaby, L., 2014. Relationships between meteorological data and grass growth over time in the south of Ireland. Ir. Geogr. 46, 175–201. https://doi.org/10.1080/00750778.2013.865364.
IPCC, 2013. Annex I: atlas of global and regional climate projections supplementary material RCP4.5. In: van Oldenborgh, G.J., Collins, M., Arblaster, J., Christensen, J. H., Marotzke, J., Power, S.B., Rummukainen, M., Zhou, T. (Eds.), Climate Change 2013: the Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, USA, pp. 1–158. AISM.
Jenkinson, D.S., Potts, J.M., Perry, J.N., Barnett, V., Coleman, K., Johnston, A.E., 1994. Trends in herbage yields over the last century on the Rothamsted long-term continuous hay experiment. J. Agric. Sci. 122, 365–374. https://doi.org/10.1017/S0021859600067290.
Jones, E., Oliphant, E., Peterson, P., Al, E., 2001. SciPy: Open Source Scientific Tools for Python.
Karrer, G., 2011. Dynamics of biomass production in extensively managed meadows at the eastern edge of the Alps. In: Pötsch, E., Krautzer, B., Hopkins, A. (Eds.), EGF 2011: Grassland Farming and Land Management Systems in Mountainous Regions. Organising Committee of the 16th Symposium of the European Grassland Federation 2011 and Agricultural Research and Education Centre (AREC). Raumberg-Gumpenstein, pp. 598–600.
Kidd, J., Manning, P., Simkin, J., Peacock, S., Stockdale, E., 2017. Impacts of 120 years of fertilizer addition on a temperate grassland ecosystem. PLoS One 12. https://doi.org/10.1371/journal.pone.0174632.
Kirwan, L., Connolly, J., Brophy, C., Baadshaug, O., Belanger, G., Black, A., Carnus, T., Collins, R., Čop, J., Delgado, I., De Vliegher, A., Elgersma, A., Frankow-Lindberg, B., Golinski, P., Grieu, P., Gustavsson, A.-M., Helgadóttir, Á., Höglind, M., Huguenin-Elie, O., Jørgensen, M., Kadžiulienė, Ž., Lunnan, T., Lüscher, A., Kurki, P., Porqueddu, C., Sebastia, M.-T., Thumm, U., Walmsley, D., Finn, J., 2014. The Agrodiversity Experiment: three years of data from a multisite study in intensively managed grasslands. Ecology 95, 2680. https://doi.org/10.1890/14-0170.1.
Klumpp, K., Tallec, T., Guix, N., Soussana, J.-F., 2011. Long-term impacts of agricultural practices and climatic variability on carbon storage in a permanent pasture. Glob. Chang. Biol. 17, 3534–3545. https://doi.org/10.1111/j.1365-2486.2011.02490.x.
Kopeć, M., Gondek, K., 2014. Attempt at an application of neural networks for assessment of the nitrogen content in meadow sward on the basis of long-term fertilizer experiments. J. Elem. 19, 127–136. https://doi.org/10.5601/jelem.2014.19.1.574.
Korhonen, P., Palosuo, T., Persson, T., Höglind, M., Jégo, G., Van Oijen, M., Gustavsson, A.-M., Bélanger, G., Virkajärvi, P., 2018. Modelling grass yields in northern climates – a comparison of three growth models for timothy. Field Crop. Res. 224, 37–47. https://doi.org/10.1016/J.FCR.2018.04.014.
Lobell, D.B., Burke, M.B., 2010. On the use of statistical models to predict crop yield responses to climate change. Agric. For. Meteorol. 150, 1443–1452. https://doi.org/10.1016/J.AGRFORMET.2010.07.008.
Marissink, M., Pettersson, R., Sindhøj, E., 2002. Above-ground Plant Production under Elevated Carbon Dioxide in a Swedish Semi-natural Grassland. Ecosystems and Environment.
Metherell, A.K., Harding, L.A., Cole, C.V., Parton, W.J., 1993. CENTURY Soil Organic Matter Model Environment: Technical Documentation v4.0.
Morrison, J., Jackson, M.V., Sparrow, P.E., 1980. The Response of Perennial Ryegrass to Fertilizer Nitrogen in Relation to Climate and Soil. Hurley, UK.
Necpálová, M., Anex, R., Fienen, M., Del Grosso, S., Castellano, M., Sawyer, J., Iqbal, J., Pantoja, J., Barker, D., 2015. Understanding the DayCent model: calibration, sensitivity, and identifiability through inverse modeling. Environ. Model. Softw 66, 110–130. https://doi.org/10.1016/J.ENVSOFT.2014.12.011.
Niklaus, P.A., Leadley, P.W., Schmid, B., Körner, C., 2001. A long-term field study on biodiversity x elevated CO2 interactions in grassland. Ecol. Monogr. 71, 341–356. https://doi.org/10.1890/0012-9615(2001)071[0341:ALTFSO]2.0.CO;2.
