Modelling climate change impacts on European grassland-based livestock systems

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Declaration

I, Martha Dellar, declare that the work in this thesis was written by myself and is my own. Furthermore, this work has not been submitted for any other degree or professional qualification. All sources of information and contributions have been acknowledged. This thesis includes multiple jointly-authored publications. In each case, I was the lead author and performed the entirety of the analysis and writing. Other authors provided suggestions as to the methodology, and for chapter three, Dr David Holmes assisted with writing the computer code to optimise the Century model parameters.

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Abstract

Climate change is leading to higher temperatures and altered rainfall patterns across Europe. These changes are likely to have major impacts on plant life. This is particularly relevant for livestock production systems which are dependent on grass and forage. Farmers need to know what they can expect in the future so that they can be well prepared and ensure that their livestock will have enough to eat. This thesis aims to quantify the impacts of rising atmospheric CO_2 concentrations, higher temperatures and changes in water availability on the yield and protein content of European grasslands.

The first approach used was a meta-analysis. Data from experiments in which the climate had been artificially altered was collected and divided according to geographic region (Alpine, Atlantic, continental, northern and southern) and plant type (graminoids, legumes, forbs and shrubs). Using Markov Chain Monte Carlo (MCMC) simulations, mixed models were developed to estimate the expected changes to plant yield and protein (i.e. nitrogen (N)) concentration under different climatic changes. The results showed that areas predicted to become warmer and wetter (i.e. northern Europe and parts of Alpine and continental Europe) will benefit from higher plant yields, but reduced plant N concentration. Areas which will become warmer and drier (i.e. southern Europe and parts of continental Europe) will see decreases in both yield and N concentration. The Atlantic region is the area where climate change is expected to be the least extreme and the effects on plant life will be relatively minor. Shrubs will particularly benefit from rising atmospheric CO_2 concentrations, though will also suffer large decreases in N concentration, as will forbs.

The next approach considered different methodologies for modelling grassland yield and N yield. One method involved developing a statistical model using data from long-term grassland experiments across Europe. Through stepwise linear regression, equations were developed to model grassland yield and N yield based on various weather and managerial variables. The other method used a pre-existing process-based model (Century), which was applied to six sites across Europe. Both approaches produced reasonable estimates of grassland yield and N yield. The prediction error was lower for the Century model while the regression methodology produced better correlations between observations and predictions. Both models

were quite sensitive to uncertainties in weather parameters, particularly precipitation, with little sensitivity to soil properties. Overall, the regression approach was found to be suitable for considering general trends over large spatial scales, while the Century model was more appropriate for local-scale analysis.

The two models described above were used to quantify the effects of two different climate change scenarios (one midrange and one more extreme) on the five European regions listed above. The two models generally produced similar predictions, indicating that grassland yields will increase in most areas though there may be slight decreases in southern Europe. Also, plant N concentrations will decrease. Generally permanent grasslands responded more positively to climate change than temporary ones. The impact of climate change tends to be less than the impact of fertiliser, geographic region or grassland type, suggesting that appropriate changes to grassland management practices should be able to mitigate the negative effects of climate change.

The modelling described above was all performed using a monthly time-step. This is computationally efficient, but means that short-term extreme weather events are not accounted for. Extreme weather events such as heavy rainfall, droughts and heat waves are predicted to become both more frequent and more intense in the future and it is important to consider the impacts they will have on grasslands and therefore livestock.

Two methodologies were used to quantify the effects of extreme weather events on grasslands. The first uses multiple regression analysis and incorporates terms such as ‘number of days in a month with temperature greater than 30°’ to account for weather extremes. The equations developed had a good fit with observed data. They were found to be predominantly sensitive to uncertainties in precipitation rather than in temperature or grassland species composition. Two projected future weather datasets were applied to the equations; both followed the same climate change scenario, but one included extreme events and the other was smoothed to reduce the extremes. Comparing the model outputs from the two datasets showed that smoothing the data increased the predicted yields and N yields, demonstrating that extreme weather events are detrimental to grasslands. In general, the yield of temporary grasslands decreased over time, while for permanent grasslands it increased. There was little change in N yield over time.

The other methodology used the pre-existing process-based model DailyDayCent, which is very similar to the Century model, but is based on a daily rather than a monthly time-step. DailyDayCent was applied to six sites across Europe and was found to have reasonably good fit, though struggled to capture inter-annual variability. The model was predominantly sensitive to uncertainties in rainfall measurements rather than temperature. Two climate change datasets, with and without extreme events, were applied to the model for each of the six sites. Predicted yields and N yields were similar to those found with the Century model. The presence or absence of extreme events usually had little effect, but this may have been due to limitations of the model. The exception was for a site in southern Europe, where the presence of extreme events led to increases in yield and N yield in the short-term, but large decreases in the long-term.

Overall, grassland yields are expected to increase in the future in response to climate change (except possibly in southern Europe), particularly for permanent grasslands, while plant N concentration will decrease. Increased yields are generally good for livestock, though reduced N concentrations indicate that grazing animals will need to have a higher intake in order to receive the same amount of protein. Extreme weather events are an important consideration, leading to reductions in grassland yield and N yield. Farmers need to be prepared to meet the challenges presented by such events, for example through using more resilient plant species or increasing plant species richness.

Lay Summary

Climate change is leading to higher temperatures and altered rainfall patterns across Europe. These changes are likely to have major impacts on plant life. This is particularly relevant for livestock production systems which are dependent on grass and forage. Farmers need to know what they can expect in the future so that they can be well prepared and ensure that their livestock will have enough to eat. This thesis takes several different approaches to quantifying the impacts of rising atmospheric CO_2 concentrations, higher temperatures and changes in water availability on the yield and protein content of European grasslands. It also considers the likely effects of these changes on grassland-based livestock systems.

Firstly, data from previous experiments in which the climate had been artificially altered was collected and divided according to geographic region (Alpine, Atlantic, continental, northern and southern) and plant type. The data was analysed to determine the expected changes to plant yield and protein concentration under different climatic changes. The results showed that areas predicted to become warmer and wetter (i.e. northern Europe and parts of Alpine and continental Europe) will benefit from higher plant yields, but reduced plant protein concentration. Areas which will become warmer and drier (i.e. southern Europe and parts of continental Europe) will see decreases in both yield and protein concentration. Climate change in the Atlantic region is expected to be the least extreme and the effects on plant life will be relatively minor. Shrubs will particularly benefit from rising atmospheric CO_2 concentrations though will also suffer large decreases in protein concentration.

The next approach considered different methodologies for modelling grassland yield and protein content. One method involved developing a statistical model using data from long-term grassland experiments across Europe. Equations were developed to model grassland yield and protein content based on various weather and managerial variables. The other method used a pre-existing model (Century), which was applied to six sites across Europe. Both approaches produced reasonable estimates of grassland yield and protein content. Overall, the first approach was found to be suitable for considering general trends over large spatial scales, while the latter model was more appropriate for analysis at a local scale.

The two models described above were used to quantify the effects of two different climate change scenarios (one midrange and one more extreme) on the five

European regions listed above. The two models generally produced similar predictions, indicating that grassland yields will increase in most areas, though there may be slight decreases in southern Europe. Also, plant protein concentrations will decrease. The impact of climate change tends to be less than the impact of fertiliser, geographic region or grassland type, suggesting that appropriate changes to grassland management practices should be considered to mitigate the negative effects of climate change.

The modelling described above was all performed on a monthly time-scale. Although this is computationally efficient, short-term extreme weather events are not captured properly. Extreme weather events such as heavy rainfall, droughts and heat waves are predicted to become both more frequent and more intense in the future and it is important to consider the impacts they will have on grasslands and livestock.

Two methodologies were used to quantify the effects of extreme weather events on grasslands. The first involved developing a statistical model. Two future weather datasets were applied to this model; these both followed a midrange climate change scenario, but one included extreme weather events and one did not. Comparing the results from the two datasets showed that including extreme events led to lower grassland yields and protein content, demonstrating that extreme weather events are detrimental to grasslands. In general, grasslands which have existed for a long time experienced increasing yields, while more short-term grasslands (e.g. those which are part of a crop rotation) experienced decreasing yields. There was little change in protein content over time.

The other methodology was to use another pre-existing model (DailyDayCent), which is very similar to the Century model, but uses a daily rather than a monthly time-step. It was applied to six sites across Europe. Two climate change datasets, with and without extreme events, were applied to the model for each of the sites. Predicted yields and protein content were similar to those found with the Century model. The presence or absence of extreme events usually had little effect, but this may have been due to limitations of the model. The exception was for a site in southern Europe, where the presence of extreme events led to increases in yield and protein content in the short-term, but large decreases in the long-term.

Overall, grassland yields are expected to increase in the future (except possibly in southern Europe), particularly for long-term ‘permanent’ grasslands, while plant protein concentration will decrease across Europe. Increased yields are generally good for livestock, though reduced protein concentrations indicate that grazing animals will need to eat more in order to receive the same amount of protein. Extreme weather events are an important consideration, leading to reductions in grassland yield and protein content. Farmers need to be prepared to meet the challenges presented by such events, for example through using more resilient plant species or increasing plant species diversity.

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Publications

Journal articles

Dellar, M., Topp, C.F.E., Banos, G. and Wall, E., 2018. A meta-analysis on the effects of climate change on the yield and quality of European pastures, *Agriculture, Ecosystems and Environment*, 265, p413-420

Dellar, M., Topp, C.F.E., Pardo, G., del Prado, A., Fitton, N., Holmes, D., Banos, G. and Wall, E., 2019. Empirical and dynamic approaches for modelling the yield and N content of European grasslands, *Environmental Modelling and software*, 122

Conference proceedings

Dellar, M., Topp, C.F.E., Banos, G. and Wall, E., 2018. How will the nutritional quality of European pastures be affected by climate change? Proceedings of the British Society of Animal Science, 9(s1), 9 – 11 April 2018, Dublin, Ireland, p3

Dellar, M., Topp, C.F.E., Banos, G. and Wall, E., 2018. A meta-analysis on the impacts of climate change on the yield of European pastures. Sustainable meat and milk production from grasslands, Grassland Science in Europe, 23, European Grassland Federation General Meeting, 17 – 21 June 2018, Cork, Ireland, p.535 – 537

Dellar, M., Topp, C.F.E., Banos, G., del Prado, A., Pardo, G., Fitton, N. and Wall, E., 2019. Modelling the impact of climate change on the yield of western European reseeded grasslands. Proceedings of the British Society of Animal Science, 9 – 11 April 2019, Edinburgh, UK, p203

Dellar, M., Topp, C.F.E., Pardo, G., del Prado, A., Banos, G. and Wall, E., 2019. Modelling the impact of climate change on the yield of European pastures. Book of Abstracts of the 70th Annual Meeting of the European Federation of Animal Science, 26 – 30 August 2019, Ghent, Belgium

List of abbreviations

AGDW – Above ground dry weight

Alt - Altitude

ANPP – Aboveground net primary production

C – Carbon

CO_2 – Carbon dioxide

DM – Dry matter

FACE – Free air carbon enrichment

IPCC – Intergovernmental Panel on Climate Change

LP – legume percentage

MCMC – Markov Chain Monte Carlo

N – Nitrogen

NF – Nitrogen fertiliser

P – Phosphorus

PFG – Plant functional group

ppm – parts per million

RCP – Representative concentration pathway

REML – Restricted maximum likelihood

RMSE – Root mean squared error

SD – Standard deviation

SE – Standard error

sed – Standard error of difference

↑C – Elevated atmospheric CO_2 concentration

↑T – Elevated temperature

↑W – Increased water availability

↓W – Reduced water availability

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CHAPTER 1 Introduction

1.1 Background

1.1.1 European grasslands

1.1.1.1 Grassland types

In Europe, 20.7% of land area consists of grassland. This varies from 56.3% of land area in Ireland to just 4.4% in Finland (Eurostat, 2017). Grassland can be either *permanent* or *temporary*. Permanent grasslands have been used continuously as grassland for at least five years. Temporary grasslands have been used as grassland for less than five years and are often part of a rotation. Temporary grasslands tend to produce higher yields. Grasslands also vary according to the intensity of their management, i.e. fertiliser application, number of harvests per year and livestock stocking density. Grasslands with intensive management practices are referred to as *intensive grasslands*, while grasslands with little management are referred to as *extensive grasslands*. Grasslands are typically used for grazing or silage/hay production, though in some cases plant quality is too poor for these purposes. In these cases the grasslands still perform valuable ecosystem services in terms of biodiversity, carbon storage and water catchment (Lesschen et al., 2014).

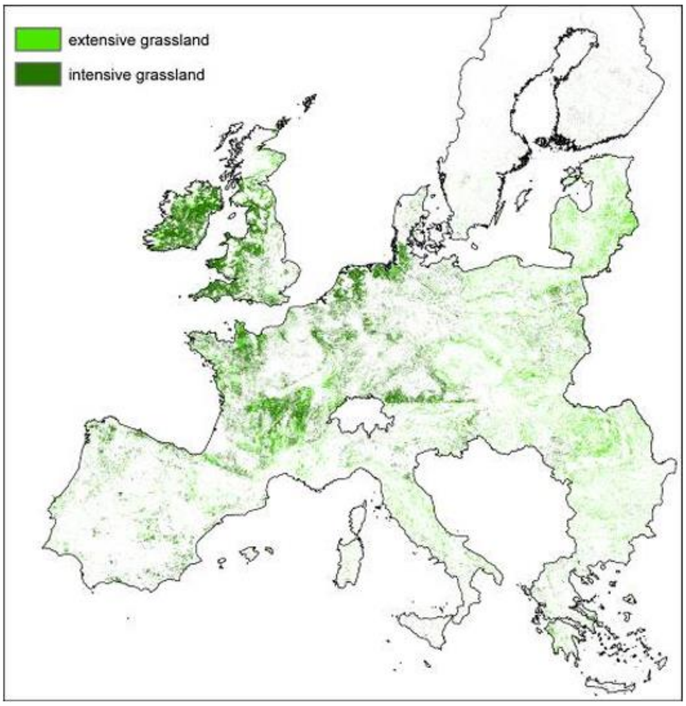

Figure 1.1: *Distribution of extensive and intensive grassland in the EU (Environmental Geography, 2018)*

Intensive grasslands are dominant in Ireland, as well as in parts of the UK, France, Germany and the Netherlands, while extensive grasslands prevail in other areas (figure 1.1). Permanent grasslands tend to dominate in the UK, as well as in Austria, Bulgaria and northern Spain (Lesschen et al., 2014). As one would expect, the distribution of intensive grasslands matches up well with the distribution of highly productive grassland (figure 1.2).

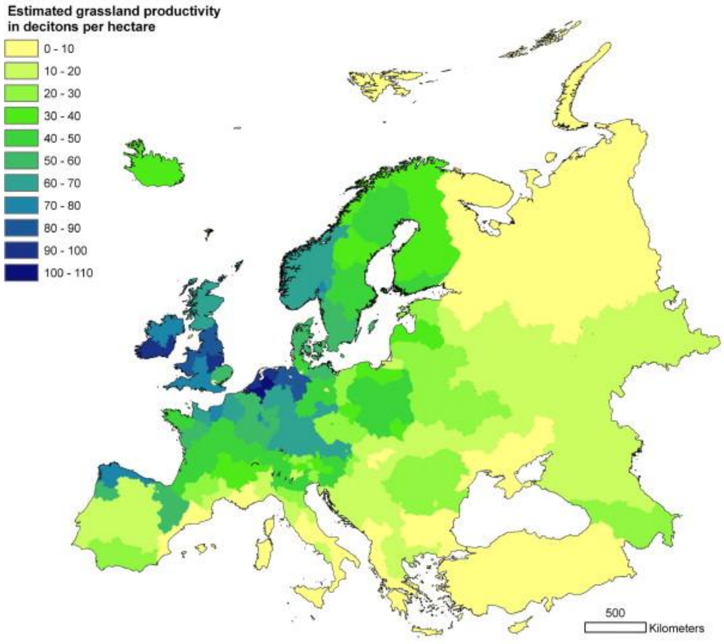

Figure 1.2: *Estimated grassland productivity in Europe (Smit et al., 2008)*

From figures 1.1 and 1.2, it can be seen that there is a large degree of variation in grassland systems across Europe. In England, Wales, Ireland and the Netherlands, there are highly productive intensive systems, while Scotland favours extensive systems, though still has highly productive grasslands. Extensive farming is widely used throughout southern and eastern Europe, and these grasslands are much less productive. Other areas have more of a mix of systems.

In terms of land use, in Iceland, Norway, Scotland and Ireland, a large proportion of total agricultural land area is permanent grassland, while Sweden and Finland have very little grassland at all (Eurostat, 2017). In southern Europe, there is more land devoted to silvo-pastoral systems than there is to open grassland (Malek and Verburg, 2017).

1.1.1.2 Plant species

Permanent grasslands are dominated by one or more species of grass, though may include many different plant types, including shrubs, forbs and legumes. All plant species are perennial or else self-seeding. Temporary grasslands are usually 100% grass or else a grass/legume mixture. Species may be perennial, biennial or annual. Common grasses include ryegrasses (particularly perennial ryegrass (*Lolium perenne*) and Italian ryegrass (*L. multiflorum*)), cocksfoot (*Dactylis glomerata*), fescues (*Festuca*) and timothy (*Phleum pratense*) (Velthof et al., 2014). Common legumes include white clover (*Trifolium repens*), red clover (*T. pratense*), subterranean clover (*T. subterraneum*) and lucerne (*Medicago sativa*) (Molle et al., 2008). European species are mostly C3, though some C4 species can be found in southern Europe. Intensive systems tend to have lower plant species diversity than extensive systems (Pakeman et al., 2017).

1.1.2 Climate change in Europe

1.1.2.1 Temperature

Temperatures across Europe continue to increase, with the 2002-2011 European land area decadal average being 1.3 ± 0.11°C above the 1850-1899 average (Kovats et al., 2014). Warming has been greatest in northern Europe during the winter and in southern Europe during the summer (EEA, 2012), and this pattern is expected to continue in the future (Christensen et al., 2013; Jacob et al., 2014). Under a midrange prediction (Representative Concentration Pathway (RCP) 4.5) (Collins et al., 2013), average annual temperatures are expected to rise by 1.0 to 4.5°C by 2100.

Since the 1960s, the frequency of high temperature extremes (hot days, tropical nights and heat waves) has increased across Europe, while the frequency of low temperature extremes (cold spells and frost days) has decreased (EEA, 2012). Heatwaves are expected to occur increasingly often in future, especially in southern Europe (Kovats et al., 2014). The drier, hotter conditions in southern and parts of continental Europe also mean that the wildfire risk will increase, by 150% in some areas (EEA, 2012), with the period of risk extending by up to a month (Giannakopoulos et al., 2009).

1.1.2.2 Precipitation

Annual precipitation has been increasing in the north of Europe and decreasing in the south since the 1960s (EEA, 2012). This is predicted to continue in the future, with average annual precipitation expected to increase by up to 25% in northern and eastern Europe under a midrange scenario, while decreasing by 25% in parts of southern Europe (compared with 1971 – 2000) (Jacob et al., 2014). This increased rainfall will fall in the winter months; most areas will see a reduction in summer precipitation. Heavy rain events will become more frequent (especially in the north) and dry spells will become longer (especially in the south) (Christensen et al., 2013; Forzieri et al., 2014; Kovats et al., 2014). Floods will become more common across large parts of Europe, with the exception of northern and north-eastern areas, where warmer winters mean there is less snowfall and thus less snowmelt in spring (Madsen et al., 2014; Rojas et al., 2012). Drought events in southern Europe are already becoming both longer and more intense and this trend is expected to continue and to spread into central Europe (Kovats et al., 2014). The increasing variation in aridity in Mediterranean areas (with increases in both heavy rain events and dry spells) is likely to lead to soil degradation and in extreme cases desertification (EEA, 2012).

1.1.2.3 Other climatic changes

There have been no strong trends in wind speeds across Europe over the last 140 years (Bett et al., 2013). Small increases in extreme wind speed are predicted for central and northern Europe with medium confidence, though the picture is less clear in other areas. Wind speeds may possibly decrease in southern Europe, though this has been predicted with low confidence (Kovats et al., 2014).

Mean sea level is increasing (except in the northern Baltic) and extreme levels have increased. Extreme events are predicted to increase with high confidence. Significant increases are expected along the eastern North Sea and west of the UK and Ireland. Trends for the southern North Sea, the Dutch coast and the Adriatic are less clear (Kovats et al., 2014).

1.1.3 How the climate affects grasslands and why does it matter?

1.1.3.1 Climate and grasslands

Grass growth and nutritional quality are affected by the climate. Growing seasons and phenology are largely determined by temperature (Ansquer et al., 2009; Madakadze et al., 2003) and soil moisture (primarily from rainfall) affects both growth and nutrient uptake (Parton et al., 1993). Changes in air temperature and water availability have been found to affect grassland productivity and nutritional quality, as will be discussed further in section 1.2. However, it seems that this requires relatively severe climatic changes. Smit et al. (2008) looked at the measured productivity of permanent grasslands in Europe between 1973 and 2005 and found that it remained roughly constant. The productivity of temporary grasslands increased by 0.35% per year in the same period, though this was attributed to genetic improvements rather than the changing climate. However, more extreme climatic events do have effects. During the 2003 heatwave there was a 60% green fodder deficit in France (FAO, 2016). During the 2018 heatwave grass in the UK stopped growing, causing farmers to have to use their winter forage rations (Ffoulkes, 2018). Extremely heavy rainfall in the UK in 2014 led to 25% of pastures becoming unviable in some regions, requiring full cultivation and replacement and leading to forage losses of up to 30% (ADAS, 2014). As climate change becomes more severe and the frequency of such extreme events increases, it is likely that there will be major consequences for European grasslands.

1.1.3.2 Consequences for livestock

There are approximately 88.4 million bovine animals in Europe (mainly in France, Germany and the UK), as well as 86.8 million sheep (mainly in the UK and Spain) and 12.7 million goats (mainly in Greece and Spain) (Eurostat, 2018). Dairy cattle tend to be associated with intensive systems, though the amount of grazing time varies hugely from country to country. In Ireland, 98% of cows have access to grass, while in Bulgaria grazing is almost non-existent (DG for Health and Food Safety, 2017). Beef cattle may be farmed intensively or extensively, though there is a tendency for all cattle farming to move towards more intensive systems (DG for Health and Food Safety, 2017; English Nature, 2006). Sheep are mainly found in extensive grazing systems and particularly in Less Favoured Areas, given their ability to adapt to disadvantageous conditions and the difficulties of using the land for anything else. In Spain, 82% of sheep are found in such areas and 69% in Britain

(Brunagel et al., 2008). Goat farming systems vary across Europe, though goat grazing is generally extensive. Northern countries tend to rely on grass and rough grazing, while Mediterranean systems also make use of housing, woodland, stubbles and arable by-products (SAC and INRA, 2000).

Around 40% of livestock feed intake (by dry matter) in Europe comes from grass (Lesschen et al., 2014). Indeed, for intensively grazed pastures, about 85% of herbage is consumed by ruminants (Rychnovská, 1993). It follows that future changes to grassland productivity and nutritional quality are likely to affect livestock.

If forage availability decreases, this could require longer grazing times and lead to reduced feed intake (Allison, 1985). On the other hand, if there is an increase in herbage then this could increase feed intake and generate higher milk yields (assuming animals are not already achieving their maximum intake capacity) (Morand-Fehr et al., 2007). Changes in forage availability may require changes in stocking density (Moran et al., 2009; Nardone et al., 2010).

Pasture quality is also an important consideration. Silanikove (2000) found that some Mediterranean pastures are already failing to provide sufficient nitrogen (N) and energy to meet the requirements for the maintenance and pregnancy of sheep. If livestock do not receive sufficient energy and nutrients in their diet, this can lead to weight loss, reduced growth, lower milk yields and reduced sexual function (Hogan et al., 2008; Morand-Fehr et al., 2007; Sevi et al., 2009). On the other hand, if pasture quality were to improve, as may happen in some areas, this would likely lead to increased growth rates and higher milk yields (McMillin, 2010; Morand-Fehr et al., 2007).

In terms of meat production, a reduction in food intake for small ruminants produces leaner, less fatty meat (Sañudo et al., 1998). A low quality diet can lead to stressed, poor quality meat (Sañudo et al., 1998), whereas a high energy diet means that carcasses have more fat and are more tender with less problematic pH’s (the pH of meat can affect both its toughness and its shelf-life) (Devine et al., 1993; Sañudo et al., 1998). In terms of milk production, a high feed intake produces better milk (Morand-Fehr et al., 2007), whereas feed restriction increases the milk’s fat content (Sevi et al., 2009). Consumption of legumes (i.e. protein) increases the conjugated linoleic acid content of milk (Cabiddu et al., 2005), while a low protein diet makes for low protein milk (Bencini and Pulina, 1997).

Poor forage quality can lead to a number of health problems for grazing livestock. Nutritional stress from reduced protein digestibility can increase an animal's susceptibility to parasites and diseases (Sotiraki et al., 2013). Also, plants with poor digestibility have a longer rate of passage, reducing total intake and potentially causing muscle and fat catabolism, and in extreme cases death (Milchunas et al., 2005). A reduction in appealing plants could reduce an animal's feed intake (Hogan et al., 2008), or else lead them to eat toxic plants instead (Banik et al., 2015).

1.2 State of the art

1.2.1 Approaches for determining the effects of climate change on grasslands

1.2.1.1 Experimental research

A large number of experiments have been performed, investigating the impacts of climate change on European grasslands. These generally look at three possible changes: increasing atmospheric CO_2 concentration, increasing temperature and changes in water availability. The majority of experiments consider these changes individually, though some look at combinations of changes (e.g. Farfan-Vignolo and Asard, 2012; Stevnbak et al., 2012; Zwicke et al., 2013). Those experiments considering multiple simultaneous climatic changes have often found that they produce opposing effects (for example increased growth due to elevated CO_2, but decreased growth due to higher temperatures). This makes it hard to determine what the net effect of simultaneous changes might be.

Increases in atmospheric CO_2 concentrations are usually implemented using a climate chamber or FACE (Free Air Carbon Enrichment) array (e.g. Diaz et al., 1998; Hebeisen et al., 1997). Temperature increases are often implemented using a climate chamber or greenhouse (e.g. Hakala and Mela, 1996; Jonasson et al., 1999), but other methods include night-time screening (e.g. Sardans et al., 2008), infrared heating systems (e.g. Sanaullah et al., 2014), buried heating wires (e.g. Schuerings et al., 2013) and transplants (e.g. Cantarel et al., 2013). For outdoor experiments, reductions in water availability are usually implemented through shelters (e.g. Jung et al., 2014; Walter et al., 2012), while increases are implemented through irrigation systems (e.g. Khan et al., 2014). Other experiments are conducted in climate chambers or greenhouses and water availability is controlled through irrigation systems or manual watering (e.g. De Luis et al., 1999; Küchenmeister et al., 2014).

Experiments provide very accurate information at a site-specific level, especially if they are conducted *in situ* rather than in a greenhouse, climate chamber or similar. Long-term experiments in particular are very useful as they provide information on plant adaptations over time and on legacy effects between years. The disadvantages are that they are time-consuming and it is difficult to extrapolate the results to a larger geographic scale.

1.2.1.2 Meta-analysis

Meta-analyses circumvent some of the disadvantages of experimental research, by enabling the results from multiple experiments to be generalised to have a wider range of application. Several meta-analyses have been performed looking at the effects of climate change on grasslands, usually at a global scale. Many of these focus on just a single climatic change (e.g. Lee et al., 2017; Wang, 2007; Wellstein et al., 2017), most likely due to the lack of experiments including multiple simultaneous changes. Even those meta-analyses which look at multiple climatic changes do not consider those changes happening simultaneously and they are treated as separate effects (e.g. Dumont et al., 2015). The exception is the meta-analysis of Wang et al. (2012), which looked at the combined effect of elevated CO_2 concentrations and increased temperature on plant physiology and growth. They found that the effect of elevated CO_2 concentrations varied depending on the temperature treatment, highlighting the importance of considering multiple simultaneous changes to growing conditions.

1.2.1.3 Modelling

Grassland models generally fall into one of two categories: statistical or process-based. Statistical models are usually based on multiple regression analysis and thus are only concerned with statistical trends, they do not account for biological processes. Process-based models are more complex and aim to accurately simulate known biological interactions and activity.

Statistical grassland models can be site-specific or can be applied at a larger (e.g. regional or even national) scale (Armstrong et al., 1997; Hurtado-Uria et al., 2014; Trnka et al., 2006). They are generally fairly simple and require minimal inputs. This simplicity comes with costs. They are restricted to a single output (Qi et al., 2017), are subject to issues with co-linearity between predictor variables, assume that past relationships will hold in the future and tend to have low signal-to-noise ratios when comparing yields with weather conditions (Lobell and Burke, 2010).

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 statistical meta-model derived from the outputs of the same process-based model. While the statistical model accounted for less variation (as would be expected), it still produced ‘sufficiently precise’ estimations of pasture yield. On the other hand, Jenkinson et al. (1994) used regression equations to model interactions between weather conditions and herbage yield for a long-term grassland experiment and found several difficulties with this method. They found that there were such a large number of relevant variables and interactions of variables, many of which were correlated with one another, were non-linear or which varied according to the time of year, that it became incredibly complex and the number of variables could be greater than the number of observations. They suggested that using principal component analysis might be more effective, though acknowledged that this can be difficult to interpret biologically. They also found that extreme climatic events could have an influence lasting multiple years, further complicating the analysis.

Lobell and Burke (2010) compared three types of statistical models: (i) those based on time-series data from a single area, (ii) those based on data from various sites at a single time, and (iii) those based on variations in both time and space. They found that the first type gave the best results for evaluating yield under changing precipitation, but performed less well for changes in temperature, while the other two types produced more accurate responses for temperature than precipitation. Lobell and Burke (2010) also concluded that statistical models become more appropriate as spatial scales increase and recommend such models when considering the large-scale impacts of climate change.

Process-based or dynamic models have been developed as a way of analysing grassland systems (and ecosystems in general), for example PaSIM (Riedo et al., 1998), NGAUGE (Brown et al., 2005) and Century (Parton et al., 1987). These provide highly detailed information and assess a wide variety of parameters, for example carbon (C) and N fluxes, N_2O emissions and organic matter decomposition. They are usually applied on a site-specific basis and require a large number of inputs. Korhonen et al. (2018) applied several different process-based models to timothy grass swards in northern Europe and Canada and found that the more detailed the model, the more accurate the results.

Applying such models on a larger scale would require an unrealistic amount of data. Also, it would be necessary to parameterise the model for each of the multitude of existing pasture types in order to accurately capture all the processes in each system, which is also unrealistic (Trnka et al., 2006). Attempts have been made to apply process-based ecosystem models 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. Another drawback of process-based models is that they generally have a considerably longer run-time than purely statistical methods, due to their complexity.

Previous attempts to model the effects of climate change on grasslands have usually been conducted at relatively small spatial scales. A regression approach was used for Atlantic calcareous grasslands (Duckworth et al., 2000), concluding that little change was expected. Several studies have used process-based models, but generally at a site-specific or else national scale (Abdalla et al., 2010; Graux et al., 2013; Thornley and Cannell, 1997; Vital et al., 2013). The Century model was used to predict the effects of climate change on grassland net primary productivity (among other things) at several sites worldwide (Hall et al., 1995), though none of these sites were in Europe. They found that grassland productivity generally increased.

1.2.2 Effects of climate change on grasslands

1.2.2.1 Elevated atmospheric CO_2 concentrations

Atmospheric CO_2 concentrations have been rising since the industrial revolution and the rate of change is increasing. In the early 1700s it was around 280ppm and today it is around 408ppm (Lindsey, 2019). Under a midrange climate change scenario (RCP4.5), average global CO_2 concentration is expected to reach 538ppm by 2100, but it could reach 936ppm under an extreme scenario (RCP8.5) (IPCC, 2013a).

Many studies have confirmed that elevated CO_2 increases plant growth and yields, providing a fertilisation effect (Tubiello et al., 2007). When no other climatic factors are considered, trees and shrubs have the greatest response to elevated CO_2, followed by legumes, with grasses having a relatively low response; also C_3 plants respond to increased CO_2 levels, while C_4 species do not (Ainsworth and Long, 2004; Vanuytrecht and Thorburn, 2017). It is however necessary to have increased nutrients to support this increased growth. With low soil N, the CO_2 stimulation (particularly among non-legumes) is reduced (Kimball et al., 2002). Climatic factors can also have an effect. For example, Hovenden et al. (2014) and Hovenden and Newton (2018) found that for permanent grasslands in Australia, the extent of plants' response to CO_2 is dependent on seasonal rainfall amounts, in fact certain conditions completely negated the fertilisation effect. Obermeier et al. (2017) found a similar result for an extensive grassland in Germany, in that the fertilisation effect could be reduced or negated by extremes of wetness, dryness or high temperatures.

In terms of plant quality, many experiments have shown that elevated atmospheric CO_2 levels reduce plant crude protein (i.e. N) concentration (e.g. Goverde et al., 2002; Marissink et al., 2002; Zanetti et al., 1997). This has been attributed to increased plant growth (greater carbon content without increases in N inputs will inevitably reduce N concentrations), changes in how plants allocate N (Cotrufo et al., 1998) and changes in Rubisco activity (the first major stage in a plant's conversion of CO_2 to energy-rich molecules) (Leakey et al., 2009). On the other hand, elevated atmospheric CO_2 concentrations may also increase nutrient uptake capacity by enhancing mycorrhizal associations (Rillig et al. 1998; Sardans and Peñuelas 2013); they have also been found to favour legumes over grasses, (Grünzweig and Dumbur, 2012; Navas et al., 1997), and a higher sward legume content may partially counteract the decreasing plant N concentrations (Thornton et al., 2009).

Elevated CO_2 concentrations tend to increase total non-structural carbohydrates in plant-life, though there does not appear to be any significant effect on digestibility (Dumont et al., 2015). Also, Reyes-Fox et al. (2014) found that elevated CO_2 concentrations can lengthen the growing season for a temperate grassland, through enabling plants to conserve more water and thus remain active longer. They note that this does not affect the length of the reproductive season.

In summary, higher atmospheric CO_2 concentrations tend to lead to increased plant growth and reduced plant protein concentrations, though this is dependent on plant species, nutrient availability and climatic factors.

1.2.2.2 Elevated temperature

The effect of increasing air temperatures on plant growth is closely related to water availability. In mid to high latitudes and in mountainous regions, increasing temperatures are expected to have a positive effect on plant production (Dumont et al., 2015; Graux et al., 2013; Hopkins and Del Prado, 2007; Watson et al., 1997), provided there are sufficient water resources to support this growth (Graux et al., 2013). This is in part due to the longer growing season (Höglind et al. 2013; Kipling et al. 2016; Trnka et al. 2011; Kenyon et al. 2009).

Southern Europe is expected to experience reduced forage production when climate change impacts alone are considered (up to 30% reduction by 2050 in some areas) due to a combination of drought and very high temperatures (Rötter and Höhn, 2015). For example, during the summer heat wave of 2003, France had a 60% green fodder deficit (FAO, 2016). The increase in temperature and lack of water is expected to lead to shorter growing seasons, which will reduce total plant yields (Del Prado et al., 2014). There is evidence that plants can acclimatise to higher temperatures to a certain extent, for example through increasing their optimal temperature for photosynthesis or down-regulating photochemical efficiency, though there are likely to be limits to these mechanisms (Niu et al., 2014). The seasonality of temperature changes is also important. In experiments conducted in Germany, Grant et al. (2017) found that whether temperature increases occurred in the winter or the summer affected both grassland productivity and composition.

In northern Europe, higher temperatures will lead to less snow cover. There is disagreement among authors about how this will affect grass growth. In their modelling study, Thorsen and Höglind (2010) found that the risk of winter-related damage will decrease, while Rapacz et al. (2014) predicted that the reduced snow cover could increase the chance of frost damage. In experiments around the world, Henry et al. (2018) found that frost effects (from reduced winter precipitation) led to decreased plant growth, and not just in the coldest regions. In experiments in Germany, Zeeman et al. (2017) observed that reduced snow cover enhanced grassland productivity by extending the growing season, though this was dependent on elevation and environmental conditions.

Most studies agree that warming tends to reduce nutrient availability in plants, particularly in terms of N concentration (Dumont et al., 2015; Jonasson et al., 1999). However, in experiments on a low-fertility grassland, Hovenden et al. (2017) found that elevated temperatures increased soil N availability and that this more than counteracted the decrease in plant N caused by elevated atmospheric CO_2 concentrations, leading to a net gain. Nitrogen allocation within plants can also be affected, as has been found in experiments in Mediterranean shrublands, although the nature of the response varies between different species (Gavrichkova et al., 2017; Sardans et al., 2008). The effect of temperature on plant digestibility also seems to be variable, with different experiments producing conflicting results (Carter et al., 1999; Dumont et al., 2015; Sanz-Saez et al., 2012). In their meta-analysis of climate change experiments, Lee et al. (2017) found that neutral detergent fibre increased by 0.9 ± 0.3% (mean ± se) for every 1°C rise in mean annual temperature.

In summary, plant life in areas which are currently quite cold will benefit from higher temperatures, though there are still questions about the effects of reduced snow cover. Areas which currently experience high temperatures are expected to have reduced forage production. Warming tends to reduce nutrient availability in plants.

1.2.2.3 Changes in water availability

Total annual precipitation is a strong indicator of aboveground net primary production (ANPP) (Golodets et al., 2015; La Pierre et al., 2016), though not as strong as seasonal precipitation or nutrient availability (La Pierre et al., 2016). Precipitation variability also has an effect on plant life; Grant et al. (2014) found that increased variability reduced the yield but raised the quality of a temperate grassland in Germany and Grant et al. (2017) found that it affected the composition of the same grassland.

Southern Europe is predicted to receive less rainfall and the risk of drought will increase, reducing both forage yields and forage quality (Dumont et al., 2015; Golodets et al., 2015; Sardans and Peñuelas, 2013). Modelling approaches have suggested that since increasing CO_2 concentrations have a fertilisation effect and increase water use efficiency, that this will counteract the negative effects of higher temperatures and reduced water availability (Osborne et al., 2000; Rötter and Höhn, 2015), though with drought conditions in southern Europe predicted to worsen it may be that these benefits become insignificant (Nijs et al., 2000; Sardans and Peñuelas, 2013). Indeed, Brookshire and Weaver (2015) found that long-term increases in aridity led to a decline in grassland productivity for a mountain meadow in Montana, US, despite increases in atmospheric CO_2 concentrations and N deposition. Harrison et al. (2018) found a similar trend in California, with extreme rainfall events failing to compensate for a long dry period. Timing of droughts is also key. In experiments in Kansas, Denton et al. (2017) found that while spring droughts had little effect on grassland productivity, summer drought led to significant reductions. Alpine regions are also vulnerable to droughts (Schmid et al., 2011), though are generally expected to see increased growth (Trnka et al., 2011).

Drought conditions have been found to greatly reduce the soil N available to forage species (Hofer et al., 2017; Kunrath et al., 2018), while conversely, N limitation has been found to reduce water use efficiency in tall fescue grass (Kunrath et al., 2018). In their meta-analysis, He and Dijkstra (2014) found that droughts decrease plant N and phosphorus (P), reducing their nutritional value. Surprisingly, the reductions were more severe in the short-term (less than 90 days) than the long term (more than 90 days) and when occasional wetting was included as part of the drought treatment there was no effect on plant N or P.

In experiments in Germany and Belgium respectively, Carlsson et al. (2017) and Elst et al. (2017) found that grasses tend to be more drought resistant than forbs or legumes. However, in a temperate grassland experiment in Switzerland, Hofer et al. (2017) found that legumes have better drought resistance than other functional groups, since they are less N-limited. In experiments in the Alps, Stampfli et al. (2018) found that forbs are especially negatively affected by droughts, an effect that increased with high land-use intensities. Grasses have been found to take up to a year to recover from the effects of a drought, while shrubs can take up to two years (Wu et al., 2018). Elst et al. (2017) also found that species-rich communities tend to experience more leaf senescence than monocultures, particularly among N-fixers, as a result of extreme drought events; they hypothesise that this could be due to diverse communities requiring more water. There is also some evidence that repeated exposure to droughts increases plant tolerance to such events (Walter et al., 2013), reducing mortality. In experiments on perennial ryegrass in the French Alps, Legay et al. (2018) found that soil legacy effects can mean that after one drought, there can be beneficial effects of future droughts for plant life in terms of increased resistance and recovery. However, drought acclimated plants tend to have smaller leaves, thicker leaf cell walls and be prone to early senescence, making them less desirable forage (Niu et al., 2014). On the other hand, in a meta-analysis Stuart-Haëntjens et al. (2018) found that grasslands in areas with higher mean annual precipitation are both more resistant and more resilient to droughts than those in drier areas. They suggest that this is because of general water limitations in dry areas or else because dry areas experience higher plant mortality during a drought than wetter areas.

