Report to The Stapledon Memorial Trust on research carried out supported by a Stapledon Travelling Fellowship

Development of meta-models to predict future pasture yield and quality under various climate change scenarios for different European regions

Martha Dellar[1,2]

E-mail: Martha.Dellar@sruc.ac.uk

Contact address: SRUC, Roslin Institute, Easter Bush Campus, Midlothian, EH25 9RG

Supervisors: Kairsty Topp[1], Georgios Banos[1,2] and Eileen Wall[1]

[1] Scotland's Rural College

[2] University of Edinburgh

UK lead organisation:

Scotland's Rural College

Peter Wilson Building

Kings Buildings

West Mains Road

Edinburgh

EH9 3JG

Contact: Eileen Wall

E-mail: Eileen.Wall@sruc.ac.uk

Supervising institute:

BC3-Basque Centre for Climate Change-Klima Aldaketa Ikergai

Parque Científico de UPV/EHU

Barrio Sarriena s/n, 48940 Leioa

Spain

Contacts: Agustin del Prado and Guillermo Pardo

E-mail: agustin.delprado@bc3research.org / guillermo.pardo@bc3research.org

Fellowship dates:

7th May – 1st June 2018

Objective of fellowship

The fellowship was awarded to enable the recipient to spend four weeks working at the Basque Centre for Climate Change developing models to predict pasture yield and quality under climate change. Specifically, the trip was an opportunity to learn to use the Century ecosystem model from people who had experience with it and to consider alternative modelling approaches from experts in the field. This work forms part of the recipients PhD research. The trip was timed to coincide with the iSAGE (Innovation for Sustainable Sheep and Goat Production in Europe) AGM. The models developed will be used by iSAGE as input for a whole-farm model.

Introduction

By 2100, significant climatic changes are expected across Europe. Under a midrange prediction (Representative Concentration Pathway (RCP) 4.5), 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 will 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. Two modelling approaches have been implemented, one using an existing dynamic model (Century) and the other developing empirical models. Results from the two methodologies are compared and contrasted.

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. Century has also historically produced good results (Parton et al., 1993). The main relevant inputs are grassland type, temperature, precipitation, management and soil texture.

The empirical models used are regression equations. Datasets from grassland experiments across Europe were gathered to contribute to the development of the models. Empirical models have 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).

As a dynamic model based on ecosystem processes, Century is able to predict the yield and quality of future grazing systems under different climate change scenarios, but it requires a relatively large number of inputs (compared with 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. By using both approaches, we will be able to get a general picture of the responses of European grazing systems to climate change.

Methodology

Division by region and grassland type

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 three distinct types of grazing system. 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. The three grazing systems are permanent grassland, reseeded grassland and heathland. Permanent grasslands are dominated by one or more species of grass, though may include many different plant types. They have remained unsown for at least five years. Reseeded grasslands are found in more intensive systems. They are usually 100% grass or else a grass/legume mixture and produce high yields. They have been reseeded within the last five years. Heathlands are areas which are dominated by at least one shrub species. They are used as rough grazing in very extensive farming systems. In making these divisions by region and grassland type, we aim to account for as much of the existing variation as possible while still being able to group grazing systems in a manageable way.

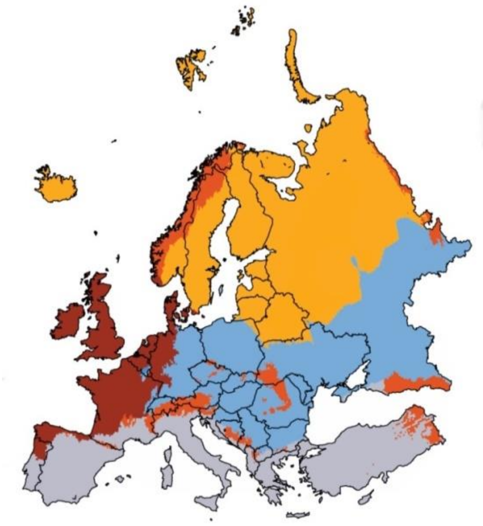

Figure 1: Division of Europe into five regions based on climatic zones (Kovats et al., 2014)

Data collection

In order to develop the empirical models and to test the results of the Century model, it was necessary to collect data from grazing systems across Europe. This was done both by searching published literature and by contacting experts in the field. We collected data on above ground dry weight (AGDW) and nitrogen (N) content. It was also necessary to collect meteorological data and details on soil types. In some cases there was a weather station on site, but in other cases nearby weather station data was used or if this was not available then large-scale meteorological datasets were used. Monthly weather data was used for all analysis. If site-specific soil data was unavailable then it was taken from existing soil datasets (Batjes, 2000; Scotland's soils, 2018; UKSO, 2017). The datasets collected for the Atlantic region are summarised in table 1. Data has also been collected for other regions but the analysis is still ongoing.

