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Table 1 – Key information

Country	**UK**
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Abstract

With rising temperatures, changes in precipitation and increasing atmospheric CO2 concentrations, European grasslands are likely to undergo significant changes in the coming decades. We used three approaches to model how the yield and nitrogen (N) content of European grasslands are likely to change in the future. The first approach was a meta-analysis. We looked at how different plant functional groups responded to artificial changes in atmospheric CO_2, temperature and water availability in different geographic regions. We then developed empirical models based on linear regression of climatic and grassland management variables. Finally we applied an existing dynamic model, Century, to several sites around Europe. The fit of the empirical and dynamic models was assessed before using them to predict future grassland yield and N content under two different climate change scenarios. All three methodologies agreed that yields will increase in Alpine and northern regions. For the Atlantic region yields may increase slightly or else stay the same (depending on fertiliser use). For the continental and southern regions the results were less clear, with different methodologies predicting different results. N content per hectare was generally predicted to remain constant, though if yields increase this suggests decreasing plant N concentrations. The exception was in northern Europe where N content is expected to increase. It should be possible to mitigate any negative impacts of climate change through changes in grassland management practices.

Contents

1. Introduction

By 2100, significant climatic changes are expected across Europe. Under a midrange prediction (Representative Concentration Pathway (RCP) 4.5) (Collins et al., 2013), average annual temperatures are expected to rise by 1 to 4.5°C by 2100 and average annual precipitation is expected to increase by up to 25% in northern and eastern Europe, while decreasing by 25% in parts of southern Europe (IPCC, 2013). Since plant growth is dependent on temperature and water availability (among other things), these climatic changes are likely to have an impact on both the yield and nutritional quality of future European grazing systems.

In order to know how grazing systems are likely to change in the future, it is necessary to have accurate models. Three modelling approaches have been implemented, the first being a meta-analysis, the second developing empirical models and the third using an existing dynamic model (Century (Parton et al., 1987)).These methodologies are used to evaluate the impact of climate change on the yield and nitrogen (N) content of both permanent and temporary grasslands, as well as on individual plant types. This will give us information about the quantity of grazing available to livestock in the future and also the protein content of that grazing.

The meta-analysis used data from studies in which the climate was artificially altered and the resulting effects on plant yield and nitrogen concentration were measured. A meta-analysis enables us to use small-scale experimental data to get a general picture of overall effects over a large spatial scale. Koricheva and Gurevitch (2014) describe meta-analysis as a highly important tool when considering the impacts of environmental drivers in the field of plant ecology.

The empirical models used are linear regression equations. Datasets from grassland experiments across Europe were gathered to contribute to the development of the models. 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 than process-based models and require less input data. Empirical models have also been found to be more effective than dynamic models at predicting crop responses to climate change over large spatial scales, suggesting that this could be an effective approach (Lobell and Burke, 2010). Qi et al. (2017) compared the outputs of a process-based model for the productivity at 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. Empirical models are only relevant within the confines of the experiments which contributed to their development. They cannot be used to predict grassland yield or quality under climate conditions different from those original experiments. They are however useful in determining trends in responses to weather variation.

Dynamic models simulate the different processes in a system, looking at how the system changes over time. 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 impossible to apply more complex models to sites where only limited data is available. Century is a dynamic model designed for ecosystem analysis and can be applied to croplands, forests and a broad range of 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 (compared with many other dynamic pasture models), thus requiring few inputs. 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 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.

Each approach has its benefits and limitations. The meta-analysis uses data from experiments where the climate was actually changed, rather than just making predictions. This is useful for understanding how plants respond to different changes, but doesn't account for plants adapting over time to the new climate. Century does account for long-term climatic changes and is able to predict the yield and quality of future grazing systems under different climate change scenarios, but it requires more inputs than the empirical models and has to be run separately for each site it is applied to. The empirical models apply over a wide geographic area, but are only relevant within the confines of the experiments which contributed to their development. They cannot be used to predict grassland yield or quality under climate conditions different from those original experiments. They are however useful in determining trends in responses to weather variation. In this study we use the three methodologies to predict future yields and N content of different European grazing systems. The accuracy of the different methodologies is assessed, climate change scenarios are applied and the results are compared. By using all three approaches, we are able to mitigate the drawbacks of each and get a general picture of the responses of European grazing systems to climate change.