Increased water availability, as is predicted for northern Europe, in general promotes plant growth and increases its quality (Matías et al., 2011; Sardans and Peñuelas, 2013), though the amount of growth is very dependent on the type and diversity of plant species present (Byrne et al., 2013). However, rainfall is expected to become more intense and be punctuated by longer dry periods, increasing the risk of soil erosion and potentially leading to greater leaching of nutrients from the soil (Del Prado et al., 2014; Hopkins and Del Prado, 2007; Kipling et al., 2016). Heavy rainfall can also increase the risk of damage to pastures from poaching (Brown et al., 2016) and prolonged rainfall may make it difficult for farmers to find suitable times for management activities such as fertilisation and harvesting (Ergon et al., 2018). Certain areas will face increased risk of flooding (EEA, 2016). The effects of floods vary considerably and plant resilience is heavily dependent on species type (AHDB, 2014; NASD, 2009). Effects include spread of weeds (Griffiths, 2009), reduced plant energy content (Donath et al., 2004) and in the most severe cases land may require full cultivation and replacement (ADAS, 2014). Summer floods tend to cause more damage than winter floods (Griffiths, 2009; Morris et al., 2010; Morris and Hess, 2008) and very mild flooding can see plants actually benefiting from the increased availability of water and nitrate resources (Wright et al., 2015).

In summary, droughts are expected to become more common in southern Europe, reducing both the yield and nutritional quality of grasslands. Precipitation will increase in northern Europe, increasing plant yields and quality, although extremely heavy rainfall events can have a detrimental effect on grasslands.

1.2.3 Conclusions

Climate change, and especially extreme climatic events, are likely to have significant impacts on European grasslands. It is important to consider the effects of multiple climatic changes simultaneously. The effects of some changes can cancel one another out to some extent, making it difficult to know what the net effect will be. Also, plants' response to one change (e.g. increasing temperature) can be affected by other changes (e.g. increasing or decreasing water availability). There is still a lack of data on the effect of multiple simultaneous changes, making it difficult to know what to expect, though modelling approaches are attempting to fill this gap.

There is a huge amount of variation in plants' responses to climatic changes. The same experiment carried out on different species, different grassland types or in different locations can produce completely contrasting results. This makes it difficult to determine overall trends.

There are several approaches to dealing with these challenges. While experimental research tells us what will happen at a specific site under a particular set of circumstances, it is not so helpful for determining a more general picture. Meta-analyses, and statistical and process-based models can all be used to get a broader perspective, though each comes with certain limitations. In the past, they have tended to be applied at either a global scale or at a particular site, with some applications on a national scale.

It is important to know how European grasslands will be affected by climate change. A large proportion of European livestock is dependent on grazing and harvested grass for their feed intake and changes in the quantity and quality of their feed can have major impacts on their productivity, product quality and welfare. Knowing what will happen in the future enables researchers to determine the most appropriate adaptation measures to take and will allow farmers to properly prepare.

1.3 Aims and objectives

The aim of this thesis is to quantify the impacts of climate change on the yield and nutritional quality (N yield) of European grasslands. This will encompass increasing atmospheric CO_2 concentrations, increasing temperatures and changes in water availability, including both average changes and extreme events. It will account for regional variation and differences due to plant and grassland types. The specific objectives are as follows:

1. Conduct a meta-analysis on the effects of elevated atmospheric CO_2 concentrations, elevated temperature and changes in water availability, both individually and simultaneously, on grassland plant species. This accounts for variation between geographic regions and plant functional groups – *Chapter 2*
2. Investigate the efficacy of different modelling approaches (both statistical and process-based) to simulate the yield and N yield of European grasslands. Determine under which circumstances each approach is most effective and investigate the models' sensitivity to variations in inputs – *Chapter 3*
3. Use the models from chapter three to estimate the impacts of climate change on the yield and N yield of European grasslands up to 2100. Check agreement between the different approaches and draw appropriate conclusions as to what is likely to happen in future and the appropriateness of the different methodologies. Consider the likely impacts on grazing livestock and make recommendations for how farmers could respond to coming changes – C*hapter 4*
4. Develop and implement a statistical model for simulating the effects of future extreme weather events on the yield and N yield of European grasslands. Investigate the model's sensitivity to variation in inputs and consider the likely impacts on grazing livestock – *Chapter 5*
5. Use a process-based model to simulate the effects of future extreme weather events on the yield and N yield of European grasslands. Investigate the model's sensitivity to variation in inputs and compare the results with those from chapter four – *Chapter 6*

CHAPTER 2 Meta-analysis on the effects of climate change on the yield and quality of European pastures

2.1 Chapter introduction

This chapter is a meta-analysis on the effects of climate change on the yield and N concentration of European grasslands. This uses data from experiments in which the climate has been artificially manipulated and as such should be an accurate representation of the likely impacts of climate change. As described in section 1.2.1.2, previous meta-analyses on this subject tend to be conducted on a global scale and to focus on a single climatic change. Focusing on a single geographic area (Europe) should give more accurate results compared with a global approach and all the experiments in this study were conducted in Europe or else in controlled laboratory conditions representative of a European climate. In addition, while the effects of individual climatic changes are considered, combinations of these changes are also included, as far as this is possible with the experimental data available. As such, this meta-analysis goes further than previous work in this area and provides reasonable estimates of the effects of climate change on European grasslands.

This research was published in *Agriculture, Ecosystems and Environment* (Dellar et al., 2018) and the manuscript is included below. Martha Dellar is the lead author on this paper. She assembled the experimental data, determined the statistical methodology, conducted the analysis and wrote the paper. Other authors advised on the methodology and provided feedback on the paper.

2.2 A meta-analysis on the effects of climate change on the yield and quality of European pastures

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2.2.1 Abstract

As has been widely reported, climate change will be felt throughout Europe, though effects are likely to vary dramatically across European regions. While all areas are expected to experience elevated atmospheric CO_2 concentrations (↑C) and higher temperatures (↑T), the north east will get considerably wetter (↑W) while the south much drier (↓W). It is likely that these changes will have an impact on pastures and consequently on grazing livestock. This study aims to evaluate the expected changes to pasture yield and quality caused by ↑C, ↑T, ↑W and ↓W across the different European regions and across different plant functional groups (PFGs). Data was collected from 143 studies giving a total of 998 observations. Mixed models were used to estimate expected changes in above ground dry weight (AGDW) and nitrogen (N) concentrations and were implemented using Markov Chain Monte Carlo simulations. The results showed an increase in AGDW under ↑C, particularly for shrubs (+71.6%), though this is likely to be accompanied by a reduction in N concentrations (-4.8%). ↑T will increase yields in Alpine and northern areas (+82.6%), though other regions will experience little change or else decreases. ↑T will also reduce N concentrations, especially for shrubs (-13.6%) and forbs (-18.5%). ↓W will decrease AGDW for all regions and PFGs, though will increase N concentrations (+11.7%). Under ↑W there was a 33.8% increase in AGDW. While there is a need for further research to get a more complete picture of future pasture conditions, this analysis provides a general overview of expected changes and thus can help European farmers prepare to adapt their systems to meet the challenges presented by a changing climate.

Key words: Climate change, meta-analysis, pastures, above ground dry weight

2.2.2 Introduction

Depending on global emissions, global average atmospheric CO_2 concentrations are expected to rise to between 421 and 936 ppm by 2100 (IPCC, 2013a). Under a mid-range emissions scenario (IPCC representative concentration pathway (RCP) 4.5), Europe can expect average annual temperature increases of between 1 and 4.5°C, with the greatest warming in the south in summer and in the north-east in winter (EEA, 2017). Annual precipitation is predicted to increase for northern and large parts of continental Europe (up to 25% increase under RCP4.5), while decreasing in southern Europe (up to 25% reduction under RCP4.5) (Jacob et al., 2014). Extreme events (heat-waves, heavy precipitation events and droughts) will all become more common across the continent (Kovats et al., 2014).

A great deal is already known about how specific plant species respond to specific climatic changes in specific ecosystems. However, it is useful to generalise this knowledge to a wider scale in order to make appropriate management and policy decisions. Changes in pasture yield and quality will have knock-on effects on the livestock production sector and it is important for farmers, policy makers and researchers to know what to expect.

Elevated atmospheric CO_2 levels (↑C) generally increase plant yields, though results are conflicting when considering the relative responses of different plant functional groups (PFGs) (Ainsworth and Long, 2004; Nowak et al., 2004; Wang et al., 2012). In terms of plant quality, Dumont et al. (2015) found that ↑C decreases forage nitrogen (N) content, though to varying extents for different geographic areas.

The effect of increasing air temperatures (↑T) on plant growth is closely related to water availability. In mid to high latitudes and in mountainous regions, it is predicted that ↑T will increase plant production (Dumont et al., 2015; Hopkins and Del Prado, 2007; Watson et al., 1997); this is partly due to the longer growing season (Kipling et al., 2016; Trnka et al., 2011). However, Alpine regions have been observed to be vulnerable to droughts (Schmid et al., 2011), which would have a negative effect on growth, making it hard to know what the overall impact will be. Northern Europe will experience increased water availability (↑W), which promotes plant growth and has a positive effect on plant quality (Matías et al., 2011; Sardans and Peñuelas, 2013).

Southern Europe, by contrast, is expected to experience decreased forage production when climate change impacts alone are considered (up to 30% reduction by 2050 in Portugal and southern France) due to a combination of drought and very high temperatures (Dumont et al., 2015; Rötter and Höhn, 2015), although it is not clear what the net result will be when combined with the fertilisation effect of ↑C. Meta-analyses have shown that warming and drought tend to reduce nutrient availability in plants, particularly in terms of N content, though again there is regional variation (Lee et al. 2017; Dumont et al. 2015).

Given the expected geographic variation in the effects of climate change on pastures, it is useful to consider these effects on a regional basis. It is also helpful to consider the effects on different PFGs, as these could lead to changes in pasture composition. In this study we use a meta-analysis to quantify the effects of ↑C, ↑T, ↑W and ↓W on both the yield and quality of pasture and forage species across five European regions. We also investigate the impacts on yield and quality for different PFGs and consider the effects of multiple simultaneous climatic changes.

2.2.3 Methods

The search for studies for this meta-analysis was conducted in January 2017 using the Web of Science database. Additional studies were taken from grey literature, previous meta-analyses on a similar topic, bibliographies of key review articles, expert consultation and internet searches (see Supplementary Material A for full details of the search terms used). Only studies written in English were used due to limitations on resources; no limits were set on the publication date. To be included, a study had to meet the following criteria:

- Conducted in Europe, or else in controlled laboratory conditions;
- Includes at least one desirable forage species commonly found in Europe;
- Assesses the effect of ↑C, ↑T, ↑W or ↓W on plant life;
- Provides quantitative data on changes in plant yield or quality, including mean, standard deviation (SD) (or equivalent) and sample size.

Where plants were sampled several times over a period, only data from the final sampling was used. Several studies compared different cultivars or genotypes of the same species; these were taken as replicates. For the purposes of the present study, plants were grouped into shrubs, forbs, legumes and graminoids. The vast majority of plant species included in the analysis were perennial types with a C3 photosynthetic pathway. Some studies did not report the precise mix of plant species used so it is possible that some C4 species were present; these were treated as 'mixed species' experiments. Each study was assigned to one of five geographical regions: Alpine, Atlantic, continental, northern and southern (see figure 2.1). Laboratory studies were assigned a region based on the climatic conditions applied and the plant species used.

Figure 2.1: *Regional classification (Kovats et al., 2014)*

In total, 143 studies were used in this meta-analysis (see Supplementary Material B and C for full details), providing 998 observations (one observation is counted as a value under climate change conditions together with the associated control value). Eighty-two studies investigated the effects of ↑C, with an average increase of 284 ± 79 ppm (mean ± SD) (number of observations *n* = 476) over an average period of 475 days; 45 studies looked at the effects of ↑T, with an average increase of 3.2 ± 1.7°C (*n* = 301) over an average of 418 days; 59 studies looked at the effects of reduced water availability (↓W), with an average water reduction of 79 ± 26% compared with control treatments (*n* = 357) over an average of 70 days (mainly in summer); 9 studies considered the impact of increased water availability (↑W), with an average water increase of 117 ± 96% (n = 48) over an average of 189 days (around half during summer, with others during winter and spring). Of these studies, 32 considered the effects of multiple simultaneous climatic changes (162 observations). This CO_2 increase was in the middle of the predicted range for 2100 atmospheric concentrations and the temperature increase also falls within the expected range. The ↑W and ↓W treatments were both quite extreme but are over much shorter time periods than the ↑C and ↑T treatments; they could be seen to represent a particularly wet or dry season.

The natural logarithm of the response ratio (L) was used to estimate the effect of the different climate treatments, where $L_i = ln(\bar{X}_{Ti}/\bar{X}_{Ci})$ ($\bar{X}_{Ti}$ and $\bar{X}_{Ci}$ are the mean outcomes for experiment i under test and control conditions respectively). Assuming $\bar{X}_{Ti}$ and $\bar{X}_{Ci}$ are normally distributed, the variance of L_i (S_i) can be approximated as:

$$S_i = \frac{(SD_{Ti})^2}{n_{Ti}\bar{X}_{Ti}^2} + \frac{(SD_{Ci})^2}{n_{Ci}\bar{X}_{Ci}^2}$$

(Hedges et al., 1999)

where SD_{Ti} and SD_{Ci} are the standard deviations and n_{Ti} and n_{Ci} are the sample sizes of experiment i under test and control conditions.

Mixed models were used in most cases, with fixed effects relating to plant type, climatic treatment, management practices and experimental methodology and with the individual studies as a random effect. Fixed effects models were used for yield under ↑T and ↑W since in these cases the random effect of the individual studies was found to be insignificant (using a likelihood ratio test). The choice of fixed effects was determined through REML analysis in GenStat 16th Ed. (VSNi, 2013) and the model was implemented in WinBUGS 1.4.3 (MRC, 2007).

The model can be described as follows:

$$L_i \sim N(\theta_i, S_i^2)$$

with

$$\theta_i \sim N(\mu, \tau^2)$$

where θ_i is the true mean of L_i; μ denotes true overall effect across all studies and τ^2 is the between-study variance. To incorporate fixed effects, μ is generalised to a regression function:

$$\mu = \beta_0 + \beta_1 Q_1 + \beta_2 Q_2 + \cdots + \beta_p Q_p + \alpha_0 R$$

where $Q_1, \dots, Q_p$ represent *p* fixed effects (e.g. fertiliser use, treatment time, European region, etc.) and *R* represents the random effect. Since this models the natural logarithm of the response ratio, the overall effect μ was converted to percentage change using the following equation:

$$Percentage\ change = e^{\mu} - 1$$

WinBUGS fits Bayesian models using Markov Chain Monte Carlo (MCMC) simulations. Non-informative priors were used and all observations were weighted according to their variance. The model was run with three chains to check sensitivity to different initial conditions. Fifty-thousand iterations were sufficient to ensure convergence for all models, with the first 1,000 discarded as burn-in. Bias and homogeneity of the studies was assessed by means of funnel plots. The goodness-of-fit of the models was assessed using posterior predictive p-values (Meng, 1994) and by comparing the cumulative frequency distributions of predicted and observed data (Ntzoufras, 2009).

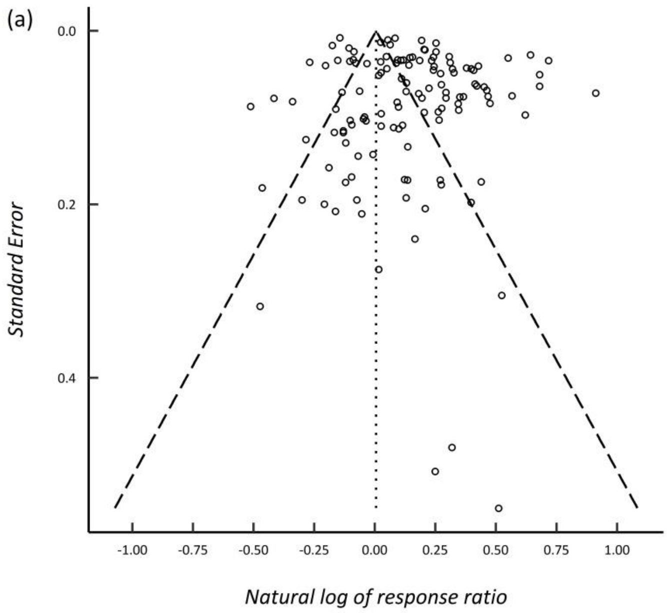
Analyses were performed looking at the effects of ↑C, ↑T, ↓W and ↑W on plant above ground dry weight (AGDW) and on above ground N concentration for different plant functional groups (PFGs) across the five European regions. Studies which looked at multiple simultaneous climatic treatments were used to assess the effects of the different combinations. Where region or PFG was not a significant factor (or when there were only a small number of observations available), then their results are grouped. Analyses were only run when data from at least five different studies was available. This had the effect that the only plant quality measure used was N concentration.

2.2.4 Results

2.2.4.1 Bias and sensitivity analysis

In all cases, the models were found to have an acceptable fit. The observed cumulative frequency distribution fell within the 95% credible interval of the predicted cumulative frequency distribution in almost all cases. For some models (N concentration under ↓W and both AGDW and N concentration for different combinations of treatments), a few points were just outside the interval at the upper end of the distribution, suggesting that these models slightly over-predict results at the upper extreme. Posterior predictive p-values ranged from 0.487 to 0.537 across all models.

Funnel plots were made for each analysis (examples in figure 2.2). The plots shown here are representative of all plots, with those for AGDW generally not showing signs of bias but indicating considerable heterogeneity between studies. Exceptions were plots for forbs under ↓W conditions and the continental region under ↑T, where higher standard errors of measurement were associated with greater negative response to the climatic change. Funnel plots for N concentration generally revealed bias and also high levels of heterogeneity. The plot for N concentration under ↑C was biased towards a greater negative response. For ↓W the overall effect was positive though the bias was towards a reduced or even negative response. For all PFGs except legumes under ↑T the effect was negative and the bias was towards a reduced or positive response; for legumes the bias was towards a more negative response.



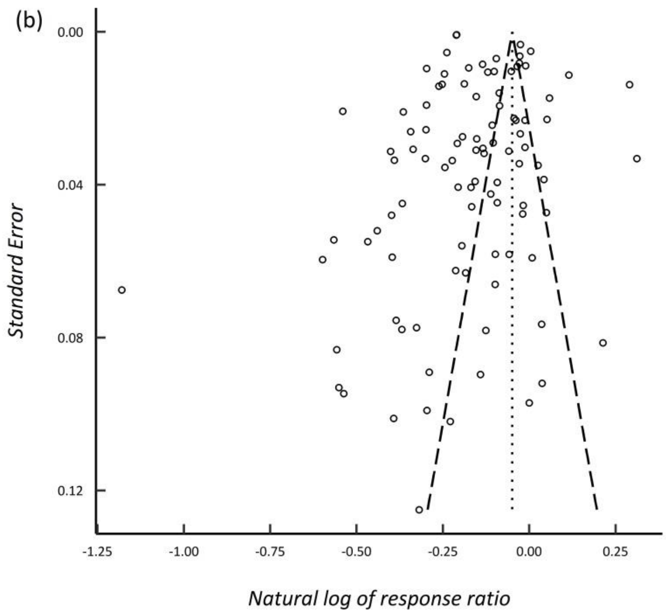


Figure 2.2: *Funnel plots for (a) above ground dry weight of graminoids under elevated atmospheric CO_2 concentration and (b) N concentration under elevated atmospheric CO_2 concentration. The x-axis shows the natural logarithm of the response ratio of results under climatically altered and control conditions. The dashed lines show pseudo 95% confidence limits and the dotted line indicates the overall effect estimate*

2.2.4.2 Above ground dry weight

Shrubs exhibit a considerably higher growth increase than other PFGs under ↑C (+71.6% growth increase), with forbs, legumes and graminoids being more similar in their responses (figure 2.3). Graminoids are less likely to experience elevated growth under ↑C than legumes or forbs (with the chances of increased growth being 55.7%, 94.6% and 96.9% respectively, calculated from the posterior distribution) and generally exhibit less growth than legumes, which in turn exhibit less growth than forbs (mean increases of +0.6%, +8.5% and +13.0% for graminoids, legumes and forbs respectively).

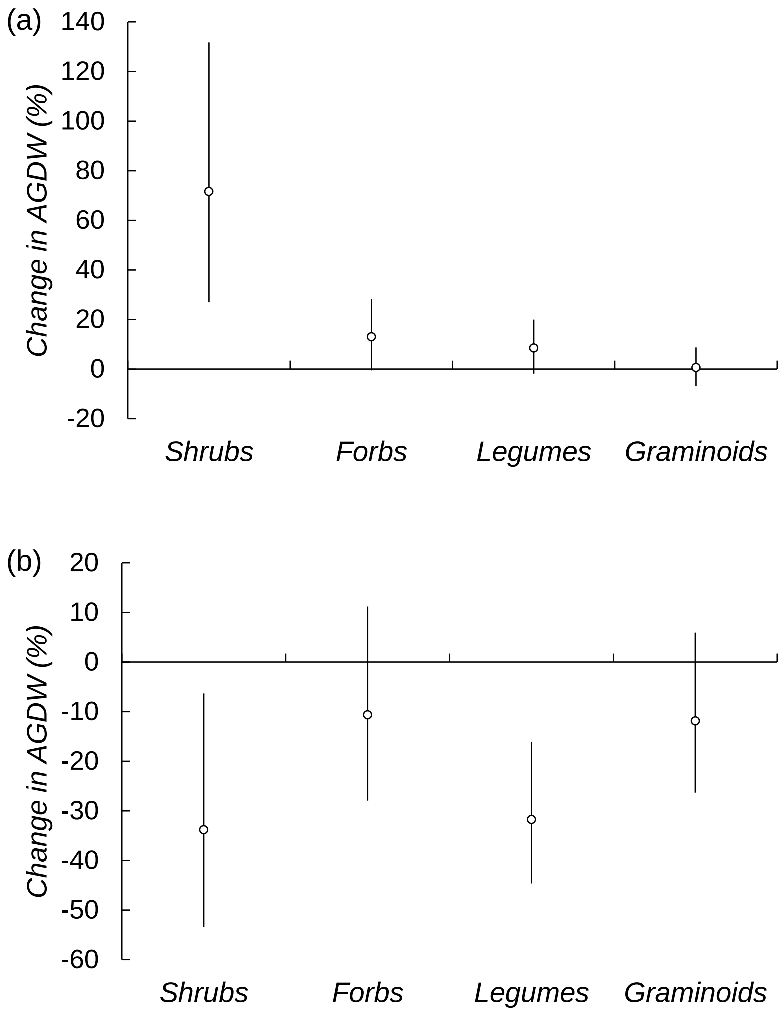


Figure 2.3: *Mean change in above ground dry weight (AGDW) under (a) elevated atmospheric CO2 concentration and (b) reduced water availability, grouped by plant functional group. Error bars represent 95% credible intervals*

Shrubs and legumes both experience significant yield reductions under ↓W (-33.8% and -31.8% respectively). Forbs, and graminoids are both likely to have decreased yields (84.8% and 91.5% likelihoods respectively), with mean decreases of -10.7% and -11.9%. There were no significant differences between PFGs under ↑T and insufficient data for ↑W.

Changes in AGDW for different European regions under ↑T and ↓W are shown in figure 2.4. The southern region is missing for ↑T due to a lack of available data and the northern region is missing for ↓W as this is not an expected consequence of climate change. ↑T increases growth in Alpine and northern areas (+82.6%) and reduces it in the continental region (-32.6%). There is negligible effect on plant yield in the Atlantic region. Under ↓W, there is a significant decrease in AGDW in the continental region (-42.2%) and likely decreases everywhere else, (the likelihoods of a reduction are 87.4%, 95.9% and 84.9% for the Alpine, Atlantic and southern regions respectively). For ↑W, all the data came from the Alpine, continental and northern regions, which are all areas which are predicted to receive increased rainfall under climate change, at least for part of the year. AGDW increases under ↑W (+57.1%), though with a large credible interval (17.2 – 110.4%), possibly due to the small dataset and the wide regional variation; unfortunately there was insufficient data for a regional division under ↑W. There were no significant regional differences for ↑C.

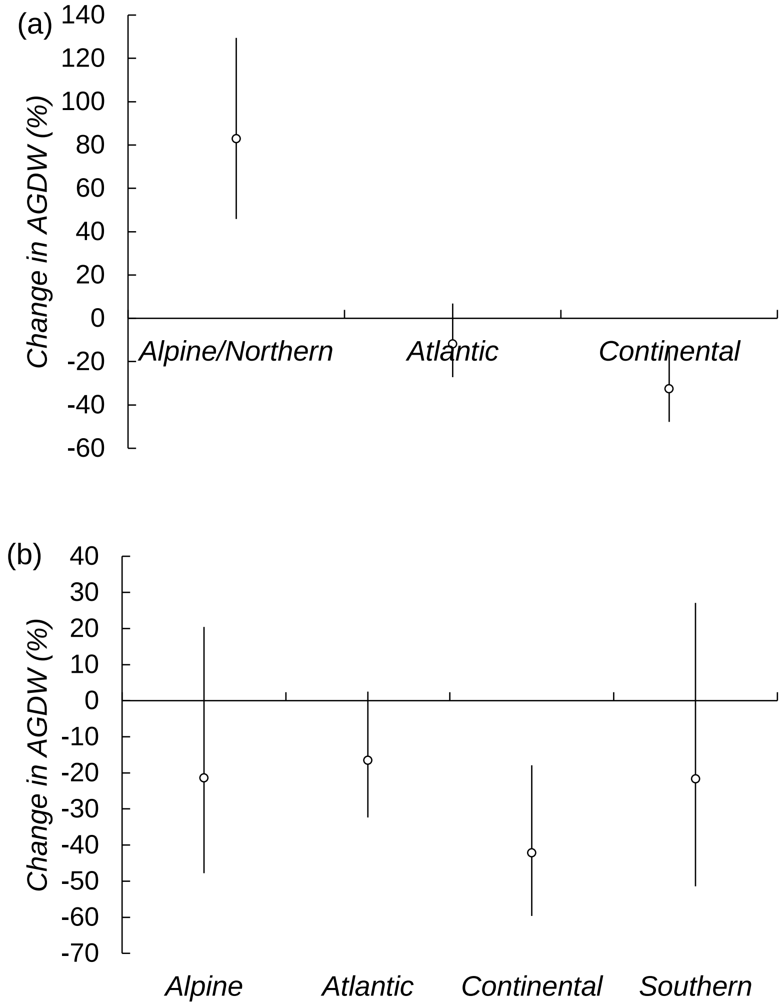


Figure 2.4: *Mean change in above ground dry weight (AGDW) under (a) elevated air temperature and (b) reduced water availability, grouped by region. Error bars represent 95% credible intervals*

So far only single climatic changes have been considered (though data from experiments with multiple treatments was used, with the additional treatments included in the models as a fixed effect). The expected changes in AGDW under different combinations of climatic treatments are shown in figure 2.5. ↑C+↑T increases plant growth (+32.8%), while ↑T+↓W and ↑C+↑T+↓W are likely to lead to reductions. For ↑C+↓W, the two effects seem to cancel each other out, producing very little change in AGDW. Combining ↑W with ↑T is likely to increase growth (80.3% chance of an increase), though the credible interval is very large, which is likely a result of the small amount of data available for ↑W+↑T.

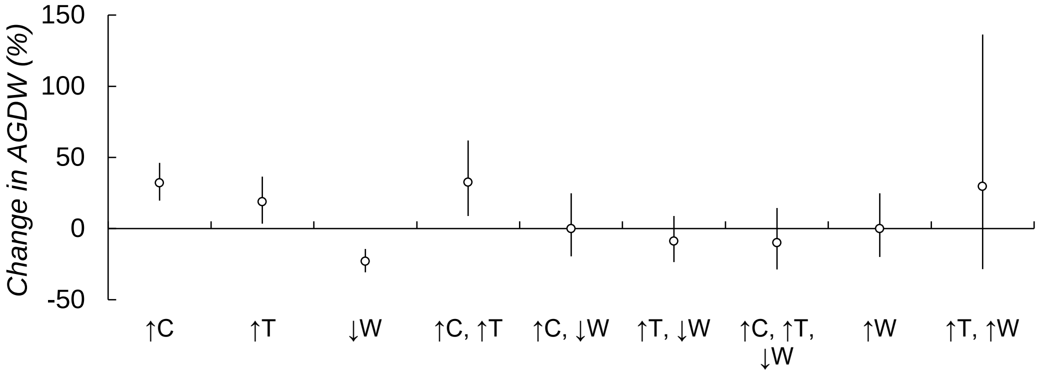


Figure 2.5: *Mean change in above ground dry weight (AGDW) for different combinations of climate treatments, including elevated atmospheric CO2 concentration (↑C), elevated air temperature (↑T), reduced water availability (↓W) and elevated water availability (↑W). Error bars represent 95% credible intervals*

2.2.4.3 Nitrogen concentration

The expected changes in N concentration under ↑T for different PFGs are shown in figure 2.6. Shrubs and forbs both display significant reductions in N concentration (-13.6% and -18.5% reductions respectively), while N concentration in graminoids is likely to decrease (average reduction of -5.6% with a 94.3% chance of a decrease).

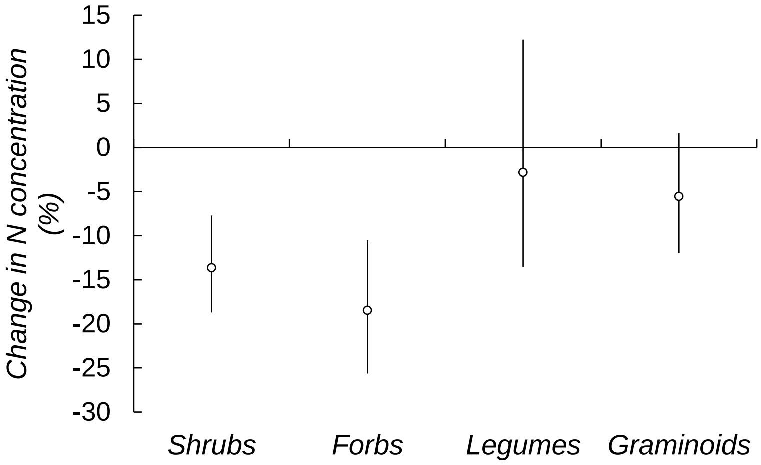


Figure 2.6: *Mean change in N concentration under elevated air temperature, grouped by plant functional group. Error bars represent 95% credible intervals*

Neither PFG nor region had a significant effect for the other climatic changes and so overall average changes are shown (figure 2.7). Under ↓W there was a significant increase in N concentration (+11.7%), while it is likely to decrease under ↑C (-4.8% with a 84.8% chance of a decrease).

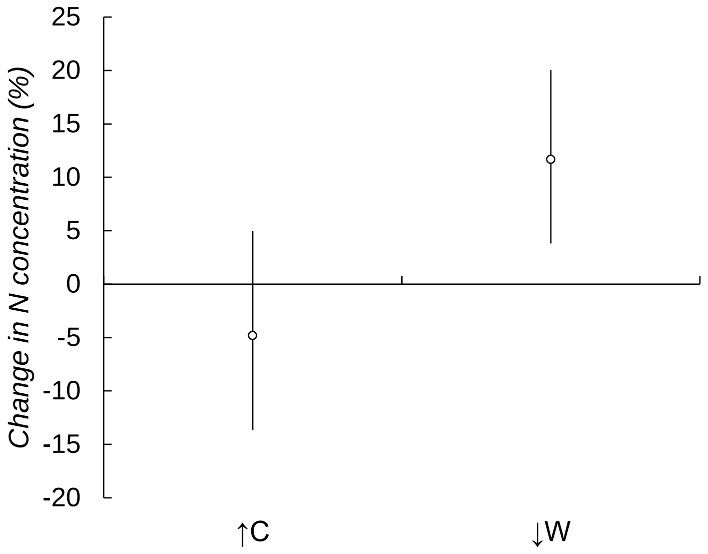


Figure 2.7: *Mean change in N concentration under elevated atmospheric CO2 concentration (↑C) and reduced water availability (↓W). Error bars represent 95% credible intervals*

It is interesting to note, when comparing how N concentration changes for different combinations of climate treatments (figure 2.8), that ↓W produces little change in N concentration when considered alone, while in the previous analysis (figure 2.7) it produced an increase. This is because all treatments involving ↓W were included in figure 2.7, including e.g. ↑C+↓W, ↑T+↓W, etc. It appears that ↑C+↓W decreases N concentration (-12.8%) and ↑W increases it (11.8%), but other combinations produce a slight but non-significant reduction.

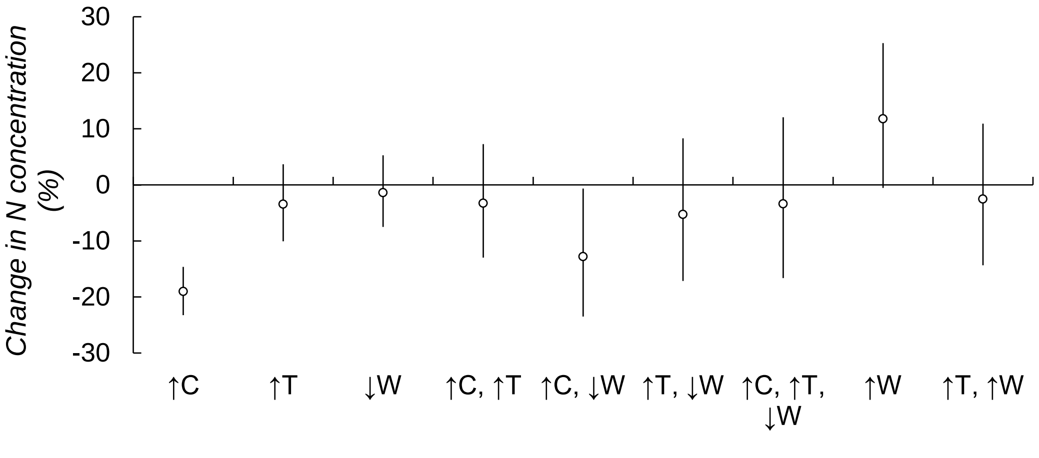


Figure 2.8: *Mean change in N concentration for different combinations of climate treatments, including elevated atmospheric CO_2 concentration (↑C), elevated air temperature (↑T), reduced water availability (↓W) and elevated water availability (↑W). Error bars represent 95% credible intervals*

2.2.5 Discussion

The present study set out to quantify the effects of ↑C, ↑T, ↑W and ↓W on pasture yield and quality across Europe. The impacts of these changes on yield and quality for different PFGs were also assessed. The results presented above address these objectives.

2.2.5.1 Bias and sensitivity analysis

For all funnel plots there was a large degree of heterogeneity. This is to be expected given the differing methodologies, plant species, locations and soil types across the studies. At least some of this variability is accounted for in the analysis through the fixed and random effects. There are several possible explanations for the bias that was recorded. It may be that some categories (plant species, locations, etc.) are over-represented, there may be publication bias, or it may be that due to the small number of observations for some PFGS and regions that it is not possible to make an accurate estimate. For shrubs in particular there were only a small number of studies available and these results should be treated with caution. Due to the bias found it may be that the results for N concentration under ↓W and ↑T should show a greater negative response and that those under ↑C should have a smaller response. The more extreme observations which have a large standard error should not have too great an influence as the observations were weighted according to their variance.

2.2.5.2 Above ground dry weight

Looking at the change in AGDW under ↑C (figure 2.3), the results show that shrubs exhibit a larger degree of growth than other PFGs. In this analysis, the average CO_2 increase for experiments involving shrubs was 184 ppm, whereas it was 290 ppm for all other PFGs, making this result particularly surprising. Ainsworth and Long (2004) had a similar finding for trees, but other studies (Nowak et al., 2004; Wang et al., 2012) found contrasting results. This is an area that would benefit from further independent studies.

When looking at ↓W, there was a greater reduction in AGDW for shrubs and legumes than for forbs and graminoids. Elst et al. (2017) suggest that grasses may be more resistant to drought than legumes due to their generally deeper rooting depth, giving them greater access to the limited water resources. The large reduction in shrub yield compared to graminoids could be attributed to competition effects, as proposed by Kreyling et al. (2008).

For ↑T the effect across functional groups was very similar, there being a slight increase in AGDW, although it should be noted that there were comparatively few studies looking at ↑T for southern Europe where high temperatures are expected to have especially negative effects, which could have skewed the results.

In general, it seems that in areas which are not water-limited, all functional groups will benefit to some extent, though particularly shrubs. An increase in shrub encroachment could have variable effects on pastures, some positive and some negative (Eldridge et al., 2011; Rivest et al., 2011). In water-limited areas it is harder to predict which functional groups will benefit the most when all climate change effects are considered, however given the variation in responses between groups it seems likely that there will be changes in pasture composition.

Looking at change in AGDW by region (figure 2.4), the increase in growth for the Alpine and northern regions under ↑T is unsurprising since these are areas which are often temperature-limited and which will benefit from longer growing seasons. The increased growth under ↑W conditions is also to be expected as it reduces the chance of growth being limited by lack of water, though water-logging may become an issue if the ↑W becomes too extreme. The results show a great deal of uncertainty about how large the growth might be; comparatively few studies were found which dealt with the effects of ↑W, making more precise estimates practically impossible. Given that annual precipitation is predicted to increase over a large part of northern and continental Europe, this is certainly an area worthy of further investigation. Under ↓W conditions it is interesting to note that a greater decrease in AGDW is predicted for the continental region than the southern, where droughts are expected to be more of a problem. This may be because plants in the southern region are already partially adapted to ↓W conditions (Pugnaire et al., 1999; Volaire et al., 2009).

When comparing the different combinations of climatic treatments (figure 2.5), the most interesting results are for ↑C+↑T and ↑C+↑T+↓W, since these combinations most accurately represent future conditions (EEA, 2017). While ↑C+↑T will cause yields to go up, adding in the effect of ↓W negates the positive growth response. It may be that irrigating pastures, particularly in southern and continental Europe, will become increasingly necessary as conditions become drier, though this will put an increased strain on diminishing water resources (EEA, 2017). It is unfortunate that no studies could be found looking at the effects of ↑C+↑T+↑W, since this would be useful for predicting future plant growth in northern Europe; however, given that both the ↑C and ↑T+↑W results show a positive response in AGDW, it seems safe to assume that yields will increase in this region.

2.2.5.3 Nitrogen concentration

Looking at N concentration under ↑T, the general decreasing trend can be explained as a natural consequence of increased growth: as plants get bigger their N concentration becomes more diluted. The relatively minor reduction in legumes is likely due to an enhancement of N fixing caused by warming (Sardans et al., 2008; Zavalloni et al., 2012). Different PFGs have also been found to allocate N in different ways as a response to warming, which could be having an effect here (Sardans et al., 2008). There may also be competition effects at play (most of these experiments were conducted on multi-species swards), as suggested by Andresen et al. (2009). With some PFGs showing higher growth increases and others showing lower reductions in N concentration under ↑T, it seems that swards containing multiple PFGs are better for livestock than those with only a single PFG, as they enable livestock to benefit from the higher yields while at the same time still having sufficient access to protein.

No regional differences were found for N concentration for any of the climatic treatments. The likely reduction under ↑C conditions has been widely documented and can be attributed to some combination of increased growth, changes in Rubisco activity (Leakey et al., 2009) and changes in N allocation (Cotrufo et al., 1998). The increase in N concentration under ↓W is likely due to the reduced growth and also to changes in allocation (Sardans et al., 2008).

Looking at combinations of climate treatments (figure 2.8), ↑C+↓W shows a clear decrease in N concentration, but other combinations exhibit very little change. This may be due to there being a lot of different factors in play which may be cancelling one another out (for example changes in growth, Rubisco activity, allocation and N uptake). It should also be noted that some of these treatment combinations only featured in a very small number of studies. Further research would provide a clearer picture of the likely outcomes of these combinations of climatic changes.

2.2.5.4 Impacts on livestock

Increases in AGDW are a positive result from a livestock perspective. Assuming grazing animals were not already at their maximum intake capacity then there is considerable scope to increase feed intake, leading to increased performance. Of course decreases in yields will have the opposite effect. In terms of forage quality, the general reduction in N concentration indicates decreased protein content, which can have a wide range of negative impacts on livestock (Landau et al., 2000; Schröder et al., 2003). It is likely that farmers will need to make increased use of concentrate feeds to compensate for the drop in protein. Irrigation may also become increasingly necessary (where feasible) to counteract the negative effects of droughts. Where irrigation is not possible, farmers may need to consider using different breeds or species, or else moving to other areas.