Table 1: Summary of datasets for the Atlantic region

Experiment	Location	Duration	Data collected	System type	Nitrogen fertiliser (kg/year)	Cuts per year	Grazing	Average annual air temperature (°C)	Average total annual rainfall (mm)	Average total annual global radiation (MJ/m^2)	Source of weather data
Palace Leas	Cockle Park, Newcastle, England	1897 - 2015	AGDW	Permanent grassland	Various	1	Sheep and cattle	8.0	792	3804	Met Office (2012); NASA (2018); NOAA (2016)
Park Grass	Rothamsted, England	1856 - 2017	AGDW	Permanent grassland	Various	1 - 2	None	9.3	688	3367	Local weather station
Williams et al. (2003)	Aberystwyth, Wales	1992 - 2001	AGDW	Reseeded grassland	Various	5	Sheep	10.2	1038	3981	Local weather station, NASA (2018)
Schils and Snijders (2004)	Lelystad, Netherlands	1994 - 1998	AGDW, N content	Reseeded grassland	Various	5	None	9.7	799	3565	KNMI (2017)
GM20	21 sites across England and Wales	1970 - 1973	AGDW, N content	Reseeded grassland	Various	6 - 7	None	N/A	N/A	N/A	UEA CRU et al. (2017)
Culardoch experiment, JHI	Culardoch, Scotland	2001 - 2016	AGDW, N content	Heathland	None	0	None	4.5	808	3220	Local weather station, NASA (2018)
Reinsch et al. (2017)	Clocaenog, Wales	1998 - 2012	AGDW	Heathland	None	0	None	7.4	1263	3598	NASA (2018); UEA CRU et al. (2017)
Reinsch et al. (2017)	Mols, Denmark	1998 - 2012	AGDW	Heathland	None	0	None	8.7	669	3931	NASA (2018); UEA CRU et al. (2017)
Reinsch et al. (2017)	Brandbjerg, Denmark	2004 - 2012	AGDW	Heathland	None	0	None	9.4	757	4025	NASA (2018); UEA CRU et al. (2017)
Reinsch et al. (2017)	Oldebroek, Netherlands	1998 - 2012	AGDW	Heathland	None	0	None	8.9	1005	3999	NASA (2018); UEA CRU et al. (2017)

Century model

Thus far, the Century model has been applied to one of the GM20 sites (Hurley Research Institute, Berkshire). It was initially parameterised with one level of N fertiliser, then tested with other N treatments and parameterised further. Model fit is assessed by calculating the mean square error (MSE) and the correlation between the observed and predicted results. MSE is divided into variance and bias using the following equation:

$$MSE = Bias^2 + Variance$$

Different climate change scenarios are then applied (i.e. increases in temperature and atmospheric CO_2 concentrations as well as seasonal changes in water availability). These adjustments are based on the different RCP scenarios as defined by the IPCC (Collins et al., 2013). Expected changes for Hurley Research Institute under a midrange climate change scenario (RCP4.5) are shown in table 2. This same process will be applied to other sites for which data has been collected; these sites will be selected to include all regions and grassland types.

Table 2: Expected climatic changes by 2100 for Hurley Research Institute under RCP4.5 (IPCC, 2013) relative to the average from 1986 – 2005.

Atmospheric CO_2 concentration (ppm)		538.4
Temperature change (°C)	Dec – Feb	+1.75
	Mar – May	+1.25
	Jun – Aug	+2.50
	Sep – Nov	+1.75
Precipitation change (%)	Oct – Mar	+5.0
	Apr – Sept	-5.0

The experiment at Hurley took place from 1970 – 1973, however we are assuming that there was little climatic difference between this time period and the 1986 – 2005 baseline, and so we will use these proposed changes without further adjustments.