Some of the information from this deliverable (the empirical models) is used as input to improve the predictions of forage change production and quality in the farm model developed in WP4.

2. Methods

2.1 Grouping by region, plant type and grazing system

Across Europe there is a huge variety of grazing systems. These include intensive grass monocultures, mountain meadows, heather moorlands, silvo-pastoral systems and many more. For this reason, this research divides Europe into five regions and looks at distinct types of plants and grazing systems. The regional division is shown in figure 1. There are the same regions as those used by the Intergovernmental Panel on Climate Change and are based on climatic zones.

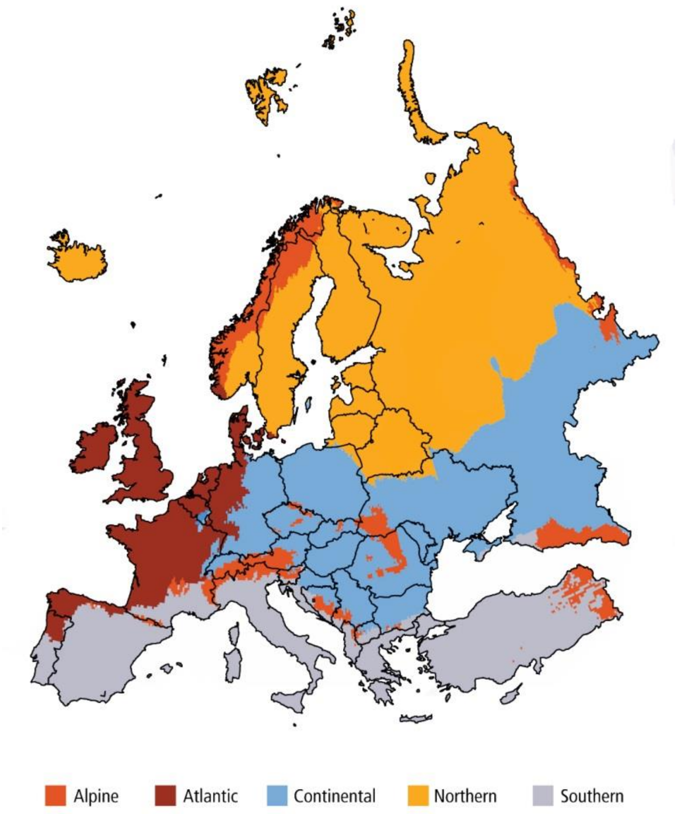

Figure 1: European climatic zones (Kovats et al., 2014)

For the meta-analysis, the studies used generally looked at individual plant species rather than whole grazing systems. For this reason the analysis was divided by plant functional group (i.e. graminoids, legumes, forbs and shrubs). The data for the Century and regression analyses tended to come from more system-wide experiments and so was split by grassland type: permanent and temporary. Permanent grasslands are dominated by one or more species of grass, though may include many different plant types. They have been used as grassland for at least five years and are often associated with extensive grazing systems. Temporary grasslands are usually 100% grass or else a grass/legume mixture and produce high yields. They have used as grassland for less than five years and tend to be associated with more intensive grazing systems. In making these divisions by region, plant type and grazing system, we aim to account for as much of the existing variation in grazing systems as possible while still being able to group them in a manageable way.