2.2.5.5 Other factors

Only three of the studies used involved grazing livestock on the study area. To get a realistic idea of the effects of climate change on forage, it would be useful if there was more data available for grazed plant-life, since the presence of livestock would also have an influence. There are also other factors which play a role; our analysis generally shows ↑W as having positive effects, but if the ↑W is the result of extreme rainfall events then the effect could be deleterious. Increases in ozone concentrations (Fuhrer, 2009; ICP Vegetation, 2011) and changes in the distribution and destructiveness of pests and pathogens (Bale et al., 2002; Jaggard et al., 2010) will also affect forage species. More research is needed to determine how all these different factors will interact in the future.

2.2.6 Conclusion

The present study highlights future trends in pasture yield and quality in different European regions. The general results of the meta-analysis can be used to inform farmers and policy makers around future land-use scenarios and animal management options.

↑C increases AGDW, particularly for shrubs (+71.6%), though is likely to reduce N concentrations (-4.8%). ↑T will increase yields in Alpine and northern areas (+82.6%), though other regions will experience little change or else decreases. ↑T will also reduce N concentrations, especially for shrubs (-13.6%) and forbs (-18.5%).

↓W will decrease AGDW for all regions and PFGs, though will increase N concentrations (+11.7%). Under ↑W there was a 33.8% increase in AGDW.

In general, areas which will become warmer and wetter (in particular the northern region and parts of the Alpine and continental regions) can expect higher yields, though this will likely be accompanied by reductions in N concentration. Where conditions become warmer and drier (particularly southern Europe and parts of the continental region), there will be reductions in both yield and probably also N concentration. In areas where predicted climatic changes are less extreme (for example the Atlantic region), changes in pastures will be more moderate, though a reduction in N concentration is likely. How yields will be affected in such areas will largely depend on water availability.

2.3 Chapter conclusion

This research determined the impacts of elevated atmospheric CO_2 concentrations, elevated temperatures and changes in water availability on the yield and N concentration of European grasslands. The experiments used in this research artificially altered the climate, meaning that they provide very accurate indications of how plants respond to such changes. This meta-analysis made good use of this data, however, the work did have some limitations. There was evidence of bias in the collected experiments, particularly for N concentration. In addition, the analysis which could be performed was limited by the data available. Few experiments included grazing livestock, which is unfortunate as it is known that grazing activity can affect plants' response to climate change (Christensen et al., 2004; Deléglise et al., 2015; Thornley & Cannell, 1997). There was also insufficient data for some climatic changes and regions to perform an analysis (e.g. elevated temperatures in southern Europe). While it was possible to consider the effects of multiple simultaneous climatic changes, the results would be more robust if more experimental data had been available. As it was, it was not possible to divide the results by region or plant functional group, which could have provided valuable insights.

Overall, this study provided useful results, but there is still more to be explored. Chapters three to six use alternative methodologies for analysing the effects of climate change on European grasslands. These address some of the limitations found in this meta-analysis. The regression models developed in chapters three and five consider the effects of changes in temperature and precipitation simultaneously on a regional basis. The process-based models used in chapters three, four and six do the same, while also allowing for changing atmospheric CO_2 concentrations and the effects of grazing. The different methodologies complement one another, each having their own strengths and providing new insights. By using different approaches, the limitations of each can be mitigated and a detailed picture of the effects of climate change can be achieved.

2.4 Supplementary materials

2.4.1 Supplementary material A: Search terms and sources used to find studies for the meta-analysis

Web of Science search terms

AND TOPIC: ("climat* change*" or "environmental change*" or weather or "global warming" or "climat* varia*" or temperature$ or precipitation or rainfall or "extreme event$" or "extreme weather event$" or drought$ or "water availability" or CO2 or "carbon dioxide" or nutrient$ or nitrogen or "moisture deficit" or "water deficit")

AND TOPIC: ("N concentration" or "N content" or "C$N ratio" or "total non$structural carbohydrate$" or "water-soluble carbohydrate$" or "neutral detergent fib??$" or digestibility or "acid detergent fib??$" or "acid detergent lignin$" or "sugar content" or "starch content" or quality or "nutrient level$" or "dry-weight" or biomass or yield)

AND TOPIC: (pasture* or pastoral or forage or graz* or C3 or C4 or herb* or shrub$ or *grass* or bent or cocksfoot or *clover or timothy or lucerne or alfalfa or matgrass or "sweet vernal" or heather or saltbush or orach$ or broom or trefoil or gorse or furze or whin or achillea or acinos or adonis or agrostis or "alopecurus pratensis" or "anthoxanthum odoratum" or anthyllis or Arrhenather* or "aster linosyris" or atriplex or bromus or "calluna vulgaris" or campanula or carex or centaur* or cerastium or cirsium or cistus or "coronilla minima" or "corynephorus canescens" or "crepis capillaris" or "Crupina vulgaris" or Cynosurion or Cytisus or dactyl* or "deschampsia flexuosa" or dianthus or erica or eriophorum or Euphrasia or fescue* or festuca or Galium or genista or globularia or hippocrepis or "holcus lanatus" or Koeleria or lathyrus or leontodon or lolium or Lotus or medicago or "mibora minima" or minuartia or "molinia caerulea" or nardus or Onobrychis or Ononis or phleum or "pimpinella saxifraga" or plantago or poa or potentilla or ranunculus or "rumex acetosa" or salsola or sanguisorba or "Silene dioica" or taraxacum or tragopogon or trifolium or ulex or Vaccinium or vicia)

NOT TOPIC: (marine or river or aqua* or fish or urea or herbicide or fungicide or biofuel$ or *mercury or *bean* or rice or cotton or maize or wheat or onion$ or cheese$)

NOT TITLE: (tree$ or forest* or modelling)

Grey literature

The following websites were searched for relevant studies:

- FACCE/JPI
- MACSUR
- DEFRA: Science and research projects
- ANIMALCHANGE
- MultiSward
- Legume Futures
- Climate-ADAPT
- EU Science Hub

Previous meta-analyses

The studies used in these two previous meta-analyses were checked for relevance:

Dumont et al., 2015; Wang et al., 2012

Bibliographies

The bibliographies of the following papers were checked for relevant studies:

Dieleman et al., 2012; Dumont et al., 2015; Fuhrer, 2003; Kipling et al., 2016; Lüscher et al., 2004; Reyer et al., 2013; Tubiello et al., 2007; Wang et al., 2012; Wang, 2007

Internet searches

Internet searches were performed using both Google and Google Scholar using the following search terms:

Experiment Europe climate change global warming weather temperature precipitation rain drought CO2 nutrient nitrogen quality biomass yield carbohydrate fibre digestibility dry-weight pasture forage grass legume shrub graze

2.4.2 Supplementary material B: Studies included in the meta-analysis

Aerts, R., Callaghan, T. V., Dorrepaal, E., van Logtestijn, R.S.P., Cornelissen, J.H.C., 2009. Seasonal climate manipulations result in species-specific changes in leaf nutrient levels and isotopic composition in a sub-arctic bog. Funct. Ecol. 23, 680–688. doi:10.1111/j.1365-2435.2009.01566.x

Agrell, J., Anderson, P., Oleszek, W., Stochmal, A., Agrell, C., 2004. Combined Effects of Elevated Co 2 and Herbivore Damage on Alfalfa and Cotton. J. Chem. Ecol. 30, 2309–2324. doi:10.1023/B:JOEC.0000048791.74017.93

Akmal, M., Janssens, M.J.J., 2004. Productivity and light use efficiency of perennial ryegrass with contrasting water and nitrogen supplies. F. Crop. Res. 88, 143–155. doi:10.1016/j.fcr.2003.12.004

Andresen, L.C., Michelsen, A., Jonasson, S., Beier, C., Ambus, P., 2009. Glycine uptake in heath plants and soil microbes responds to elevated temperature, CO2 and drought. Acta Oecologica 35, 786–796. doi:10.1016/j.actao.2009.08.010

Annicchiarico, P., Pecetti, L., Tava, A., 2013. Physiological and morphological traits associated with adaptation of lucerne (Medicago sativa) to severely drought-stressed and to irrigated environments. Ann. Appl. Biol. 162, 27–40. doi:10.1111/j.1744-7348.2012.00576.x

Aranjuelo, I., Perez, P., Hernandez, L., Irigoyen, J.J., Zita, G., Martinez-Carrasco, R., Sanchez-Diaz, M., 2005. The response of nodulated alfalfa to water supply, temperature and elevated CO2: photosynthetic downregulation. Physiol. Plant. 123, 348–358. doi:10.1111/j.1399-3054.2005.00459.x

Araujo, S.S., Duque, A.S., Silva, J.M., Santos, D., Silva, A.B., Fevereiro, P., 2013. Water deficit and recovery response of Medicago truncatula plants expressing the ELIP-like DSP22. Biol. Plant. 57, 159–163. doi:10.1007/s10535-012-0235-7

Baxter, R., Ashenden, T.W., Farrar, J.F., 1997. Effect of elevated CO2 and nutrient status on growth, dry matter partitioning and nutrient content of Poa alpina var vivipara L. J. Exp. Bot. 48, 1477–1486. doi:10.1093/jxb/48.7.1477

Baxter, R., Ashenden, T.W., Sparks, T.H., Farrar, J.F., 1994. Effects of elevated carbon-dioxide on 3 montane grass species. 1. Growth and dry-matter partitioning. J. Exp. Bot. 45, 305–315. doi:10.1093/jxb/45.3.305

Beierkuhnlein, C., Thiel, D., Jentsch, A., Willner, E., Kreyling, J., 2011. Ecotypes of European grass species respond differently to warming and extreme drought. J. Ecol. 99, 703–713. doi:10.1111/j.1365-2745.2011.01809.x

Benot, M.-L., Saccone, P., Pautrat, E., Vicente, R., Colace, M.-P., Grigulis, K., Clement, J.-C., Lavorel, S., 2014. Stronger Short-Term Effects of Mowing Than Extreme Summer Weather on a Subalpine Grassland. Ecosystems 17, 458–472. doi:10.1007/s10021-013-9734-4

Bezemer, T.M., Jones, T.H., 2012. The effects of CO2 and nutrient enrichment on photosynthesis and growth of Poa annua in two consecutive generations. Ecol. Res. 27, 873–882. doi:10.1007/s11284-012-0961-5

Bloor, J.M.G., Pichon, P., Falcimagne, R., Leadley, P., Soussana, J.-F., 2010. Effects of Warming, Summer Drought, and CO2 Enrichment on Aboveground Biomass Production, Flowering Phenology, and Community Structure in an Upland Grassland Ecosystem. Ecosystems 13, 888–900. doi:10.1007/s10021-010-9363-0

Cantarel, A.A.M., Bloor, J.M.G., Soussana, J.-F., 2013. Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. J. Veg. Sci. 24, 113–126. doi:10.1111/j.1654-1103.2012.01452.x

Dale, H., Press, M.C., 1998. Elevated atmospheric CO2 influences the interaction between the parasitic angiosperm Orobanche minor and its host Trifolium repens. New Phytol. 140, 65–73. doi:10.1046/j.1469-8137.1998.00247.x

De Boeck, H.J., Bassin, S., Verlinden, M., Zeiter, M., Hiltbrunner, E., 2016. Simulated heat waves affected alpine grassland only in combination with drought. New Phytol. 209, 531–541. doi:10.1111/nph.13601

De Boeck, H.J., Dreesen, F.E., Janssens, I.A., Nijs, I., 2011. Whole-system responses of experimental plant communities to climate extremes imposed in different seasons. New Phytol. 189, 806–817. doi:10.1111/j.1469-8137.2010.03515.x

De Luis, I., Irigoyen, J.J., Sanchez-Diaz, M., 1999. Elevated CO2 enhances plant growth in droughted N-2-fixing alfalfa without improving water status. Physiol. Plant. 107, 84–89. doi:10.1034/j.1399-3054.1999.100112.x

Deléglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B., Buttler, A., 2015. Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. Agric. Ecosyst. Environ. 213, 94–104. doi:10.1016/j.agee.2015.07.020

den Berge, J., Naudts, K., De Boeck, H.J., Ceulemans, R., Nijs, I., 2014. Do interactions with neighbours modify the above-ground productivity response to drought? A test with two grassland species. Environ. Exp. Bot. 105, 18–24. doi:10.1016/j.envexpbot.2014.04.002

denHertog, J., Stulen, I., Fonseca, F., Delea, P., 1996. Modulation of carbon and nitrogen allocation in Urtica dioica and Plantago major by elevated CO2: Impact of accumulation of nonstructural carbohydrates and ontogenetic drift. Physiol. Plant. 98, 77–88. doi:10.1034/j.1399-3054.1996.980109.x

Diaz, S., Fraser, L.H., Grime, J.P., Falczuk, V., 1998. The impact of elevated CO2 on plant-herbivore interactions: experimental evidence of moderating effects at the community level. Oecologia 117, 177–186. doi:10.1007/s004420050646

Dreesen, F.E., De Boeck, H.J., Janssens, I.A., Nijs, I., 2014. Do successive climate extremes weaken the resistance of plant communities? An experimental study using plant assemblages. Biogeosciences 11, 109–121. doi:10.5194/bg-11-109-2014

Erice, G., Louahlia, S., Jose Irigoyen, J., Sanchez-Diaz, M., Avice, J.-C., 2010. Biomass partitioning, morphology and water status of four alfalfa genotypes submitted to progressive drought and subsequent recovery. J. Plant Physiol. 167, 114–120. doi:10.1016/j.jplph.2009.07.016

Erice, G., Sanz-Saez, A., Aroca, R., Manuel, Ruiz-Lozano, J., Avice, J.-C., Jose Irigoyen, J., Sanchez-Diaz, M., Aranjuelo, I., Manuel Ruiz-Lozano, J., Avice, J.-C., Jose Irigoyen, J., Sanchez-Diaz, M., Aranjuelo, I., 2014. Photosynthetic downregulation in N-2-fixing alfalfa under elevated CO2 alters rubisco content and decreases nodule metabolism via nitrogenase and tricarboxylic acid cycle. Acta Physiol. Plant. 36, 2607–2617. doi:10.1007/s11738-014-1631-8

Farfan-Vignolo, E.R., Asard, H., 2012. Effect of elevated CO2 and temperature on the oxidative stress response to drought in Lolium perenne L. and Medicago sativa L. Plant Physiol. Biochem. 59, 55–62. doi:10.1016/j.plaphy.2012.06.014

Fenner, N., Ostle, N.J., McNamara, N., Sparks, T., Harmens, H., Reynolds, B., Freeman, C., 2007. Elevated CO2 effects on peatland plant community carbon dynamics and DOC production. Ecosystems 10, 635–647. doi:10.1007/s10021-007-9051-x

Ferris, R., Nijs, I., Behaeghe, T., Impens, I., 1996. Contrasting CO2 and temperature effects on leaf growth of perennial ryegrass in spring and summer. J. Exp. Bot. 47, 1033–1043. doi:10.1093/jxb/47.8.1033

Ferris, R., Taylor, G., 1995. Contrasting effects of elevated CO2 and water deficit on two native herbs. New Phytol. 131, 491–501. doi:10.1111/j.1469-8137.1995.tb03086.x

Ferris, R., Taylor, G., 1993. Contrasting effects of elevated CO2 on the root and shoot growth of 4 native herbs commonly found in chalk grasssland. New Phytol. 125, 855–866. doi:10.1111/j.1469-8137.1993.tb03934.x

Franzaring, J., Holz, I., Fangmeier, A., 2008. Different responses of Molinia caerulea plants from there origins to CO2 enrichment and nutrient supply. Acta Oecologica 33, 176–187. doi:10.1016/j.actao.2007.10.006

Frehner, M., Luscher, A., Hebeisen, T., Zanetti, S., Schubiger, F., Scalet, M., 1997. Effects of elevated partial pressure of carbon dioxide and season of the year on forage quality and cyanide concentration of Trifolium repens L. from a FACE experiment. Acta Oecologica 18, 297–304. doi:10.1016/S1146-609X(97)80018-5

Friedrich, U., von Oheimb, G., Kriebitzsch, W.-U., Schlesselmann, K., Weber, M.S., Haerdtle, W., 2012. Nitrogen deposition increases susceptibility to drought - experimental evidence with the perennial grass Molinia caerulea (L.) Moench. Plant Soil 353, 59–71. doi:10.1007/s11104-011-1008-3

Fuchslueger, L., Bahn, M., Hasibeder, R., Kienzl, S., Fritz, K., Schmitt, M., Watzka, M., Richter, A., 2016. Drought history affects grassland plant and microbial carbon turnover during and after a subsequent drought event. J. Ecol. 104, 1453–1465. doi:10.1111/1365-2745.12593

Gellesch, E., Wellstein, C., Beierkuhnlein, C., Kreyling, J., Walter, J., Jentsch, A., 2015. Plant community composition is a crucial factor for heath performance under precipitation extremes. J. Veg. Sci. 26, 975–984. doi:10.1111/jvs.12304

Gilgen, A.K., Buchmann, N., 2009. Response of temperate grasslands at different altitudes to simulated summer drought differed but scaled with annual precipitation. Biogeosciences 6, 2525–2539.

Goverde, M., Arnone, J.A., Erhardt, A., 2002. Species-specific reactions to elevated CO2 and nutrient availability in four grass species. Basic Appl. Ecol. 3, 221–227. doi:10.1078/1439-1791-00095

Grant, O.M., Incoll, L.D., McNeilly, T., 2005. Variation in growth responses to availability of water in Cistus albidus populations from different habitats. Funct. Plant Biol. 32, 817–829. doi:10.1071/FP05020

Hakala, K., Mela, T., 1996. The effects of prolonged exposure to elevated temperatures and elevated CO2 levels on the growth, yield and dry matter partitioning of field-sown meadow fescue. Agric. Food Sci. Finl. 5, 285–298.

Hanley, M.E., Trofimov, S., Taylor, G., 2004. Species-level effects more important than functional group-level responses to elevated CO2: evidence from simulated turves. Funct. Ecol. 18, 304–313. doi:10.1111/j.0269-8463.2004.00845.x

Hansen, A.H., Jonasson, S., Michelsen, A., Julkunen-Tiitto, R., 2006. Long-term experimental warming, shading and nutrient addition affect the concentration of phenolic compounds in arctic-alpine deciduous and evergreen dwarf shrubs. Oecologia 147, 1–11. doi:10.1007/s00442-005-0233-y

Harmens, H., Williams, P.D., Peters, S.L., Bambrick, M.T., Hopkins, A., Ashenden, T.W., 2004. Impacts of elevated atmospheric CO2 and temperature on plant community structure of a temperate grassland are modulated by cutting frequency. Grass Forage Sci. 59, 144–156. doi:10.1111/j.1365-2494.2004.00414.x

Hartwig, U.A., Wittmann, P., Raun, R.B., Hartwig-Raz, B., Jansa, J., Mozafar, A., Luscher, A., Leuchtmann, A., Frossard, E., Nosberger, J., 2002. Arbuscular mycorrhiza infection enhances the growth response of Lolium perenne to elevated atmospheric pCO(2). J. Exp. Bot. 53, 1207–1213. doi:10.1093/jexbot/53.371.1207

Haworth, M., Moser, G., Raschi, A., Kammann, C., Gruenhage, L., Mueller, C., 2016. Carbon dioxide fertilisation and supressed respiration induce enhanced spring biomass production in a mixed species temperate meadow exposed to moderate carbon dioxide enrichment. Funct. Plant Biol. 43, 26–39. doi:10.1071/FP15232

Hebeisen, T., Luscher, A., Zanetti, S., Fischer, B.U., Hartwig, U.A., Frehner, M., Hendrey, G.R., Blum, H., Nosberger, J., 1997. Growth response of Trifolium repens L and Lolium perenne L as monocultures and bi-species mixture to free air CO2 enrichment and management. Glob. Chang. Biol. 3, 149–160. doi:10.1046/j.1365-2486.1997.00073.x

Heijmans, M., Klees, H., Berendse, F., 2002. Competition between Sphagnum magellanicum and Eriophorum angustifolium as affected by raised CO2 and increased N deposition. Oikos 97, 415–425. doi:10.1034/j.1600-0706.2002.970311.x

Hofer, D., Suter, M., Haughey, E., Finn, J.A., Hoekstra, N.J., Buchmann, N., Luscher, A., 2016. Yield of temperate forage grassland species is either largely resistant or resilient to experimental summer drought. J. Appl. Ecol. 53, 1023–1034. doi:10.1111/1365-2664.12694

Holub, P., Tuma, I., Zahora, J., Fiala, K., 2015. Biomass production of different grassland communities under artificially modified amount of rainfall. Polish J. Ecol. 63, 320–332. doi:10.3161/15052249PJE2015.63.3.003

Hoorens, B., Aerts, R., Stroetenga, M., 2003. Is there a trade-off between the plant's growth response to elevated CO2 and subsequent litter decomposability? Oikos 103, 17–30. doi:10.1034/j.1600-0706.2003.12276.x

Huber, R., 1994. Changes in plant-species richness in a calcareous grassland following changes in environmental conditions. Folia Geobot. Phytotaxon. 29, 469–482.

Inauen, N., Koerner, C., Hiltbrunner, E., 2012. No growth stimulation by CO2 enrichment in alpine glacier forefield plants. Glob. Chang. Biol. 18, 985–999. doi:10.1111/j.1365-2486.2011.02584.x

Jakobsen, I., Smith, S.E., Smith, F.A., Watts-Williams, S.J., Clausen, S.S., Gronlund, M., 2016. Plant growth responses to elevated atmospheric CO2 are increased by phosphorus sufficiency but not by arbuscular mycorrhizas. J. Exp. Bot. 67, 6173–6186. doi:10.1093/jxb/erw383

Jonasson, S., Michelsen, A., Schmidt, I.K., Nielsen, E. V, 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. Ecology 80, 1828–1843. doi:10.1890/0012-9658(1999)080{[}1828:RIMAPT]2.0.CO;2

Jongen, M., Fay, P., Jones, M.B., 1996. Effects of elevated carbon dioxide and arbuscular mycorrhizal infection on Trifolium repens. New Phytol. 132, 413–423. doi:10.1111/j.1469-8137.1996.tb01861.x

Jongen, M., Jones, M.B., 1998. Effects of elevated carbon dioxide on plant biomass production and competition in a simulated neutral grassland community. Ann. Bot. 82, 111–123. doi:10.1006/anbo.1998.0654

Jonsdottir, I.S., Khitun, O., Stenstrom, A., 2005. Biomass and nutrient responses of a clonal tundra sedge to climate warming. Can. J. Bot. Can. Bot. 83, 1608–1621. doi:10.1139/b05-129

Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G., Spiegelberger, T., 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. J. Ecol. 102, 45–53. doi:10.1111/1365-2745.12177

Kaarlejarvi, E., Eskelinen, A., Olofsson, J., 2013. Herbivory prevents positive responses of lowland plants to warmer and more fertile conditions at high altitudes. Funct. Ecol. 27, 1244–1253. doi:10.1111/1365-2435.12113

Khan, M.A.S.A., Grant, K., Beierkuhnlein, C., Kreyling, J., Jentsch, A., 2014. Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland. Plant Soil 379, 161–175. doi:10.1007/s11104-014-2050-8

Khan, M.A.S.A., Kreyling, J., Beierkuhnlein, C., Jentsch, A., 2016. Ecotype-specific improvement of nitrogen status in European grasses after drought combined with rewetting. Acta Oecologica 77, 118–127. doi:10.1016/j.actao.2016.10.004

Klanderud, K., Totland, O., 2005. Simulated climate change altered dominance hierarchies and diversity of an alpine biodiversity hotspot. Ecology 86, 2047–2054. doi:10.1890/04-1563

Körner, C., Miglietta, F., 1994. Long term effects of naturally elevated CO2 on mediterranean grassland and forest trees. Oecologia 99, 343–351. doi:10.1007/BF00627748

Kuechenmeister, F., Kuechenmeister, K., Kayser, M., Wrage-Moennig, N., Isselstein, J., 2014. Effects of Drought Stress and Sward Botanical Composition on the Nutritive Value of Grassland Herbage. Int. J. Agric. Biol. 16, 715–722.

Kyriazopoulos, A.P., Orfanoudakis, M., Abraham, E.M., Parissi, Z.M., Serafidou, N., 2014. Effects of Arbuscular Mycorrhiza Fungi on Growth Characteristics of Dactylis glomerata L. under Drought Stress Conditions. Not. Bot. Horti Agrobot. Cluj-Napoca 42, 132–137.

Leadley, P.W., Niklaus, P.A., Stocker, R., Korner, C., 1999. A field study of the effects of elevated CO2 on plant biomass and community structure in a calcareous grassland. Oecologia 118, 39–49. doi:10.1007/s004420050701

Leadley, P.W., Stöcklin, J., 1996. Effects of elevated CO2 on model calcareous grasslands: community, species, and genotype level responses. Glob. Chang. Biol. 2, 389–397. doi:10.1111/j.1365-2486.1996.tb00089.x

Lemmens, C.M.H.M., De Boeck, H.J., Zavalloni, C., Nijs, I., Ceulemans, R., 2008. How is phenology of grassland species influenced by climate warming across a range of species richness? Community Ecol. 9, 33–42. doi:10.1556/ComEc.9.2008.S.6

Maestre, F.T., Reynolds, J.F., 2007a. Amount or pattern? Grassland responses to the heterogeneity and availability of two key resources. Ecology 88, 501–511. doi:10.1890/06-0421

Maestre, F.T., Reynolds, J.F., 2007b. Biomass responses to elevated CO2, soil heterogeneity and diversity: an experimental assessment with grassland assemblages. Oecologia 151, 512–520. doi:10.1007/s00442-006-0577-y

Mamolos, A.P., Veresoglou, D.S., Noitsakis, V., Gerakis, A., 2001. Differential drought tolerance of five coexisting plant species in Mediterranean lowland grasslands. J. Arid Environ. 49, 329–341. doi:10.1006/jare.2001.0792

Manderscheid, R., Bender, J., Schenk, U., Weigel, H.J., 1997. Response of biomass and nitrogen yield of white clover to radiation and atmospheric CO2 concentration. Environ. Exp. Bot. 38, 131–143. doi:10.1016/S0098-8472(97)00007-5

Marchi, S., Tognetti, R., Vaccari, F.P., Lanini, M., Kaligaric, M., Miglietta, F., Raschi, A., 2004. Physiological and morphological responses of grassland species to elevated atmospheric CO2 concentrations in FACE-systems and natural CO2 springs. Funct. Plant Biol. 31, 181–194. doi:10.1071/FP03140

Marissink, M., Pettersson, R., Sindhoj, E., 2002. Above-ground plant production under elevated carbon dioxide in a Swedish semi-natural grassland. Agric. Ecosyst. Environ. 93, 107–120. doi:10.1016/S0167-8809(01)00356-5

Martinez-Fernandez, D., Walker, D.J., Romero, P., Martinez-Ballesta, M.C., Correal, E., 2012. The Response of the Leguminous Fodder Plant Bituminaria bituminosa to Water Stress. J. Agron. Crop Sci. 198, 442–451. doi:10.1111/j.1439-037X.2012.00515.x

Meisser, M., Deleglise, C., Mosimann, E., Signarbieux, C., Mills, R., Schlegel, P., Buttler, A., Jeangros, B., 2013. Effects of a severe drought on a permanent meadow in the Jura mountains. Agrar. Schweiz 4, 476–483.

Meyer-Gruenefeldt, M., Friedrich, U., Klotz, M., Von Oheimb, G., Haerdtle, W., 2015. Nitrogen deposition and drought events have non-additive effects on plant growth - Evidence from greenhouse experiments. Plant Biosyst. 149, 424–432. doi:10.1080/11263504.2013.853699

Miranda-Apodaca, J., Perez-Lopez, U., Lacuesta, M., Mena-Petite, A., Munoz-Rueda, A., 2015. The type of competition modulates the ecophysiological response of grassland species to elevated CO2 and drought. Plant Biol. 17, 298–310. doi:10.1111/plb.12249

Molau, U., 2010. Long-term impacts of observed and induced climate change on tussock tundra near its southern limit in northern Sweden. Plant Ecol. Divers. 3, 29–34. doi:10.1080/17550874.2010.487548

Mortensen, L.M., 1999. Effects of different carbon dioxide and ozone concentrations on shoot growth of Phleum pratense L. and Betula pubescens Ehrh. as influenced by day length and irradiance. Acta Agric. Scand. Sect. B - Soil Plant Sci. 49, 50–56. doi:10.1080/09064719950135704

Mortensen, L.M., Saebo, A., 1996. The effect of elevated CO2 concentration on growth of Phleum pratense L in different parts of the growth season. Acta Agric. Scand. Sect. B - Soil Plant Sci. 46, 128–134.

Moser, B., Fridley, J.D., Askew, A.P., Grime, J.P., 2011. Simulated migration in a long-term climate change experiment: invasions impeded by dispersal limitation, not biotic resistance. J. Ecol. 99, 1229–1236. doi:10.1111/j.1365-2745.2011.01841.x

Mraz, P., Tarbush, E., Mueller-Schaerer, H., 2014. Drought tolerance and plasticity in the invasive knapweed Centaurea stoebe s.l. (Asteraceae): effect of populations stronger than those of cytotype and range. Ann. Bot. 114, 289–299. doi:10.1093/aob/mcu105

Naudts, K., den Berge, J., Farfan, E., Rose, P., AbdElgawad, H., Ceulemans, R., Janssens, I.A., Asard, H., Nijs, I., 2014. Future climate alleviates stress impact on grassland productivity through altered antioxidant capacity. Environ. Exp. Bot. 99, 150–158. doi:10.1016/j.envexpbot.2013.11.003

Naudts, K., den Berge, J., Janssens, I.A., Nijs, I., Ceulemans, R., 2013. Combined effects of warming and elevated CO2 on the impact of drought in grassland species. Plant Soil 369, 497–507. doi:10.1007/s11104-013-1595-2

Naudts, K., den Berge, J., Janssens, I.A., Nijs, I., Ceulemans, R., 2011. Does an extreme drought event alter the response of grassland communities to a changing climate? Environ. Exp. Bot. 70, 151–157. doi:10.1016/j.envexpbot.2010.08.013

Norton, L.R., Firbank, L.G., Blum, H., 1999. Effects of free-air CO2 Enrichment (FACE) on experimental grassland communities. Funct. Ecol. 13, 38–44. doi:10.1046/j.1365-2435.1999.00006.x

Padilla, F.M., Miranda, J.D., Jorquera, M.J., Pugnaire, F.I., 2009. Variability in amount and frequency of water supply affects roots but not growth of arid shrubs. Plant Ecol. 204, 261–270. doi:10.1007/s11258-009-9589-0

Pang, J., Yang, J., Ward, P., Siddique, K.H.M., Lambers, H., Tibbett, M., Ryan, M., 2011. Contrasting responses to drought stress in herbaceous perennial legumes. Plant Soil 348, 299–314. doi:10.1007/s11104-011-0904-x

Parsons, A.N., Welker, J.M., Wookey, P.A., Press, M.C., Callaghan, T. V, Lee, J.A., 1994. Growth-responses of 4 sub-Arctic dwarf shrubs to simulated environmental change. J. Ecol. 82, 307–318. doi:10.2307/2261298

Picon-Cochard, C., Teyssonneyre, F., Besle, J.M., Soussana, J.-F.F., 2004. Effects of elevated CO2 and cutting frequency on the productivity and herbage quality of a semi-natural grassland. Eur. J. Agron. 20, 363–377. doi:10.1016/S1161-0301(03)00040-6

Prechsl, U.E., Burri, S., Gilgen, A.K., Kahmen, A., Buchmann, N., 2015. No shift to a deeper water uptake depth in response to summer drought of two lowland and sub-alpine C-3-grasslands in Switzerland. Oecologia 177, 97–111. doi:10.1007/s00442-014-3092-6

Press, M.C., Potter, J.A., Burke, M.J.W., Callaghan, T. V, Lee, J.A., 1998. Responses of a subarctic dwarf shrub heath community to simulated environmental change. J. Ecol. 86, 315–327. doi:10.1046/j.1365-2745.1998.00261.x

Ramo, K., Kanerva, T., Nikula, S., Ojanpera, K., Manninen, S., 2006. Influences of elevated ozone and carbon dioxide in growth responses of lowland hay meadow mesocosms. Environ. Pollut. 144, 101–111. doi:10.1016/j.envpol.2006.01.009

Rouhier, H., Read, D.J., 1998. The role of mycorrhiza in determining the response of Plantago lanceolata to CO2 enrichment. New Phytol. 139, 367–373. doi:10.1046/j.1469-8137.1998.00200.x

Roumet, C., Laurent, G., Canivenc, G., Roy, J., 2002. Genotypic variation in the response of two perennial grass species to elevated carbon dioxide. Oecologia 133, 342–348. doi:10.1007/s00442-002-1041-2

Roumet, C., Laurent, G., Roy, J., 1999. Leaf structure and chemical composition as affected by elevated CO2: genotypic responses of two perennial grasses. New Phytol. 143, 73–81. doi:10.1046/j.1469-8137.1999.00437.x

Sæbø, A., Mortensen, L.M., 1995. Growth and regrowth of Phleum pratense, Lolium perenne, Trifolium repens and Trifolium pratense at normal and elevated CO2 concentration. Agric. Ecosyst. Environ. 55, 29–35. doi:10.1016/0167-8809(95)00607-T

Sanaullah, M., Chabbi, A., Girardin, C., Durand, J.-L., Poirier, M., Rumpel, C., 2014. Effects of drought and elevated temperature on biochemical composition of forage plants and their impact on carbon storage in grassland soil. Plant Soil 374, 767–778. doi:10.1007/s11104-013-1890-y

Sanz-Saez, A., Erice, G., Aguirreolea, J., Munoz, F., Sanchez-Diaz, M., Jose Irigoyen, J., 2012. Alfalfa forage digestibility, quality and yield under future climate change scenarios vary with Sinorhizobium meliloti strain. J. Plant Physiol. 169, 782–788. doi:10.1016/j.jplph.2012.01.010

Sardans, J., Penuelas, J., Estiarte, M., Prieto, P., 2008. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. Glob. Chang. Biol. 14, 2304–2316. doi:10.1111/j.1365-2486.2008.01656.x

Schappi, B., Korner, C., 1996. Growth responses of an alpine grassland to elevated CO2. Oecologia 105, 43–52. doi:10.1007/BF00328790

Schenk, U., Jager, H.J., Weigel, H.J., 1997. The response of perennial ryegrass white clover mini-swards to elevated atmospheric CO2 concentrations: effects on yield and fodder quality. Grass Forage Sci. 52, 232–241. doi:10.1046/j.1365-2494.1997.00069.x

Schmid, S., Hiltbrunner, E., Spehn, E., Lüscher, A., Scherer-Lorenzen, M., 2011. Impact of experimentally induced summer drought on biomass production in alpine grassland, in: Pötsch, E., Krautzer, B., Hopkins, A. (Eds.), Grassland Farming and

Land Management Systems in Mountainous Region. Organising Committee of the 16th Symposium of the European Grassland Federation 2011 and Agricultural Research and Education Centre (AREC), Raumberg-Gumpenstein, Austria, pp. 214–216.

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. doi:10.1111/j.1365-2486.2004.00803.x

Schuerings, J., Beierkuhnlein, C., Grant, K., Jentsch, A., Malyshev, A., Penuelas, J., Sardans, J., Kreyling, J., 2013. Absence of soil frost affects plant-soil interactions in temperate grasslands. Plant Soil 371, 559–572. doi:10.1007/s11104-013-1724-y

Schuerings, J., Jentsch, A., Walter, J., Kreyling, J., 2014. Winter warming pulses differently affect plant performance in temperate heathland and grassland communities. Ecol. Res. 29, 561–570. doi:10.1007/s11284-014-1174-x

Sebastia, M.-T., 2007. Plant guilds drive biomass response to global warming and water availability in subalpine grassland. J. Appl. Ecol. 44, 158–167. doi:10.1111/j.1365-2664.2006.01232.x

Sheppard, C.S., Alexander, J.M., Billeter, R., 2012. The invasion of plant communities following extreme weather events under ambient and elevated temperature. Plant Ecol. 213, 1289–1301. doi:10.1007/s11258-012-0086-5

Soussana, J.F., Casella, E., Loiseau, P., 1996. Long-term effects of CO2 enrichment and temperature increase on a temperate grass sward .2. Plant nitrogen budgets and root fraction. Plant Soil 182, 101–114. doi:10.1007/BF00010999

Stevnbak, K., Scherber, C., Gladbach, D.J., Beier, C., Mikkelsen, T.N., Christensen, S., 2012. Interactions between above- and belowground organisms modified in climate change experiments. Nat. Clim. Chang. 2, 805–808. doi:10.1038/NCLIMATE1544

Stöcklin, J., Schweizer, K., Körner, C., 1998. Effects of elevated CO2 and phosphorus addition on productivity and community composition of intact monoliths from calcareous grassland. Oecologia 116, 50–56. doi:10.1007/s004420050562

Suter, D., Nosberger, J., Luscher, A., 2001. Response of perennial ryegrass to free-air CO2 enrichment (FACE) is related to the dynamics of sward structure during regrowth. Crop Sci. 41, 810–817.

Taylor, S.H., Ripley, B.S., Woodward, F.I., Osborne, C.P., 2011. Drought limitation of photosynthesis differs between C-3 and C-4 grass species in a comparative experiment. Plant, Cell Environ. 34, 65–75. doi:10.1111/j.1365-3040.2010.02226.x

Utrillas, M.J., Alegre, L., Simon, E., 1995. Seasonal changes in production and nutrient content of Cynodon dactylon. (L.) Pers. subjected to water deficits. Plant Soil 175, 153–157.

Van De Velde, H., Bonte, D., AbdElgawad, H., Asard, H., Nijs, I., 2015. Combined elevated CO2 and climate warming induces lagged effects of drought in Lolium perenne and Plantago lanceolata. Plant Ecol. 216, 1047–1059. doi:10.1007/s11258-015-0488-2

van Heerwaarden, L.M., Toet, S., van Logtestijn, R.S.P., Aerts, R., 2005. Internal nitrogen dynamics in the graminoid Molinia caerulea under higher N supply and elevated CO2 concentrations. Plant Soil 277, 255–264. doi:10.1007/s11104-005-7140-1

van Kleunen, M., Stephan, M.A., Schmid, B., 2006. CO2- and density-dependent competition between grassland species. Glob. Chang. Biol. 12, 2175–2186. doi:10.1111/j.1365-2486.2006.01248.x

Verlinden, M., Van Kerkhove, A., Nijs, I., 2013. Effects of experimental climate warming and associated soil drought on the competition between three highly invasive West European alien plant species and native counterparts. Plant Ecol. 214, 243–254. doi:10.1007/s11258-012-0163-9

Walter, J., Grant, K., Beierkuhnlein, C., Kreyling, J., Weber, M., Jentsch, A., 2012a. Increased rainfall variability reduces biomass and forage quality of temperate grassland largely independent of mowing frequency. Agric. Ecosyst. Environ. 148, 1–10. doi:10.1016/j.agee.2011.11.015

Walter, J., Hein, R., Auge, H., Beierkuhnlein, C., Löffler, S., Reifenrath, K., Schädler, M., Weber, M., Jentsch, A., 2012b. How do extreme drought and plant community composition affect host plant metabolites and herbivore performance? Arthropod. Plant. Interact. 6, 15–25. doi:10.1007/s11829-011-9157-0

Warwick, K.R., Taylor, G., Blum, H., 1998. Biomass and compositional changes occur in chalk grassland turves exposed to elevated CO2 for two seasons in FACE. Glob. Chang. Biol. 4, 375–385. doi:10.1046/j.1365-2486.1998.00159.x

Werkman, B.R., Callaghan, T. V, 2002. Responses of bracken and heather to increased temperature and nitrogen addition, alone and in competition. Basic Appl. Ecol. 3, 267–276. doi:10.1078/1439-1791-00103

Whitehead, S.J., Caporn, S.J.M., Press, M.C., 1997. Effects of elevated CO2, nitrogen and phosphorus on the growth and photosynthesis of two upland perennials: Calluna vulgaris and Pteridium aquilinum. New Phytol. 135, 201–211. doi:10.1046/j.1469-8137.1997.00651.x

Winkler, J.B., Herbst, M., 2004. Do plants of a semi-natural grassland community benefit from long-term CO2 enrichment? Basic Appl. Ecol. 5, 131–143. doi:10.1078/1439-1791-00219

Woodin, S., Graham, B., Killick, A., Skiba, U., Cresser, M., 1992. Nutrient limitation of the long-term response of heather (Calluna vulgaris (L) Hull) to CO2 enrichment. New Phytol. 122, 635–642.