Olofsson, J., Shams, H., 2007. Determinants of plant species richness in an alpine meadow. J. Ecol. 95, 916–925. https://doi.org/10.1111/j.1365-2745.2007.01284.x.
Parton, W.J., Schimel, D.S., Cole, C.V., Ojima, D.S., 1987. Analysis of factors controlling soil organic matter levels in great plains grasslands. Soil Sci. Soc. Am. J. 51, 1173–1179. https://doi.org/10.2136/sssaj1987.03615995005100050015x.
Parton, W.J., Scurlock, J.M.O., Ojima, D.S., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.-C., Seastedt, T., Garcia Moya, E., Kamnalrut, A., Kinyamario, J.I., 1993. Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. Glob. Biogeochem. Cycles 7, 785–809. https://doi.org/10.1029/93GB02042.
Peratoner, G., Gottardi, S., Werth, E., Figl, U., Bodner, A., Kasal, A., 2010. Suitability of seed mixtures for intensively farmed permanent meadows in a mountain environment. In: Schnyder, H., Isselstein, J., Taube, F., Auerswald, K., Schellberg, J., Wachendorf, M., Herrmann, A., Gierus, M., Wrage, N., Hopkins, A. (Eds.), EGF 2010: Grassland in a Changing World. Organising Committee of the 23rd General Meeting of the European Grassland Federation and Arbeitsgemeinschaft Grünland und Futterbau der Gesellschaft für Pflanzenbauwissenschaften, pp. 536–538. Kiel, Germany.
Qi, A., Murray, P.J., Richter, G.M., 2017. Modelling productivity and resource use efficiency for grassland ecosystems in the UK. Eur. J. Agron. 89, 148–158. https://doi.org/10.1016/J.EJA.2017.05.002.
R Core Team, 2017. R: A Language and Environment for Statistical Computing.
Rafique, R., Kumar, S., Luo, Y., Kiely, G., Asrar, G., 2015. An algorithmic calibration approach to identify globally optimal parameters for constraining the DayCent model. Ecol. Model. 297, 196–200. https://doi.org/10.1016/J.ECOLMODEL.2014.11.022.
Rancane, S., Berzins, P., Stesele, V., Jansons, A., 2016. Breeding of cocksfoot (Dactylis glomerata L.) with improved forage quality. In: Höglind, M., Bakken, A.K., Hovstad, K.A., Kallioniemi, E., Riley, H., Steinshamn, H., Østrem, L. (Eds.), EGF 2016: the Multiple Roles of Grassland in the European Bioeconomy. Organising Committee of the 26th General Meeting of the European Grassland Federation, NIBIO, Trondheim, Norway, pp. 314–316.
Rose, S.K., 2014. Integrated assessment modeling of climate change adaptation in forestry and pasture land use: a review. Energy Econ. 46, 548–554. https://doi.org/10.1016/J.ENECO.2014.09.018.
Samuil, C., Vintu, V., Iacob, T., Saghin, G., Trofin, A., 2009. Management of permanent grasslands in North-Eastern Romania. In: Cagaš, B., Macháč, R., Nedělník, J. (Eds.), EGF 2009: Alternative Functions of Grassland. Organising Committee of the 15th European Grassland Federation Symposium 2009. Research Institute for Fodder Crops Ltd, Troubsko (RIFC), OSEVA PRO Ltd, Grassland Research Station at Zubri (GRS), Brno, Czech Republic, pp. 234–237.
Samuil, C., Vintu, V., Sirbu, C., Saghin, G., Muntianu, I., Ciobanu, C., 2011. Low input management of Agrostis capillaris + Festuca rubra grasslands in Romania. In: Pötsch, E.M., Krautzer, B., Hopkins, A. (Eds.), EGF 2011: Grassland Farming and Land Management Systems in Mountainous Regions. Organising Committee of the 16th Symposium of the European Grassland Federation 2011 and Agricultural Research and Education Centre (AREC). Raumberg-Gumpenstein, pp. 335–337.
Sándor, R., Barcza, Z., Acutis, M., Doro, L., Hidy, D., Köchy, M., Minet, J., Lellei-Kovács, E., Ma, S., Perego, A., Rolinski, S., Ruget, F., Sanna, M., Seddaiu, G., Wu, L., Bellocchi, G., 2017. Multi-model simulation of soil temperature, soil water content and biomass in Euro-Mediterranean grasslands: uncertainties and ensemble performance. Eur. J. Agron. 88, 22–40. https://doi.org/10.1016/J.EJA.2016.06.006.
Schellberg, J., Moseler, B., Kuhbauch, W., Rademacher, I., 1999. Long-term effects of fertilizer on soil nutrient concentration, yield, forage quality and floristic composition of a hay meadow in the Eifel mountains, Germany. Grass Forage Sci. 54, 195–207. https://doi.org/10.1046/j.1365-2494.1999.00166.x.