Empirical models

For each grassland type, the datasets were reduced until they were all approximately the same size as the smallest, with the entries to be cut selected randomly. Three quarters of each dataset was then randomly selected to be used for model development. Stepwise regression was implemented in R (v.3.4.3, R Core Team, 2017) on this data to determine the best fitting model. Covariates included rainfall, temperature and radiation (all on a monthly basis), management details (e.g. number of harvests and N fertiliser) and various soil parameters where these were available. Both squared and interaction terms were included. The final model was then tested against the remaining quarter of the data and the mean square error and correlation coefficient were calculated. The type of model output depends on the type of input data available. For example, for the Atlantic region, for permanent grasslands the output is peak biomass, while for reseeded grasslands it is total annual harvested dry matter (i.e. the sum of multiple harvests). This is due to the nature of the data available. For heathlands in the Atlantic region the Clocaenog site was excluded from the analysis as the yields reported were dramatically different (by an order of magnitude) from the other sites.

It is not possible to apply the same climatic changes to the empirical models as were used in the Century model, as the empirical models are only valid within the climate in which the original experiments were conducted. However, small changes (which fall within the natural variability at the time of the experiments) can be applied. For the Hurley site, we can reduce average spring/summer rainfall by 5% (as per the expected changes detailed in table 2) and slightly increase spring/summer temperatures (the minimum average spring/summer temperature at the site can be raised by 1°C and it still falls within the range of observed temperatures).

Preliminary results

Data analysis is still ongoing, however some preliminary results for the Atlantic region have been achieved.

Century model

We are still working on parameterising the Century model and hope that the fit can be improved. For N additions of 150 and 450 kg per year, the model predicts very similar yields for every year (see figure 2). This is in contrast to the observed yields which are much lower in 1971 and 1972 for the 150N treatment and for the 450N treatment the observed yields were slightly lower in 1972. The model also predicts very similar results for the two N treatments. For the 0N treatment, the predicted yields are in approximately the right range, though there are some large differences between the predicted and observed values. Table 3 summarises the fit of the model for the different N treatments.

Table 3: Estimations of the goodness-of-fit of the Century model.

	0N	150N	450N
MSE	0.140	1.330	0.732
Variance	0.140	0.756	0.732
Bias	0.006	0.758	0.003
Correlation	0.245	0.552	0.690