Xi, N., Carrere, P., Bloor, J.M.G., 2015. Plant community responses to precipitation and spatial pattern of nitrogen supply in an experimental grassland ecosystem. Oecologia 178, 329–338. doi:10.1007/s00442-015-3289-3

Ylanne, H., Stark, S., Tolvanen, A., 2015. Vegetation shift from deciduous to evergreen dwarf shrubs in response to selective herbivory offsets carbon losses: evidence from 19 years of warming and simulated herbivory in the subarctic tundra. Glob. Chang. Biol. 21, 3696–3711. doi:10.1111/gcb.12964

Zanetti, S., Hartwig, U.A., vanKessel, C., Luscher, A., Hebeisen, T., Frehner, M., Fischer, B.U., Hendrey, G.R., Blum, H., Nosberger, J., 1997. Does nitrogen nutrition restrict the CO2 response of fertile grassland lacking legumes? Oecologia 112, 17–25. doi:10.1007/s004420050278

Zavalloni, C., Gielen, B., Lemmens, C.M.H.M., De Boeck, H.J., Blasi, S., den Bergh, S., Nijs, I., Ceulemans, R., 2008. Does a warmer climate with frequent mild water shortages protect grassland communities against a prolonged drought? Plant Soil 308, 119–130. doi:10.1007/s11104-008-9612-6

Zavalloni, C., Vicca, S., Buscher, M., de la Providencia, I.E., de Boulois, H.D., Declerck, S., Nijs, I., Ceulemans, R., 2012. Exposure to warming and CO2 enrichment promotes greater above-ground biomass, nitrogen, phosphorus and arbuscular mycorrhizal colonization in newly established grasslands. Plant Soil 359, 121–136. doi:10.1007/s11104-012-1190-y

Zwicke, M., Alessio, G.A., Thiery, L., Falcimagne, R., Baumont, R., Rossignol, N., Soussana, J.-F., Picon-Cochard, C., 2013. Lasting effects of climate disturbance on perennial grassland above-ground biomass production under two cutting frequencies. Glob. Chang. Biol. 19, 3435–3448. doi:10.1111/gcb.12317

2.4.3 Supplementary material C: Summary of the experiments used in the meta-analysis

Table 2.1: *Summary of abbreviations used in table 2.2*

Growing area		Methodology	
CC	Climate chamber or similar	CC	Climate chamber or similar
F	Field study	Cover	Ground-level covering during the night
GH	Greenhouse or similar	FACE	Free air carbon dioxide enrichment
		GH	Greenhouse or similar
		HC	Ground-level or subterranean heating cables
		HL	Heating lamps
		OTC	Open top chamber
		SACC	Screen-aided carbon dioxide control
		Shelter	Above ground-level shelter
		TGT	Temperature-gradient tunnel
		Trans	Transplantation

Table 2.2: *The regions, climatic treatments, yield and quality parameters, plant functional groups and methodologies used in each study*

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
Aerts et al. (2009)	Alpine	↑T, ↑W	N	Shrub, Forb	F	OTC	None
Agrell et al. (2004)	Southern	↑C	AGDW, N	Legume	CC	CC	None
Akmal & Janssens (2004)	Continental	↓W	AGDW	Grass	F	Shelter	None
Andresen et al. (2009)	Continental	↑C, ↑T, ↓W	N	Shrub, Grass	F	FACE	None
Annicchiarico et al. (2013)	Continental	↓W	AGDW	Legume	F	Shelter	Cut

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
Aranjuelo et al. (2005)	Southern	↑C, ↑T, ↓W	N	Legume	GH	TGT	None
Araujo et al. (2013)	Southern	↓W	AGDW	Legume	CC	CC	None
Baxter et al. (1997)	Atlantic	↑C	AGDW, N	Grass	CC	CC	None
Baxter et al. (1994)	Atlantic	↑C	AGDW	Grass	F	OTC	None
Beierkuhnlein et al. (2011)	Continental	↑T, ↓W	AGDW	Grass	F	Shelter, Cover	Cut
Benot et al. (2014)	Alpine	↑T, ↓W	AGDW, N	Grass	F	Shelter, HL	None
Bezemer & Jones (2012)	Atlantic	↑C	AGDW	Grass	CC	CC	None
Bloor et al. (2010)	Continental	↑C, ↑T, ↓W	AGDW	Mix	F	Trans, shelter, FACE	Cut
Cantarel et al. (2013)	Continental	↑C, ↑T, ↓W	N	Mix	F	Trans, shelter, FACE	Cut
Dale & Press (1998)	Atlantic	↑C	AGDW, N	Legume	CC	CC	None
De Boeck et al. (2016)	Alpine	↓W	AGDW	Forb, Grass, Legume	F	Shelter	None
De Boeck et al. (2011)	Atlantic	↑T, ↓W	AGDW	Mix	F	Shelter, HL	Cut
De Luis et al. (1999)	Southern	↑C, ↓W	N	Legume	CC	CC	None
Deléglise et al. (2015)	Alpine	↓W	AGDW, N	Mix	F	Shelter	Grazed
den Berge et al. (2014)	Atlantic	↓W	AGDW	Grass, Forb	GH	GH	None
denHertog et al. (1996)	Atlantic	↑C	N	Forb	CC	CC	None
Diaz et al. (1998)	Atlantic	↑C	AGDW	Forb, Grass, Legume	GH	GH	None
Dreesen et al. (2014)	Atlantic	↑T, ↓W	AGDW	Forb	F	Shelter, HL	None
Erice et al. (2010)	Southern	↓W	AGDW	Legume	GH	GH	None
Erice et al. (2014)	Southern	↑C	AGDW, N	Legume	CC	CC	None
Farfan-Vignolo & Asard (2012)	Atlantic	↑C, ↑T, ↓W	AGDW	Grass, Legume	CC	CC	None
Fenner et al. (2007)	Atlantic	↑C	AGDW	Mix	GH	GH	None

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
Ferris & Taylor (1993)	Atlantic	↑C	AGDW	Forb, Legume	CC	CC	None
Ferris & Taylor (1995)	Atlantic	↑C, ↓W	AGDW	Forb, Legume	CC	CC	None
Ferris et al. (1996)	Atlantic	↑C, ↑T	AGDW	Grass	GH	CC_NL	Cut
Franzaring et al. (2008)	Continental	↑C	AGDW	Grass	CC	CC	None
Frehner et al. (1997)	Alpine	↑C	N	Legume	F	FACE	Cut
Friedrich et al. (2012)	Atlantic	↓W	AGDW, N	Grass	GH	GH	None
Fuchslueger et al. (2016)	Alpine	↓W	AGDW, N	Mix	F	Shelter	Grazed
Gellesch et al. (2015)	Continental	↓W, ↑W	AGDW	Shrub	F	Shelter, Irrigation	None
Gilgen & Buchmann (2009)	Continental, Alpine	↓W	AGDW	Mix	F	Shelter	Cut, None
Goverde et al. (2002)	Continental	↑C	AGDW, N	Grass	GH	GH	None
Grant et al. (2005)	Atlantic	↓W	AGDW	Shrub	GH	GH	None
Hakala & Mela (1996)	Northern	↑C, ↑T	AGDW, N	Grass	F, GH	OTC, GH	Cut
Hanley et al. (2004)	Atlantic	↑C	AGDW	Mix	CC	CC	Cut
Hansen et al. (2006)	Alpine	↑T	N	Shrub	F	OTC	None
Harmens et al. (2004)	Atlantic	↑C, ↑T	AGDW	Grass, Forb	GH	GH	Cut
Hartwig et al. (2002)	Continental	↑C	N	Grass	CC	CC	None
Haworth et al. (2016)	Atlantic	↑C	AGDW, N	Grass, Forb	F	FACE	Cut
Hebeisen et al. (1997)	Alpine	↑C	AGDW	Grass, Legume	F	FACE	Cut
Heijmans et al. (2002)	Atlantic	↑C	AGDW	Grass	GH	GH	None
Hofer et al. (2016)	Continental, Atlantic	↓W	AGDW	Grass, Forb, Legume	F	Shelter	Cut
Holub et al. (2015)	Continental	↓W, ↑W	AGDW	Mix	F	Shelter	None
Hoorens et al. (2003)	Atlantic	↑C	AGDW, N	Grass, Forb	GH	GH	None
Huber (1994)	Northern	↑W	AGDW	Mix	F	Irrigation	None
Inauen et al. (2012)	Alpine	↑C	AGDW, N	Grass	F	FACE	None

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
Jakobsen et al. (2016)	Southern	↑C	AGDW	Legume	CC	CC	None
Jonasson et al. (1999)	Alpine	↑T	AGDW, N	Shrub, Mix	F	OTC	None
Jongen & Jones (1998)	Atlantic	↑C	AGDW	Grass	F	OTC	Cut
Jongen et al. (1996)	Atlantic	↑C	AGDW, N	Legume	GH	GH	None
Jonsdottir et al. (2005)	Alpine	↑T	AGDW, N	Grass	F	OTC	None
Jung et al. (2014)	Alpine	↓W	N	Grass, Forb, Legume	F	Shelter	None
Kaarlejarvi et al. (2013)	Alpine	↑T	AGDW	Forb	F	OTC	None
Khan et al. (2014)	Continental	↓W, ↑W	N	Grass, Forb, Legume	F	Shelter, Irrigation	Cut
Khan et al. (2016)	Continental	↓W	N	Grass	F	Shelter, Cover	Cut
Klanderud & Totland (2005)	Alpine	↑T	AGDW	Mix	F	OTC	None
Körner & Miglietta (1994)	Southern	↑C	N	Forb	F	Natural CO_2 spring	None
Kuechenmeister et al. (2014)	Continental	↓W	N	Grass, Forb, Legume, Mix	CC	CC	Cut
Kyriazopoulos et al. (2014)	Southern	↓W	AGDW	Grass	F	Irrigation	None
Leadley & Stöcklin (1996)	Continental	↑C	AGDW	Grass, Legume	GH	GH	None
Leadley et al. (1999)	Continental	↑C	AGDW	Grass, Forb, Legume	F	SACC	Cut
Lemmens et al. (2008)	Atlantic	↑T	AGDW	Grass, Forb, Legume	GH	GH	Cut
Maestre & Reynolds (2007a)	Atlantic	↓W	AGDW	Mix	GH	GH	None
Maestre & Reynolds (2007b)	Continental	↑C	AGDW	Grass, Forb, Mix	CC	CC	None
Mamolos et al. (2001)	Southern	↓W	AGDW	Grass	GH	GH	None
Manderscheid et al. (1997)	Atlantic	↑C	N	Legume	F	OTC	Cut
Marchi et al. (2004)	Southern	↑C	AGDW	Grass, Legume	F	FACE	Cut

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
Marissink et al. (2002)	Northern	↑C	AGDW, N	Grass, Forb, Mix	F	OTC	None
Martinez-Fernandez et al. (2012)	Southern	↓W	AGDW	Shrub	GH	GH	None
Meisser et al. (2013)	Alpine	↓W	AGDW, N	Mix	GH	GH	Cut, Grazed
Meyer-Gruenefeldt et al. (2015)	Atlantic	↓W	AGDW, N	Shrub	GH	GH	None
Miranda-Apodaca et al. (2015)	Southern	↑C, ↓W	AGDW	Grass, Legume	CC	CC	None
Molau (2010)	Alpine	↑T	AGDW	Grass, Forb, Shrub	F	OTC	None
Mortensen (1999)	Northern	↑C	AGDW	Grass	CC	CC	None
Mortensen & Sæbø (1996)	Northern	↑C	AGDW	Grass	F	OTC	None
Moser et al. (2011)	Atlantic	↑T, ↓W	AGDW	Grass	F	Shelter, HC	Grazed
Mraz et al. (2014)	Continental	↓W	AGDW	Forb	CC	CC	None
Naudts et al. (2014)	Atlantic	↑C, ↑T, ↓W	AGDW	Mix	GH	GH	None
Naudts et al. (2011)	Atlantic	↑C, ↑T, ↓W	AGDW	Mix	GH	GH	None
Naudts et al. (2013)	Atlantic	↑C, ↑T, ↓W	AGDW	Mix	GH	GH	None
Norton et al. (1999)	Alpine	↑C	AGDW	Grass, Forb	F	FACE	None
Padilla et al. (2009)	Southern	↓W	AGDW	Legume, Shrub	GH	GH	None
Pang et al. (2011)	Southern	↓W	AGDW	Legume	GH	GH	None
Parsons et al. (1994)	Alpine	↑T, ↑W	AGDW	Shrub	F	OTC, Irrigation	None
Picon-Cochard et al. (2004)	Continental	↑C	AGDW	Mix	F	FACE	Cut
Prechsl et al. (2015)	Continental, Alpine	↓W	AGDW	Mix	F	Shelter	Cut, None
Press et al. (1998)	Alpine	↑T, ↑W	AGDW	Grass, Forb	F	OTC, Irrigation	None
Ramo et al. (2006)	Northern	↑C	AGDW, N	Grass, Forb	F	OTC	None
Rouhier & Read (1998)	Atlantic	↑C	AGDW	Forb	GH	GH	None

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
Roumet et al. (1999)	Southern	↑C	N	Grass	GH	GH	None
Roumet et al. (2002)	Southern	↑C	AGDW	Grass	GH	GH	None
Sæbø & Mortensen (1995)	Northern	↑C	AGDW	Grass, Legume	F	OTC	Cut
Sanaullah et al. (2014)	Atlantic	↑T	N	Grass	F	HL	None
Sanz-Saez et al. (2012)	Southern	↑C, ↑T	AGDW	Legume	GH	TGT	None
Sardans et al. (2008)	Southern	↑T, ↓W	N	Legume, Shrub	F	Shelter	None
Schappi & Korner (1996)	Alpine	↑C	AGDW	Grass, Forb, Mix	F	OTC	None
Schenk et al. (1997)	Continental	↑C	AGDW, N	Grass, Legume, Mix	F	OTC	Cut
Schmid et al. (2011)	Alpine	↓W	AGDW	Grass, Forb, Legume, Shrub	F	Shelter	None
Schneider et al. (2004)	Alpine	↑C	AGDW	Grass	F	FACE	Cut
Schuerings et al. (2013)	Continental	↑T	AGDW, N	Grass, Mix	F	HC	Cut
Schuerings et al. (2014)	Continental	↑T	AGDW	Grass, Forb, Shrub	F	HL, HC	Cut, None
Sebastia (2007)	Alpine	↑T, ↓W	AGDW	Grass, Forb	F	Trans	Cut
Sheppard et al. (2012)	Continental	↑T, ↓W, ↑W	AGDW	Mix	F	Shelter, Cover, Irrigation	None
Soussana et al. (1996)	Continental	↑C, ↑T	AGDW, N	Grass	GH	GH	Cut
Stevnbak et al. (2012)	Continental	↑C, ↑T, ↓W	AGDW	Grass	F	FACE	None
Stöcklin et al. (1998)	Continental	↑C	AGDW	Grass, Forb, Legume	GH	GH	Cut
Suter et al. (2001)	Alpine	↑C	AGDW	Grass	F	FACE	Cut
Taylor et al. (2011)	Southern	↓W	N	Grass	CC	CC	None
Utrillas et al. (1995)	Southern	↓W	AGDW	Grass	F	Irrigation	Cut
Van De Velde et al. (2015)	Atlantic	↑C, ↑T, ↓W	AGDW	Grass, Forb	CC	CC	None
van Heerwaarden et al. (2005)	Atlantic	↑C	AGDW, N	Grass	CC	CC	None

Study	Region	Climatic treatment	Parameter	Plant functional group	Growing area	Methodology	Defoliation
van Kleunen et al. (2006)	Alpine	↑C	AGDW	Grass	F	FACE	None
Verlinden et al. (2013)	Atlantic	↑T	AGDW	Forb	GH	CC_NL	None
Walter et al. (2012)	Continental	↓W	AGDW, N	Grass, Mix	F	Shelter	Cut
Walter et al. (2012)	Continental	↓W	N	Grass	F	Shelter	None
Warwick et al. (1998)	Alpine	↑C	AGDW	Grass, Forb, Legume	F	FACE	Cut
Werkman & Callaghan (2002)	Atlantic	↑T	AGDW	Shrub	F	Shelter	None
Whitehead et al. (1997)	Atlantic	↑C	AGDW, N	Shrub	CC	CC	None
Winkler & Herbst (2004)	Continental	↑C	AGDW, N	Grass, Forb, Legume	F	FACE	Cut, None
Woodin et al. (1992)	Atlantic	↑C	N	Shrub	CC	CC	None
Xi et al. (2015)	Continental	↓W, ↑W	AGDW	Grass, Forb, Legume	F	Shelter, Irrigation	None
Ylanne et al. (2015)	Alpine	↑T	N	Shrub	F	OTC	None
Zanetti et al. (1997)	Alpine	↑C	N	Grass	F	FACE	Cut
Zavalloni et al. (2008)	Atlantic	↑T	AGDW	Mix	GH	GH	Cut
Zavalloni et al. (2012)	Atlantic	↑C, ↑T	AGDW, N	Grass, Forb, Legume	GH	GH	None
Zwicke et al. (2013)	Continental	↑T, ↓W	AGDW	Grass, Forb, Legume	F	HL, Shelter	Cut

CHAPTER 3 Empirical and dynamic approaches for modelling the yield and N yield of European grasslands

3.1 Chapter introduction

This chapter uses two different approaches to model the yield and N yield (referred to in this chapter as 'N content') of European grasslands. The first involves developing statistical models using multiple regression analysis. The second is a pre-existing process-based model known as Century. Both approaches use data from long-running grassland experiments and their associated weather data. These differ from those experiments used in the meta-analysis, in that here there is no artificial manipulation of the climate. Instead, for each site, annual yields and N yields over a period of several years are used. This type of statistical model for grassland yield has not previously been applied at a Europe-wide level and there has been no previous attempt to model N yield over large spatial scales anywhere. Previously, the Century model has mostly been used to model soil C and N dynamics. It has been used to model grassland productivity (Parton et al., 1993), though not in Europe and it has not generally been used for plant N yield. This chapter provides valuable information about the effectiveness of these modelling approaches in the European context.

This research was published in *Environmental Modelling and Software* (Dellar et al., 2019b) and the manuscript is included below. Martha Dellar is the lead author on this paper. She assembled the experimental data, determined the statistical methodology, conducted the analysis and wrote the paper. David Holmes assisted with writing the computer code to optimise the Century model parameters. Other authors advised on the methodology and provided feedback on the paper.

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

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3.2.1 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.

Key words: Grasslands, Yield, Nitrogen, Modelling

3.2.2 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.

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.

3.2.3 Methods

3.2.3.1 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 figure 3.1. 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).

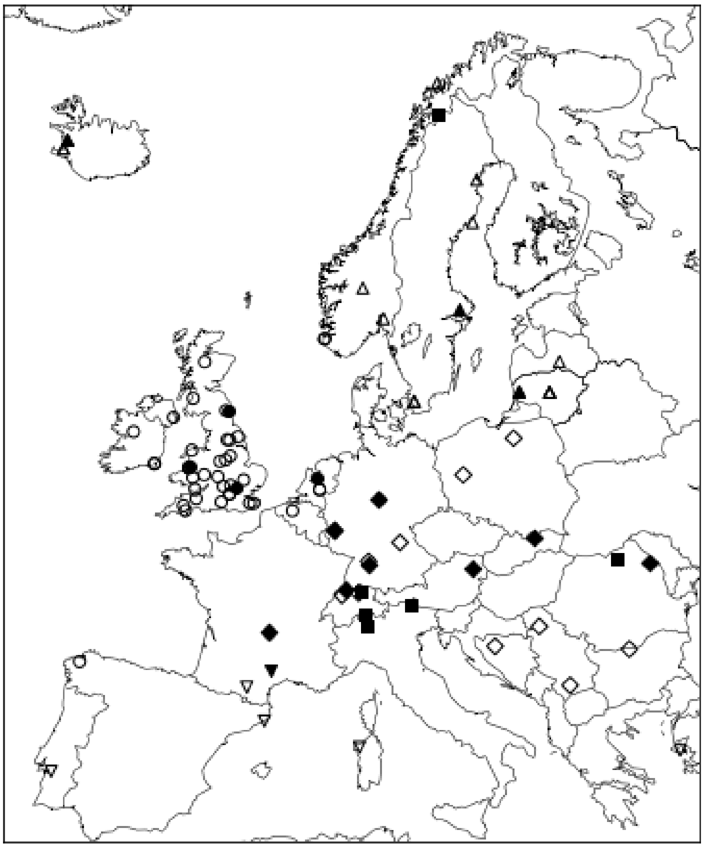


Figure 3.1: *Locations of sites used, by geographic region and grassland type. Regions are Alpine (■), Atlantic (●), Continental (◆), Northern (▲) and Southern (▼). Open shapes denote temporary grasslands, while solid shapes denote permanent grasslands*

3.2.3.2 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:

$$\text{Yield (t DM/ha)} = \alpha_0 + \alpha_{REGION} + \alpha_1 Rain_{JFM} + \alpha_2 Rain_{AMJ} + \alpha_3 Rain_{JA} + \alpha_4 Temp_{FM} + \alpha_5 Temp_{AMJ} + \alpha_6 Temp_{JA} + \alpha_7 Rain_{JFM}^2 + \alpha_8 Rain_{AMJ}^2 + \alpha_9 Rain_{JA}^2 +$$

$\alpha_{10}Temp_{JA}^2 + \alpha_{11}Altitude + \alpha_{12}Cuts + \alpha_{13}NF + \alpha_{14}Cuts^2 + \alpha_{15}NF^2 + \alpha_{16}NF*Rain_{JFM} + \alpha_{17}NF*Temp_{JA}$

Applicable to the Alpine, Atlantic, continental and northern regions

Yield, temporary grassland:

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

Applicable to the Atlantic, continental, northern and southern regions

N content, permanent grassland:

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

Applicable to the continental region

N content, temporary grassland:

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

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 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.

3.2.3.3 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 3.1. 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.

Table 3.1: *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

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 3.2.

Table 3.2: *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

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.

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:

$$X = SoilC + \sum_{i} (Y_i + N_i)$$

$Y_i = RMSE(P_Y, O_Y)/\overline{O_Y}$ *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

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.

3.2.3.4 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.

3.2.3.5 Sensitivity analysis

We looked at the sensitivity of the model predictions to uncertainty in different input parameters. These are shown in table 3.3, along with ranges for their potential uncertainty (based on Fitton et al. (2014) and Gottschalk et al. (2007)).

Table 3.3: *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	±30mm per month	Regression and Century
Temperature	±1°C	Regression and Century
Legume percentage	±25%	Regression
Soil pH	±1.5pH unit	Century
Soil clay content	±30%	Century
Soil bulk density	±0.3g/cm^3	Century

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.

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 5,000 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 3.1).

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:

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

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).

3.2.4 Results

3.2.4.1 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 3.4. In all cases, the fit was reasonably good, with high correlations but also relatively high RMSEs, though the latter were due entirely to variation 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.

Table 3.4: *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)*	0.89 *(0.00)*	28.1 *(0.0)*

3.2.4.2 Century model

The goodness-of-fit of the parameterised models is shown in table 3.5. 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.

Table 3.5: *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, 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

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
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	1.57 *(0.11)*	1.55 *(0.04)*	21.6 *(0.2)*	0.63	NA	10.0 *(0.4)*	NA	NA
	65	5.25 *(0.29)*	5.31 *(0.07)*	25.7 *(0.2)*	0.36	NA	47.1 *(0.8)*	NA	NA

3.2.4.3 Sensitivity analysis

3.2.4.3.1 Regression model

The sensitivity analysis results for the regression model are shown in table 3.6. 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.

3.2.4.3.2 Century model

The standard deviations of the total uncertainty (σ_g) for each site are shown in figure 3.2. 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 figure 3.3. 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 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.

Table 3.6: *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*

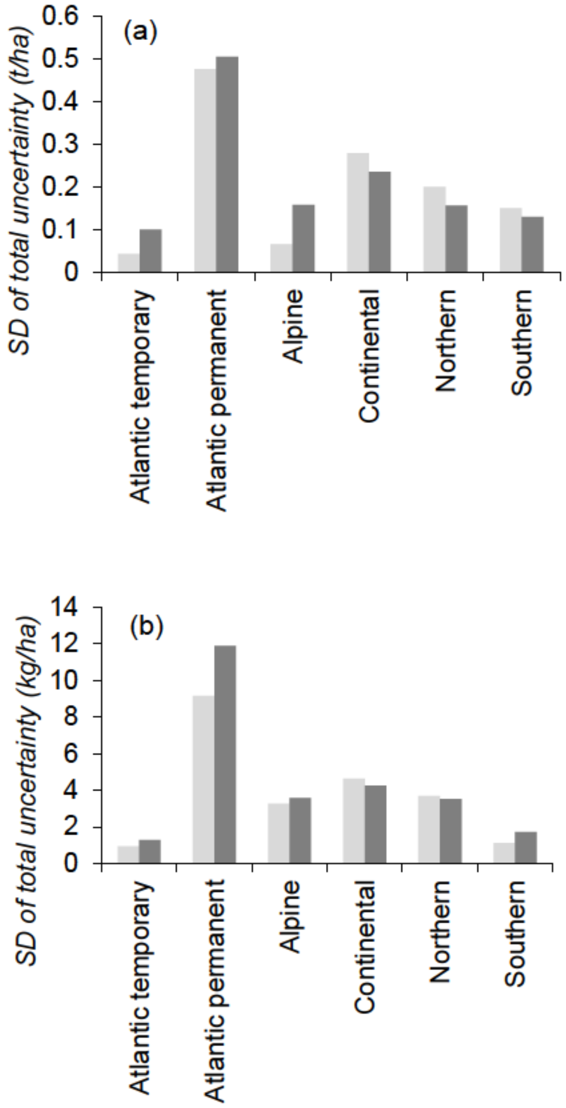
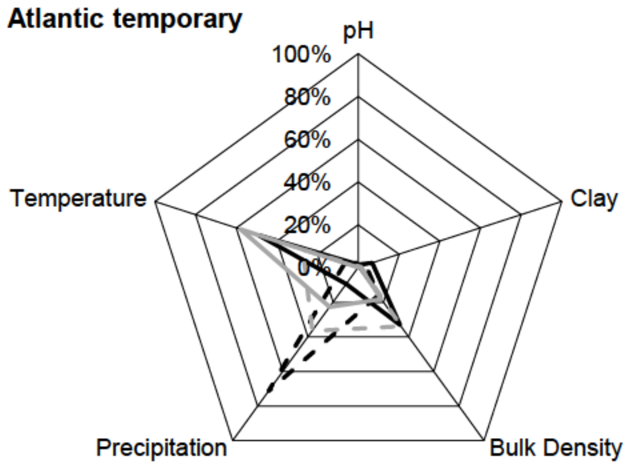


Figure 3.2: *Standard deviations of the total uncertainty in (a) yield and (b) N content predictions in the Century model when precipitation, temperature, soil pH, soil clay content and soil bulk density are allowed to vary. Light grey bars denote the no/low fertiliser treatment, dark grey bars denote the with/high fertiliser treatment*



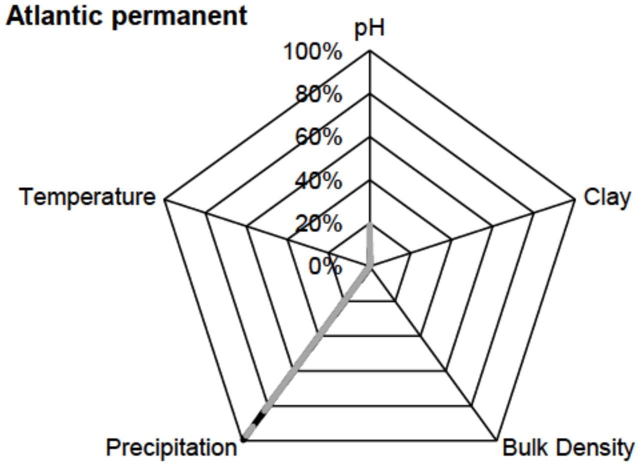


Figure 3.3: *Contribution indices, representing the contribution of each parameter to the total uncertainty, for the six sites to which the Century model has been applied. Black lines indicate results for yield and grey lines results for N content. Solid lines indicate the no/low fertiliser treatment and dashed lines indicate the with/high fertiliser treatment (continued on following pages)*

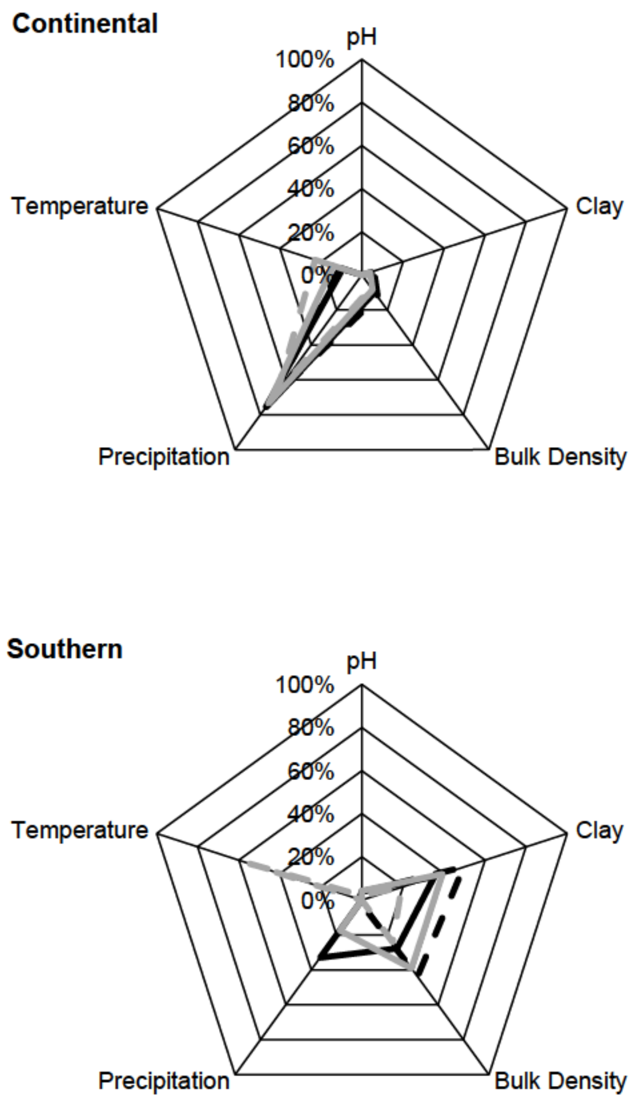
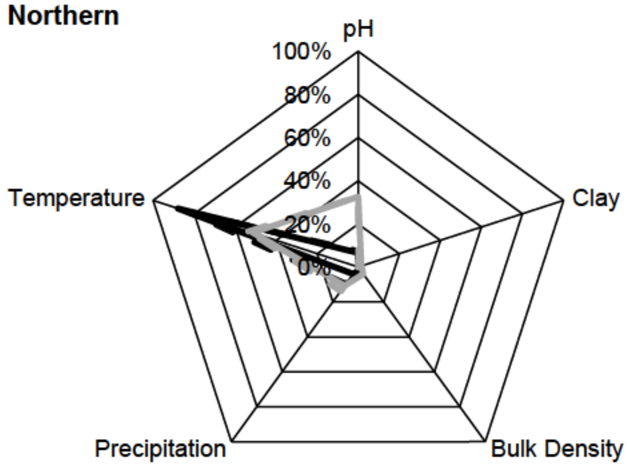


Figure 3.3 (continued): *Contribution indices, representing the contribution of each parameter to the total uncertainty, for the six sites to which the Century model has been applied. Black lines indicate results for yield and grey lines results for N content. Solid lines indicate the no/low fertiliser treatment and dashed lines indicate the with/high fertiliser treatment* *(continued on following page)*



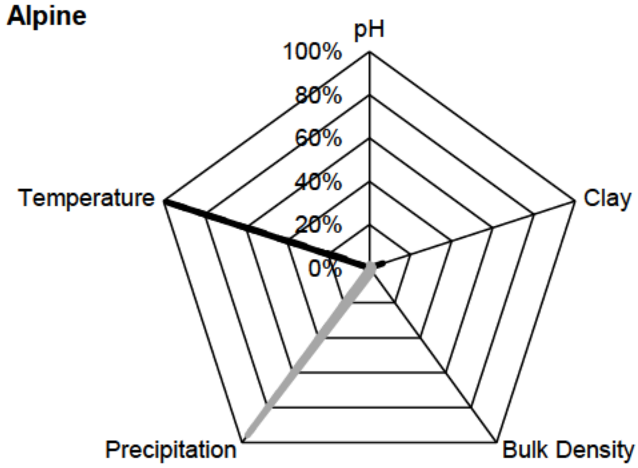


Figure 3.3 (continued): *Contribution indices, representing the contribution of each parameter to the total uncertainty, for the six sites to which the Century model has been applied. Black lines indicate results for yield and grey lines results for N content. Solid lines indicate the no/low fertiliser treatment and dashed lines indicate the with/high fertiliser treatment*

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.

3.2.5 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.

3.2.5.1 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 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.

3.2.5.2 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.

3.2.5.3 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 1mm a day then they can be wrong by up to 30mm 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, 2013b), 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 3.2), 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 3.5). 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.

3.2.5.4 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.

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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.

3.3 Chapter conclusion

This research determined the effectiveness of two modelling approaches (statistical and process-based) for estimating the yield and N yield of European grasslands. Statistical models for N yield over large spatial scales had not previously been developed and this paper demonstrated that such an approach can be very effective. It also produced statistical models for the yield of permanent and temporary grasslands in Europe, which had not previously been achieved. It was also determined that the Century model can be a useful tool for modelling the mean annual yields and N yields of European grasslands, though it was less effective when it came to detecting inter-annual variation.

The work did have some limitations. For instance, there was insufficient data to develop separate regression models for each region. Instead ‘region’ was included as a term in the model. This assumes that each region has similar responses to changes in temperature and precipitation, which is unlikely to be the case. It was also not possible to have each regression model be applicable to all regions, again due to data availability.

Nevertheless, this research provides valuable insights into the factors affecting the yield and N yield of European grasslands and provides useful tools for further research. The next chapter will use these models to investigate the likely impacts of climate change on European grasslands.

3.4 Appendices

3.4.1 Appendix A – Sites used for regression modelling

Table 3.7: *Permanent and temporary grassland 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)

Dataset / Location	Climatic region	Data available	Source
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)
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)

3.4.2 Appendix B – Coefficients of regression equations

Table 3.8: *Coefficients of regression equations*

i	α_i	β_i	γ_i	δ_i
0	15.1128199	-19.9492871	-171.2297218	-379.6930803
REGION	Alpine:	Atlantic:	NA	Atlantic:
	0	0		0
	Atlantic:	Continental:		Continental:
	-3.2947027	-1.0002833		5.2174092
	Continental:	Northern:		Northern:
	-2.0093908	-2.3116753		-70.2426315
	Northern:	Southern:		
	-2.8885051	-1.2554504		
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

i	α_i	β_i	γ_i	δ_i
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		

3.5 Supplementary materials

Table 3.9: *Sensitivity analysis results for the Century model when parameters were varied individually*

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
N	Bulk density	France	0	13.38	12.61	-0.06	14.96	0.12	0.96	-3.763	3.913	NA	NA	NA
N	Clay content	France	0	13.38	14.53	0.09	12.10	-0.10	0.99	-123.664	1254.581	-4626.077	7418.650	-4407.584
N	pH	France	0	13.38	13.40	0.00	13.38	0.00	0.91	-5.823	3.268	-0.674	0.061	-0.002
N	Precipitation	France	0	13.38	11.59	-0.13	12.55	-0.06	0.98	-0.071	0.139	-0.219	0.002	0.009
N	Temperature	France	0	13.38	13.27	-0.01	13.51	0.01	0.42	0.020	0.086	NA	NA	NA
N	Bulk density	France	65	49.56	48.50	-0.02	51.55	0.04	0.97	-4.940	5.106	NA	NA	NA
N	Clay content	France	65	49.56	50.83	0.03	48.04	-0.03	0.95	4.621	-11.687	NA	NA	NA
N	pH	France	65	49.56	49.49	0.00	49.56	0.00	1.00	-15.657	7.371	-1.297	0.101	-0.003
N	Precipitation	France	65	49.56	49.75	0.00	48.66	-0.02	0.99	-0.036	-0.163	-0.071	-0.002	0.004
N	Temperature	France	65	49.56	47.87	-0.03	51.83	0.05	0.99	0.193	1.932	NA	NA	NA
Yield	Bulk density	France	0	2.04	1.96	-0.04	2.23	0.09	1.00	-0.301	0.710	-0.906	0.489	0.007
Yield	Clay content	France	0	2.04	2.18	0.07	1.88	-0.08	0.98	-15.933	161.665	-597.004	959.621	-571.613
Yield	pH	France	0	2.04	2.04	0.00	2.04	0.00	0.97	-0.009	0.041	-0.014	0.002	0.000
Yield	Precipitation	France	0	2.04	1.77	-0.13	1.96	-0.04	0.99	-0.006	0.035	-0.026	0.000	0.001

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
Yield	Temperature	France	0	2.04	2.08	0.02	2.00	-0.02	0.93	0.006	-0.058	0.002	0.030	-0.017
Yield	Bulk density	France	65	5.61	5.51	-0.02	5.80	0.03	0.96	-0.468	0.488	NA	NA	NA
Yield	Clay content	France	65	5.61	5.75	0.02	5.45	-0.03	0.94	0.496	-1.253	NA	NA	NA
Yield	pH	France	65	5.61	5.60	0.00	5.61	0.00	1.00	-2.278	1.072	-0.189	0.015	0.000
Yield	Precipitation	France	65	5.61	5.48	-0.02	5.52	-0.02	0.98	-0.003	0.004	-0.015	0.000	0.000
Yield	Temperature	France	65	5.61	5.54	-0.01	5.64	0.01	0.93	0.007	0.040	0.005	0.007	-0.040
N	Bulk density	Germany	0	42.90	44.30	0.03	41.05	-0.04	0.99	5.154	-5.209	NA	NA	NA
N	Clay content	Germany	0	42.90	41.57	-0.03	43.73	0.02	0.95	-3.254	8.031	NA	NA	NA
N	pH	Germany	0	42.90	43.13	0.01	42.90	0.00	0.99	122.715	-58.710	10.500	-0.832	0.025
N	Precipitation	Germany	0	42.90	34.49	-0.20	47.16	0.10	1.00	0.295	1.167	0.272	0.101	-0.059
N	Temperature	Germany	0	42.90	44.95	0.05	44.08	0.03	0.63	0.477	0.669	2.118	-1.271	-1.094
N	Bulk density	Germany	With	117.72	118.36	0.01	116.94	-0.01	0.99	2.172	-2.204	NA	NA	NA
N	Clay content	Germany	With	117.72	116.72	-0.01	118.25	0.00	0.99	-67.545	647.189	-2330.850	3718.802	-2203.490
N	pH	Germany	With	117.72	117.93	0.00	117.72	0.00	0.99	112.018	-53.585	9.582	-0.759	0.022
N	Precipitation	Germany	With	117.72	110.89	-0.06	121.57	0.03	0.99	0.602	0.661	0.428	0.126	-0.074
N	Temperature	Germany	With	117.72	116.96	-0.01	120.88	0.03	0.89	0.565	4.157	3.562	-3.215	-2.501
Yield	Bulk density	Germany	0	4.09	4.12	0.01	4.03	-0.01	0.96	0.143	-0.146	NA	NA	NA
Yield	Clay content	Germany	0	4.09	4.03	-0.01	4.12	0.01	0.99	-3.286	31.366	-112.753	179.793	-106.500

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
Yield	pH	Germany	0	4.09	4.10	0.00	4.09	0.00	0.99	7.127	-3.410	0.610	-0.048	0.001
Yield	Precipitation	Germany	0	4.09	3.43	-0.16	4.19	0.03	0.99	0.020	0.006	0.019	0.013	-0.006
Yield	Temperature	Germany	0	4.09	4.16	0.02	4.17	0.02	0.50	0.028	0.068	0.098	-0.071	-0.047
Yield	Bulk density	Germany	With	6.80	6.82	0.00	6.76	-0.01	0.96	0.092	-0.093	NA	NA	NA
Yield	Clay content	Germany	With	6.80	6.76	-0.01	6.82	0.00	0.99	-3.047	29.582	-107.683	173.289	-103.410
Yield	pH	Germany	With	6.80	6.80	0.00	6.80	0.00	0.99	3.846	-1.840	0.329	-0.026	0.001
Yield	Precipitation	Germany	With	6.80	6.29	-0.08	6.91	0.02	0.99	0.017	0.004	0.026	0.011	-0.006
Yield	Temperature	Germany	With	6.80	6.84	0.01	6.89	0.01	0.59	0.024	0.108	0.132	-0.098	-0.104
N	Bulk density	Hurley, UK	0	28.13	29.02	0.03	27.91	-0.01	1.00	8.431	-18.903	14.523	-4.473	0.421
N	Clay content	Hurley, UK	0	28.13	27.84	-0.01	28.47	0.01	1.00	-1.031	6.910	NA	NA	NA
N	pH	Hurley, UK	0	28.13	28.29	0.01	28.13	0.00	1.00	35.974	-16.986	2.998	-0.234	0.007
N	Precipitation	Hurley, UK	0	28.13	28.96	0.03	27.94	-0.01	0.92	0.037	0.039	-0.011	-0.022	0.004
N	Temperature	Hurley, UK	0	28.13	26.15	-0.07	27.14	-0.04	0.90	-0.022	1.014	-3.163	-0.543	1.735
N	Bulk density	Hurley, UK	150	81.30	81.98	0.01	81.16	0.00	1.00	15.094	-51.843	70.793	-45.187	11.146
N	Clay content	Hurley, UK	150	81.30	80.99	0.00	81.64	0.00	1.00	-1.060	7.102	NA	NA	NA
N	pH	Hurley, UK	150	81.30	81.39	0.00	81.30	0.00	0.99	21.572	-10.160	1.789	-0.139	0.004
N	Precipitation	Hurley, UK	150	81.30	80.91	0.00	81.44	0.00	-0.03	-0.063	0.010	0.075	0.003	-0.010
N	Temperature	Hurley, UK	150	81.30	79.19	-0.03	80.33	-0.01	0.88	-0.019	1.149	-3.374	-0.607	1.903