Schils, R., Snijders, P., 2004. The combined effect of fertiliser nitrogen and phosphorus on herbage yield and changes in soil nutrients of a grass/clover and grass-only sward. Nutrient Cycl. Agroecosyst. 68, 165–179. https://doi.org/10.1023/B:FRES.0000019045.90791.a4.
Schneider, M.K., Luscher, A., Richter, M., Aeschlimann, U., Hartwig, U.A., Blum, H., Frossard, E., Nosberger, J., 2004. Ten years of free-air CO2 enrichment altered the mobilization of N from soil in Lolium perenne L. swards. Glob. Chang. Biol. 10, 1377–1388. https://doi.org/10.1111/j.1365-2486.2004.00803.x.
Skuodienė, R., Repšienė, R., 2008. Productivity and quality of perennial ryegrass (Lolium perenne L.) in western Lithuania. In: Hopkins, A., Gustafsson, T., Bertilsson, J., Dalin, G., Nilsdotter-Linde, N., Spörndly, E. (Eds.), EGF 2008: Biodiversity and Animal Feed - Future Challenges for Grassland Production. Organising Committee of the 22nd General Meeting of the European Grassland Federation. Swedish University of Agricultural Sciences, Uppsala, Sweden, pp. 320–322.
Stampfli, A., 2001. Did recent climatic shifts affect productivity of grass-dominated vegetation in southern Switzerland? In: Walther, G., Burga, C., Edwards, P. (Eds.), "Fingerprints" of Climate Change: Adaped Behaviour and Shifting Species Ranges. Kluwer Academic/Plenum Publishers, Ascona, Switzerland, pp. 249–261.
Thumm, U., Tonn, B., 2010. Effect of precipitation on dry matter production of a meadow with varied cutting frequency. In: Schnyder, H., Isselstein, J., Taube, F., Auerswald, K., Schellberg, J., Wachendorf, M., Herrmann, A., Gierus, M., Wrage, N., Hopkins, A. (Eds.), EGF 2010: Grassland in a Changing World. Organising Committee of the 23rd General Meeting of the European Grassland Federation and Arbeitsgemeinschaft Grünland und Futterbau der Gesellschaft für Pflanzenbauwissenschaften, pp. 90–92. Kiel, Germany.
Timsina, J., Humphreys, E., 2003. Performance and Application of CERES and SWAGMAN Destiny Models for Rice-Wheat Cropping Systems in Asia and Australia: a Review.
Trnka, M., Eitzinger, J., Gruszczynski, G., Buchgraber, K., Resch, R., Schaumberger, A., 2006. A simple statistical model for predicting herbage production from permanent grassland. Grass Forage Sci. 61, 253–271. https://doi.org/10.1111/j.1365-2494.2006.00530.x.
UEA CRU, Harris, I., Jones, P.D., 2017. CRU TS4.01: climatic Research Unit (CRU) Time-Series (TS) version 4.01 of high-resolution gridded data of month-by-month variation in climate. Cent. Environ. Data Anal. https://doi.org/10.5285/58a8802721c94c66ae45c3baa4d814d0 (Jan. 1901- Dec. 2016) [WWW Document].
Vasilev, E., 2012. Productivity of wheatgrass (Agropyron cristatum (L.) Gaertn.) as a component of pasture mixtures for the conditions of the Danube Plain. In: Goliński, P., Warda, M., Goliński, P. (Eds.), EGF 2012: Grassland - a European Resource? Organizing Committee of the 24th General Meeting of the European Grassland Federation and Polish. Grassland Society, Lublin, Poland, pp. 190–192.
Wang, F., Mladenoff, D.J., Forrester, J.A., Keough, C., Parton, W.J., 2013. Global sensitivity analysis of a modified CENTURY model for simulating impacts of harvesting fine woody biomass for bioenergy. Ecol. Model. 259, 16–23. https://doi.org/10.1016/j.ecolmodel.2013.03.008.
Williams, T.A., Evans, D.R., Rhodes, I., Abberton, M.T., 2003. Long-term performance of white clover varieties grown with perennial ryegrass under rotational grazing by

sheep with different nitrogen applications. J. Agric. Sci. 140, 151–159. https://doi.org/10.1017/S0021859603002958.

Wu, Y., Liu, S., Huang, Z., Yan, W., 2014. Parameter optimization, sensitivity, and uncertainty analysis of an ecosystem model at a forest flux tower site in the United States. J. Adv. Model. Earth Syst. 6, 405–419. https://doi.org/10.1002/2013MS000298.

Xiong, W., Holman, I., Conway, D., Lin, E., Li, Y., 2008. A crop model cross calibration for use in regional climate impacts studies. Ecol. Model. 213, 365–380. https://doi.org/10.1016/J.ECOLMODEL.2008.01.005.