2.2 Meta-analysis

For the meta-analysis, 131 studies (providing a total of 797 observations) were collected, examining the effects of elevated atmospheric CO_2 concentration, elevated temperature and changes in water availability on commonly grazed European plant species. Specifically they considered the impacts on plant yield and/or N concentration. The majority of these studies looked at the effects of changing a single climatic variable, although some (26 studies) considered the effects of multiple simultaneous climatic changes. The average CO_2 and temperature increases across the experiments were within the range of expected climate change for 2100. The changes in water availability were quite extreme, but were over relatively short time periods. They could be seen to represent particularly wet or dry seasons. Mixed models were used to evaluate the effects of the climatic treatments, with fixed effects relating to experimental methodology, region and plant type. The models were fitted using Markov Chain Monte Carlo (MCMC) simulations. Full details of the methodology can be found in Dellar et al. (2018).

2.3 Data

The Century and regression approaches required data from grassland experiments across Europe. These experiments differed from those used in the meta-analysis in that they did not involve artificial climatic changes, but instead recorded plant yield and N content under ambient climatic conditions. The analysis looked at how these measurements were affected by normal variations in temperature and rainfall. The experimental data was assembled from published literature and through contacting experts and relevant institutions. The locations of these experiments, including grassland type and climatic region, are shown in figure 2. The full list of sites is in appendix A. Weather data for all sites was taken from the Climatic Research Unit gridded dataset (UEA CRU et al., 2017).