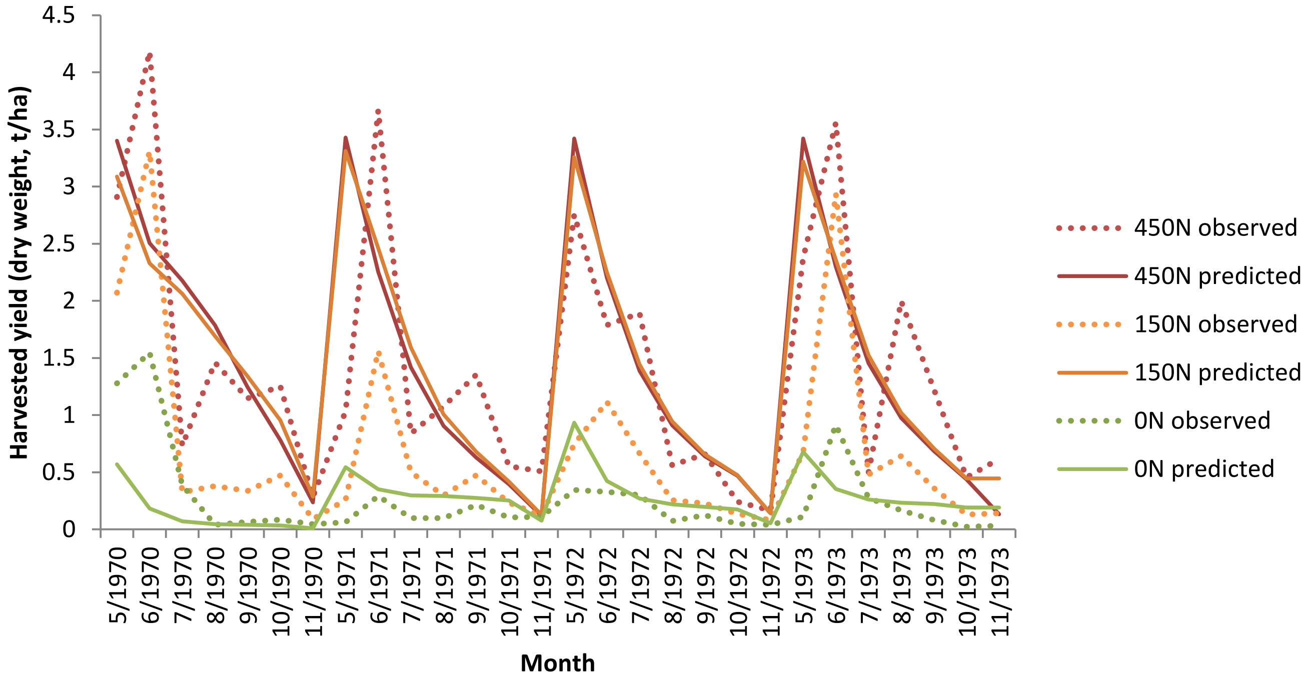

Figure 2: Observed yields (dotted lines) and Century predicted yields (solid lines) for different fertilisation treatments (kg N per hectare per year) at Hurley Research Institute, 1970 - 1973

Applying the temperature and precipitation changes as described in table two produces negligible effect on the average annual total harvested biomass (figure 3). This does not include changes in atmospheric CO_2 concentrations.

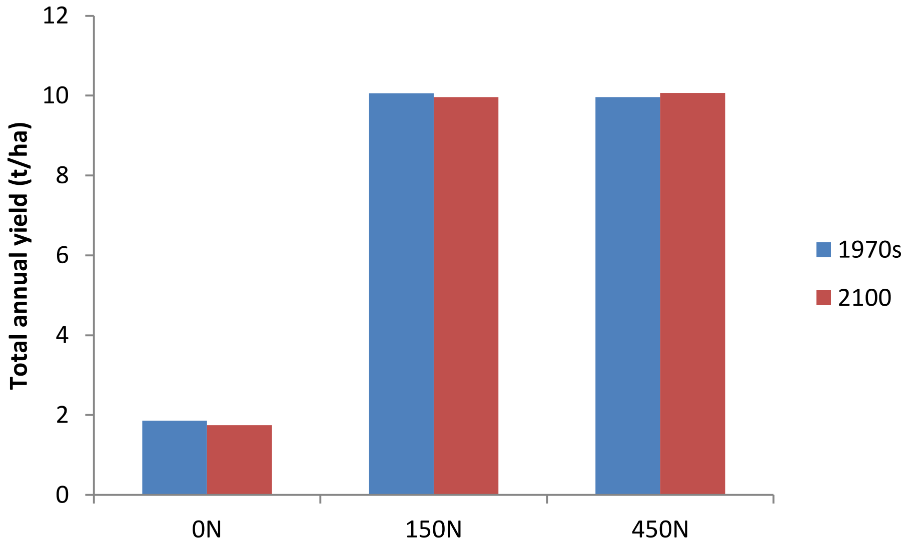

Figure 3: Predicted average annual yield from the Century model for the Hurley Research Institute under 1970's climate and the expected 2100 climate under RCP4.5 for different N treatments

Empirical models

Empirical models have been developed for permanent grasslands, reseeded grasslands and heathlands in the Atlantic region using the datasets listed in table 1. The final models are as follows:

Permanent grasslands:

Peak biomass (t DM/ha) = $\alpha_0 + \alpha_1 * Rain_{MAM} + \alpha_2 * Rain_{MAM}^2 + \alpha_3 * Rain_{JJ} + \alpha_4 * Temp_{JF} + \alpha_5 * Temp_{JJ} + \alpha_6 * Rad_{JJ} + \alpha_7 * N + \alpha_8 * SAWC + \alpha_9 * N * Temp_{JJ} + \alpha_{10} * N * Rad_{JJ} + \alpha_{11} * N * SAWC$

Reseeded grasslands:

Total annual harvested biomass (t DM/ha) = $\beta_0 + \beta_1 * Rain_{MAMJJA} + \beta_2 * Rain_{MAMJJA}^2 + \beta_3 * Temp_{AMJJA} + \beta_4 * Temp_{AMJJA}^2 + \beta_5 * N + \beta_6 * N^2 + \beta_7 * SAWC + \beta_8 * Clover + \beta_9 * N * Rain_{MAMJJA} + \beta_{10} * N * SAWC + \beta_{11} * N * Clover$

Total annual harvested N (kg/ha) = $\gamma_0 + \gamma_1 * Rain_{JF} + \gamma_2 * Rain_{MAMJJA} + \gamma_3 * Temp_{MJJ} + \gamma_4 * N + \gamma_5 * N^2 + \gamma_6 * SAWC + \gamma_7 * Clover + \gamma_8 * N * Rain_{MAMJJA} + \gamma_9 * N * SAWC + \gamma_{10} * N * Clover$