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
Yield	Bulk density	Hurley, UK	0	1.62	1.68	0.04	1.59	-0.02	0.96	0.152	-0.146	NA	NA	NA
Yield	Clay content	Hurley, UK	0	1.62	1.59	-0.01	1.64	0.02	1.00	-0.081	0.545	NA	NA	NA
Yield	pH	Hurley, UK	0	1.62	1.63	0.01	1.62	0.00	1.00	2.934	-1.382	0.243	-0.019	0.001
Yield	Precipitation	Hurley, UK	0	1.62	1.61	-0.01	1.60	-0.01	0.51	0.003	0.004	-0.001	-0.001	0.000
Yield	Temperature	Hurley, UK	0	1.62	1.52	-0.06	1.53	-0.05	0.92	-0.009	-0.008	-0.162	0.014	0.080
Yield	Bulk density	Hurley, UK	150	6.37	6.38	0.00	6.36	0.00	0.96	0.038	-0.037	NA	NA	NA
Yield	Clay content	Hurley, UK	150	6.37	6.35	0.00	6.39	0.00	1.00	-0.066	0.439	NA	NA	NA
Yield	pH	Hurley, UK	150	6.37	6.38	0.00	6.37	0.00	0.99	1.571	-0.735	0.128	-0.010	0.000
Yield	Precipitation	Hurley, UK	150	6.37	6.08	-0.04	6.34	0.00	0.95	-0.007	-0.026	0.010	0.007	-0.003
Yield	Temperature	Hurley, UK	150	6.37	6.24	-0.02	6.28	-0.01	0.97	-0.001	0.040	-0.201	-0.017	0.099
N	Bulk density	Iceland	0	65.26	64.85	-0.01	65.98	0.01	0.88	-71.914	1579.463	-10900.643	29633.693	-27635.270
N	Clay content	Iceland	0	65.26	64.86	-0.01	65.86	0.01	0.99	-1.698	8.678	NA	NA	NA
N	pH	Iceland	0	65.26	57.45	-0.12	65.96	0.01	1.00	-39.089	-8.446	10.647	-2.109	0.125
N	Precipitation	Iceland	0	65.26	64.59	-0.01	61.98	-0.05	0.86	-0.128	-0.330	-0.292	-0.024	0.014
N	Temperature	Iceland	0	65.26	61.17	-0.06	69.26	0.06	1.00	-0.067	3.918	NA	NA	NA
N	Bulk density	Iceland	100	123.69	123.40	0.00	123.96	0.00	0.88	-124.914	2758.044	-19090.188	51948.611	-48475.626
N	Clay content	Iceland	100	123.69	123.38	0.00	123.84	0.00	0.90	19.089	-424.943	3375.164	-11495.048	14307.600
N	pH	Iceland	100	123.69	116.62	-0.06	124.11	0.00	1.00	-10.800	-25.409	14.365	-2.463	0.138

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
N	Precipitation	Iceland	100	123.69	122.41	-0.01	121.12	-0.02	0.59	0.010	0.084	-0.370	-0.052	0.024
N	Temperature	Iceland	100	123.69	120.18	-0.03	127.85	0.03	0.93	-0.145	3.467	NA	NA	NA
Yield	Bulk density	Iceland	0	6.19	6.17	0.00	6.22	0.00	0.88	-7.236	159.746	-1105.297	3006.840	-2804.655
Yield	Clay content	Iceland	0	6.19	6.17	0.00	6.20	0.00	0.96	-0.046	0.237	NA	NA	NA
Yield	pH	Iceland	0	6.19	5.95	-0.04	6.20	0.00	1.00	-4.570	2.387	-0.433	0.030	-0.001
Yield	Precipitation	Iceland	0	6.19	6.16	0.00	6.11	-0.01	0.75	-0.018	-0.013	NA	NA	NA
Yield	Temperature	Iceland	0	6.19	5.85	-0.05	6.43	0.04	0.99	-0.035	0.286	NA	NA	NA
Yield	Bulk density	Iceland	100	7.18	7.17	0.00	7.20	0.00	0.88	-8.406	185.807	-1286.574	3501.047	-3266.428
Yield	Clay content	Iceland	100	7.18	7.17	0.00	7.19	0.00	0.86	0.458	-10.091	79.291	-266.750	327.014
Yield	pH	Iceland	100	7.18	7.00	-0.02	7.19	0.00	1.00	-2.361	0.975	-0.098	-0.005	0.001
Yield	Precipitation	Iceland	100	7.18	7.16	0.00	7.14	-0.01	0.34	-0.002	0.000	-0.004	-0.001	0.000
Yield	Temperature	Iceland	100	7.18	6.91	-0.04	7.36	0.02	0.98	-0.037	0.209	NA	NA	NA
N	Bulk density	Rothamsted	0	42.67	42.45	-0.01	42.29	-0.01	0.98	12.200	-48.371	67.089	-38.784	7.828
N	Clay content	Rothamsted	0	42.67	42.00	-0.02	43.33	0.02	1.00	-2.190	9.922	NA	NA	NA
N	pH	Rothamsted	0	42.67	61.51	0.44	42.35	-0.01	0.99	609.650	-328.024	62.840	-4.932	0.124
N	Precipitation	Rothamsted	0	42.67	24.61	-0.42	47.55	0.11	1.00	0.003	4.692	-1.093	-0.099	0.040
N	Temperature	Rothamsted	0	42.67	43.98	0.03	41.70	-0.02	0.86	-0.150	-1.059	NA	NA	NA
N	Bulk density	Rothamsted	144	155.25	155.73	0.00	153.47	-0.01	1.00	-12.857	35.469	-29.845	8.380	-0.801

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
N	Clay content	Rothamsted	144	155.25	153.78	-0.01	156.71	0.01	1.00	-4.816	21.811	NA	NA	NA
N	pH	Rothamsted	144	155.25	166.68	0.07	154.80	0.00	1.00	446.176	-261.482	56.849	-5.428	0.192
N	Precipitation	Rothamsted	144	155.25	126.49	-0.19	160.90	0.04	1.00	-0.301	6.185	-1.555	-0.061	0.035
N	Temperature	Rothamsted	144	155.25	157.79	0.02	152.66	-0.02	0.98	-0.282	-2.480	NA	NA	NA
Yield	Bulk density	Rothamsted	0	2.93	2.92	0.00	2.90	-0.01	0.99	-0.367	1.288	-1.881	1.337	-0.377
Yield	Clay content	Rothamsted	0	2.93	2.90	-0.01	2.97	0.01	1.00	-0.119	0.536	NA	NA	NA
Yield	pH	Rothamsted	0	2.93	3.69	0.26	2.92	-0.01	0.99	15.361	-6.536	0.743	0.011	-0.004
Yield	Precipitation	Rothamsted	0	2.93	1.84	-0.37	3.16	0.08	1.00	0.002	0.218	-0.060	0.000	0.001
Yield	Temperature	Rothamsted	0	2.93	2.96	0.01	2.90	-0.01	0.53	-0.004	-0.015	-0.047	-0.002	0.056
Yield	Bulk density	Rothamsted	144	5.76	5.80	0.01	5.66	-0.02	1.00	0.740	-2.608	3.578	-2.093	0.400
Yield	Clay content	Rothamsted	144	5.76	5.72	-0.01	5.80	0.01	1.00	-0.149	0.667	NA	NA	NA
Yield	pH	Rothamsted	144	5.76	5.93	0.03	5.76	0.00	1.00	15.149	-10.063	2.494	-0.273	0.011
Yield	Precipitation	Rothamsted	144	5.76	4.38	-0.24	5.91	0.03	1.00	0.006	0.187	-0.080	0.008	0.001
Yield	Temperature	Rothamsted	144	5.76	5.68	-0.01	5.78	0.00	0.97	-0.003	0.037	-0.040	0.013	0.011
N	Bulk density	Switzerland	140	148.02	148.76	0.01	148.48	0.00	0.40	-70.593	315.053	-509.117	356.130	-91.339
N	Clay content	Switzerland	140	148.02	147.35	0.00	148.27	0.00	0.48	-1.088	3.843	NA	NA	NA
N	pH	Switzerland	140	148.02	147.43	0.00	148.02	0.00	0.87	-298.241	161.873	-32.798	2.940	-0.098
N	Precipitation	Switzerland	140	148.02	152.57	0.03	157.55	0.06	0.98	4.744	1.900	NA	NA	NA

Output	Parameter	Site	Fertiliser (kg/ha/yr)	Baseline (Yield: t/ha, N: kg/ha)	Maximum deviation from baseline when parameter decreases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter decreases	Maximum deviation from baseline when parameter increases (Yield: t/ha, N: kg/ha)	Maximum % change when parameter increases	R-squared of regression	Offset	Linear coefficient	Squared coefficient	Cubed coefficient	Fourth coefficient
N	Temperature	Switzerland	140	148.02	153.66	0.04	153.74	0.04	0.28	5.701	0.386	-1.678	-0.160	0.817
N	Bulk density	Switzerland	560	353.97	355.14	0.00	352.39	0.00	0.95	3.756	-3.959	NA	NA	NA
N	Clay content	Switzerland	560	353.97	352.24	0.00	354.34	0.00	0.99	40.610	-667.805	3718.249	-8600.679	7106.989
N	pH	Switzerland	560	353.97	352.17	-0.01	353.97	0.00	0.93	188.083	-122.929	28.664	-2.869	0.105
N	Precipitation	Switzerland	560	353.97	346.52	-0.02	359.19	0.01	0.97	-0.679	2.332	NA	NA	NA
N	Temperature	Switzerland	560	353.97	351.72	-0.01	353.17	0.00	0.16	0.536	0.229	-4.339	0.055	2.958
Yield	Bulk density	Switzerland	140	6.93	6.92	0.00	6.95	0.00	0.81	-0.060	0.067	NA	NA	NA
Yield	Clay content	Switzerland	140	6.93	6.91	0.00	6.93	0.00	0.03	-0.015	0.044	NA	NA	NA
Yield	pH	Switzerland	140	6.93	6.94	0.00	6.93	0.00	0.22	0.016	-0.002	NA	NA	NA
Yield	Precipitation	Switzerland	140	6.93	7.25	0.05	7.27	0.05	0.95	0.313	0.006	0.001	0.001	-0.001
Yield	Temperature	Switzerland	140	6.93	7.31	0.06	7.24	0.04	0.98	0.326	-0.097	-0.037	-0.003	-0.011
Yield	Bulk density	Switzerland	560	12.41	12.38	0.00	12.42	0.00	0.89	-0.079	0.075	NA	NA	NA
Yield	Clay content	Switzerland	560	12.41	12.38	0.00	12.39	0.00	0.99	0.760	-12.252	66.785	-149.079	115.165
Yield	pH	Switzerland	560	12.41	12.40	0.00	12.41	0.00	-0.11	-0.004	0.000	NA	NA	NA
Yield	Precipitation	Switzerland	560	12.41	12.37	0.00	12.36	0.00	0.86	-0.007	-0.011	-0.004	0.001	0.000
Yield	Temperature	Switzerland	560	12.41	12.61	0.02	12.12	-0.02	0.98	-0.015	-0.247	NA	NA	NA

CHAPTER 4 Modelling the impact of climate change on the yield and N yield of European grasslands

4.1 Chapter introduction

This chapter uses the models from chapter three to investigate the likely effects of climate change on the yield and N yield of European grasslands. This represents the first attempt to consider these effects at a Europe-wide scale. In chapter three it was determined that the regression approach had better correlations between observations and predictions than the process-based approach and that it is more effective over large spatial scales. However, there is a risk of extrapolation errors if it is used for a climate different to that under which the regression equations were developed. To counteract this, the climate change scenarios are bounded so that they do not change too much. This approach is also supplemented by the use of the Century process-based model which does not have this restriction. By using both approaches, the drawbacks of each are mitigated and it is possible to achieve a general picture of the responses of European grasslands to climate change.

This research has been submitted to *Royal Society Open Science* and the manuscript is included below. Martha Dellar is the lead author on this paper. She assembled the data, determined the statistical methodology, conducted the analysis and wrote the paper. Other authors advised on the methodology and provided feedback on the paper.

4.2 Modelling the impact of climate change on the yield and N yield of European grasslands

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4.2.1 Abstract

The world is experiencing rising atmospheric CO_2 concentrations, increasing temperatures and changes in rainfall patterns, all of which will continue in the future. These changes have implications for grasslands, potentially affecting both yield and nutritional quality, and thus for grass-based livestock systems. We used two modelling approaches, one involving regression on meteorological and managerial variables and the other using the Century process-based model. We applied these approaches to sites across different geographic regions in Europe (Alpine, Atlantic, continental, northern and southern) under two climate change scenarios (RCP4.5 and RCP8.5). We found that the two approaches usually agreed with one another, in that grassland yields are expected to increase, though probably less so in the Atlantic region, and there may be slight decreases in southern Europe. Both approaches agreed that plant N concentration will be reduced, indicating that livestock will need to eat more to receive the same quantity of protein. The impact of different fertiliser levels, grassland types and geographic regions on plant yield and plant N yield will be much greater than the impact of climate change. This suggests that it should be possible to mitigate negative climate change impacts through appropriate changes in grassland management practices.

Key words: Climate change, Modelling, Yield, Nitrogen

4.2.2 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 1.0 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, 2013b). 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 grasslands.

Experimental research on the effects of climate change on grasslands has usually focussed on individual climatic changes (elevated atmospheric CO_2 concentration, increased temperature or changes in water availability), with relatively few looking at combinations thereof. Those which have looked at multiple simultaneous changes have often found that the different climatic changes produce opposing effects (for example increased growth due to elevated CO_2, but decreased growth due to higher temperatures) (Farfan-Vignolo and Asard, 2012; Stevnbak et al., 2012; Zwicke et al., 2013). This makes it hard to determine what the net effect of simultaneous changes might be. Those experiments which do consider simultaneous changes give us useful information at a site-specific level, but not on a larger scale. Meta-analyses have been used to get more of a general picture of the future impacts of climate change using experimental information (Dellar et al., 2018; Dumont et al., 2015; Wang et al., 2012), but since the majority of the experimental evidence is based on a single climatic change, they too struggle to determine the effects of simultaneous changes.

Previous attempts to model the effects of climate change on grasslands have usually been conducted at relatively small spatial scales. A regression approach was used for Atlantic calcareous grasslands (Duckworth et al., 2000), concluding that little change was expected. Several previous studies have used process-based models, but generally at a site-specific or else national scale (Abdalla et al., 2010; Graux et al., 2013; Thornley and Cannell, 1997; Vital et al., 2013). The Century model was used to predict the effects of climate change on grassland net primary productivity (among other things) at several sites worldwide (Hall et al., 1995), though none of these sites were in Europe. It was found that grassland productivity generally increased.

We have previously used two approaches to model the yield and nitrogen (N) yield (i.e. protein) of European grasslands (Dellar et al., 2019b). The first is a regression model with climatic and managerial variables and the second is a dynamic process-based model, namely Century (Parton et al., 1987). Both approaches were found to predict grassland yield and N yield in Europe under the current climate reasonably well, though they have different ranges of applicability. The regression model is well suited to identifying general trends over large geographic regions, while Century gives more accurate predictions at a site-specific scale.

The present study aims to use the two approaches to predict the effects of climate change on grassland yield and N yield across Europe. Each approach has its benefits and limitations. Century accounts for long-term climatic changes and is able to predict the yield and quality of future grasslands under different climate change scenarios, but it requires more inputs than the regression model and has to be parameterised separately for each site. The regression model applies over a wide geographic area, but is only relevant within the confines of the experiments which contributed to its development. It cannot be used to predict grassland yield or quality under climate conditions different from those original experiments. It is however useful in determining trends in responses to weather variation. By using both approaches, we are able to mitigate the drawbacks of each and get a general picture of the responses of European grasslands to climate change.

4.2.3 Methods

We considered five geographic regions, based on climatic zones (figure 4.1) and both permanent and temporary grasslands. Full details are given in Dellar et al. (2019b). Monthly temperature and precipitation data for all sites were taken from the Climatic Research Unit gridded dataset (UEA CRU et al., 2017).

Figure 4.1: *Classification of the five geographic regions, based on climatic zones (Kovats et al., 2014)*

4.2.3.1 Regression model

4.2.3.1.1 Model Development

We collected data from grassland experiments across Europe. These provided yield (as harvested dry matter) and N yield measurements over time periods of at least three years. We used stepwise regression to generate equations for grassland yield and N yield for both permanent and temporary grasslands (Dellar et al., 2019b):

Yield, permanent grassland:

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

Applicable to the Alpine, Atlantic, continental and northern regions

Yield, temporary grassland:

$$\text{Yield (t/ha)} = \beta_0 + \beta_{REGION} + \beta_1 Rain_{JFM} + \beta_2 Rain_{AMJ} + \beta_3 Rain_{JA} + \beta_4 Temp_{JF} + \beta_5 Temp_{MA} + \beta_6 Temp_{MJ} + \beta_7 Temp_{JA} + \beta_8 Rain_{JFM}^2 + \beta_9 Rain_{AMJ}^2 + \beta_{10} Rain_{JA}^2 +$$

$\beta_{11}Temp_{MJ}^2 + \beta_{12}Temp_{JA}^2 + \beta_{13}Altitude + \beta_{14}Cuts + \beta_{15}Legume + \beta_{16}NF + \beta_{17}Altitude^2 + \beta_{18}Cuts^2 + \beta_{19}Legume^2 + \beta_{20}NF^2 + \beta_{21}NF{*}Rain_{JA} + \beta_{22}NF{*}Cuts$

Applicable to the Atlantic, continental, northern and southern regions

N yield, permanent grassland:

$$N\ yield\ (kg/ha) = \gamma_0 + \gamma_1Rain_{March} + \gamma_2Rain_{AM} + \gamma_3Rain_{JJA} + \gamma_4Temp_{January} + \gamma_5Temp_{August} + \gamma_6Rain_{March}^2 + \gamma_7Rain_{JJA}^2 + \gamma_8Altitude + \gamma_9Cuts + \gamma_{10}Cuts^2 + \gamma_{11}NF + \gamma_{12}NF{*}Rain_{March} + \gamma_{13}NF{*}Temp_{January} + \gamma_{14}NF{*}Temp_{August} + \gamma_{15}NF{*}Cuts$$

Applicable to the continental region

N yield, temporary grassland:

$$N\ yield\ (kg/ha) = \delta_0 + \delta_{REGION} + \delta_1Rain_{AM} + \delta_2Rain_{JJA} + \delta_3Temp_{JF} + \delta_4Temp_{MA} + \delta_5Temp_{JJA} + \delta_6Rain_{AM}^2 + \delta_7Rain_{JJA}^2 + \delta_8Temp_{JF}^2 + \delta_9Temp_{MA}^2 + \delta_{10}Temp_{JJA}^2 + \delta_{11}Altitude + \delta_{12}Cuts + \delta_{13}Legume + \delta_{14}NF + \delta_{15}Altitude^2 + \delta_{16}Cuts^2 + \delta_{17}Legume^2 + \delta_{18}NF^2 + \delta_{19}NF{*}Temp_{MA} + \delta_{20}NF{*}Cuts$$

Applicable to the Atlantic, continental and northern regions

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' indicate the number of harvests per year

'Legume' is the percentage of nitrogen-fixing plants at sowing, 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. Coefficients for the equations are given in appendix A.

We have previously examined the fit of these equations to experimental data and their sensitivity to uncertainties in the inputs (Dellar et al., 2019b). The fit was generally good (R^2 values between 0.6 and 0.8 and correlations between predictions and observations between 0.76 and 0.89). However, the root mean squared error between predictions and observations was relatively large (28.1 – 40.5% of the mean value), though this was due entirely to variation rather than bias. The equations were more sensitive to uncertainties in precipitation measurements than in anything else, which often accounted for more than 80% of the total uncertainty.

4.2.3.1.2 Climate change scenarios

We used the period 1971-2000 as a baseline. Temperature and precipitation data for this period were taken from CORDEX (CORDEX, 2018) for each experimental site. To get climate change predictions we used the estimated ranges given in Jacob et al. (2014). This gave us likely ranges for temperature and precipitation changes for 2071-2100 relative to our baseline for each of our geographic regions (where ‘likely’ means between the 17^{h} and 83rd percentile of projected changes). It also gave us median, maximum and minimum possible changes. These ranges were given for two climate change scenarios: RCP4.5 and RCP8.5. These are representative concentration pathways; RCP4.5 represents a midrange scenario while RCP8.5 is more extreme (Moss et al., 2010). We checked that the predicted 2071-2100 temperature and rainfall data for each of our experimental sites from EUROCORDEX fitted within the ranges provided by Jacob et al. (2014). The average changes for the sites within each region were usually in the ‘likely’ range and always in the min/max range. The time periods chosen are in line with the EUROCORDEX guidelines (Benestad et al., 2017), which recommend that periods of at least thirty years should be used to ensure that it is long-term climate change which is being assessed, rather than short-term variability.

The regression equations were developed using data from the ‘ambient’ climate and 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 were calculated. Predicted climatic changes were bounded so that they could not go beyond these values. To assess how much effect this had on the results, we implemented the regression equations with both the bounded and unbounded climate change scenarios. We compared the results using Welch’s t-test to see if bounding the scenarios had a significant effect (after first confirming that the samples were normally distributed).

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.

4.2.3.2 Century model

4.2.3.2.1 Model parameterisation

The Century model is an ecosystem analysis tool which models carbon (C) and N fluxes throughout the plant-soil system (Parton et al., 1987). We applied the model to six sites across Europe, listed in table 4.1. Further details on the choice of sites is given in Dellar et al. (2019b).

Table 4.1: *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 yield 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

The model was parameterised separately for each of the sites using Markov Chain Monte Carlo simulations (Dellar et al., 2019b). When compared with experimental data, the Century model generally estimated mean annual yield and N yield very well (predictions were usually within 10% of observations and were within 20% in all but one case), but often struggled to capture inter-annual variation. Errors were predominantly due to variation rather than bias. Generally the model performed best in the Atlantic region and less well for the Alpine and northern sites.

Since the Century model was proven to provide accurate estimates of mean annual yield and N yield at these sites, it was determined that it was it was suitable for use in estimating grassland response to climate change at these locations. In this analysis we focused on changes in annual means rather than variation, due to the limitations of the model.

The same climate change scenarios were applied as with the regression approach. This time we did not restrict the predicted changes, since the Century model is based on biological processes and can be used for prediction beyond the experimental conditions.

4.2.4 Results

4.2.4.1 Regression model

The regression model predictions for how yield and N yield will change under the two climate change scenarios are shown in figure 4.2 and table 4.2. Yields for permanent grasslands are expected to increase more than for temporary grasslands in the Atlantic and continental regions, though the opposite is true in the northern region. Yields will also increase in Alpine areas though will decrease in southern Europe. Changes are usually greater under the RCP8.5 scenario than the RCP4.5 scenario. For N yields, there are generally no significant changes. The only exceptions are increases for temporary grasslands in the continental and northern regions under the RCP8.5 scenario. Looking at table 4.2, it can be seen that for both yield and N yield, the impacts of different grassland types and different geographic regions are almost always greater than the impact of climate change.

Table 4.2: *Regression model predictions for grassland yield and N yield by 2071-2100 under the median climatic change expected for RCP4.5 and RCP8.5*

	Yield (t/ha/yr)			N yield (kg/ha/yr)		
	1971-2000	2071-2100		1971-2000	2071-2100	
		RCP4.5	RCP8.5		RCP4.5	RCP8.5
Temporary grasslands						
Atlantic	12.70	13.11	13.37	333.8	339.3	342.2
Continental	8.33	8.32	8.33	283.2	296.1	318.5
Northern	6.62	7.54	8.01	143.2	151.0	160.3
Southern	5.75	5.07	5.03			
Permanent grasslands						
Alpine	3.17	3.48	3.96			
Atlantic	7.63	8.07	8.35			
Continental	4.77	5.55	6.35	68.1	71.3	70.8
Northern	6.31	6.32	6.39			

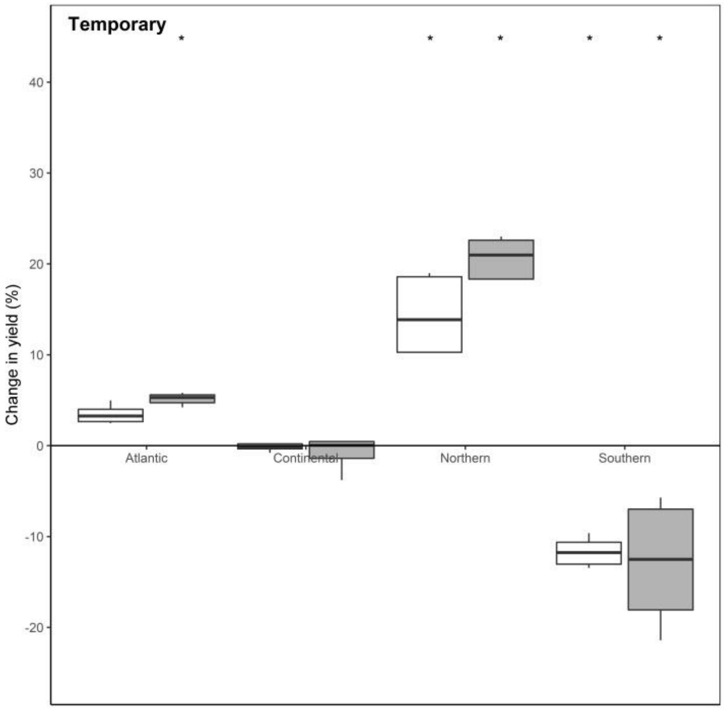
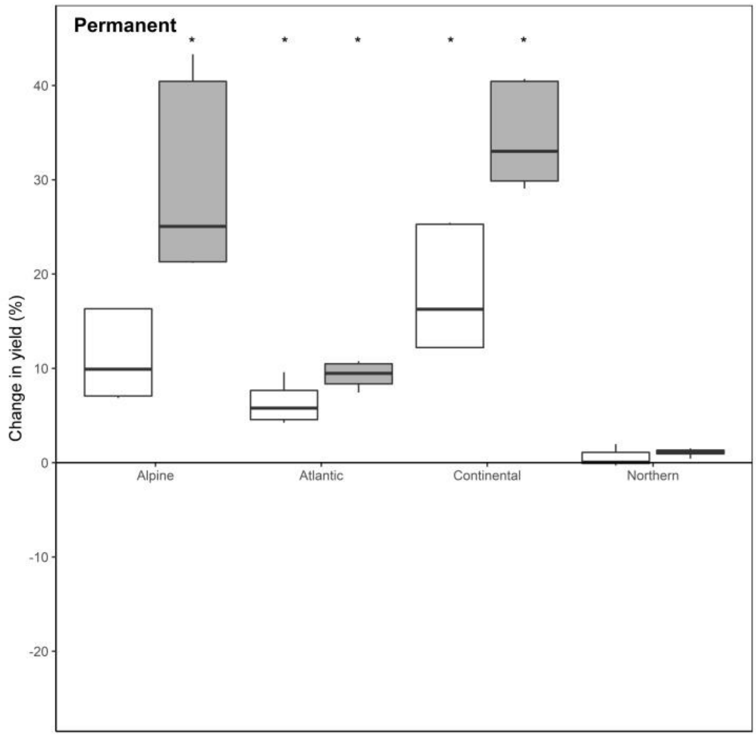


Figure 4.2: *Regression model predictions for percentage change in grassland yield and N yield by 2071-2100. White bars represent changes under the RCP4.5 scenario, while grey bars indicate changes under the RCP8.5 scenario. The bars represent the range under likely climate change (17th – 83rd percentile) while the whiskers show the range under the maximum and minimum climatic changes. The solid lines within each bar indicate the expected change under the median climatic change, asterisks indicate whether this change is significant ($p<0.05$). All changes are relative to the 1971 – 2000 baseline (continued on next page)*



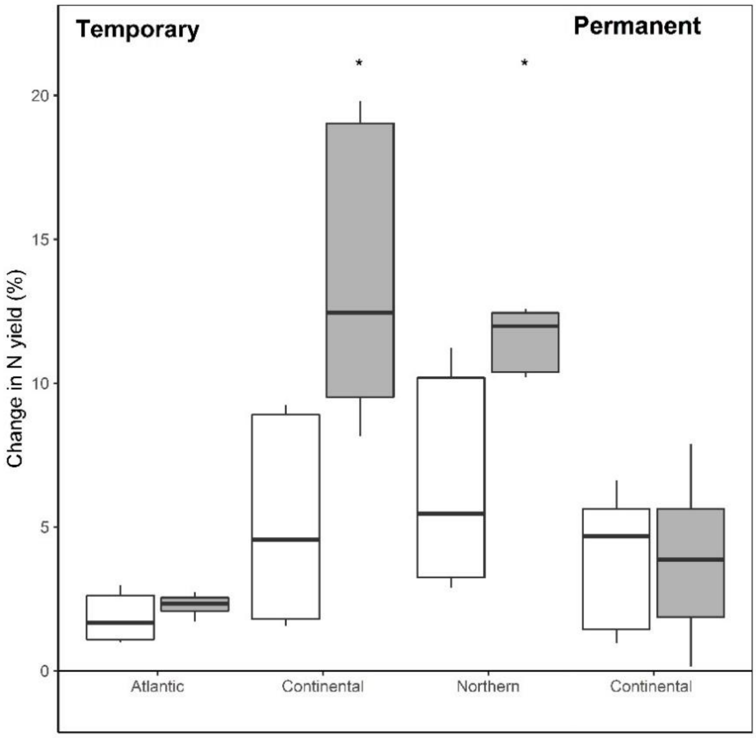


Figure 4.2 (continued): *Regression model predictions for percentage change in grassland yield and N yield by 2071-2100. White bars represent changes under the RCP4.5 scenario, while grey bars indicate changes under the RCP8.5 scenario. The bars represent the range under likely climate change (17th – 83rd percentile) while the whiskers show the range under the maximum and minimum climatic changes. The solid lines within each bar indicate the expected change under the median climatic change, asterisks indicate whether this change is significant ($p<0.05$). All changes are relative to the 1971 – 2000 baseline.*

Effect of bounding the climate change scenarios

The results above were generated using the bounded climate change scenarios. We also implemented the regression equations with the unbounded scenarios to see what effect the boundaries had. The results are shown in table 4.3. We found that for the RCP4.5 scenario, there was no significant effect on the results ($p<0.05$), except for yields of permanent grasslands in the Atlantic and northern regions under the maximum possible climatic changes, which were higher when climate change was unbounded. There were more significant differences under the RCP8.5 scenario. Here yield predictions with unbounded climate data were higher than with bounded data for permanent grasslands, but lower for temporary grasslands. For N yield, predictions were always higher with the unbounded dataset.

4.2.5 Century model

The climate change predictions from the parameterised Century models are shown in figure 4.3 and table 4.4. Predicted yields increase by a significant amount at all sites under both climate change scenarios and at all fertiliser treatment levels. Yield increases are greater under RCP8.5 than RCP4.5. For the Alpine, Atlantic and continental sites, the yield increased more under the no/low fertiliser treatment than the with/high fertiliser treatment. This trend was reversed in the southern region and fertiliser had no apparent effect on the change in yield for the northern region.

Most changes in N yield were not significant. Changes in the Alpine and Atlantic regions were particularly small. The greatest changes were in the continental and southern regions, where increases in plant N yield are predicted. Looking at table 4.4, it can be seen that for both yield and N yield, the impacts of different fertiliser levels and different geographic regions are much greater than the impact of climate change.

Table 4.3: *Significance of differences in predictions of grassland yield and N yield using bounded and unbounded climatic data. 'Minimum' and 'maximum' indicate the smallest and largest possible climatic changes while 'lower likely' and 'higher likely' indicate the 17th and 83rd percentiles of projected changes. 'ns', *, ** and *** indicate 'no significant difference' and significance with p<0.05, 0.01 and 0.001 respectively*

	Minimum		Lower likely		Median		Higher likely		Maximum	
	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5	RCP 4.5	RCP 8.5
Yield, permanent grasslands										
Alpine	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Atlantic	ns	ns	ns	ns	ns	**	ns	***	*	***
Continental	ns	ns	ns	ns	ns	ns	ns	ns	ns	*
Northern	ns	ns	ns	ns	ns	**	ns	***	*	***
Yield, temporary grasslands										
Atlantic	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Continental	ns	ns	ns	ns	ns	ns	ns	*	ns	*
Northern	ns	Ns	ns	ns	ns	ns	ns	*	ns	**
Southern	ns	**	ns	***	ns	***	ns	***	ns	***
N yield, permanent grasslands										
Continental	ns	ns	ns	ns	ns	ns	ns	*	ns	*
N yield, temporary grasslands										
Atlantic	ns	ns	ns	ns	ns	*	ns	**	ns	***
Continental	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
Northern	ns	ns	ns	ns	ns	ns	ns	**	ns	***

Table 4.4: *Century model predictions for grassland yield and N yield by 2071-2100 under the median climatic change expected for RCP4.5 and RCP8.5. Fertiliser treatments are the same as those specified in table 4.1*

	Yield (t/ha/yr)			N yield (kg/ha/yr)		
	1971-2000	2071-2100		1971-2000	2071-2100	
		RCP4.5	RCP8.5		RCP4.5	RCP8.5
No/low fertiliser						
Alpine	6.79	7.65	8.73	154.3	152.2	151.2
Atlantic temporary	0.75	0.88	1.07	14.9	14.9	14.7
Atlantic permanent	3.08	3.40	3.72	43.2	44.5	45.3
Continental	4.20	4.76	5.39	46.3	49.1	51.6
Northern	5.20	6.46	7.80	67.2	68.1	70.4
Southern	2.40	2.75	3.26	17.1	18.0	20.2
With/high fertiliser						
Alpine	12.25	13.42	14.57	368.2	365.9	350.9
Atlantic temporary	5.82	6.47	7.33	75.2	74.9	74.4
Atlantic permanent	5.89	6.38	6.51	155.0	156.7	157.3
Continental	6.75	7.36	8.00	118.0	124.8	129.8
Northern	5.88	7.30	8.80	103.1	110.5	111.8
Southern	5.70	6.59	8.00	51.5	53.6	53.0

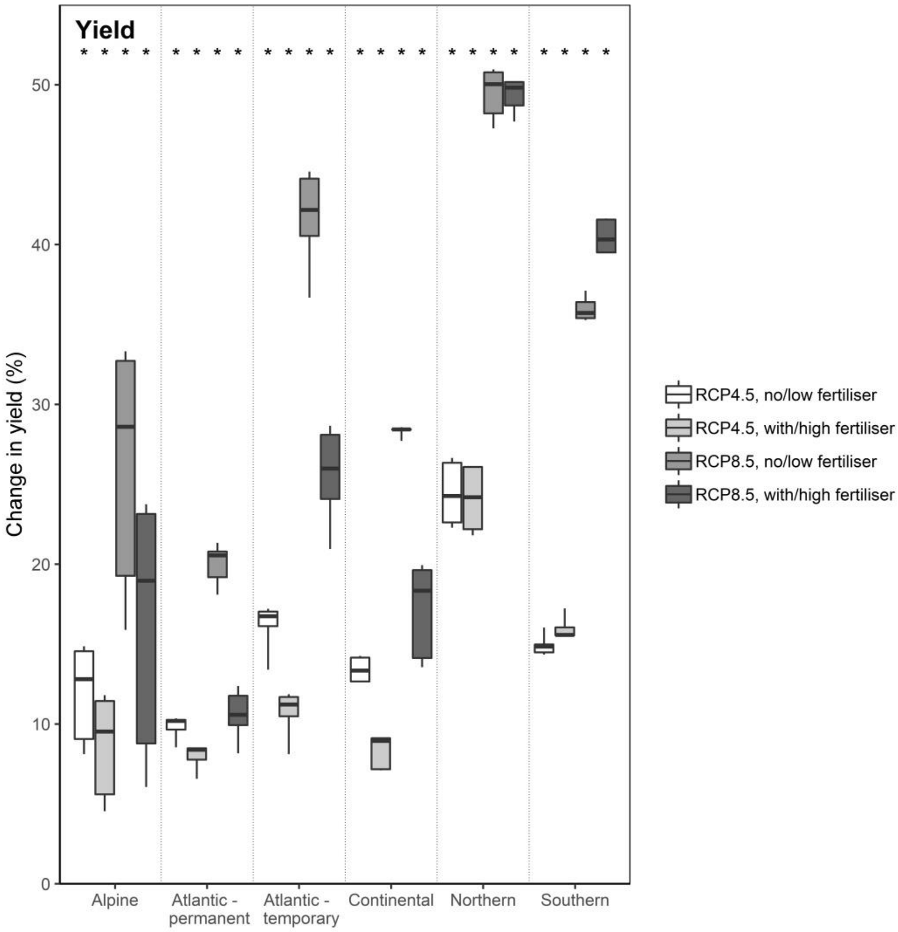


Figure 4.3: *Century model predictions for percentage change in grassland yield and N yield by 2071-2100. Fertiliser treatments are the same as those specified in table 4.1. The bars represent the range under likely climate change (17th – 83rd percentile) while the lines show the range under the maximum and minimum climatic changes. The solid lines within each bar indicate the expected change under the median climatic change, asterisks indicate whether this change is significant (p<0.05). Changes are relative to the 1971 – 2000 baseline (continued on following page)*

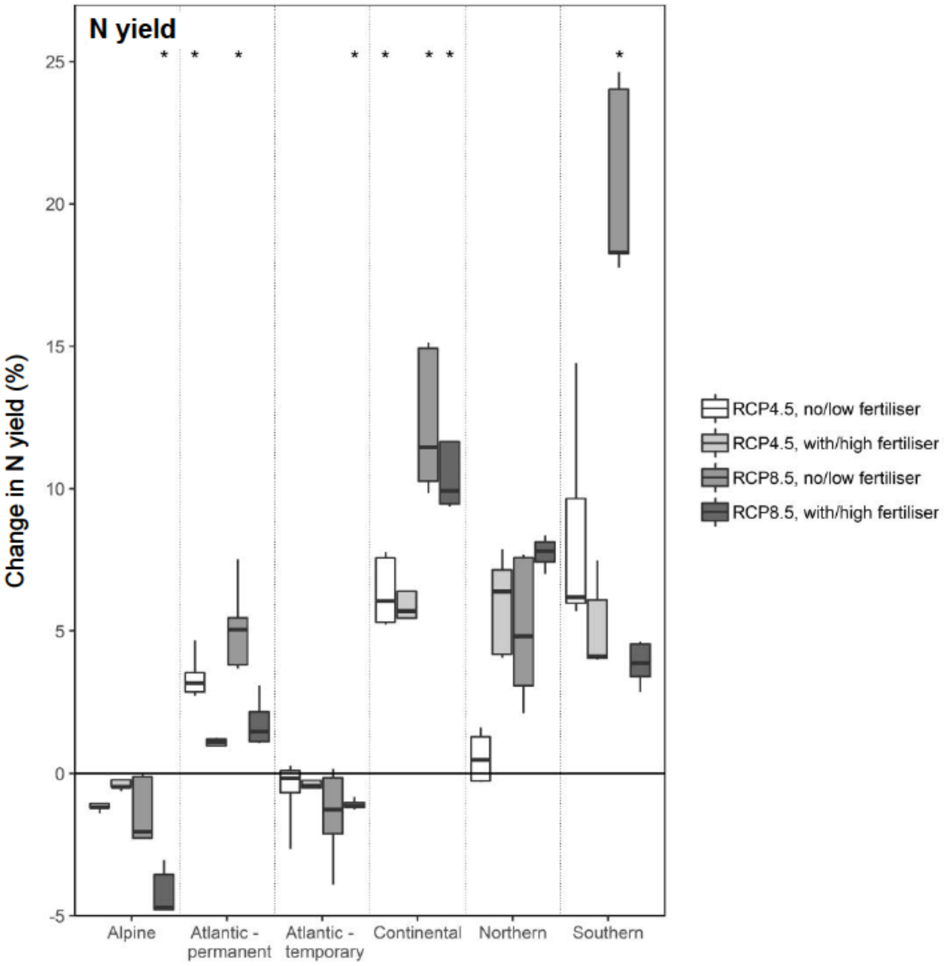


Figure 4.3 (continued): *Century model predictions for percentage change in grassland yield and N yield by 2071-2100. Fertiliser treatments are the same as those specified in table 4.1. The bars represent the range under likely climate change (17th – 83rd percentile) while the lines show the range under the maximum and minimum climatic changes. The solid lines within each bar indicate the expected change under the median climatic change, asterisks indicate whether this change is significant ($p<0.05$). Changes are relative to the 1971 – 2000 baseline.*

4.2.6 Discussion

This study set out to model the effects of climate change on grassland yield and N yield across Europe using both an empirical (regression analysis) and a dynamic approach. The results presented above address this objective.