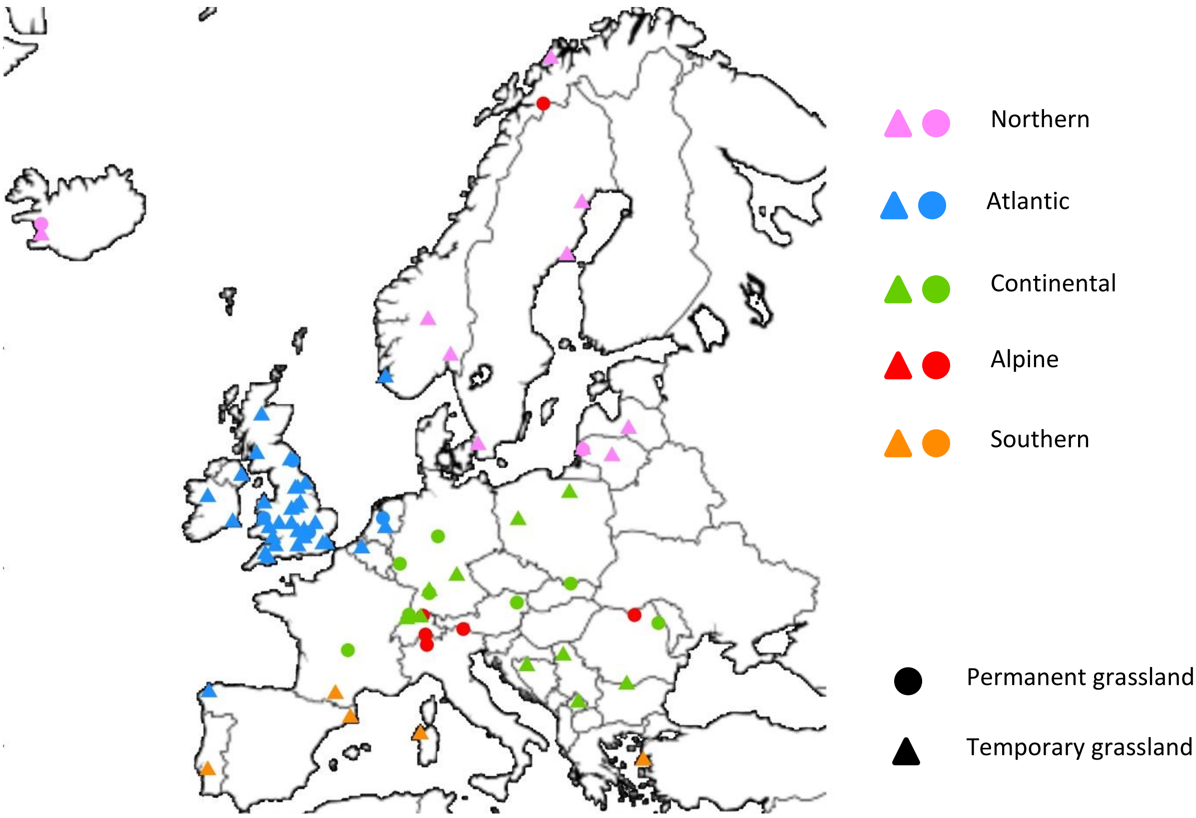

Figure 2: Locations of sites used for the regression and Century models

2.4 Linear regression model

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

Yield, permanent grassland:

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

Applicable to the Alpine, Atlantic, continental and northern regions

Yield, temporary grassland:

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

Applicable to the Atlantic, continental, northern and southern regions

N content, permanent grassland:

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

Applicable to the continental region

N, content, temporary grassland:

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

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/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.

Two climate change scenarios were used (RCP4.5 and 8.5) (Collins et al., 2013), with the predicted climate change data taken from CORDEX (CORDEX, 2018). This climate data was used as input for the regression equations, to get predictions for future grassland yields and N content. Because the regression equations were developed using data from the ambient climate, this is the only climate for which they are valid. For this reason, for each region the maximum and minimum monthly temperature and rainfall data from the input experiments was calculated. Predicted climatic changes were bounded so that they could not go beyond these values. This had the effect that the climate change scenarios used were not as extreme as they will likely be in reality. The results therefore indicate expected trends in grassland yield and quality, rather than absolute predictions. This is particularly true for RCP8.5 and predictions for the 2071 – 2100 period, since changes in temperature and precipitation were 'capped' for a large proportion of the months in these scenarios. When implementing the regression equations with the climate change scenarios, values for legume percentage, cuts per year, N fertiliser and altitude were taken as the average for the sites used to develop the equations.

2.5 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 had all the necessary requirements. Finally six sites were selected; these were chosen for both the availability of necessary information and also to get 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. It was possible for Hurley because data from each of its seven annual harvests was available, rather than just an annual total.

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

Site	Region	Grassland type	Fertiliser treatments (kg N ha^{-1} a^{-1})	Plant N measured?	Time span used for modelling (years)
Eschikon, Switzerland	Alpine	Permanent	140 / 560	✓	10
Hurley, UK	Atlantic	Temporary	0 / 150	✓	4
Rothamsted, UK	Atlantic	Permanent	0 / 144		58
Göttingen, Germany	Continental	Permanent	0 / equal to that removed the previous year	✓	40
Hvanneyri, Iceland	Northern	Permanent	0 / 100	✓	25
Larzac Causse, France	Southern	Permanent	0 / 65		25

In order to parameterise the Century model, the input parameters having the greatest effect on plant yield and N content were 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 and a list of relevant parameters was identified (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 occasionally led to over-fitting and produced unrealistic predictions when the model was applied to climate change scenarios. Instead, reasonable values for these parameters were chosen based on preliminary model runs 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

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

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

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

$N_i = RMSE(P_N, O_N)/\overline{O_N}$ *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 * gradient of total soil carbon at end of spin-up period)^3 ‡

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

Once the model was parameterised, it was run under two climate change scenarios. These were the same scenarios as were used for the linear regression models (but without the additional boundaries).

2.6 Model fit and significance testing

To assess the goodness-of-fit of the Century model, the mean yield and N content of predictions and observations were compared, as well as their standard errors. In addition, for both the Century and the linear regression models, the RMSE and correlation between predicted and observed yields and N content were calculated, with the RMSE divided into bias and variance terms.

For the climate change predictions, we first checked the assumptions of normality and homogeneity of variance, then used either the student's t-test or the Mann-Whitney U-test (as appropriate) to check the significance of the predicted changes.