Heathlands:

Peak biomass (t DM/ha) = $\delta_0 + \delta_1 * Rad_{AM} + \delta_2 * SAWC + \delta_3 * SAWC * Rad_{AM}$

Where:

$Rain_{JF}$ = Total precipitation from January to February (mm)

$Rain_{MAM}$ = Total precipitation from March to May (mm)

$Rain_{JJ}$ = Total precipitation from June to July (mm)

$Rain_{MAMJJA}$ = Total precipitation from March to August (mm)

$Temp_{JF}$ = Average temperature from January to February (°C)

$Temp_{MJJ}$ = Average temperature from May to July (°C)

$Temp_{JJ}$ = Average temperature from June to July (°C)

$Temp_{AMJJA}$ = Average temperature from April to August (°C)

Rad_{AM} = Total global radiation from April to May (MJ/m^2)

Rad_{JJ} = Total global radiation from June to July (MJ/m^2)

N = Annual N fertiliser application (kg/ha)

SAWC = Soil available water capacity (mm/m)

Clover = Clover percentage at seeding (%, e.g. 5% = 5.0)

Values of the coefficients are given in table 4:

Table 4: Coefficients for regression equations, standard error is given in brackets

α_0	-6.13358 (3.06008)	β_0	59.42659 (14.82263)	γ_0	-196.69113 (56.29059)	δ_0	37.56100 (24.92949)
α_1	0.02435 (0.00916)	β_1	0.02567 (0.00499)	γ_1	-0.21942 (0.04872)	δ_1	-0.02713 (0.02340)
α_2	-0.00006 (0.00003)	β_2	-0.00002 (0.00001)	γ_2	0.27919 (0.05661)	δ_2	-0.29452 (0.14607)
α_3	0.00840 (0.00206)	β_3	-10.71480 (2.38474)	γ_3	8.79092 (3.27093)	δ_3	0.00028 (0.00014
α_4	0.18270 (0.06432)	β_4	0.43906 (0.09448)	γ_4	0.62806 (0.08277)		
α_5	0.00753 (0.15544)	β_5	0.02268 (0.00229)	γ_5	-0.00053 (0.00006)		
α_6	0.00012 (0.00133)	β_6	-0.00003 (<0.00001)	γ_6	0.51293 (0.19283)		
α_7	-0.03975 (0.03214)	β_7	0.01769 (0.00522)	γ_7	14.09994 (1.72169)		
α_8	0.03294 (0.01081)	β_8	0.40557 (0.03805)	γ_8	0.00039 (0.00011)		
α_9	-0.00238 (0.00164)	β_9	0.00001 (<0.00001)	γ_9	0.00129 (0.00043)		
α_{10}	0.00002 (0.00001)	β_{10}	0.00004 (0.00001)	γ_{10}	-0.03772 (0.01192)		
α_{11}	0.00048 (0.00012)	β_{11}	-0.00143 (0.00026)				

These models have been tested against the data that was kept aside for validation purposes. The results can be seen in figures 4 to 7 and table 5.

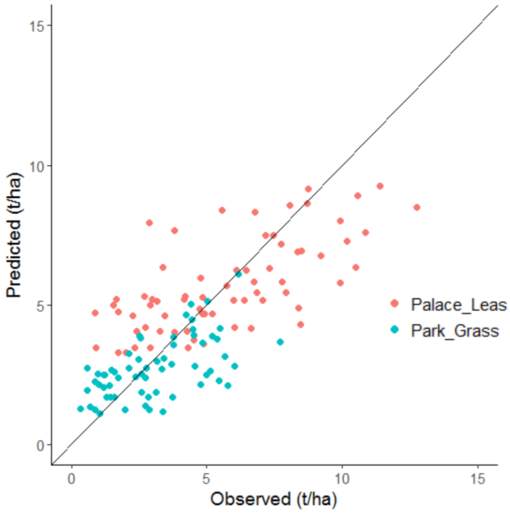

Figure 5: Observed vs predicted peak biomass for permanent grasslands in the Atlantic region. Data taken from two sites (Palace Leas and Park Grass). The straight line indicates the x = y line