4.2.6.1 Regression model

Grassland yield increases in most areas are to be expected, particularly in the Alpine and northern regions. These are areas where growth is limited due to the short growing seasons. Higher temperatures will lengthen the growing seasons and will therefore enable more growth. The decrease in yield in the southern region is also unsurprising. This area is already relatively hot and dry and is expected to become warmer and drier. The expected future decreases in plant growth in this region have been well documented (Del Prado et al., 2014; Rötter and Höhn, 2015). The Atlantic will experience relatively small changes in grassland yields, and is the region which is expected to experience the mildest climatic changes (Jacob et al., 2014). The continental region is predicted to experience large yield increases for permanent grasslands but no significant change for temporary grasslands. On the other hand, the northern region shows the opposite trend. There are various factors that could be involved here. Grasslands which receive high levels of fertiliser are in a good position to take advantage of improving climatic conditions, and the temporary grasslands in this study tended to receive more fertiliser than the permanent ones. On the other hand, multiple studies have shown that highly diverse pastures are better able to adapt to a changing climate than monocultures (Craine et al., 2012; Isbell et al., 2015; Wright et al., 2015). Permanent pastures tend to have considerably greater plant species diversity than temporary ones. For the continental region, it is also worth noting that it 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.

For N yield, most changes were not significant, the exceptions being the increases for temporary continental and northern grasslands under RCP8.5. These are surprising, especially since they do not match the predicted changes in yield. It has been found that warming and drought can affect the N allocation within plants in Mediterranean shrublands (Sardans et al., 2008) and it may be that this is having an effect here. They also found that warming could potentially increase soil extractable ammonium and nitrate, which would explain the trend of increasing plant N yield, since more N is available to plants. It should be noted that the predicted increases in N yield are almost always less than the increases in yield, indicating that plant N concentrations will decrease in the future.

Bounding the expected climatic changes had the effect that the climate change scenarios used for RCP8.5 were not as extreme as they will likely be in reality (for RCP4.5 it made little difference). The results therefore indicate expected trends in grassland yield and quality, rather than absolute predictions. This is particularly true for the southern region, where grassland yields with the unbounded climatic changes were always significantly lower than with the bounded version.

4.2.6.2 Century model

According to this model, yield is expected to increase significantly for all regions, fertiliser levels and climate change scenarios. The Century model accounts for increasing atmospheric CO_2 concentrations, increasing the rate of photo-synthesis (Metherell et al., 1993), which the regression model does not. The additional CO_2 has a fertilisation effect, causing plants to grow more, so the greater yield increases with the Century model are to be expected. It is particularly interesting that Century predicted increasing yields in the southern region. Several studies have predicted a reduction in plant yields for this region (Rötter and Höhn, 2015; Trnka et al., 2011), due to the increasingly detrimental climate. 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. Also, the southern European site to which Century was applied was in southern France, in one of the more northerly areas of the southern region. It may be that a site situated further south would not experience such high increases in yield.

For the Alpine, Atlantic and continental sites, the yield increased more under the no/low fertiliser treatment than the with/high fertiliser treatment. It may be that plants receiving little or no fertiliser have more potential for improvement and thus benefit more from improved growing conditions. Plants receiving fertiliser are closer to their maximum potential growth and so yields do not increase as much. On the other hand, this trend was reversed in the southern region. This is an area where the climate is predicted to worsen for plant life and these results suggest that fertiliser is necessary for plants to overcome the climatic changes and fully benefit from the potential yield increases offered by increasing atmospheric CO_2 concentrations.

As for the results with the regression model, most of the predicted changes in N yield were not statistically significant but tended towards increasing quantities of N. There are conflicting effects at play here within the Century model. As atmospheric CO_2 concentrations rise, the model increases plant N-use efficiency (Metherell et al., 1993), reducing N uptake from the soil. 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 greatest changes were in the continental and southern regions, areas which will experience the highest temperatures in future. This may be attributable to the changes in N allocation and availability under warming found by Sardans et al. (2008) and described above. Once again the increases in N yield were less than the changes in yield, indicating reduced plant N concentrations in future. This is consistent with multiple other studies which have found that elevated atmospheric CO_2 concentrations tends to decrease plant N concentrations (Dumont et al., 2015; Hopkins and Del Prado, 2007).

4.2.6.3 Model comparison

The two modelling approaches generally agreed with one another. Grassland yields will mostly increase, probably less so in the Atlantic region than in other areas, and it is possible that there will be slight decreases in southern Europe. Changes in N yield are usually not significant, though it may increase in warmer areas. Both approaches agreed that plant N concentration will be reduced. This agreement between contrasting methodologies enables us to have more confidence in our results. There are areas where the models do not agree, for example the yield of permanent northern and southern grasslands. Some disagreement is to be expected. The regression model does not account for increasing atmospheric CO_2 concentrations, meaning that it will tend to under-predict yields. It also uses bounded climate change scenarios, which had a significant effect in some cases. The scale of the two models is also a factor. The regression model applies to large geographic areas, while Century is applied to a single site. There will be considerable variability in the effects of climate change in regions of this size, due to differences in location, management practices, soil and other factors. It is not possible for the individual sites to which we applied Century to be representative of whole regions.

4.2.6.4 Management vs climate change

In looking at the results from both the Century and regression models (tables 4.2 and 4.4), it is clear that the impact of different fertiliser levels, grassland types and geographic regions on plant yield and N yield is 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.

4.2.6.5 Limitations

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. Furthermore, neither of the methodologies account for future changes in the grasslands themselves (for example through becoming more adapted to future climates or changing species compositions) (Parton et al., 1993). In addition, the regression analysis uses bounded climate change scenarios, does not account for changing atmospheric CO_2 concentrations and does not consider legacy effects from weather conditions in previous years (Petrie et al., 2018). On the other hand, the Century model was applied to just six sites due to data availability limitations, making it difficult to draw regional trends from the results. These limitations emphasise the value of using the two different modelling approaches together. While each method has its drawbacks, they complement one another and are able to make up for each other's potential shortcomings. The fact that they agree with one another about general trends suggests that they are performing well.

4.2.6.6 Implications for livestock farming

Most regions are likely to see grassland yields either increase or stay the same, which is good or at least 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 resilience, adaptability and efficiency. All areas will experience 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.

4.2.7 Acknowledgements

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4.3 Chapter conclusion

This chapter produced estimates of how European grassland yields and N yield are likely to be affected by climate change. The meta-analysis in chapter two achieved the same thing, but using a very different methodology as well as different input data (the meta-analysis used data from experiments where the climate was artificially altered, whereas this analysis was based on ambient weather conditions). Using different approaches means that a more complete picture can be achieved. In chapter seven, the results from the different methodologies will be compared to see if they agree with one another and to identify possible reasons for any disagreement.

While this chapter produced interesting results, it did have several limitations. In particular because it operates on a monthly time step it was not possible to account for the effects of extreme weather events. Extreme weather events are expected to become both more frequent and more intense in future and can potentially have major impacts on grasslands (see section 1.1.3.1). The following two chapters aim to address this issue by exploring ways of accounting for the effects of extreme weather events.

4.4 Appendix A: Coefficients of regression equations

This is provided in section 3.4.2.

CHAPTER 5 Statistical models for estimating the impacts of future extreme weather events on European grasslands

5.1 Chapter introduction

This chapter and the next aim to address one of the major limitations of the previous chapter, in that the models used did not account for the effects of extreme weather events. This chapter develops statistical models similar to those developed in chapter three, but investigates different ways of including terms which represent the prevalence of extreme weather events. Two future weather datasets are then applied to the models (one with weather extremes and one in which these are reduced) as a way of quantifying the effect of including extreme events. Using this type of statistical approach to model the effects of extreme weather events has not previously been performed in any field. This paper provides a new methodology for quickly estimating the effects of such events over a large spatial scale.

This research has been submitted to *Global Change Biology* and the manuscript is included below. Martha Dellar is the lead author on this paper. She assembled the experimental data, determined the statistical methodology, conducted the analysis and wrote the paper. David Holmes formally defined the concept of '*right kurtosis*' (kurtosis of values in a distribution which lie above the median) and proposed this as a possible way of representing high temperature events. This was ultimately not used, but provided valuable insights into how best to represent the prevalence of extreme weather events. Other authors advised on the methodology and provided feedback on the paper.

5.2 Modelling the impacts of future extreme weather events on European grasslands

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5.2.1 Abstract

As the climate changes, extreme weather events such as droughts, heatwaves and heavy rainfall will become both more frequent and more intense. These events can have a major effect on grasslands, and therefore on grassland-based livestock systems. We developed models using multiple regression analysis to predict grassland yield and nitrogen (N) yield, accounting for temperature and precipitation extremes. We used data from seventy-four grassland experiments across Europe, distinguishing between four climatic regions. The fit of the models was generally good, with the model for N yield from temporary grasslands performing best and that for yield of permanent grasslands having the least good fit. Permanent grasslands were more sensitive to uncertainties in the model inputs than temporary ones. Uncertainty associated with precipitation measurements was almost always the largest contributor to total uncertainty, and was particularly dominant for N yield. We input future weather data to the models, based on the A1B climate change scenario and generated using a regional climate model. We also generated a smoothed version of this weather dataset using weighted moving averages, i.e. with reduced extreme events. Comparing the model outputs using both the original weather data and the smoothed data showed that smoothing the data increased the predicted yields by 4.0% and 13.8% for temporary and permanent grasslands respectively and increased predicted N yields by 10.4%. This demonstrates that extreme weather events lead to reduced grassland yields and N yields. In general, the yield of

temporary grasslands decreased over time, while for permanent grasslands it increased. There was little change in N yield over time, except in northern Europe where it increased by around 19%. In future, farmers would benefit from increasing the resilience of their grasslands to extreme weather events, perhaps through making more use of multi-species swards or through switching to more resilient plant species.

5.2.2 Introduction

As the climate changes, extreme weather events are expected to become both more frequent and more intense. In Europe, under a midrange climate change scenario (Representative Concentration Pathway (RCP) 4.5 (Collins et al., 2013)), heavy rainfall events will increase by up to 25% by 2071-2100 (compared with 1971-2000). Summer heatwaves are not expected to increase much under this midrange scenario, but under an extreme scenario (RCP8.5) there will be two to nine more events per year. Droughts will become longer, increasing by up to 24 and 32 days under the midrange and extreme scenarios respectively (Kovats et al., 2014).

Such events can have a major effect on grasslands, and thus on grass-based livestock systems. The 2003 summer heatwave led to a 60% green fodder deficit in France (FAO, 2016) and heavy rainfall in 2014 led to forage losses of 30% and a quarter of pastures requiring full cultivation and replacement in some regions of the UK (ADAS, 2014). In Europe, grass accounts for approximately 40% of livestock feed intake (by dry matter, Lesschen et al., 2014). If livestock farmers are to adequately prepare to meet the challenge of climate change, it is important that we understand how grasslands will be affected by extreme weather events.

While understanding the effects of extreme weather events is clearly very important, grassland models often do not account for them. This may be because they use weather data which have been smoothed to remove the extremes or, in a few cases, because they run on a monthly time-step, making it difficult to include short-term weather events (Abdalla et al., 2010; Dellar et al., 2019a; Graux et al., 2013; Hall et al., 1995). Wilcox et al. (2017) performed a meta-analysis to look at the effects of extreme rainfall and drought on grasslands, using experiments where water availability was artificially manipulated. They found that above-ground net primary productivity was more sensitive to increased precipitation than decreased precipitation. Also, the MODEXTREME project (Bellocchi et al., 2014) worked to improve process-based modelling techniques to accurately predict the effects of extreme climatic events on crops. While they have looked at the effects on some specific crops, these do not yet include grasslands. Similarly, process-based models have been used to investigate how the yields of wheat at sites in the UK and France (Semenov and Porter, 1995) and maize in the Czech Republic (Dubrovský et al., 2000) respond to changes in climatic variability. It was found that increasing the prevalence of extreme weather events led to lower crop yields and that changes to climatic variability could have a greater effect on yields than changes to mean temperature or precipitation. Process-based models are usually applied at a specific site and, while they can provide very detailed and accurate predictions for that location, they are less useful for determining how crops will generally be affected over a large geographical area. There is a need for a model which can predict the effects of both temperature and precipitation extremes and which can be quickly applied over a large spatial scale. This will enable researchers to determine the effects of extreme weather events on grasslands and the likely consequences for livestock farming.

The present study will develop statistical models using regression on locational, meteorological and managerial variables. These will be used to analyse the effects of extreme weather events on the yield and nitrogen (N) yield of grasslands across Europe. Nitrogen is an indicator of protein content and is helpful in determining the nutritional quality of grass for livestock. Similar models have been developed and used to estimate climate change effects on grasslands (Dellar et al., 2019a, 2019b), however these did not account for extreme weather events. This study will also make comparisons with those results to see how much difference is made by including extreme weather events.

5.2.3 Methods

5.2.3.1 Data

Data were assembled from grassland experiments across Europe, taken from published literature and through contacting experts in the field. In total, seventy-four experimental sites were used, with all experiments lasting a minimum of three years. The full list of sites is given in the supplementary material. These sites were divided by geographical region (based on local climatic zones (Kovats et al., 2014)) and into temporary and permanent grasslands. Temporary grasslands are defined as those which have been used as grassland for less than five years. They are usually part of a crop rotation and tend to be mono-cultures or to have a very small number of plant species present. Permanent grasslands have been used as grassland for more than five years and tend to have a highly diverse range of plant species. Figure 5.1 shows the site locations, regions and grassland types.

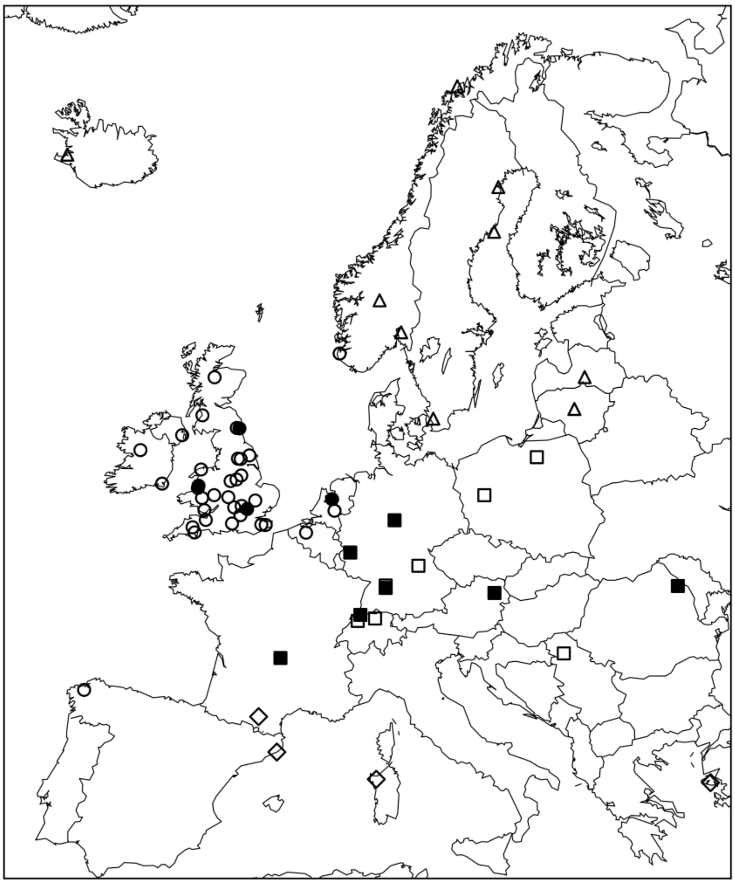

Figure 5.1: *Locations of sites used, by geographic region and grassland type. Regions are Atlantic (●), Continental (■), Northern (▲) and Southern (◆). Open shapes denote temporary grasslands, while solid shapes denote permanent grasslands*

For each experimental site, weather data were either collected as part of the experiment, or was taken from the nearest weather station, provided this was within 50km of the site (89% were within 20km). Weather station data were taken from the EUSTACE/ECA&D dataset (Squintu et al., 2019), as well as the national meteorological services of the UK (Met Office, 2019), Germany (DWD, 2019), Sweden (SMHI, 2019), the Netherlands (KNMI, 2019) and Latvia (LVĢMC, 2019).

For some regions and grassland types there were insufficient data available to conduct an analysis. Due to the difficulties of accessing reliable weather data for a specific location, no mountainous sites were included. Also, either weather data could not be found or there were insufficient experiments looking at yield for permanent grasslands in northern or southern Europe, or for N yield for permanent grasslands or for N yield for reseeded grasslands in southern Europe.

Data from each experimental site were edited so that all those for a given region and grassland type contributed approximately the same number of data points; this was to ensure that no single site dominated the analysis. Three quarters of the data from each site were used for model development, with the remaining quarter kept for validation.

5.2.3.2 Model development

We considered several possible predictor variables to include in the regression models to account for the prevalence of extreme events. These are listed in table 5.1.

We tried different combinations of extreme event variables, avoiding combinations of variables which were very highly correlated to avoid issues of multicollinearity, though we found that some correlation between variables was inevitable. We also tried different monthly groupings, as we did not have enough data to support listing all months individually with all their separate extreme events terms. No more than three months were grouped together at a time. Quadratic terms were included, as were interaction terms. We ran linear regression on all these possible combinations. This was done separately for the yield of permanent grasslands, the yield of temporary grasslands and the N yield from temporary grasslands. The regression equations producing the best fit (determined using the adjusted R-squared value) were identified and were applied to the validation datasets.

The models were validated using the remaining quarter of the experimental data. The root mean squared error (RMSE) and correlation between predicted and observed yields and N yields were calculated and the RMSEs were divided into bias and variance terms. All analysis was performed using R (R Core Team, 2017).

5.2.3.3 Sensitivity analysis

The sensitivity analysis methodology was based on that used by Fitton et al. (2014) and Gottschalk et al. (2007). Uncertainties in model inputs can affect the accuracy of predictions; we investigated how the models responded to small variations in certain inputs. We chose those inputs which are most prone to uncertainty, possibly due to measurement errors or, in the case of weather data, because the nearest weather station is often located away from the experimental site. The inputs varied are listed in table 5.2, along with their uncertainty ranges.

Table 5.1: *Possible predictor variables for accounting for extreme weather events*

Temperature variables	Precipitation variables
Mean/Minimum/Maximum monthly temperature *(TMean / TMin / TMax)*	Total monthly precipitation *(PTotal)*
Variance of mean/maximum monthly temperatures $(TVar_{mean} / TVar_{max})$	Number of days in a month with precipitation greater than 10mm $(PDays_{>10})$
Skewness of mean monthly temperatures $(TSkew_{mean})$	Greatest number of consecutive days in a month with precipitation less than 1mm *(PDryspell)*
Kurtosis of mean/maximum monthly temperatures $(TKurtosis_{mean} / TKurtosis_{Max})$	Variance of monthly rainfall *(PVar)*
Variance of mean/maximum monthly temperatures above the median $(TRight\_var_{mean} / TRight\_var_{max})$	
Kurtosis of mean/maximum monthly temperatures above the median $(TRight\_kurtosis_{mean} / TRight\_kurtosis_{max})$	
Number of days in a month with minimum temperature below 0°C $(TDays_{<0})$	
Number of days in a month with maximum temperature above 25°C/30°C $(TDays_{>25} / TDays_{>30})$	

Table 5.2: *Parameters tested as part of the sensitivity analysis and corresponding uncertainly ranges*

Parameter	Uncertainty range
Precipitation	±1mm per day
Temperature	±1°C
Legume percentage	±25%

For each site and year of the experiment, we determined the total uncertainty in the model and calculated what percentage of this was attributable to uncertainties in each parameter. To do this, we freely varied all parameters simultaneously within their uncertainty ranges, running the model multiple times until the standard deviation of the results (σ_g) converged (approximately 10,000 runs). For reasons of computational efficiency, the parameter values for each model run were determined using Latin hypercube sampling. This process was then repeated three times, keeping one of the parameters at its original value while allowing the other two to vary. This enabled us to calculate the standard deviation of the results when parameter *i* is held constant (σ_i,). The σ_g and σ_i values were averaged across the years in each site, and then averaged again across the sites in each region. These averaged values were used to calculate the contribution index for each parameter *i* using the following formula:

$$c_i = \frac{\sigma_g - \sigma_i}{\sum_{j=1}^{3}(\sigma_g - \sigma_j)} \times 100$$

The higher the c_i, the greater the contribution of that parameter to the total uncertainty.

5.2.3.4 Climate change and extreme weather events

We used the daily future climate dataset produced by the REMO model (GERICS, 2019) under the A1B climate change scenario (rapid economic growth with a balanced approach to fossil-fuel vs sustainable energy sources (Nakicenovic et al., 2000)). This has not been smoothed and thus includes expected extreme weather events. From this dataset we reduced the variance using weighted moving averages to generate a new dataset with fewer and less intense extremes. For temperature we used a 5-day moving average with weighting [0.1,0.2,0.4,0.2,0.1] and for precipitation we used a 3-day moving average with weighting [0.1,0.8,0.1]. These weightings achieved an overall reduction in variance of around 25%, which was chosen to match the reduction in variance used by Beer et al. (2014) when they made a similar reduced-variance dataset. Beer et al. used a different methodology for reducing the variance, based on Taylor approximations. We chose not to use this methodology because while reducing the overall variance, it actually increases the variance amongst datapoints close to the mean. Also, it appears to involve Taylor expanding a function at a point where it is not differentiable. While numerically the formula given seems to produce reasonable results, this makes us unsure how robust the performance is. Using weighted moving averages does not have these drawbacks and also preserves monthly mean values.

We looked at three time periods: 2010 – 2030, 2045 – 2065 and 2080 – 2100. For each experimental site, we ran the regression models for each year in each time period for each of our datasets (‘with extremes’ and smoothed), using the average values for fertiliser, legume percentage and harvests per year for that site. We averaged the results over each time period and then used REML to determine the relative impacts of dataset, region and time period, using the interaction of region and experimental site as a random effect. The interaction between region and time period was included in the fixed effects (preliminary testing showed that the interactions with dataset were not significant). For temporary grasslands, yield and N yield predictions were squared to meet the normality assumption for REML. The Bonferroni multiple comparison test was used to establish the significance of the results and the REML was performed using Genstat (VSNi, 2013). By comparing the effects of the two datasets, we could determine the impact of extreme weather events. All references to statistical significance relate to $p<0.05$.

5.2.4 Results

5.2.4.1 Models

The combinations of predictor variables producing the best model fit are shown in table 5.3; interestingly, all include higher statistical moments. These also performed well when tested against the separate validation dataset.

Table 5.3: *Combinations of predictor variables producing the best model fit*

Model	Predictor variables
Yield, temporary grasslands	TMean, $TVar_{mean}$, $TSkew_{mean}$, $TKurtosis_{mean}$, PTotal, PDryspell, Pvar
Yield, permanent grasslands	TMean, $TRight\_var_{max}$, $TRight\_kurtosis_{max}$, PTotal, PDryspell, Pvar
N yield, temporary grasslands	TMean, $TVar_{mean}$, $TSkew_{mean}$, $TKurtosis_{mean}$, PTotal, PDryspell, Pvar

However, when the future climate datasets were applied to the models, the results produced were nonsensical. Further testing showed that focussing on more tangible measures rather than purely statistical ones was more effective. With this in mind, the final regression equations are as follows:

Yield, temporary grasslands:

Yield(t DM/ha) = *f*(Region, Alt, Cuts, LP, $Tmean^{JF,MA,MJ,JA}$, $TDays_{<0}^{JF,MA}$, $TDays_{>30}^{MJ,JA}$, $PDays_{>10}^{JF,MA,MJ,JA}$, $PDryspell^{JF,MA,MJ,JA}$, Alt^2, $Cuts^2$, LP^2, $Tmean^2$, $TDays_{<0}^{2}$, $TDays_{>30}^{2}$, $PDays_{>10}^{2}$, $PDryspell^2$, NF*(Cuts, LP, Tmean, $TDays_{<0}$, $TDays_{>30}$, $PDays_{>10}$, PDryspell))

Applicable to the Atlantic, continental, northern and southern regions

Yield, permanent grasslands:

Yield (t DM/ha) = *g*(Region, Alt, Cuts, $Tmean^{JF,MA,MJ,JA}$, $TDays_{<0}^{JF,MA}$, $TDays_{>25}^{MJ,JA}$, $PTotal^{JF,MA,MJ,JA}$, $PDryspell^{JF,MA,MJ,JA}$, Alt^2, $Cuts^2$, $Tmean^2$, $TDays_{<0}^{2}$, $TDays_{>25}^{2}$, $PTotal^2$, $PDryspell^2$, NF*(Cuts, Tmean, $TDays_{<0}$, $TDays_{>25}$, PTotal, PDryspell))

Applicable to the Atlantic and continental regions

N yield, temporary grasslands:

N yield (kg/ha) = h(Region, Alt, Cuts, LP, $Tmean^{JF,MA,MJ,JA}$, $TDays_{<0}^{JF,MA}$, $TDays_{>25}^{MJ,JA}$, $PTotal^{JF,MA,MJ,JA}$, $PDryspell^{JF,MA,MJ,JA}$, Alt^2, $Cuts^2$, LP^2, $Tmean^2$, $TDays_{<0}^{\ 2}$, $TDays_{>25}^2$, $PTotal^2$, $PDryspell^2$, NF*(Cuts, LP, Tmean, $TDays_{<0}$, $TDays_{>25}$, PTotal, PDryspell))

Applicable to the Atlantic, continental and northern regions

f, *g* and *h* are linear functions. Superscript letters indicate the monthly groupings, for example 'JF' is January and February. 'Alt' is altitude (m), 'Cuts' indicates the number of harvests per year, 'LP' is the percentage of nitrogen-fixing plants at seeding (e.g. 5% would be taken as 5.0), 'NF' is the amount of nitrogen fertiliser used per year (kg N/ha). Coefficients for both these equations and those in table 5.3 are provided in the supplementary materials.

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

5.2.4.2 Model fit

The goodness-of-fit of the regression equations is evaluated in table 5.4. R^2 values were calculated during model development and are based on the training dataset. Correlation and RMSEs were calculated on the validation dataset. The fit was generally good, with high correlations. The RMSEs are relatively high, though are due entirely to variation rather than bias. The equation for N yield had better fit than those for yield, having higher R^2 values and correlations and a lower RMSE. The model for the yield of temporary grasslands has slightly better fit than that for permanent grasslands.

5.2.4.3 Sensitivity analysis

The sensitivity analysis results for the regression model are shown in table 5.5. The level of uncertainty (σ_g) was fairly similar between regions, though the continental region tended to have greater uncertainty than the others. Permanent grasslands exhibited slightly more uncertainty than temporary ones, despite the fact that fewer parameters were varied. Uncertainty associated with precipitation measurements was almost always the largest contributor to total uncertainty and was particularly dominant for N yield. Uncertainty associated with legume percentage was always very small (<7%).

Table 5.4: *Goodness-of-fit of regression equations*

	Grassland type	R^2	Correlation	Root mean squared error as a percentage of mean observed value *(percentage of which is due to bias)*
Yield	Permanent	0.59	0.72	43.0 *(0.3)*
	Temporary	0.66	0.79	32.1 *(1.1)*
N yield	Temporary	0.84	0.92	25.2 *(0.0)*

Table 5.5: *Standard deviation of the total uncertainty (σ_g, units are t DM/ha for yield and kg/ha for N yield) 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*

Grassland type	Region	σ_g	c_{Temp} *(%)*	c_{Prec} *(%)*	c_{Leg} *(%)*
Yield					
Temporary	Atlantic	0.53	37.1	61.5	1.3
	Continental	0.88	48.7	49.3	2.0
	Northern	0.59	18.3	75.4	6.3
	Southern	0.87	72.7	24.5	2.8
Permanent	Atlantic	1.12	25.3	74.7	*NA*
	Continental	1.22	26.8	73.2	*NA*
N yield					
Temporary	Atlantic	38.4	5.8	93.8	0.3
	Continental	86.1	4.6	94.5	0.9
	Northern	29.0	5.7	90.3	4.0

5.2.4.4 Impact of climate change and extreme weather events

The results of the REML to determine the effects of geographic region, time period and choice of weather data ('with extremes' or smoothed) are shown in table 5.6 and figures 5.2 and 5.3. All factors were highly significant ($p<0.02$), though for the yield of permanent grasslands, region was only significant when interacted with time period. The Atlantic region was predicted to have the highest yields and N yields, though it should be noted that the experiments based in this region had the highest levels of fertiliser use. Looking at grassland yield changes over time for each region, most changes were not statistically significant but there were some clear trends. Later time periods usually led to lower yields of temporary grasslands, most notably for the continental (-25.3% for 2080-2100 compared with 2010-2030) and southern (-24.7%) regions. The yields of permanent grasslands increased over time across all regions (Atlantic: +13.0%; continental: +26.0%). The N yield of temporary grasslands mostly experienced little change, though for the northern region there was a noticeable increase (+17.4%). For all models, the REML showed that including weather extremes led to significantly lower yields and N yields. Using the smoothed weather data increased the predicted yields by 4.0% and 13.8% for temporary and permanent grasslands respectively and increased predicted N yields by 10.4%. Uncertainty was smallest for the Atlantic region and greatest for the southern region; this is due to the availability of experimental data for developing the models.

Table 5.6: *Predicted means and* sed *from the REML on the effects of region, time period and choice of weather dataset (with extremes or smoothed) on grassland yield and N yield*

	Interaction term	Region: Atlantic	Region: Continental	Region: Northern	Region: Southern	Time period: 2010-2030	Time period: 2045-2065	Time period: 2080-2100	Dataset: With extremes	Dataset: Smoothed
Yield, Permanent grasslands – t/ha										
Mean		8.06	7.93	*NA*	*NA*	7.25^{a}	8.09^{b}	8.65^{c}	7.48	8.51
sed/p-value			*1.63/0.938*				*0.16/<0.001*		*0.12/<0.001*	
Mean	Atlantic					7.44^{ab}	8.34^{abcd}	8.41^{abcd}		
	Continental					7.05^{a}	7.85^{bc}	8.89^{bd}		
sed/p-value							*1.07/0.006*			
Yield, Temporary grasslands (transformed)										
Mean		125.63^{a}	75.00^{b}	52.93^{b}	41.72^{b}	83.40^{a}	74.72^{b}	63.34^{c}	70.90	76.75
sed/p-value			*19.64/<0.001*				*2.15/<0.001*		*1.18/<0.001*	
Mean	Atlantic					136.25^{g}	121.42^{bfgh}	119.23^{bfgh}		
	Continental					96.36^{abceg}	74.81^{abcef}	53.84^{abcd}		
	Northern					51.33^{abc}	55.32^{abcde}	52.15^{abc}		
	Southern					49.67^{ab}	47.34^{ab}	28.16^{a}		
sed/p-value							*17.03/<0.001*			

		Region				Time period			Dataset	
	Interaction term	Atlantic	Continental	Northern	Southern	2010-2030	2045-2065	2080-2100	With extremes	Smoothed
Yield, Temporary grasslands (back transformed) – t/ha										
Mean		11.21	8.66	7.28	6.46	9.13	8.64	7.96	8.42	8.76
Mean	Atlantic					11.67	11.02	10.92		
	Continental					9.82	8.65	7.34		
	Northern					7.16	7.44	7.22		
	Southern					7.05	6.88	5.31		
N yield, Temporary grasslands (transformed)										
Mean		131240^{a}	76502^{b}	19323^{c}	*NA*	72354^{a}	79841^{b}	74870^{a}	68201	83176
sed/p-value			*10357/<0.001*				*1848/<0.001*		*1214/<0.001*	
Mean	Atlantic					127967^{d}	133351^{d}	132402^{d}		
	Continental					73070^{bc}	86302^{c}	70136^{b}		
	Northern					16025^{a}	19871^{a}	22073^{a}		
sed/p-value							*8765/0.013*			
N yield, Temporary grasslands (back transformed) – kg/ha										
Mean		362.3	276.6	139.0	*NA*	269.0	282.6	273.6	261.2	288.4
Mean	Atlantic					357.7	365.2	363.9		
	Continental					270.3	293.8	264.8		
	Northern					126.6	141.0	148.6		

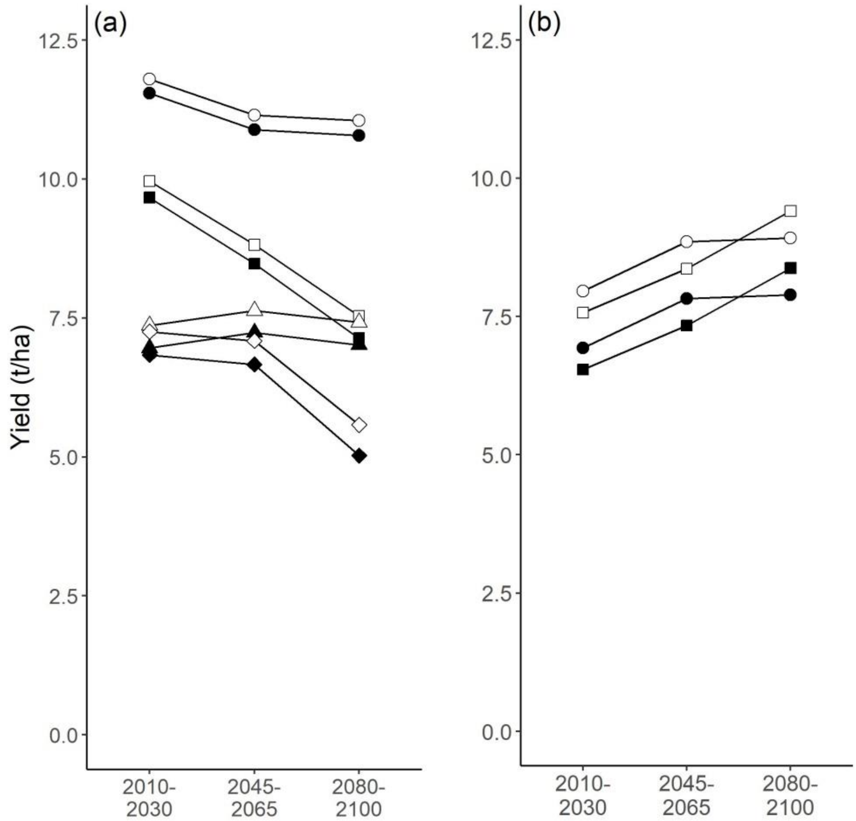

Figure 5.2: *Predicted mean yields of (a) temporary and (b) permanent grasslands. Regions are Atlantic (●), Continental (■), Northern (▲) and Southern (◆).Solid shapes indicate that the 'with extremes' dataset was used, while open shapes indicate that the smoothed dataset was used*

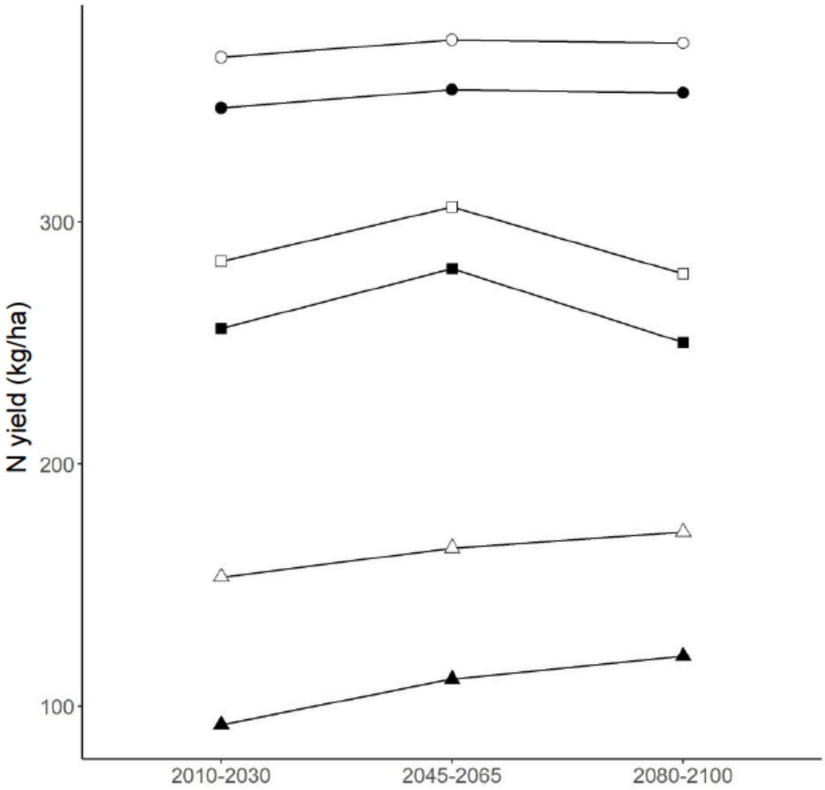

Figure 5.3: *Predicted mean N yields of (a) temporary and (b) permanent grasslands. Regions are Atlantic (●), Continental (■) and Northern (▲). Solid shapes indicate that the 'with extremes' dataset was used, while open shapes indicate that the smoothed dataset was used*

5.2.5 Discussion

5.2.5.1 Model selection and fit

The best model fit was achieved by including higher statistical moments, though these failed when applying future climate change scenarios. Including terms such as variance, skewness and kurtosis of temperatures means that the general shape of the temperature distribution is very well represented in the model, much more so than by using terms such as 'number of days with temperature greater than 30°'. However, the results of applying this model to future climate change were not biologically plausible. This should not be surprising, as the general shape of the distribution under climate change is rather far from the range exhibited by our data. We are therefore extrapolating to these new distribution shapes using parameters (such as the kurtosis) which have no biological basis, and so there is no good reason to expect that they will give good predictions of yield and N yield under these new distributions. On the other hand, measures such as 'number of days with temperature greater than 30°', while not capturing the shape of the distribution as well, do a much better job of capturing features actually relevant to plant growth. When we then use these for extrapolation to new temperature distributions under climate change, it is much more reasonable to expect that they will produce meaningful predictions.

The final models had a good fit, although the RMSEs were relatively high, especially for permanent grasslands. There was a great deal of variation between all the experiments which accounts for the high RMSEs. Permanent grasslands in particular tend to be more diverse than temporary grasslands with a wider range of plant species; they will therefore tend to have a higher degree of variability and be less predictable. The high correlations between observations and predictions and the negligible bias in the models indicate that these equations have the capacity to be useful predictive tools.

5.2.5.2 Sensitivity analysis

The continental region exhibited a higher level of uncertainty than the other regions. This is likely because this region is very large and encompasses a huge amount of variation. Similarly, permanent grasslands showed more uncertainty than temporary ones, and are also more varied.

Model predictions were generally more sensitive to uncertainties in precipitation than in temperature, particularly for N yield. Plant N uptake is known to be highly dependent on water availability (Abreu et al., 1993; Cregger et al., 2014), with both extremely wet and extremely dry conditions reducing uptake. Dellar et al. (2019a) performed a similar analysis but without any consideration of extreme weather events and they found the same thing, though the emphasis on precipitation was considerably more pronounced in their study. Including terms in the equations representing weather extremes has had a significant effect on the distribution of model uncertainty and it suggests that temperature extremes are an important consideration when conducting this type of analysis.

It is important to note that the methodology for conducting the sensitivity analysis affects different model parameters in different ways. Varying precipitation by 1mm a day means that total precipitation over a two month period can vary by up to 60mm; however varying temperature by 1° a day will only ever vary the mean temperature over a two month period by the same amount. All the extreme events terms used (e.g. number of days with temperature above 25°) have the same cumulative response to the sensitivity analysis as total precipitation, which is likely a contributing factor to this analysis having more balance in the distribution of uncertainty between temperature and precipitation, while the analysis of Dellar et al. (2019a) without any extreme events terms was so heavily skewed towards precipitation.