3. Results

3.1 Meta-analysis

The meta-analysis found that elevated atmospheric CO_2 concentrations led to increased plant yields, most notably for shrubs (+71.6%), though it also tended to reduce plant N concentrations (-4.8%). Increasing temperatures caused yields to increase in the Alpine and northern regions (+82.6%), while they decreased in continental Europe (-32.6%). Higher

‡ 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 ensure 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.

temperatures also led to reductions in N concentrations, particularly for forbs (-13.6%) and shrubs (-18.5%). Reduced water availability tended to decrease yields while increased availability led to more growth (+57.1%). Less water also tended to increase plant N concentrations (+11.7%). When multiple climatic changes were combined, the effects often cancelled one another out, for example the combination of elevated CO_2, elevated temperature and reduced water availability indicated no significant changes in either yield or N concentration. Full results can be found in Dellar et al. (2018).

3.2 Linear regression model

The goodness-of-fit of the equations is evaluated in table 3. In all cases, the fit was very good, with high correlations and low RMSEs, and the latter being due entirely to variation rather than bias.

Table 3: Goodness-of-fit of regression model equations. For the root mean square error results, yield has the unit is t/ha and N content has the unit kg/ha

	Grassland type	R-squared *(SE)*	Correlation *(SE)*	Root mean squared error *(percentage of which is due to bias)*
Yield	Permanent	0.59 *(0.00)*	0.76 *(0.01)*	2.26 *(0.0)*
	Temporary	0.59 *(0.00)*	0.76 *(0.01)*	2.73 *(0.0)*
N content	Permanent	0.72 *(0.04)*	0.80 *(0.03)*	24.68 *(0.2)*
	Temporary	0.80 *(0.00)*	0.89 *(0.00)*	64.90*(0.0)*

The regression model predictions for how yield and N content will change under the two climate change scenarios is shown in table 4. Yields are predicted to mostly stay the same or increase, though there is a slight decrease for temporary grasslands in the southern region. Nitrogen content is generally unchanged, except for a slight increase for temporary grasslands in the northern region. In almost all cases, the change under both climate change scenarios is roughly the same.

Table 4: Linear regression model predictions for percentage change in grassland yield and N content. Changes are relative to the 1971 – 2000 baseline. Bold text indicates that the change is significant at $p < 0.05$

		2021 - 2050		2071 - 2100	
		RCP4.5	RCP8.5	RCP4.5	RCP8.5
Yield					
Permanent	Alpine	3.05	6.79	10.63	**46.03**
	Atlantic	**4.44**	1.59	2.84	**6.51**
	Continental	**11.87**	**11.72**	**15.61**	**30.25**
	Northern	3.04	1.60	3.59	2.99
Temporary	Atlantic	4.02	4.15	**4.43**	0.45
	Continental	-0.22	-3.64	-2.40	**-7.23**
	Northern	**10.51**	**12.45**	**13.93**	**18.83**
	Southern	**-8.17**	**-8.05**	**-10.98**	**-10.56**
N content					
Permanent	Continental	**6.53**	**7.09**	**7.19**	-0.13
Temporary	Atlantic	1.40	-3.02	0.50	-3.64
	Contnental	1.07	-0.39	0.80	1.08
	Northern	4.02	3.76	**5.88**	**12.54**

3.3 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 (the exception being the Hurley site when fertiliser was used). 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.

The climate change predictions from the parameterised Century models are shown in table 6. Predicted yields tended to increase, often by a significant amount, with especially large increases in Iceland. Most changes in N content were not significant, though there were occasional significant decreases, particularly under RCP8.5. The exception was the site in Iceland, where a significant increase in N content was predicted.