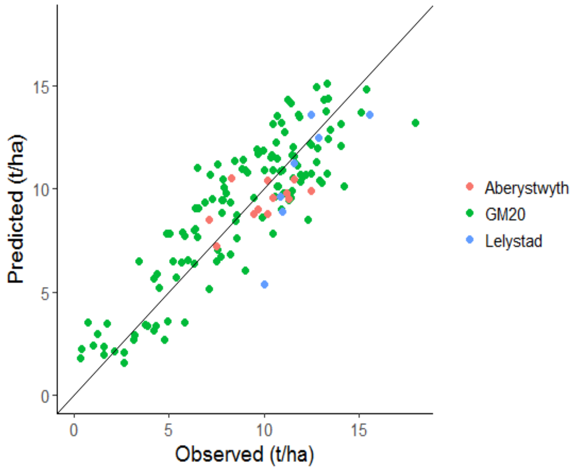

Figure 4: Observed vs predicted total annual harvested biomass for reseeded grasslands in the Atlantic region. Data taken from twenty-three sites (twenty-one GM20 sites, Aberystwyth and Lelystad). The straight line indicates the x = y line

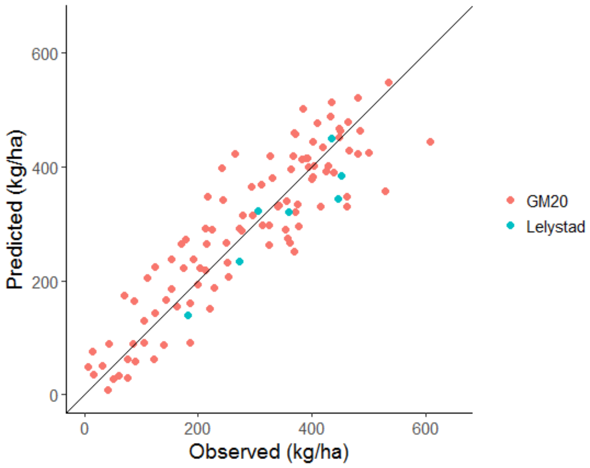

Figure 6: Observed vs predicted total annual harvested nitrogen for reseeded grasslands in the Atlantic region. Data taken from twenty sites (nineteen GM20 sites and Lelystad). The straight line indicates the x = y line

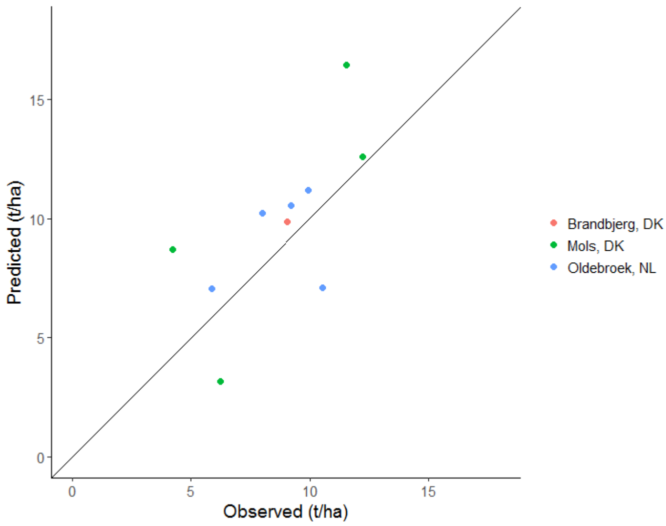

Figure 7: Observed vs predicted peak biomass for heathlands in the Atlantic region. Data taken from three sites (Brandbjerg, Mols and Oldebroek). The straight line indicates the x = y line

Table 5: Estimations of the goodness-of fit of the empirical models for the Atlantic region

	Permanent grasslands (peak biomass)	Reseeded grasslands (total annual harvested biomass)	Reseeded grasslands (total annual harvested N)	Heathlands (peak biomass)
MSE	4.08	3.29	4173.8	7.59
Variance	4.04	3.26	4150.4	6.58
Bias	0.21	0.20	4.8	1.00
Correlation	0.73	0.87	0.89	0.66

We can reduce average spring/summer rainfall by 5% and increase spring/summer temperatures by 1°C (as described in the methods section) and apply these changes to the reseeded grassland yield model. This produces small (non-significant) increases in annual yield for all N fertilisation treatments (see figure 8).