5.2.5.3 Impact of climate change and extreme weather events

While very few of the regional changes in yield and N yield over time were statistically significant, they nevertheless indicated clear trends. There were generally high levels of uncertainty around the results, more so in regions in which fewer experiments were used. If more experimental data were to become available, it seems likely that these results would display significant changes. For the Atlantic region, a lot of data were available and uncertainty was quite small, but there was also relatively little expected change in this region, which is why no significant changes were predicted. For the southern region, large changes were predicted, but there were only four experimental sites from which to draw data which meant that the confidence intervals were also very large.

The expected drop in temporary grassland yields for southern Europe has been well documented (Del Prado et al., 2014; Rötter and Höhn, 2015) and can be attributed to high temperatures, reduced rainfall and shorter growing seasons. Conversely, longer growing seasons will lead to a slight increase in northern European yields. For permanent grasslands, yields tend to increase over time. This is likely because permanent grasslands usually have a higher level of species richness, which has been found to increase resilience to climatic changes (Craine et al., 2012; Isbell et al., 2015; Wright et al., 2015). Changes in N yield over time were relatively small, with the greatest change being the increase in the northern region, which is consistent with previous findings (Dellar et al., 2019a). Plant N yield may increase due to changes in N allocation or to increases in soil extractable ammonium and nitrate, both of which have been found to be possible consequences of higher air temperatures (Sardans et al., 2008).

Using the smoothed weather dataset always led to higher predicted yields and N yields compared with the dataset including weather extremes. This clearly demonstrates that the increasing weather variability which is expected in the future will be detrimental to grasslands. This is likely because including the extremes means there is a higher probability of days where conditions are unfavourable for plant growth, such as being too hot, cold, wet or dry. This matches previous findings relating to wheat (Semenov and Porter, 1995) and maize (Dubrovský et al., 2000).

The expected changes in yield and N yield are more pessimistic than those found in Dellar et al. (2019b), which developed similar models but made no allowance for extreme weather events. That analysis used different climate change scenarios (RCP4.5 and 8.5) so is not directly comparable, however the A1B scenario used in this study falls between those two in terms of expected CO_2 emissions (Jubb and Dix, 2016). This emphasises how important it is to consider the impacts of extreme weather events. The smoothed dataset produced higher yield predictions than that including extreme events, but the analysis which did not account for extreme events at all (only considering monthly mean temperature and total monthly rainfall) produced very different results.

5.2.5.4 Limitations

There are other factors which it was not possible to account for in this study but which would benefit from further research. In particular, the effect of rising atmospheric CO_2 concentrations will tend to increase plant yields, but it is not known how this will be affected by weather extremes. It is also expected that there will be changes in grassland composition, particularly for permanent grasslands, as certain species will be more or less suited to the future climate, which will affect grassland yield and nutritional quality. This study also only considers relationships between weather and plant yield / N yield in a given year, however extreme climatic events may have an influence lasting multiple years (Jenkinson et al., 1994). Despite these drawbacks, this research nevertheless provides an overview of expected changes to grassland yield and N yield in the coming decades and emphasises the importance of accounting for the effects of extreme weather events.

5.2.5.5 Consequences for livestock

Reductions in the yield of temporary grasslands will have negative consequences for grass-based livestock systems and may result in increasing demand for bought-in feed. This will predominantly affect intensive farming systems. Extensive systems using permanent pastures will benefit from increased grassland yields, at least in the Atlantic and continental regions. The expected increase in the frequency and intensity of extreme weather events will reduce both the quantity and quality of grasslands. Farmers will need to explore options for making grasslands more resilient to such events, such as using multi-species swards, irrigating grasslands and switching to more resilient plant species.

5.2.6 Acknowledgements

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We would also like to thank Dr Matthias Kuhnert of the University of Aberdeen for provision of the REMO dataset.

5.3 Chapter conclusion

This chapter developed effective models for estimating the future yield and N yield of European grasslands, accounting for extreme weather events. The models provided valuable estimates for how grasslands will change in the future as well as demonstrating the importance of considering the effects of weather extremes. This research also introduced a novel methodology for modelling the impacts of such events.

The main limitation of this research is that the models are applied to a climatic situation different to that under which the models were developed. This means there is a risk of extrapolation errors. It was found that judicious choice of terms within the models could minimise this risk, however this does not discount the risk entirely. The models also do not account for the effects of increasing atmospheric CO_2 concentrations, which are likely to have a positive effect on grassland productivity (see section 1.2.2.1). In the next chapter, an alternative approach for modelling the effects of extreme weather events in considered. This is a process-based model (DailyDayCent) and does not have either of these drawbacks.

5.4 Supplementary materials

5.4.1 Supplementary material 1: Sites used for regression modelling

Table 5.7: Sites used for regression modelling

Dataset / Location	Climatic region	Data available	Source
Permanent grasslands			
Rothamsted, England	Atlantic	AGDW	*Private communication*
Cockle Park, England	Atlantic	AGDW	Kidd et al. (2017)
Lelystad, the Netherlands	Atlantic	AGDW	Schils and Snijders (2004)
Aberystwyth, Wales	Atlantic	AGDW	Williams et al. (2003)
Vienna, Austria	Continental	AGDW	Karrer (2011)
Auvergne, France	Continental	AGDW	Klumpp et al. (2011)
Göttingen, Germany	Continental	AGDW, N	*Private communication*
Stuttgart, Germany	Continental	AGDW	Thumm and Tonn (2010)
Eifel Mountains, Germany	Continental	AGDW	Schellberg et al. (1999)
Eifel Mountains, Germany	Continental	AGDW	Hejcman et al. (2010)
Iasi County, Romania	Continental	AGDW	Samuil et al. (2009)
North-western Switzerland	Continental	AGDW	Niklaus et al. (2001)
Temporary grasslands			
The Agrodiversity Experiment, 24 sites used	Atlantic, Continental, Northern, Southern	AGDW, N	Kirwan et al. (2014)
BIODEPTH, 4 sites used	Continental, Northern, Southern	AGDW	Hector et al. (1999)

Dataset / Location	Climatic region	Data available	Source
FAO sub-network for lowland grasslands, 10 sites used	Atlantic	AGDW	*Private communication*
GM20, 21 sites across England and Wales	Atlantic	AGDW, N	Morrison et al. (1980)
Novi Sad, Serbia	Continental	AGDW, N	Ćupina et al. (2017)
Tomaszkowo, Poland	Continental	N	Bałuch-Małecka and Olszewska (2007)
Central Latvia	Northern	AGDW	Rancane et al. (2016)

5.4.2 Supplementary material 2: Final regression equation coefficients

Table 5.8: *Final regression equation coefficients for the yield of temporary grasslands*

	Yield of temporary grasslands	
	Estimate	SE
(Intercept)	-12.26236	5.4235
Region: Continental	-1.20969	0.6456
Region: Northern	-1.58122	0.6253
Region: Southern	0.92556	1.0930
Alt	-0.00478	0.0038
NF	0.00855	0.0115
LP	0.16180	0.0321
Cuts	3.32486	0.4434
$Tmean^{JF}$	-0.23316	0.1414
$Tmean^{MA}$	0.44960	0.1747
$Tmean^{MJ}$	0.29757	0.5415
$Tmean^{JA}$	0.78790	0.7937
$TDays_{<0}{}^{JF}$	0.01304	0.0689
$TDays_{<0}{}^{MA}$	-0.02159	0.0602
$TDays_{>30}{}^{MJ}$	-0.09974	0.1610
$TDays_{>30}{}^{JA}$	0.26908	0.0710
$PDays_{>10}{}^{JF}$	0.41820	0.1163
$PDays_{>10}{}^{MA}$	-0.29556	0.1603
$PDays_{>10}{}^{MJ}$	0.03253	0.1383
$PDays_{>10}{}^{JA}$	0.54092	0.1293
$PDryspell^{JF}$	0.03394	0.0489
$PDryspell^{MA}$	-0.19441	0.0784
$PDryspell^{MJ}$	-0.22430	0.0692
$PDryspell^{JA}$	-0.10311	0.0461
Alt^2	0.00001	0.000008
NF^2	-0.00003	0.000002
LP^2	-0.00225	0.0008
$Cuts^2$	-0.33432	0.0522
$(Tmean^{JF})^2$	-0.02756	0.0115
$(Tmean^{MA})^2$	0.03402	0.0160
$(Tmean^{MJ})^2$	-0.00977	0.0209
$(Tmean^{JA})^2$	-0.02746	0.0244
$(TDays_{<0}{}^{JF})^2$	0.00088	0.0008
$(TDays_{<0}{}^{MA})^2$	0.00150	0.0010
$(TDays_{>30}{}^{MJ})^2$	-0.01148	0.0051
$(TDays_{>30}{}^{JA})^2$	0.00022	0.0013
$(PDays_{>10}{}^{JF})^2$	-0.01336	0.0082
$(PDays_{>10}{}^{MA})^2$	-0.00467	0.0150
$(PDays_{>10}{}^{MJ})^2$	-0.01181	0.0129
$(PDays_{>10}{}^{JA})^2$	-0.03153	0.0095

	Yield of temporary grasslands	
	Estimate	SE
$(PDryspell^{JF})^2$	-0.00135	0.0007
$(PDryspell^{MA})^2$	0.00792	0.0028
$(PDryspell^{MJ})^2$	0.00224	0.0022
$(PDryspell^{JA})^2$	0.00003	0.0007
NF*LP	-0.00004	0.0002
NF*Cuts	0.00108	0.0008
NF*$Tmean^{JF}$	0.00036	0.0007
NF*$Tmean^{MA}$	-0.00080	0.0009
NF*$Tmean^{MJ}$	-0.00086	0.0006
NF*$Tmean^{JA}$	0.00165	0.0007
NF*$TDays_{<0}{}^{JF}$	0.00005	0.0001
NF*$TDays_{<0}{}^{MA}$	-0.00015	0.0001
NF*$TDays_{>30}{}^{MJ}$	0.00370	0.0008
NF*$TDays_{>30}{}^{JA}$	-0.00308	0.0004
NF*$PDays_{>10}{}^{JF}$	0.00007	0.0002
NF*$PDays_{>10}{}^{MA}$	0.00055	0.0004
NF*$PDays_{>10}{}^{MJ}$	-0.00006	0.0003
NF*$PDays_{>10}{}^{JA}$	0.00030	0.0002
NF*$PDryspell^{JF}$	-0.00007	0.0002
NF*$PDryspell^{MA}$	-0.00003	0.0001
NF*$PDryspell^{MJ}$	0.00049	0.0001
NF*$PDryspell^{JA}$	0.00016	0.0001

Table 5.9: *Final regression equation coefficients for the yield of permanent grasslands and the N yield of temporary grasslands*

	Yield of permanent grasslands		*N yield of temporary grasslands*	
	Estimate	SE	Estimate	SE
(Intercept)	17.82355	22.7847	-458.03261	337.4461
Region: Continental	5.87550	1.2277	-78.13442	25.4747
Region: Northern	NA	NA	-124.94562	30.1257
Alt	-0.01639	0.0046	0.01878	0.1229
NF	0.14723	0.0684	-0.07610	0.4008
LP	NA	NA	4.39905	0.9650
Cuts	2.97569	0.5699	85.72372	26.0512
$Tmean^{JF}$	1.79162	0.4148	5.78800	6.8017
$Tmean^{MA}$	1.65746	1.3689	11.49529	6.3942
$Tmean^{MJ}$	-8.26483	1.7330	21.73156	35.4199
$Tmean^{JA}$	3.22714	2.8440	25.45962	46.2628
$TDays_{<0}{}^{JF}$	-0.28414	0.1180	0.73315	2.2535
$TDays_{<0}{}^{MA}$	-0.35312	0.1349	-4.73131	2.2085
$TDays_{>25}{}^{MJ}$	0.19261	0.1195	-0.51614	2.3947

	Yield of permanent grasslands		*N yield of temporary grasslands*	
	Estimate	SE	Estimate	SE
$TDays_{>25}^{JA}$	-0.26832	0.1046	-1.72397	2.4353
$PTotal^{JF}$	0.00696	0.0099	0.08022	0.2079
$PTotal^{MA}$	-0.00457	0.0165	0.34184	0.2962
$PTotal^{MJ}$	0.03402	0.0201	0.48142	0.4263
$PTotal^{JA}$	0.04246	0.0222	1.69221	0.3556
$PDryspell^{JF}$	0.14038	0.1490	-14.81159	3.8061
$PDryspell^{MA}$	0.14416	0.1897	3.94979	3.6740
$PDryspell^{MJ}$	-0.04059	0.3210	-4.89121	2.6158
$PDryspell^{JA}$	-0.23977	0.1780	-5.92568	3.8464
Alt^2	0.00001	0.000005	0.00030	0.0003
NF^2	-0.00004	0.00002	-0.00048	0.0001
LP^2	NA	NA	-0.02575	0.0261
$Cuts^2$	-0.32666	0.0751	-13.10991	2.6237
$(Tmean^{JF})^2$	-0.19626	0.0403	0.03508	0.5396
$(Tmean^{MA})^2$	-0.19058	0.0957	-0.06536	0.5612
$(Tmean^{MJ})^2$	0.29756	0.0661	-0.19648	1.4821
$(Tmean^{JA})^2$	-0.06655	0.0854	-1.29361	1.6083
$(TDays_{<0}^{JF})^2$	0.00727	0.0022	0.02789	0.0295
$(TDays_{<0}^{MA})^2$	0.00586	0.0041	0.10084	0.0346
$(TDays_{>25}^{MJ})^2$	-0.00821	0.0032	-0.21756	0.0791
$(TDays_{>25}^{JA})^2$	0.00204	0.0020	0.13233	0.0537
$(PTotal^{JF})^2$	0.000002	0.00002	-0.00010	0.0007
$(PTotal^{MA})^2$	0.00005	0.0001	-0.00092	0.0008
$(PTotal^{MJ})^2$	-0.00007	0.0001	-0.00089	0.0014
$(PTotal^{JA})^2$	-0.00013	0.0001	-0.00394	0.0011
$(PDryspell^{JF})^2$	-0.00478	0.0051	0.59042	0.1466
$(PDryspell^{MA})^2$	-0.00518	0.0076	-0.04759	0.1345
$(PDryspell^{MJ})^2$	-0.00483	0.0141	0.13450	0.0859
$(PDryspell^{JA})^2$	0.00974	0.0074	0.28819	0.1261
NF*LP	NA	NA	-0.00347	0.0046
NF*Cuts	-0.00060	0.0015	0.21889	0.0341
$NF*Tmean^{JF}$	-0.00627	0.0026	-0.00802	0.0256
$NF*Tmean^{MA}$	0.00315	0.0043	-0.07843	0.0237
$NF*Tmean^{MJ}$	-0.00035	0.0035	-0.04157	0.0197
$NF*Tmean^{JA}$	-0.00596	0.0036	0.04131	0.0274
$NF*TDays_{<0}^{JF}$	-0.00150	0.0005	0.00026	0.0041
$NF*TDays_{<0}^{MA}$	0.00079	0.0006	-0.00932	0.0037
$NF*TDays_{>30}^{MJ}$	-0.00052	0.0006	0.00658	0.0064
$NF*TDays_{>30}^{JA}$	0.00107	0.0005	0.00510	0.0058
$NF*PTotal^{JF}$	-0.00006	0.00005	0.00006	0.0003
$NF*PTotal^{MA}$	-0.00003	0.0001	-0.00016	0.0004
$NF*PTotal^{MJ}$	0.00001	0.00005	0.00034	0.0004
$NF*PTotal^{JA}$	0.00003	0.0001	0.00060	0.0003
$NF*PDryspell^{JF}$	-0.00078	0.0005	-0.00271	0.0044

	Yield of permanent grasslands		*N yield of temporary grasslands*	
	Estimate	SE	Estimate	SE
NF*PDryspell^{MA}	0.00006	0.0006	-0.00992	0.0037
NF*PDryspell^{MJ}	0.00081	0.0006	0.00123	0.0031
NF*PDryspell^{JA}	0.00042	0.0006	-0.00449	0.0034

5.4.3 Supplementary material 3: Preliminary regression equation coefficients and model fit

Table 5.10: *Goodness-of-fit of preliminary regression equations provided in table 5.3*

	Grassland type	R^2	Correlation	Root mean squared error as a percentage of mean observed value *(percentage of which is due to bias)*
Yield	Permanent	0.64	0.73	46.4 *(2.4)*
	Temporary	0.73	0.81	31.0 *(3.3)*
N yield	Temporary	0.87	0.93	23.0 *(0.1)*

Table 5.11: *Preliminary regression equation coefficients for the yield of temporary grasslands for the equation provided in table 5.3*

	Yield of temporary grasslands	
	Estimate	SE
(Intercept)	-21.57685	5.62038
Region: Continental	-2.05813	0.67309
Region: Northern	-0.74208	0.58663
Region: Southern	-5.32782	1.08696
Alt	0.00547	0.00416
NF	0.03000	0.01063
LP	0.10857	0.02945
Cuts	1.88822	0.46027
$TMean^{JF}$	-0.36238	0.11063
$TMean^{MA}$	0.27286	0.14287
$TMean^{MJ}$	1.30124	0.65270
$TMean^{JA}$	-1.06452	0.80205
$TVar^{JF}$	-0.02683	0.05358
$TVar^{MA}$	0.11223	0.04477
$TVar^{MJ}$	0.09001	0.10920
$TVar^{JA}$	0.41453	0.20638
$TSkew^{JF}$	3.99639	0.52807
$TSkew^{MA}$	-0.18227	0.46694
$TSkew^{MJ}$	-0.27697	0.40125
$TSkew^{JA}$	-1.82733	0.52956
$TKurtosis^{JF}$	-0.88076	0.39124
$TKurtosis^{MA}$	2.41697	1.06756
$TKurtosis^{MJ}$	10.20702	2.32975

	Yield of temporary grasslands	
	Estimate	SE
(Intercept)	-21.57685	5.62038
$TKurtosis^{JA}$	-0.36989	0.94637
$PTotal^{JF}$	-0.00491	0.00922
$PTotal^{MA}$	0.02537	0.01091
$PTotal^{MJ}$	0.04790	0.01157
$PTotal^{JA}$	-0.02036	0.01070
$PDryspell^{JF}$	-0.17750	0.05307
$PDryspell^{MA}$	-0.01233	0.08801
$PDryspell^{MJ}$	-0.02526	0.06659
$PDryspell^{JA}$	0.00604	0.04959
$PVar^{JF}$	0.03589	0.03574
$PVar^{MA}$	-0.03179	0.03503
$PVar^{MJ}$	-0.10266	0.02473
$PVar^{JA}$	0.00015	0.01894
Alt^2	-0.00001	0.00001
NF^2	-0.00003	0.000002
LP^2	-0.00110	0.00069
$Cuts^2$	-0.20406	0.05292
$(TMean^{JF})^2$	0.02434	0.00956
$(TMean^{MA})^2$	0.01314	0.01411
$(TMean^{MJ})^2$	-0.02922	0.02471
$(TMean^{JA})^2$	0.02485	0.02457
$(TVar^{JF})^2$	-0.00201	0.00083
$(TVar^{MA})^2$	-0.00163	0.00064
$(TVar^{MJ})^2$	-0.00060	0.00331
$(TVar^{JA})^2$	-0.00680	0.01067
$(TSkew^{JF})^2$	2.32469	0.62919
$(TSkew^{MA})^2$	0.91842	0.50128
$(TSkew^{MJ})^2$	1.68023	0.63678
$(TSkew^{JA})^2$	1.31894	0.66582
$(TKurtosis^{JF})^2$	-0.00095	0.05225
$(TKurtosis^{MA})^2$	-0.31259	0.16182
$(TKurtosis^{MJ})^2$	-1.55587	0.41946
$(TKurtosis^{JA})^2$	0.03103	0.14537
$(PTotal^{JF})^2$	-0.00001	0.00002
$(PTotal^{MA})^2$	-0.00010	0.00003
$(PTotal^{MJ})^2$	-0.00007	0.00003
$(PTotal^{JA})^2$	0.00008	0.00002
$(PDryspell^{JF})^2$	0.00014	0.00063
$(PDryspell^{MA})^2$	0.00408	0.00292
$(PDryspell^{MJ})^2$	-0.00165	0.00178
$(PDryspell^{JA})^2$	-0.00190	0.00075
$(PVar^{JF})^2$	-0.00011	0.00022
$(PVar^{MA})^2$	0.00034	0.00049

	Yield of temporary grasslands	
	Estimate	SE
(Intercept)	-21.57685	5.62038
$(PVar^{MJ})^2$	0.00050	0.00009
$(PVar^{JA})^2$	-0.00038	0.00014
NF*LP	0.00012	0.00017
NF*Cuts	0.00207	0.00091
$NF*TMean^{JF}$	0.00028	0.00063
$NF*TMean^{MA}$	0.00139	0.00090
$NF*TMean^{MJ}$	-0.00340	0.00070
$NF*TMean^{JA}$	0.00149	0.00089
$NF*TVar^{JF}$	0.00022	0.00017
$NF*TVar^{MA}$	0.00037	0.00016
$NF*TVar^{MJ}$	0.00033	0.00021
$NF*TVar^{JA}$	-0.00064	0.00045
$NF*TSkew^{JF}$	-0.00411	0.00181
$NF*TSkew^{MA}$	0.00036	0.00183
$NF*TSkew^{MJ}$	0.00096	0.00168
$NF*TSkew^{JA}$	0.00640	0.00174
$NF*TKurtosis^{JF}$	0.00032	0.00065
$NF*TKurtosis^{MA}$	-0.00213	0.00100
$NF*TKurtosis^{MJ}$	-0.00463	0.00127
$NF*TKurtosis^{JA}$	0.00013	0.00114
$NF*PTotal^{JF}$	0.00006	0.00002
$NF*PTotal^{MA}$	-0.00006	0.00002
$NF*PTotal^{MJ}$	-0.00002	0.00002
$NF*PTotal^{JA}$	0.00003	0.00002
$NF*PDryspell^{JF}$	0.00032	0.00018
$NF*PDryspell^{MA}$	-0.00058	0.00015
$NF*PDryspell^{MJ}$	0.00033	0.00011
$NF*PDryspell^{JA}$	0.00014	0.00013
$NF*PVar^{JF}$	-0.00013	0.00011
$NF*PVar^{MA}$	0.00026	0.00007
$NF*PVar^{MJ}$	0.00004	0.00005
$NF*PVar^{JA}$	0.00006	0.00004

Table 5.12: *Preliminary regression equation coefficients for the yield of permanent grasslands for the equation provided in table 5.3*

	Yield of permanent grasslands	
	Estimate	SE
(Intercept)	35.76093	13.20308
Region: Continental	6.60176	1.29338
Alt	-0.01298	0.00466
NF	0.06921	0.03274

	Yield of permanent grasslands	
	Estimate	SE
Cuts	3.16443	0.66741
$TMean^{JFM}$	1.10967	0.35368
$TMean^{AM}$	-1.36668	1.45517
$TMean^{JJA}$	-2.75588	1.92429
$TRight\_var_{max}^{JFM}$	-0.69282	0.16664
$TRight\_var_{max}^{AM}$	-0.01410	0.17849
$TRight\_var_{max}^{JJA}$	-0.02070	0.37360
$TRight\_kurtosis_{max}^{JFM}$	1.58959	0.70150
$TRight\_kurtosis_{max}^{AM}$	-0.75521	0.71870
$TRight\_kurtosis_{max}^{JJA}$	0.35259	0.60965
$PTotal^{JF}$	-0.07649	0.02107
$PTotal^{MA}$	-0.01770	0.02483
$PTotal^{MJ}$	0.04779	0.02491
$PTotal^{JA}$	-0.01846	0.03377
$PDryspell^{JF}$	0.14597	0.14898
$PDryspell^{MA}$	0.19248	0.22219
$PDryspell^{MJ}$	-0.02084	0.33867
$PDryspell^{JA}$	-0.30766	0.19658
$PVar^{JF}$	0.19346	0.06312
$PVar^{MA}$	0.00744	0.08457
$PVar^{MJ}$	-0.08459	0.05407
$PVar^{JA}$	0.06250	0.06532
Alt^2	0.000004	0.000004
NF^2	-0.00004	0.00002
$Cuts^2$	-0.33534	0.08203
$(TMean^{JFM})^2$	-0.15268	0.05078
$(TMean^{AM})^2$	0.05172	0.06414
$(TMean^{JJA})^2$	0.08361	0.05336
$(TRight\_var_{max}^{JFM})^2$	0.01383	0.00373
$(TRight\_var_{max}^{AM})^2$	0.00324	0.00498
$(TRight\_var_{max}^{JJA})^2$	-0.01447	0.01562
$(TRight\_kurtosis_{max}^{JFM})^2$	-0.15746	0.11655
$(TRight\_kurtosis_{max}^{AM})^2$	0.15559	0.12551
$(TRight\_kurtosis_{max}^{JJA})^2$	-0.04908	0.08786
$(PTotal^{JF})^2$	0.00019	0.00006
$(PTotal^{MA})^2$	0.00010	0.00008
$(PTotal^{MJ})^2$	-0.00007	0.00008
$(PTotal^{JA})^2$	0.00003	0.00010
$(PDryspell^{JF})^2$	-0.01111	0.00452
$(PDryspell^{MA})^2$	-0.00451	0.00898
$(PDryspell^{MJ})^2$	-0.00622	0.01488
$(PDryspell^{JA})^2$	0.01119	0.00817
$(PVar^{JF})^2$	-0.00210	0.00066
$(PVar^{MA})^2$	-0.00058	0.00127

	Yield of permanent grasslands	
	Estimate	SE
$(PVar^{MJ})^2$	0.00058	0.00047
$(PVar^{JA})^2$	-0.00055	0.00058
NF*Cuts	-0.00333	0.00175
$NF*TMean^{JFM}$	0.00089	0.00206
$NF*TMean^{AM}$	-0.00228	0.00264
$NF*TMean^{JJA}$	-0.00381	0.00269
$NF*TRight\_var_{max}^{JFM}$	0.00010	0.00074
$NF*TRight\_var_{max}^{AM}$	0.00056	0.00046
$NF*TRight\_var_{max}^{JJA}$	0.00353	0.00083
$NF*TRight\_kurtosis_{max}^{JFM}$	-0.00153	0.00278
$NF*TRight\_kurtosis_{max}^{AM}$	-0.00253	0.00282
$NF*TRight\_kurtosis_{max}^{JJA}$	-0.00122	0.00201
$NF*PTotal^{JF}$	0.00003	0.00009
$NF*PTotal^{MA}$	-0.00020	0.00009
$NF*PTotal^{MJ}$	-0.00001	0.00007
$NF*PTotal^{JA}$	0.00029	0.00011
$NF*PDryspell^{JF}$	-0.00009	0.00049
$NF*PDryspell^{MA}$	-0.00083	0.00064
$NF*PDryspell^{MJ}$	-0.00007	0.00069
$NF*PDryspell^{JA}$	0.00094	0.00066
$NF*PVar^{JF}$	-0.00028	0.00036
$NF*PVar^{MA}$	0.00098	0.00039
$NF*PVar^{MJ}$	0.00015	0.00016
$NF*PVar^{JA}$	-0.00052	0.00028

Table 5.13: *Preliminary regression equation coefficients for the N yield of temporary grasslands for the equation provided in table 5.3*

	N yield of temporary grasslands	
	Estimate	SE
(Intercept)	-215.72594	343.96671
Region: Continental	-23.21807	29.64827
Region: Northern	-127.90480	42.87199
Alt	0.00560	0.12121
NF	-1.25262	0.33762
LP	4.58439	0.88044
Cuts	40.13928	27.66813
$TMean^{JF}$	-8.08194	6.26824
$TMean^{MA}$	-3.65029	6.34489
$TMean^{MJ}$	92.60793	30.22060
$TMean^{JA}$	-106.21161	41.79621
$TVar^{JF}$	-1.93325	3.62492
$TVar^{MA}$	-4.13644	2.44076

	N yield of temporary grasslands	
	Estimate	SE
$TVar^{MJ}$	-10.97962	4.81849
$TVar^{JA}$	-7.64494	9.59748
$TSkew^{JF}$	23.95213	19.07489
$TSkew^{MA}$	5.63479	25.65953
$TSkew^{MJ}$	56.06257	15.51979
$TSkew^{JA}$	-47.09427	21.97598
$TKurtosis^{JF}$	-52.34719	15.13852
$TKurtosis^{MA}$	287.89346	55.15409
$TKurtosis^{MJ}$	21.93104	85.35796
$TKurtosis^{JA}$	115.12199	49.40388
$PTotal^{JF}$	1.13427	0.40904
$PTotal^{MAM}$	0.55563	0.42449
$PTotal^{JJA}$	1.13917	0.47671
$PDryspell^{JF}$	2.31712	4.42771
$PDryspell^{MAM}$	4.74338	4.87151
$PDryspell^{JJA}$	-6.24072	4.46910
$PVar^{JF}$	-5.07437	2.12165
$PVar^{MAM}$	1.80240	1.70271
$PVar^{JJA}$	-1.11341	1.00214
Alt^2	0.00019	0.00027
NF^2	-0.00051	0.00005
LP^2	-0.02257	0.02466
$Cuts^2$	-8.40533	2.80226
$(TMean^{JF})^2$	0.11182	0.44579
$(TMean^{MA})^2$	1.09282	0.67366
$(TMean^{MJ})^2$	-3.76792	1.15588
$(TMean^{JA})^2$	3.63264	1.34519
$(TVar^{JF})^2$	-0.04996	0.05790
$(TVar^{MA})^2$	0.05595	0.03221
$(TVar^{MJ})^2$	0.30336	0.14037
$(TVar^{JA})^2$	0.56227	0.56883
$(TSkew^{JF})^2$	22.93111	22.05974
$(TSkew^{MA})^2$	10.33624	28.51462
$(TSkew^{MJ})^2$	14.06962	31.77121
$(TSkew^{JA})^2$	34.15646	29.73102
$(TKurtosis^{JF})^2$	3.37572	1.74046
$(TKurtosis^{MA})^2$	-46.73203	8.55535
$(TKurtosis^{MJ})^2$	-4.78579	15.42178
$(TKurtosis^{JA})^2$	-18.19996	7.50898
$(PTotal^{JF})^2$	-0.00394	0.00110
$(PTotal^{MAM})^2$	-0.00167	0.00091
$(PTotal^{JJA})^2$	-0.00126	0.00095
$(PDryspell^{JF})^2$	-0.01053	0.16968
$(PDryspell^{MAM})^2$	-0.13137	0.16249

	N yield of temporary grasslands	
	Estimate	SE
$(PDryspell^{JJA})^2$	0.18583	0.12423
$(PVar^{JF})^2$	0.11905	0.03543
$(PVar^{MAM})^2$	-0.00324	0.01425
$(PVar^{JJA})^2$	-0.00076	0.00803
NF*LP	-0.00578	0.00440
NF*Cuts	0.21043	0.03723
$NF*TMean^{JF}$	0.01835	0.02075
$NF*TMean^{MA}$	-0.05313	0.02258
$NF*TMean^{MJ}$	-0.02422	0.01681
$NF*TMean^{JA}$	0.06585	0.02593
$NF*TVar^{JF}$	0.05183	0.00895
$NF*TVar^{MA}$	-0.02123	0.00605
$NF*TVar^{MJ}$	0.01491	0.00670
$NF*TVar^{JA}$	-0.00437	0.01738
$NF*TSkew^{JF}$	-0.02771	0.04719
$NF*TSkew^{MA}$	-0.01978	0.05173
$NF*TSkew^{MJ}$	-0.10336	0.04935
$NF*TSkew^{JA}$	0.08481	0.04585
$NF*TKurtosis^{JF}$	0.01125	0.01738
$NF*TKurtosis^{MA}$	0.04897	0.02761
$NF*TKurtosis^{MJ}$	-0.04295	0.03316
$NF*TKurtosis^{JA}$	-0.01093	0.02917
$NF*PTotal^{JF}$	-0.00022	0.00058
$NF*PTotal^{MAM}$	0.00118	0.00052
$NF*PTotal^{JJA}$	0.00047	0.00044
$NF*PDryspell^{JF}$	-0.02872	0.00532
$NF*PDryspell^{MAM}$	-0.02007	0.00395
$NF*PDryspell^{JJA}$	0.00124	0.00258
$NF*PVar^{JF}$	0.00621	0.00352
$NF*PVar^{MAM}$	-0.00406	0.00271
$NF*PVar^{JJA}$	-0.00089	0.00129

CHAPTER 6 Modelling the effects of extreme weather events on the yield and N yield of European grasslands using the DailyDayCent model

6.1 Introduction

Extreme weather events, such as heatwaves, droughts and heavy rainfall, are projected to become both more severe and more frequent in the future (Kovats et al., 2014). These are events that can have major impacts on plant life (as described in section 1.1.3.1) and it is important to understand what their effects will be. Under a midrange climate change scenario (Representative Concentration Pathway (RCP) 4.5) (Collins et al., 2013), heavy precipitation events will increase by up to 25% across most of Europe by 2071-2100 (compared with 1971-2000), with the most extreme events occurring in winter. There will be little increase in the number of summer heatwaves under a midrange scenario, but they could increase by two to nine events a year under an extreme scenario (RCP8.5) for southern and continental Europe. The 95th percentile in the length of dry spells is expected to increase by up to 24 days in southern Europe under the midrange scenario, and up to 32 days under the extreme scenario (Kovats et al., 2014).

The DailyDayCent model (NREL, 2012) is a daily version of the Century model (described in chapter three). DailyDayCent was not used for the previous analyses in chapters three and four due to resource limitations, as DailyDayCent has a considerably longer run-time than Century. However, the work done to parameterise the Century model can be used to support the use of DailyDayCent and greatly reduce the necessary computing time. Like Century, DailyDayCent models fluxes of C and N throughout the plant-soil-atmosphere system. Plant productivity depends on genetic potential, nutrient availability, solar radiation, temperature/water stress and phenology. Plant nutrient concentrations are divided by plant components and are allowed to vary within specified limits, according to nutrient availability relative to plant demand and vegetation type (NREL, 2012).

The majority of grassland modelling uses smoothed weather data or, in a few cases, is run on a monthly time step (e.g. Abdalla et al., 2010; Graux et al., 2013; Hall et al., 1995), neither of which enable the study of short-term extreme events. By explicitly looking at the effects of extremes, the importance of accounting for the effects of such events can be determined.

The present chapter aims to quantify the effects of future extreme weather events on the yield and N yield of European grasslands using the DailyDayCent model. While this was covered in chapter five, it is helpful to try an alternate methodology.

This may help to discover any unidentified flaws in the regression approach and this site-specific view could also give more detailed insights on the impacts of extreme weather events. In chapter three, I found that the Century model gave more precise estimates of annual mean yield and N yield than the regression approach, while using the regression models were better for considering general trends. This may also be the case here and the two approaches can complement one another.

6.2 Methods

6.2.1 Sites and weather data

The DailyDayCent model was applied to six sites, spread across Europe (figure 6.1). These represent one site from each geographic region (see figure 2.1) and are all permanent grasslands, except for one of the Atlantic sites which is a temporary grassland. Full details are shown in table 6.1. Daily temperature and rainfall data were taken from local weather stations. The Rothamsted site provided data from its on-site weather station, data for all other weather stations were taken from the EUSTACE network (Squintu et al., 2019). This is different to the weather data used for the Century model which was gridded monthly data. It was necessary to use weather station data in this analysis to ensure that extreme weather events were included (gridded data is inevitably smoothed). The weather station data had slightly higher temperatures, while total monthly precipitation was about the same (on average maximum temperatures were 0.6° higher, minimum temperatures were 0.8° higher and precipitation was 0.4mm higher).

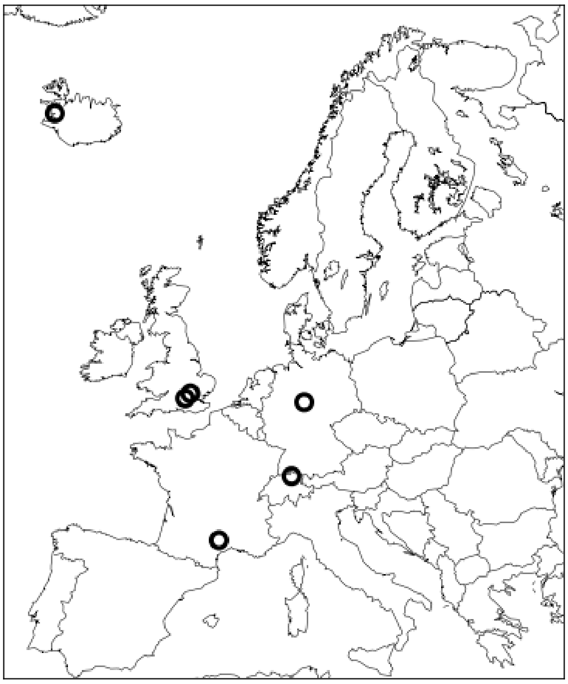

Figure 6.1: *Locations of sites to which the DailyDayCent model has been applied*

Table 6.1: *Sites to which the DailyDayCent model has been applied*

Site, Country	Geographic region	Grassland type	Fertiliser treatments (kg N ha^{-1} a^{-1})	Plant N yield available?	Experiment duration (years)	Data source
Eschikon, Switzerland	Alpine	Permanent	140 / 560	Yes	10	(Schneider et al., 2004)
Hurley, UK	Atlantic	Temporary	0 / 150	Yes	4	(Morrison et al., 1980)
Rothamsted, UK	Atlantic	Permanent	0 / 144	No	58	*Private communication*
Göttingen, Germany	Continental	Permanent	0 / equal to that removed the previous year	Yes	40	*Private communication*
Hvanneyri, Iceland	Northern	Permanent	0 / 100	Yes	25	(Brynjólfsson, 2008)
Larzac Causse, France	Southern	Permanent	0 / 65	No	25	(Chollet et al., 2014)

6.2.2 Model parameterisation

The model was parameterised in a very similar way to the method used to parameterise the Century model in chapter three. The same input parameters were optimised (see table 3.2) using Markov Chain Monte Carlo (MCMC) optimisation with the L-BFGS-B algorithm within the Python SciPy module (Jones et al., 2001). Once again, the root mean square error (RMSE) between observed and predicted values was minimised, accounting for soil carbon stabilisation during the spin-up period (for full details see section 3.2.3.3). The one difference was that with the Century model, each parameter was first optimised individually. This provided suitable initial conditions for optimising all parameters simultaneously. With DailyDayCent this was not possible due to the excessively long run-time it would require. Instead, the optimised values from the Century model were used as the initial conditions in simultaneously optimising the parameters in the DailyDayCent model, essentially using the Century values as priors.

6.2.3 Model fit and sensitivity analysis

The fit of the model was tested for each of the six sites. Predicted and observed values for average yield and N yield were compared, and corresponding standard errors were evaluated. This was done using annual yield/N yield data, except at the Hurley site where data from individual cuts were used (as the experiment at this site was of short duration and this provided additional data points). In addition, the RMSE and correlation between predicted and observed yields and N yields were calculated for both models and the RMSE were divided into bias and variance terms.

Again, restrictions on computing resources meant that it was not possible to do the full sensitivity analysis which was conducted in chapter three. However, since the Century and DailyDayCent models are very similar in terms of how they model biological processes, it is assumed that their sensitivity to different inputs is very similar. To verify this, DailyDayCent's sensitivity to changes in individual parameters was assessed. These parameters are listed in table 6.2; only weather parameters were included as the Century sensitivity analysis (section 3.2.4.3.2) showed that uncertainties in soil parameters have very little effect compared with uncertainties in weather parameters. The uncertainty ranges used are the same as those which were used for the Century sensitivity analysis and are based on those used by Fitton et al. (2014) and Gottschalk et al. (2007).

Table 6.2: *Parameters tested as part of the sensitivity analysis and corresponding uncertainly ranges*

Parameter	Uncertainty range
Precipitation	±1mm per day
Temperature	±1°C

The same methodology as was employed in chapter three for checking the linearity of uncertainty propagation was used. For each parameter, the model was run ten times, setting the parameter to ten equally-spaced steps within the uncertainty range, while leaving the other parameters at their original values. The range of yield and N yield predictions were then compared to see which parameters generated the most uncertainty when allowed to fluctuate within reasonable bounds. This was done for each of the 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).

6.2.4 Climate change and extreme weather events

For this research, two future weather datasets were used. These were the REMO dataset (as described in chapter five) and the REDVAR dataset developed by Beer et al. (2014). These give estimates of daily temperature and rainfall under the A1B climate change scenario for the years 2010 to 2100 (A1B indicates rapid economic growth with a balanced approach to fossil-fuel vs sustainable energy sources (Nakicenovic et al., 2000)). The REMO dataset includes extreme weather events and can be considered a reasonable approximation of future weather under the A1B scenario. The REDVAR dataset was derived from the REMO dataset using Taylor expansions. It has 25% lower variance for both mean temperature and mean precipitation, whilst having the same seasonal mean values. In chapter five, several disadvantages of this methodology were listed, however it does produce reasonable results. Also, the DailyDayCent model is less likely to be negatively affected by the limitations of this approach than the regression models, since it models biological processes rather than statistical trends. The reduced variability in the REDVAR dataset means that extreme weather events are fewer and less intense. By applying DailyDayCent to both datasets it is possible to determine the impact that extreme events are likely to have on grassland yield and quality in the future.