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 ha^{-1} a^{-1})	Mean *(SE)* predicted yield (t 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, Switzerland	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
	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, UK	0	2.72 *(0.16)*	2.93 *(0.04)*	41.7 *(3.5)*	0.36	NA	42.7 *(0.8)*	NA	NA
	144	6.86 *(0.25)*	5.76 *(0.07)*	30.6 *(27.2)*	0.33	NA	155.3 *(1.8)*	NA	NA
Göttingen, Germany	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
	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, Iceland	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
	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 Causse, France	0 65	1.57 *(0.11)* 5.25 *(0.29)*	1.55 *(0.04)* 5.31 *(0.07)*	21.6 *(0.2)* 25.7 *(0.2)*	0.63 0.36	NA NA	10.0 *(0.4)* 47.1 *(0.8)*	NA NA	NA NA

Table 6 Century model predictions for percentage change in grassland yield and N content. Fertiliser treatments are the same as those specified in table 1. Changes are relative to the 1971 – 2000 baseline. Bold text indicates that the change is significant at $p < 0.05$

Fertiliser	Time period	RCP	Eschikon, Switzerland	Hurley, UK	Rothamsted, UK	Göttingen, Germany	Hvanneyri, Iceland	Larzac Causse, France
Yield								
Without / Low	2021 - 2050	4.5	**9.7**	12.1	**4.6**	**8.1**	**34.2**	-1.8
		8.5	**12.7**	11.4	2.5	**8.5**	**41.4**	-1.7
	2071 - 2100	4.5	**10.6**	9.7	2.5	**9.0**	**45.5**	-1.9
		8.5	**19.3**	15.5	2.9	**15.0**	**82.4**	0.1
With / High	2021 - 2050	4.5	**7.8**	**7.2**	**4.5**	**5.4**	**37.0**	**7.4**
		8.5	**10.2**	**8.6**	**3.6**	**6.8**	**43.8**	**9.5**
	2071 - 2100	4.5	**6.9**	**8.0**	**2.7**	**5.6**	**47.5**	**9.6**
		8.5	**9.7**	**19.9**	0.6	**9.9**	**76.1**	**20.9**
N content								
Without / Low	2021 - 2050	4.5	0.3	0.9	0.2	**4.1**	-2.0	-2.5
		8.5	-0.1	-2.9	-1.9	1.0	**4.4**	-5.7
	2071 - 2100	4.5	0.5	-4.3	0.4	1.6	**8.6**	-1.1
		8.5	1.1	**-14.1**	-7.0	**-8.4**	**25.5**	-10.7
With / High	2021 - 2050	4.5	0.2	-0.1	-0.4	3.8	**18.6**	-0.6
		8.5	-0.1	-0.5	-1.3	3.0	**22.7**	-4.2
	2071 - 2100	4.5	-0.5	0.1	-1.9	2.6	**27.2**	0.2
		8.5	**-2.7**	2.0	**-3.6**	2.1	**31.7**	-4.4

4. Discussion

4.1 Model evaluation

A full analysis of the bias and sensitivity of the meta-analysis is included in Dellar et al. (2018). There was a large degree of heterogeneity amongst the studies and some bias was found in the N concentration results.

Looking at the r-squared values and the correlations for the regression equations, they had a very good fit with the observed data. Also the standard errors of these measures were very low, suggesting that the models were not over-fitted. This was slightly surprising, given the wide range of experiments used and the large geographical regions involved. Several previous studies have found difficulties with using this 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). It should be noted that the RMSEs for the regression equations were relatively high, particularly for yield, which could be due to these potential disadvantages.

For the Century model, it is not surprising that there was more variance in the correlation coefficients than the error terms, since the optimisation process minimised the RMSE but did not look at correlation. It is also not surprising that it is the Hurley site which had the largest discrepancies between predicted and observed annual totals. This experiment look place over a much shorter duration than the others, there being only four years of data to compare. 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. Since the mean was used to evaluate the impact of climate change on yield and N content, it is important that this be estimated accurately. The cases where there was little to no correlation (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 averaged monthly weather data, 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.