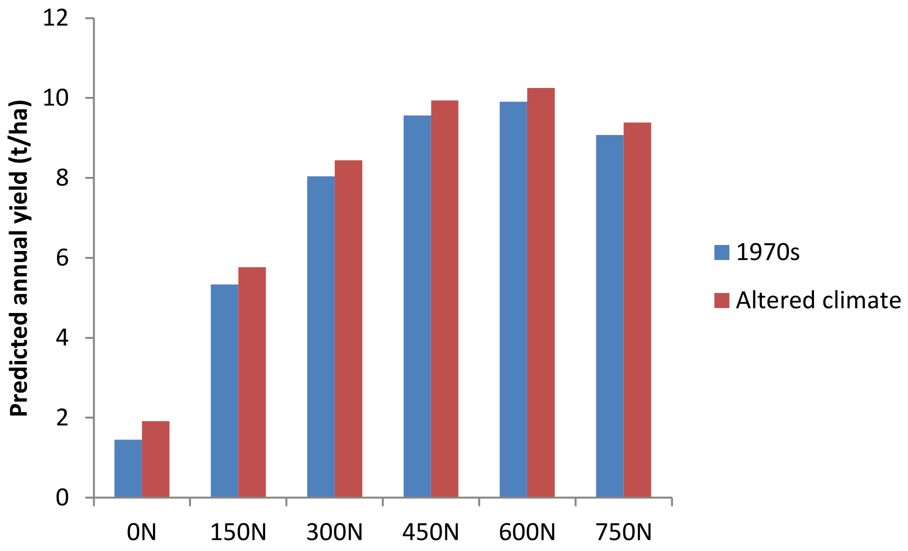

Figure 8: Predicted annual yields from a reseeded grassland empirical model under 1970's climate and a climate closer to that of 2100 (5% decrease in spring/summer rain and 1°C increase in spring/summer temperature) for different nitrogen application rates

Discussion

Century

The Century model is reasonable at estimating the maximum yield, though for some years the observed yields are much lower than this maximum. It seems there is some other factor which causes yields to be low in a given year which is not captured by the current set-up. Since Century runs on a monthly time-step, it may be that there are shorter-term events (e.g. frost) which are having an impact of growth which Century is not able to detect. Since the years with low observed growth are different for different N treatments it may be that there is some interaction between these short-term events and nitrogen availability. A model which functioned on a shorter time-step may be more effective at capturing these variations, though such a model would require more inputs.

Empirical models

All the empirical models had a good fit, with high correlations and the error predominantly coming from variance rather than bias. The heathland model was not as good as the others, though this is not surprising since the heathland datasets were much smaller than those for grasslands.

Climate change

Both modelling approaches were suggestive of no significant change in yields at the Hurley site under climate change (though the empirical models looked at a lower temperature increase). This analysis did not include changes in atmospheric CO_2 concentrations, which will be added at a later date. It is likely that elevated CO_2 concentrations will have a positive impact of yields (Ainsworth and Long, 2004; Nowak et al., 2004; Wang et al., 2012). It is also likely that other European regions will exhibit more of an impact of climate change, as the Atlantic region is the one with the smallest expected climatic changes (IPCC, 2013).

Future work

We will continue to improve the parameterisation of the Century model. We will also use Century to predict the N content of grasslands. Once this is working we will expand this analysis to look at other sites in the Atlantic region and at other regions. We will also include the impacts of elevated atmospheric CO_2 concentrations. For the empirical models, we will develop more regression equations to look at yield and N content for all grazing systems and for all European regions. Data has already been collected from sites across Europe in preparation for this.

Additional activities

While working at the Basque Centre for Climate Change, the recipient attended the iSAGE AGM which was held in Bilbao. This was an opportunity to promote her work to a wider audience and to network with academics and industry partners from across Europe. She presented some of her previous work which led into the research described here. This presentation is available on YouTube: https://www.youtube.com/watch?v=IpM3ZFql2WM.

Acknowledgements

Thank you very much to the Stapledon Memorial Trust for making this trip possible. We would also like to thank Agustin del Prado and Guillermo Pardo for welcoming the recipient at the Basque Centre for Climate Change and making the trip an enjoyable and productive experience. In addition we would like to thank Dr Andrea Britton of the James Hutton Institute for providing data from the Culardoch site. Finally, we thank the Lawes Agricultural Trust and Rothamsted Research for data from the e-RA database. The Rothamsted Long-term Experiments National Capability (LTE-NCG) is supported by the UK Biotechnology and Biological Sciences Research Council and the Lawes Agricultural Trust.

Bibliography

Ainsworth, E.A., Long, S.P., 2004. What have we learned from 15 years of free-air CO2 enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy properties and plant production to rising CO2. New Phytol. 165, 351–372. doi:10.1111/j.1469-8137.2004.01224.x

Batjes, N.H., 2000. Global Data Set of Derived Soil Properties, 0.5-Degree Grid (ISRIC-WISE). Oak Ridge, Tennessee, USA.

Collins, M., Knutti, R., Arblaster, J., Dufresne, J., Fichefet, T., Friedlingstein, P., Gao, X., Gutowski, W., Johns, T., Krinner, G., Shongwe, M., Tebaldi, C., Weaver, A., Wehner, M., 2013. Long-term Climate Change: Projections, Commitments and Irreversibility, in: Stocker, T., Qin, D., Plattner, G., Tignor, M., Allen, S., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P. (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. 1029–1136.

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, p. AISM 1-158.

KNMI, 2017. Daggegevens van het weer in Nederland [WWW Document]. K. Ned. Meteorol. Inst. URL https://www.knmi.nl/nederland-nu/klimatologie/daggegevens

Kovats, R.S.S., Valentini, R., Bouwer, L.M., Georgopoulou, E., Jacob, D., Martin, E., Rounsevell, M., Soussana, J.-F., 2014. Europe, in: Barros, V.R., Field, C.B., Dokken, D.J., Mastrandrea, M.D., Mach, K.J., Bilir, T.E., Chatterjee, M., Ebi, K.L., Estrada, Y.O., Genova, R.C., Girma, B., Kissel, E.S., Levy, A.N., MacCracken, S., Mastrandrea, P.R., White, L.L. (Eds.), Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, USA, pp. 1267–1326.

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. doi:10.1016/J.AGRFORMET.2010.07.008

Met Office, 2012. Met Office Integrated Data Archive System (MIDAS) Land and Marine Surface Stations Data (1853-current) [WWW Document]. NCAS Br. Atmos. Data Cent. URL http://catalogue.ceda.ac.uk/uuid/220a65615218d5c9cc9e4785a3234bd0

Metherell, A.K., Harding, L.A., Cole, C.V., Parton, W.J., 1993. CENTURY Soil organic matter model environment: Technical Documentation v4.0.

NASA, 2018. POWER Agroclimatology Daily Averaged Data [WWW Document]. POWER Proj. Data Sets. URL https://power.larc.nasa.gov/

NOAA, 2016. NOAA NCDC GCPS Monthly Station [WWW Document]. IRI Data Libr. URL http://iridl.ldeo.columbia.edu/SOURCES/.NOAA/.NCDC/.GCPS/.MONTHLY/.STATION/

Nowak, R.S., Ellsworth, D.S., Smith, S.D., 2004. Functional responses of plants to elevated atmospheric CO2- do photosynthetic and productivity data from FACE experiments support early predictions? New Phytol. 162, 253–280. doi:10.1111/j.1469-8137.2004.01033.x

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. Global Biogeochem. Cycles 7, 785–809. doi:10.1029/93GB02042

R Core Team, 2017. The R project for statistical computing.

Reinsch, S., Koller, E., Sowerby, A., de Dato, G., Estiarte, M., Guidolotti, G., Kovács-Láng, E., Kröel-Dulay, G., Lellei-Kovács, E., Larsen, K.S., Liberati, D., Peñuelas, J., Ransijn, J., Robinson, D.A., Schmidt, I.K., Smith, A.R., Tietema, A., Dukes, J.S., Beier, C., Emmett, B.A., 2017. Shrubland primary production and soil respiration diverge along European climate gradient. Sci. Rep. 7. doi:10.1038/srep43952

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. Nutr. Cycl. Agroecosystems 68, 165–179. doi:10.1023/B:FRES.0000019045.90791.a4

Scotland's soils, 2018. National soil map of Scotland [WWW Document]. URL http://soils.environment.gov.scot/ (accessed 7.16.18).

UEA CRU, Harris, I.C., 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 (Jan. 1901-Dec. 2016) [WWW Document]. Cent. Environ. Data Anal. URL http://dx.doi.org/10.5285/58a8802721c94c66ae45c3baa4d814d0

UKSO, 2017. United Kingdom Soil Observatory [WWW Document]. URL http://mapapps2.bgs.ac.uk/ukso/home.html? (accessed 7.16.18).

Wang, D., Heckathorn, S.A., Wang, X., Philpott, S.M., 2012. A meta-analysis of plant physiological and growth responses to temperature and elevated CO2. Oecologia 169, 1–13. doi:10.1007/s00442-011-2172-0

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. doi:10.1017/S0021859603002958