4.2 Impacts of climate change

Alpine region: All three modelling approaches indicated an expected increase in plant yield under climate change. This is logical since growth in Alpine areas is often limited by low temperatures. Century suggested that there would be no significant change in plant N content except under the most extreme conditions. Elevated atmospheric CO_2 concentrations tend to decrease plant N; this is a well-documented effect and it was demonstrated in the meta-analysis. It is represented in the Century model through an increase in plant N-use efficiency (Metherell et al., 1993). On the other hand, N flows follow C flows in Century, so if plant C increases, then so too does plant N (to some extent). The lack of a change in plant N may be due to a cancelling-out of these conflicting effects. This is consistent with reality, in that changes in N-use efficiency, Rubisco activity (the first major stage in a plant's conversion of CO_2 to energy-rich molecules) and N-allocation under elevated CO_2 concentrations suggest a decrease in plant N (Cotrufo et al., 1998; Leakey et al., 2009), while higher temperatures have been found to increase N content in mountainous areas (Dumont et al., 2015).

Atlantic region: The Century model results suggested small but significant increases in yields when fertiliser is used and no significant change when it is not used, while the regression model and the meta-analysis results indicate very little change. The climate change scenarios used in the regression analysis are less severe than those used for the Century models (as described in section 2.4) and the predicted changes are likely to be smaller than they would be in reality. Also, the regression approach does not account for the impact of increasing atmospheric CO_2 concentration, which means that it will tend to underestimate future yields, whereas Century responds to elevated CO_2 by increasing photosynthesis (Metherell et al., 1993). It seems reasonable to assume that yields will either remain constant or slightly increase in this region, depending on fertiliser use. This is to be expected in a region in where plant growth is not currently temperature-limited and which will experience increases in atmospheric CO_2 concentration and temperature. Adding fertiliser gives plants the nutrients they need to take advantage of the improving conditions. All three approaches suggest very little change in N content except under the most extreme conditions. Again, this is likely due to different effects cancelling one another out. For the most extreme scenario (RCP8.5 in the period 2071 – 2100), the estimated atmospheric CO_2 concentration reaches 936ppm. Such a high concentration could explain the significant reductions in Century's N content predictions for this scenario.

Continental region: The regression model predicted large increases for permanent grassland yields, but a significant decrease for temporary grasslands under the extreme climate change scenario. Century predicted a small increase while the meta-analysis predicted a decrease. The continental region is very large and it may be that it exhibits more variation in grassland responses to climate change than other regions. It could be beneficial for further research to separate this region into smaller areas, though this would be contingent on data availability. It is interesting to note that the regression results for permanent grasslands agree with the Century results and it is possible that permanent grasslands will benefit more from climate change than temporary ones. From a biological standpoint, this could be due to grassland composition. Permanent grasslands have a greater variety of plant species and types than temporary ones and are therefore likely to be more resilient to the negative effects of climate change (Craine et al., 2012; Isbell et al., 2015; Wright et al., 2015). All methodologies agree that there will be very little change in plant N content under either climate change scenario.

Northern region: All models predicted increases in grassland yield, although the increase was not significant for permanent grasslands under the regression model. According to the meta-analysis, an increase is very likely since expected increases in atmospheric CO_2 concentration, temperature and water availability all contribute to elevated plant growth in this region. All methodologies also show increases in plant N content (though this was not a significant increase in the meta-analysis). For Century, this is likely due to N increasing as C increases (Metherell et al., 1993). Wetter conditions may also increase nutrient uptake from the soil (Matías et al., 2011), though elevated rainfall can cause an increase in nutrient leaching (Metherell et al., 1993).

Southern region: Century predicted significant yield increases when fertiliser was applied, but no change when no fertiliser was used, while the regression model and the meta-analysis predicted a significant decrease in yield. Several previous studies have predicted a reduction in plant yields for southern Europe (Rötter and Höhn, 2015; Trnka et al., 2011), making the Century results in the present study particularly surprising. Often such predictions are based on the increasing frequency of extreme weather events such as droughts and heatwaves. Because Century runs on a monthly time-step it is not possible to include such events in the model, suggesting that the Century prediction is likely to be an over-estimate. Because of this, combined with the fact that there was generally very little data available for the southern region (for both the regression modelling and the meta-analysis), it is difficult to estimate future grassland yields here. In terms of N content, Century predicted no significant change and the meta-analysis also suggested no change. There was insufficient data to incorporate this region into the regression models.

4.3 Management vs climate change

In looking at the results from both the Century and regression models, it is clear that the impact of different fertiliser levels and different geographic regions on plant yield and N content are much greater than the impact of climate change. This is consistent with the meta-analysis of Thébault et al. (2014), who found that the strongest factors for predicting variation in grasslands were interactions of practices relating to fertilisation and defoliation, rather than anything relating to climate or CO_2 enrichment. This is encouraging as it suggests that it should be possible to mitigate negative climate change impacts through appropriate changes in grassland management practices.

4.4 Limitations

Some limitations of the models considered in the present study have already been mentioned. Both Century and the regression models rely on monthly weather data, which means that they are not able to capture the effects of extreme weather events. Since such events (heatwaves, droughts, heavy rainfall, flooding, etc.) are expected to become more frequent in the future (Kovats et al., 2014), it is useful to consider the impact they will have on grassland quality and yield. The meta-analysis did consider extreme changes in water availability, though usually not in combination with other climatic changes. Furthermore, none of the methodologies account for future changes in the growing season or in the grasslands themselves (for example through becoming more adapted to future climates or changing species compositions). In addition, the regression analysis does not account for changing atmospheric CO_2 concentrations and does not consider legacy effects from weather conditions in previous years (e.g. Petrie et al., 2018).

Furthermore, the regression model was run with less extreme climate scenarios, as it could not make predictions for situations outside its input data. Century to some extent faces the same limitation, as it was parameterised using data from the current climate. However, because it is a process-based model, Century can be used to extrapolate results to new climates to a certain extent, though users should be aware that results become less reliable as the future climate diverges further from the current one.

4.5 Implications for livestock farming

Most regions are likely to see grassland yields either increase or stay the same, which is either good or neutral for grazing livestock. The exception is southern Europe, which could see a reduction in yields, possibly necessitating the increased use of bought-in-feed and/or changes in management practices, including selective breeding for enhanced animal adaptability and efficiency. In areas where yields increase but N content remains constant, this implies a reduction in plant N concentration, meaning that animals need to eat more to receive the same amount of protein. This is something that farmers should be aware of, possibly introducing more legumes to grasslands or increasing the use of concentrate feeds.

Conclusions

The modelling approaches considered in the present study usually agree with one another and, where they do not, the discrepancy can generally be attributed to a known limitation of one of the models. Plant yields are usually predicted to either stay constant or increase, the exception being in southern Europe where there is insufficient data to be sure of the trend and we are unable to account for the impact of extreme weather events; the impact of the latter cannot be accounted for in any region, but they are expected to particularly affect southern Europe. N content is generally unchanged, except for a predicted increase in northern Europe. Management practices such as fertilisation appear to have more of an impact on pastures than climate change. This suggests that it may be possible to mitigate negative climate change effects through appropriate changes in grassland management practices.

All three modelling approaches have limitations. The meta-analysis generally considers one aspect of climate change at a time rather than multiple simultaneous changes, the regression methodology can only apply restricted climate change scenarios and Century only applies to a single site (or multiple homogeneous sites). However by using all three approaches and seeing that they corroborate one another we can have confidence in our results.

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Appendix A: Sites used for regression modelling

Permanent grasslands			
Dataset / Location	**Climatic region**	**Data available**	**Source**
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	Atlantic, Continental,	Yield, N	Kirwan et al. (2014)

Experiment, 24 sites used	Northern, Southern		
BIODEPTH, 5 sites used	Continental, Northern, Southern	Yield	Hector et al. (1999)
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 A references

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Appendix B: Coefficients of linear 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		