The difference between the two datasets was evaluated for each site and each month. In each case, the maximum and minimum temperatures, maximum precipitation and the variance and kurtosis of maximum and minimum temperatures and precipitation were calculated.

For each site, the model was run for three time periods (2010 – 2030, 2045 – 2065 and 2080 – 2100) using weather data from both the REDVAR and REMO datasets. The resulting predictions of yield and N yield were compared and the differences were tested for statistical significance ($p<0.05$) using the Mann-Whitney U-test (the normality assumption was not met in all cases so the student's t-test could not be used).

6.3 Results

6.3.1 Differences between REMO and REDVAR datasets

The maxima, minima, variances and kurtoses for each dataset, site and month are given in Appendix A. On average, maximum precipitation is 24% lower in the REDVAR dataset across the six sites. Maximum temperature is 18% lower and minimum temperature is 37% higher. Variance in the REDVAR dataset was reduced by 18%, 58% and 55% for precipitation, maximum temperature and minimum temperature respectively. Kurtosis of precipitation was 40% lower in the REDVAR dataset than the REMO dataset, but 9% and 29% higher for maximum and minimum temperature respectively. On average, monthly mean temperatures were similar across the two datasets, with mean temperatures in the REDVAR dataset being 0.4% lower.

6.3.2 Model fit

The model fit results are shown in table 6.3. There was usually little difference between the observed and predicted means and the RMSE tended to be dominated by variance rather than bias. There was more variation in the correlations between predictions and observations, ranging from relatively high correlation (Hurley) to no correlation (Iceland). The standard errors of the predicted means were always less than those of the observed means (for both yield and N yield), indicating that the predictions showed considerably less inter-annual variation than there was in reality.

The greatest differences between observed and predicted mean yields were at the German and Rothamsted sites when fertiliser was used. These sites also had some of the highest RMSEs, though many of the RMSEs were quite high. Three sites exhibited no correlation between observed and predicted yields, these being the Icelandic and Swiss sites with fertiliser and the German site without fertiliser. For N yield, the model performed very well for the Hurley site in terms of the RMSE and correlation, though produced the largest discrepancy between predicted and observed N yield of any of the sites when fertiliser was used. The model was less successful at predicting N yield at the Icelandic and Swiss sites and was particularly poor at the Swiss site when fertiliser was used. In these cases, the model produced no correlation between predicted and observed N yields and high RMSEs.

Overall the model performed best at the UK, German and French sites and was often more successful when no fertiliser was used. It performed particularly poorly at the Swiss site with high fertiliser use and at the Icelandic site.

Table 6.3: *Goodness-of-fit of the DailyDayCent 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 yields, $\bar{O}_Y$ and $\bar{O}_N$ are mean observed yield and N yield. 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 yield (kg ha^{-1} a^{-1})	Mean *(SE)* predicted N yield (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 *(0.04)*	16.1 *(0.5)*	0.30	141.2 *(8.9)*	145.1 *(3.4)*	17.2 *(2.6)*	0.45
	560	12.16 *(0.95)*	11.71 *(0.09)*	24.0 *(2.4)*	-0.09	381.4 *(41.5)*	385.5 *(6.2)*	32.2 *(0.1)*	0.18
Hurley, UK	0	1.82 *(0.56)*	1.80 *(0.26)*	15.2 *(0.0)*	0.66	34.6 *(9.1)*	32.5 *(4.9)*	11.9 *(0.6)*	0.74
	150	4.76 *(0.88)*	5.11 *(0.31)*	13.9 *(0.6)*	0.58	99.7 *(18.0)*	126.1 *(8.5)*	9.9 *(9.0)*	0.54
Rothamsted, UK	0	2.72 *(0.16)*	2.77 *(0.05)*	36.1 *(0.2)*	0.63	NA	67.5 *(1.2)*	NA	NA
	144	6.86 *(0.25)*	5.34 *(0.11)*	33.6 *(43.1)*	0.40	NA	200.7 *(3.9)*	NA	NA

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 yield (kg ha^{-1} a^{-1})	Mean *(SE)* predicted N yield (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
Göttingen, Germany	0	3.56 *(0.21)*	3.98 *(0.07)*	38.1 *(9.5)*	0.13	34.1 *(2.3)*	36.2 *(0.5)*	39.0 *(2.7)*	0.45
	Equal to previous year's N removal	6.33 *(0.31)*	8.73 *(0.18)*	30.8 *(76.9)*	0.75	135.0 *(6.7)*	132.6 *(3.3)*	21.0 *(0.8)*	0.80
Hvanneyri, Iceland	0	5.73 *(0.40)*	5.59 *(0.06)*	35.3 *(0.5)*	-0.19	82.5 *(6.8)*	75.8 *(1.3)*	43.8 *(3.5)*	-0.26
	100	7.64 *(0.23)*	7.65 *(0.11)*	16.6 *(0.0)*	-0.07	126.3 *(4.5)*	132.5 *(3.2)*	21.2 *(5.4)*	0.06
Larzac Causse, France	0	1.57 *(0.11)*	1.55 *(0.02)*	25.0 *(0.1)*	0.30	NA	11.0 *(0.2)*	NA	NA
	65	5.25 *(0.29)*	5.29 *(0.03)*	26.1 *(0.1)*	0.40	NA	60.4 *(0.2)*	NA	NA

6.3.3 Sensitivity analysis

The sensitivity analysis results are shown in figure 6.2. Temperature variations had very little effect on the model outputs. Precipitation variations did have an effect, but only at the UK and German sites, and the French site when no fertiliser was used. In almost all these cases, increasing precipitation led to increased yields and N yields. The exception was for N yields at the Hurley site when no fertiliser was used, where this pattern was reversed. For the Rothamsted, German and French sites, there was more uncertainty when no fertiliser was used than when it was applied. The greatest level of uncertainty was found at the Rothamsted site, with yields ranging from -19% to +22% from the baseline when no fertiliser was used.

6.3.4 Effects of climate change and extreme weather events

The DailyDayCent model was run for each site, time period and fertiliser treatment with both the REMO and REDVAR datasets. The results are shown in figures 6.3 and 6.4. Yields usually increased over time, less so at the UK sites than at the others. For the UK and German sites, as well as the Swiss site with low fertiliser, N yields were roughly constant. For the others, N yields slightly increased.

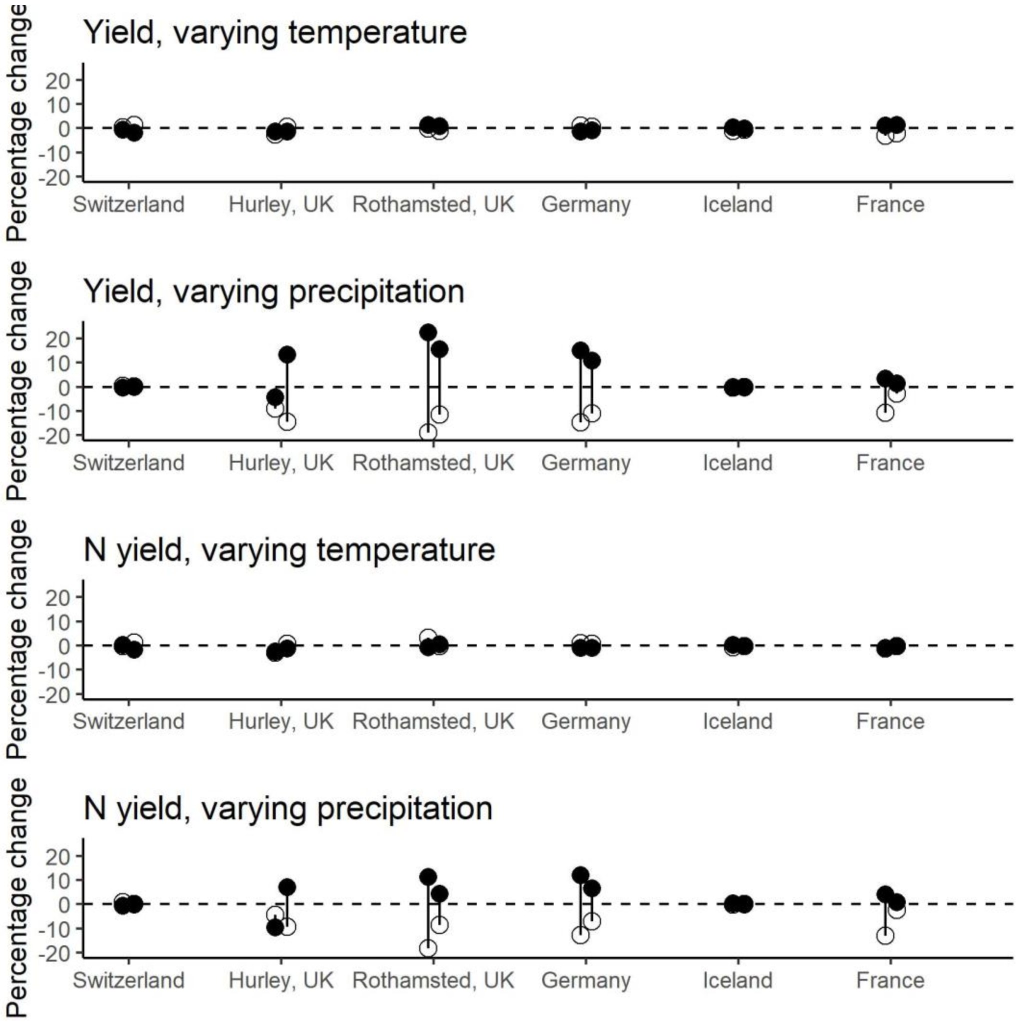

Figure 6.2: *Sensitivity of the DailyDayCent predictions of yield and N yield to changes in precipitation (±1mm per day) and temperature (±1°C). For each site, the points on the left are when no fertiliser was used (or a low level of fertiliser for Switzerland) and the points on the right are when it was used (or a high level for Switzerland). Solid circles indicate the change when the precipitation or temperature was increased and empty circles indicate they were decreased*

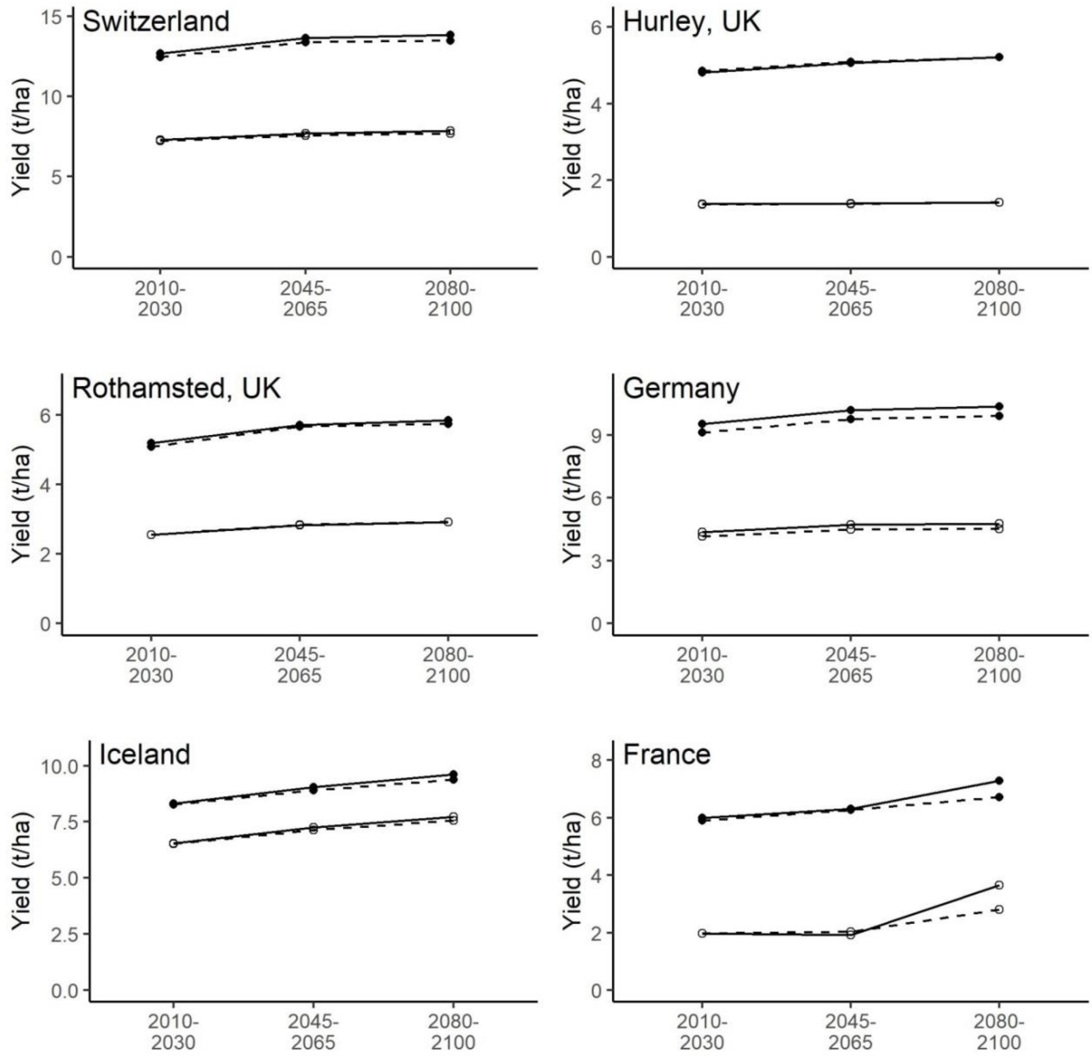

Figure 6.3: *Predicted future grassland yields using the DailyDayCent model. Solid lines denote the results using the REDVAR dataset (no extreme events) and dashed lines are for the REMO dataset (with extreme events). Solid circles indicate that fertiliser was used (or a high level of fertiliser for Switzerland) and empty circles indicate that no fertiliser was used (or a low level for Switzerland)*

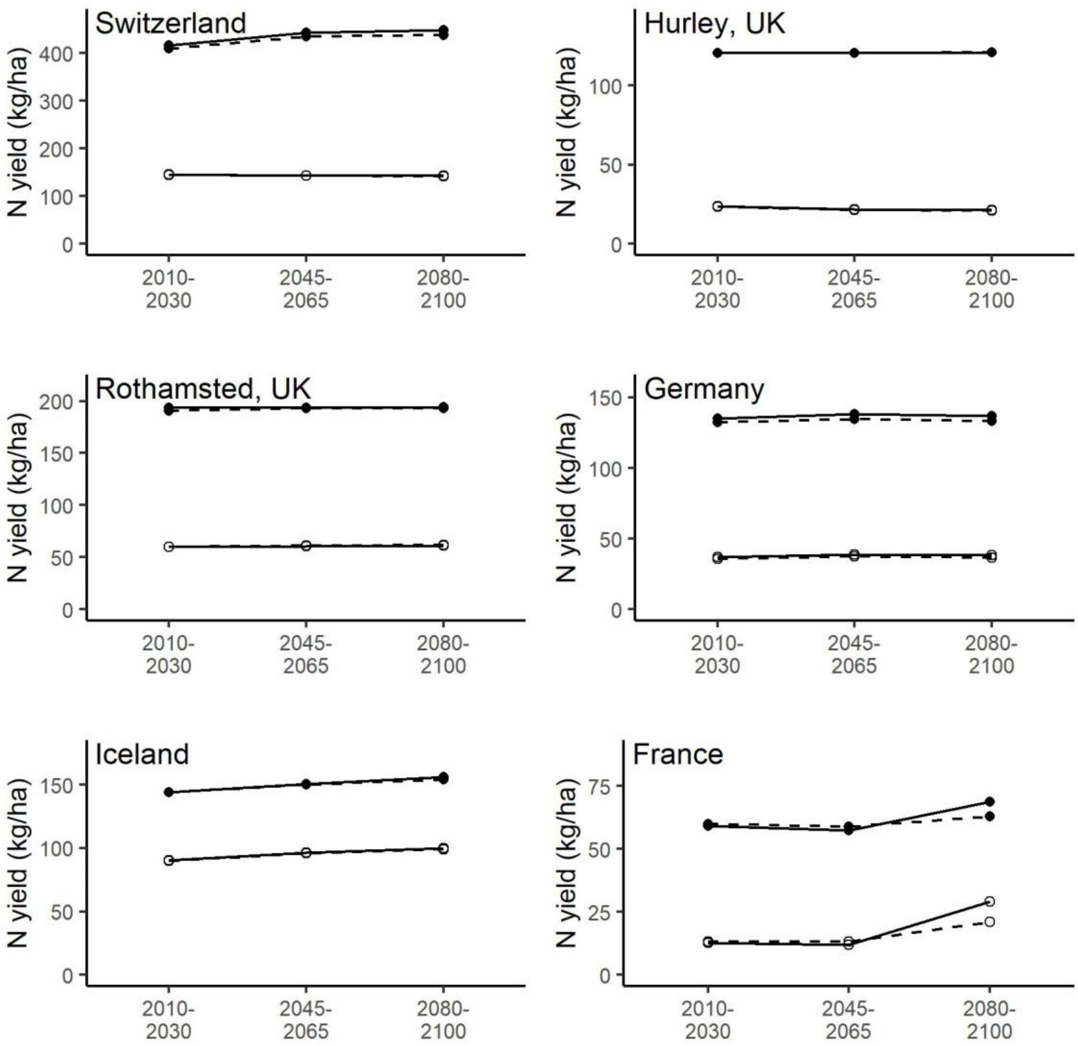

Figure 6.4: *Predicted future grassland N yields using the DailyDayCent model. Solid lines denote the results using the REDVAR dataset (no extreme events) and dashed lines are for the REMO dataset (with extreme events). Solid circles indicate that fertiliser was used (or a high level of fertiliser for Switzerland) and empty circles indicate that no fertiliser was used (or a low level for Switzerland)*

The differences between the predictions with each dataset were calculated as a percentage of the prediction with the REDVAR dataset. The results are shown in table 6.4. Predicted yield and N yield were generally lower when extreme events were included, but the difference was often not significant. Exceptions are the Swiss site, where extreme events caused small but significant yield reductions when a low fertiliser level was used, and the French site, where extreme events caused large drops in both yield and N yield for the 2080-2100 period, but increases for the 2045 – 2065 period. Extreme events also caused significant yield reductions at the Icelandic site for the 2080-2100 period with fertiliser, and also for the German site when no fertiliser was used. The German site generally experienced higher percentage differences between the results of the two datasets than any other site except the French.

Table 6.4: *Percentage difference between yield and N yield predictions using the DailyDayCent model with the REMO (with extreme events) and REDVAR (without extreme events) datasets. Results are given as a percentage of the REDVAR predictions. Negative numbers indicate that the prediction with the REDVAR dataset was less than that with the REMO dataset. Numbers in bold indicate a significant difference (p<0.05) between the predictions from the two datasets*

	Time period	Switzerland	Hurley UK	Rothamsted UK	Germany	Iceland	France
Yield							
	2010 - 2030	**1.04**	1.32	0.31	4.76	0.60	-0.21
No/low fertiliser	2045 - 2065	**1.48**	1.46	-0.27	4.45	1.77	**-5.44**
	2080 - 2100	**1.94**	0.38	0.20	**5.24**	2.26	**23.15**
	2010 - 2030	1.77	-0.64	2.12	4.07	0.75	**1.47**
With/high fertiliser	2045 - 2065	**1.97**	-0.57	0.66	4.13	1.60	0.57
	2080 - 2100	2.68	-0.06	1.77	4.50	**2.25**	**7.73**
N yield							
	2010 - 2030	0.10	1.70	-0.13	3.86	0.22	-4.22
No/low fertiliser	2045 - 2065	0.46	1.59	-0.61	3.45	0.72	**-12.15**
	2080 - 2100	0.53	0.42	-0.63	4.24	1.22	**27.95**
	2010 - 2030	1.61	0.09	1.58	2.03	-0.05	-1.14
With/high fertiliser	2045 - 2065	**1.82**	-0.06	0.27	2.49	0.43	**-2.72**
	2080 - 2100	2.47	-0.01	0.84	2.63	1.23	**8.21**

6.4 Discussion

This chapter aimed to quantify the effects of future extreme weather events under the A1B climate change scenario on the yield and N yield of European grasslands using the DailyDayCent model.

6.4.1 Model fit

DailyDayCent generally predicts mean annual yields reasonably well, but struggles to capture inter-annual variation. The Century model had the same issue (see section 3.2.4.2). It was hoped that by switching to the daily version of the model, more variability would be captured, but this was not the case. Century was initially developed for the US Great Plains, where the climate is relatively stable. While the model has been adapted to cover a wider range of areas, it may be that the ways in which both Century and DailyDayCent model the underlying biological processes are not well suited to such variable climates as are found in Europe.

The model fit results for DailyDayCent are very similar to those for Century; sometimes one model produces slightly better results, and sometimes the other. For yield, there was considerably more bias in the predictions for the Rothamsted site with the DailyDayCent model than there was with the Century model when fertiliser was used (43.1% vs 27.2%). For N yield, RMSE and bias were usually lower with DailyDayCent than with Century and correlations were either slightly higher or about the same.

It is surprising that the results were sometimes worse with DailyDayCent than with Century (albeit usually only marginally). DailyDayCent is a more detailed model than Century, accounting for more interactions between different ecosystem components, and it runs on a daily time step, suggesting that it should be better at capturing variability. The Century optimised model parameters were used as initial conditions for determining the DailyDayCent parameters, but it is possible that due to the different weather data sources, this led to DailyDayCent parameters which were not optimal. Several of the parameters included in the optimisation procedure related to temperature and the temperatures recorded by the weather stations tended to be slightly higher than in the gridded dataset, which could be responsible for the occasionally less good model fit.

However, DailyDayCent still produces reasonable estimates of mean annual yield and N yield and the fit is good enough to use the model to make estimates of the effects of extreme weather events, albeit with some caution. The fact that the model struggles to capture inter-annual variation suggests that it may not always accurately capture the effects of temperature and precipitation extremes and this should be taken into account when considering the results.

6.4.2 Sensitivity analysis

As for the Century model, the majority of the uncertainty in the model came from the precipitation inputs; this is discussed in detail in section 3.2.4.3.2. For the Century model, there was considerably more uncertainty in the predictions for the Rothamsted site than for any of the others. Here there were several sites displaying relatively high levels of uncertainty and the Rothamsted site was less of an outlier.

While it makes sense for the Rothamsted site to be more closely aligned with the others (especially the Hurley site as they are geographically very close to one another), the sensitivity analysis conducted for Century was considerably more detailed and involved varying multiple parameters simultaneously. This is a more robust methodology (Saltelli et al., 2019), but was unfortunately not possible with the DailyDayCent model due to its long run-time.

The Icelandic and Swiss sites showed the least uncertainty and these are the two sites with the highest annual rainfall, indicating that water limitation is a likely factor in model uncertainty. This is supported by yield and N yield tending to increase as precipitation increased. There generally being a greater degree of uncertainty when no fertiliser was used indicates that fertiliser is counteracting the effects of water deficit to some extent.

6.4.3 Effects of climate change and extreme weather events

The predicted yields and N yields showed similar trends to those found with the Century model (see chapter four). The predicted values were slightly different as different climate change scenarios were used (RCP4.5 and 8.5 vs A1B), however both show that yields tend to increase and N yields usually stay the same except for an increase at the French site. Century also predicted N yield increases for the German site, which were not realised here. This is likely due to differences between the climate change scenarios, or else due to functional differences between the models. Higher yields coupled with constant N yields will lead to lower plant N concentrations, indicating that livestock will need to eat more to receive the same amount of protein.

In the present study, there was usually no significant difference between the results with the REMO and REDVAR datasets. This suggests that it is generally reasonable to use smoothed weather data when considering the effects of climate change on grassland yield and N yield, though not in the southern (and possibly Alpine) region where there were large differences. This is very helpful for future modelling work. Process-based models with a monthly time-step are considerably faster to run than those with a daily time-step, but they cannot capture extreme weather events. This research suggests that in most areas in Europe this drawback is not an issue and it is reasonable to use the more computationally-efficient approach.

For the French site in southern Europe, extreme events caused large drops in both yield and N yield for the 2080-2100 period, but increases for the 2045 – 2065 period. This suggests that the milder extremes expected mid-century may be beneficial to plant-life, but that as they become more intense they have a detrimental effect. While this region will become drier on average, it will also experience increases in extremely heavy rainfall events (Jacob et al., 2014) and it may be this extra moisture at key times of year which is causing the slight increase mid-century over the scenario with no extremes. However, in the long-term, extreme weather events have a significantly negative effect, though not enough to counteract the predicted increases in yield and N yield. This demonstrates that it is very important to consider the effects of climatic extremes when modelling southern European grasslands.

6.4.4 Limitations

The DailyDayCent model struggled to capture inter-annual variation, which suggests that it was not fully picking up on the impacts of climate on grassland yield and N yield. It may be that extreme weather events will have a greater effect in reality, but these results at least indicate a general trend. It is also likely that climate change will cause changes in both the species composition of permanent grasslands and the resilience of current species (Dibari et al., 2015; Grant et al., 2014b; Pakeman et al., 2017). This will affect their response to climate change and extreme weather events, but it is unfortunately not currently possible to capture this in the DailyDayCent model.

6.4.5 Consequences for livestock

The general consequences of climate change on livestock farming have been discussed in earlier chapters. Regarding the specific effects of extreme weather events, the availability and quality of grass will not be significantly affected in most areas, beyond those changes already discussed due to ‘average’ climate change (i.e. climate change without extremes). The exception is southern Europe, where grazing livestock may benefit in the short term from improved grassland yields and protein content, but in the long-term these will be adversely affected beyond what was expected from average climate change, though a net gain is still positive. The effects on livestock of changes in grazing availability and quality are discussed in section 1.1.3.2 and in chapter four. Extreme weather events can also have direct impacts on grazing livestock, such as heat and cold stress, foot problems and increased mortality (Moran et al., 2009).

6.5 Chapter conclusion

This chapter used the DailyDayCent process-based model to consider the effects of climate change and extreme weather events on the yield and N yield of European grasslands. This follows on from similar work done in chapters three and four using the Century model and compliments the work in chapter five using a statistical approach to model the effects of extreme weather events.

Several different approaches have now been used: meta-analysis, statistical models and process-based models. The final chapter will evaluate the different methodologies and compare their results to draw appropriate conclusions about the likely impacts of climate change on European grasslands.

6.6 Appendix A: Comparison of REMO and REDVAR datasets, 2010 – 2100

Table 6.5: *Comparison of REMO and REDVAR datasets, 2010 – 2100*

Site	Parameter	Month	REDVAR variance	REMO variance	REDVAR kurtosis	REMO kurtosis	REDVAR minimum	REMO minimum	REDVAR maximum	REMO maximum
Alpine	Precipitation	1	40.67	44.31	12.21	15.55	NA	NA	58.18	70.61
		2	43.13	45.97	7.18	8.45	NA	NA	39.57	42.76
		3	47.73	50.73	11.77	13.6	NA	NA	64.43	69.86
		4	45.93	48.68	7.51	8.24	NA	NA	44.24	47.23
		5	54.28	60.79	13.93	18.1	NA	NA	68.83	82.22
		6	89.31	106.14	16.65	28.14	NA	NA	91.83	126.39
		7	84.93	96.22	18.45	22.09	NA	NA	86.4	99.31
		8	106.42	131.42	32.84	54.27	NA	NA	138.89	179.28
		9	98.46	126.2	25.35	40.98	NA	NA	104.43	161.3
		10	56.47	71.53	18.6	35.09	NA	NA	71.86	112.8
		11	59.1	62.32	8.85	10.19	NA	NA	56.9	60.61
		12	69.45	77.57	14.84	18.58	NA	NA	78.82	92.65
	Maximum temperature	1	8.47	18.7	3.38	2.73	NA	NA	13.62	18.58
		2	9.66	21.78	5.04	3.23	NA	NA	15.27	20.76
		3	9.29	22.69	3.41	2.96	NA	NA	21.39	27.28
		4	9.02	24.16	3.12	2.76	NA	NA	24.16	30.63
		5	10.94	26.55	2.66	2.46	NA	NA	30.09	34.89
		6	10.06	24.56	2.86	2.71	NA	NA	33.53	40.25
		7	8.39	22.04	3.09	2.93	NA	NA	36.34	43.5
		8	9.46	22.09	2.84	2.67	NA	NA	35.16	40.9
		9	10.13	23.19	2.82	2.55	NA	NA	32.91	37.07
		10	8.94	20.34	2.64	2.61	NA	NA	24.51	31.99
		11	7.74	16.2	3.1	3.13	NA	NA	18.75	24.74
		12	7.88	17.77	2.73	2.63	NA	NA	14.59	19.91
	Minimum temperature	1	8.69	18.2	10.17	6.54	-25.51	-25.51	NA	NA
		2	6.78	14.82	14.33	8.17	-22.74	-22.74	NA	NA
		3	4.02	9.97	4.98	3.99	-9.55	-12.19	NA	NA
		4	3.57	8.62	2.93	2.83	0.9	-1.71	NA	NA
		5	4.67	9.32	2.76	3.03	3.39	0.74	NA	NA
		6	3.83	8.35	2.98	3.11	6.29	2.83	NA	NA
		7	2.77	6.84	2.91	2.96	10.52	8.24	NA	NA
		8	3.27	6.88	2.8	2.73	9.73	6.7	NA	NA
		9	4.09	8.42	3.06	2.84	6.46	3.58	NA	NA
		10	4.88	10	2.65	2.75	2.36	-0.22	NA	NA
		11	5.4	11.49	3.7	3.85	-7.42	-12.99	NA	NA

Site	Parameter	Month	REDVAR variance	REMO variance	REDVAR kurtosis	REMO kurtosis	REDVAR minimum	REMO minimum	REDVAR maximum	REMO maximum
		12	6.69	14.54	13.56	6.54	-23.82	-23.82	NA	NA
Atlantic temporary	Precipitation	1	19.28	20.22	10.64	12.58	NA	NA	36.89	41.73
		2	11.29	12.1	10.86	12.87	NA	NA	25.37	29.29
		3	11.31	12.15	13.44	16.46	NA	NA	30.73	38.35
		4	9.33	10.54	11.58	15.23	NA	NA	23.69	32.33
		5	8.46	9.76	21.15	45.88	NA	NA	33.55	51.27
		6	8.81	9.73	19.69	29.12	NA	NA	29.74	39.22
		7	8.08	9.49	28.02	46.14	NA	NA	32.84	50.53
		8	15.55	18.6	25.34	32.11	NA	NA	45.88	46.4
		9	28.33	36.2	32.35	88.88	NA	NA	61.77	121.43
		10	28.57	33.76	20.19	24.81	NA	NA	61.4	63.46
		11	26.92	30.63	14.92	19.24	NA	NA	41.8	46.78
		12	22.94	24.67	12.44	15.51	NA	NA	47.9	52.79
	Maximum temperature	1	5.15	12.33	2.99	2.63	NA	NA	13.77	15.16
		2	5.45	12.21	4.13	3.67	NA	NA	15.2	19.55
		3	4.53	11	4.39	3.97	NA	NA	19.14	25.48
		4	6.37	16.59	3.52	3.49	NA	NA	25.36	29.84
		5	7.04	17.87	2.87	2.79	NA	NA	26.72	32.04
		6	6.93	16.86	2.83	2.59	NA	NA	28.88	33.48
		7	5.49	14.72	3	2.76	NA	NA	32.18	37.87
		8	6.41	15.56	3.14	2.94	NA	NA	34.5	37.95
		9	6.32	14.99	3.34	3.5	NA	NA	31.21	36.55
		10	5.86	12.5	3.59	4.01	NA	NA	26.36	30.78
		11	4.93	9.96	3.25	3.05	NA	NA	18.72	21.76
		12	5.81	12.84	3.29	2.95	NA	NA	13.9	16.5
	Minimum temperature	1	4.28	10.97	4.51	2.88	-13.24	-13.24	NA	NA
		2	4.81	11.59	8.58	3.95	-15.8	-15.8	NA	NA
		3	2.9	7.86	2.48	2.32	-4.01	-6.57	NA	NA
		4	2.79	6.72	3.01	3.08	0.72	-1.41	NA	NA
		5	2.74	5.77	3.45	3.73	1.83	-0.52	NA	NA
		6	2.36	4.96	2.75	3.25	6.92	4.92	NA	NA
		7	1.57	3.83	3.13	3.28	8.92	6.72	NA	NA
		8	2.15	4.88	3.06	3.07	8.09	6.08	NA	NA
		9	3.15	6.84	2.88	3.09	5.55	3.02	NA	NA
		10	5.32	11.46	3.01	2.99	0.78	-2.43	NA	NA
		11	5.39	13.36	2.66	2.51	-2.58	-5.71	NA	NA
		12	5.01	12.63	2.97	2.6	-9.41	-12.94	NA	NA

Site	Parameter	Month	REDVAR variance	REMO variance	REDVAR kurtosis	REMO kurtosis	REDVAR minimum	REMO minimum	REDVAR maximum	REMO maximum
Atlantic permanent	Precipitation	1	12.73	13.65	12.16	15.19	NA	NA	36.05	38.18
		2	9.17	9.84	10.39	13.85	NA	NA	25.39	34.47
		3	8.78	9.71	11.35	14.78	NA	NA	22.91	30.99
		4	10.82	12.36	15.5	21.24	NA	NA	29.87	39.91
		5	11.5	13.19	19.58	37.78	NA	NA	36.75	50.24
		6	13.56	16.12	30.2	46.43	NA	NA	43.59	51.06
		7	10.21	12.44	36.75	61.9	NA	NA	41.21	57.92
		8	20.85	27	27.57	40.59	NA	NA	49.31	63.53
		9	24.91	29.54	22.1	30.36	NA	NA	49.55	57.51
		10	23.59	27.88	19.54	29.01	NA	NA	49.46	66.68
		11	21.34	25.37	20.7	32.82	NA	NA	57.04	75.51
		12	17.27	18.82	13.33	16.1	NA	NA	39.94	45.58
	Maximum temperature	1	5.1	12.26	2.97	2.6	NA	NA	13.65	15.48
		2	5.25	11.8	3.99	3.52	NA	NA	14.93	19.2
		3	4.5	11	4.19	3.83	NA	NA	18.87	25.33
		4	6.37	16.24	3.59	3.52	NA	NA	25.24	30.13
		5	6.88	17.22	3	2.94	NA	NA	26.65	31.68
		6	6.51	15.84	2.88	2.72	NA	NA	28.17	32.73
		7	5.28	14.05	3.19	2.97	NA	NA	32.85	38.93
		8	6.03	14.67	3.17	3.02	NA	NA	34.01	37.55
		9	6.01	14.28	3.32	3.6	NA	NA	30.74	36.32
		10	5.82	12.32	3.41	3.9	NA	NA	25.35	30.49
		11	5.02	10.14	3.19	2.99	NA	NA	18.45	21.54
		12	5.79	12.84	3.28	2.89	NA	NA	13.76	16.5
	Minimum temperature	1	4.2	10.65	6.5	3.27	-17.63	-17.63	NA	NA
		2	4.47	10.62	7.48	3.54	-12.84	-12.84	NA	NA
		3	2.84	7.69	2.46	2.36	-3.47	-5.9	NA	NA
		4	2.75	6.63	3.06	3.08	0.87	-1.22	NA	NA
		5	2.89	6	3.48	3.73	1.43	-0.79	NA	NA
		6	2.43	5.11	2.81	3.24	6.93	4.92	NA	NA
		7	1.61	3.88	3.1	3.26	9.52	7.65	NA	NA
		8	2.13	4.86	3.08	3.1	8.59	6.07	NA	NA
		9	3.08	6.71	2.93	3.15	6.06	3.7	NA	NA
		10	5.13	11	3.07	3.01	0.72	-1.9	NA	NA
		11	5.26	12.76	2.71	2.57	-3.06	-5.88	NA	NA
		12	4.9	12.11	3.06	2.54	-9.58	-10.42	NA	NA

Site	Parameter	Month	REDVAR variance	REMO variance	REDVAR kurtosis	REMO kurtosis	REDVAR minimum	REMO minimum	REDVAR maximum	REMO maximum
Continental	Precipitation	1	16.36	18.27	13.9	22.91	NA	NA	39.63	58.3
		2	11.84	13.48	9.02	12.19	NA	NA	25.79	29.68
		3	12.98	14.19	9.19	10.68	NA	NA	26.63	29.7
		4	9.76	11.06	14.94	27.55	NA	NA	34.29	47.32
		5	17.31	19.75	23.05	30.45	NA	NA	44.83	56.64
		6	29.09	33.88	42.08	69.93	NA	NA	90.43	113.86
		7	19.29	22.38	29.35	47.34	NA	NA	55.87	73.45
		8	22.74	26.2	27.18	43.16	NA	NA	59.77	75.59
		9	25.51	29.78	20.93	28.43	NA	NA	58.59	65.35
		10	14.91	17.25	19.5	24.29	NA	NA	42.87	44.23
		11	21.72	24.57	17.89	22.48	NA	NA	49.67	56.78
		12	18.76	20.56	8.42	9.68	NA	NA	29.92	32.93
	Maximum temperature	1	9.5	21.67	4.21	2.78	NA	NA	12.41	17.94
		2	10.31	23.79	3.96	2.89	NA	NA	14.34	20.8
		3	9.39	22.56	3.05	2.9	NA	NA	18.36	25.86
		4	9.38	24.89	3.26	3.11	NA	NA	25.6	30.89
		5	10.5	26.42	2.8	2.72	NA	NA	28.71	33.6
		6	9.4	26.07	3.02	2.98	NA	NA	31	38.32
		7	8.66	24.62	3.04	3.02	NA	NA	36.31	45.67
		8	9.99	25.43	2.93	3.23	NA	NA	35.94	46.43
		9	9.53	23.5	2.88	2.92	NA	NA	31.71	36.83
		10	9.43	21.64	2.99	3.31	NA	NA	25.08	33.43
		11	7.09	14.81	3.5	3.54	NA	NA	16.78	23.47
		12	8.16	18.13	2.83	2.61	NA	NA	12.49	16.54
	Minimum temperature	1	12.45	25.84	13.33	7.04	-30.82	-30.82	NA	NA
		2	9.27	21.25	7.85	5.78	-20.98	-24.14	NA	NA
		3	4.93	12.13	9.41	5.68	-19.43	-21.88	NA	NA
		4	3.95	9.82	2.75	2.85	-2.7	-7.27	NA	NA
		5	4.43	9.73	3.06	3.29	1.86	-0.98	NA	NA
		6	3.64	8.75	3.23	3.56	6.38	3.71	NA	NA
		7	2.88	7.22	3.16	3.62	9.5	6.46	NA	NA
		8	3.44	7.69	3.09	3.27	8.05	6.55	NA	NA
		9	3.98	8.41	3.13	3.1	5.18	2.54	NA	NA
		10	5.61	12.12	2.99	3.16	-0.11	-3.29	NA	NA
		11	5.61	13.12	4.01	3.53	-11.75	-17.66	NA	NA
		12	7.89	17.9	5.25	4.95	-15.65	-22.29	NA	NA

Site	Parameter	Month	REDVAR variance	REMO variance	REDVAR kurtosis	REMO kurtosis	REDVAR minimum	REMO minimum	REDVAR maximum	REMO maximum
Northern	Precipitation	1	37.68	43.7	9.45	15.2	NA	NA	58.87	71.54
		2	45.45	53.59	10.01	14.36	NA	NA	63.2	75.04
		3	47.89	53.48	8.51	9.05	NA	NA	66.32	64.56
		4	18.48	21.99	14.65	28.65	NA	NA	56	71.34
		5	16.05	18.89	9.12	12.14	NA	NA	26.34	32.33
		6	12.3	13.69	9.37	11.81	NA	NA	27.65	32.16
		7	10.04	11.18	9.72	11.75	NA	NA	24.43	28.88
		8	26.59	29.27	8.84	10.43	NA	NA	41.47	41.61
		9	39.46	46.91	11.95	18.72	NA	NA	72.28	88.41
		10	51.99	57.46	10.72	14.56	NA	NA	83.91	97.78
		11	38.03	43.11	7.78	10.63	NA	NA	56.65	70.31
		12	46.92	53.03	10.71	13.54	NA	NA	54.75	65.66
	Maximum temperature	1	6	15.76	3.2	2.84	NA	NA	11.04	15.99
		2	4.74	12.78	3.5	2.84	NA	NA	10.67	15.03
		3	9.11	20.99	4.31	2.96	NA	NA	14.31	19.8
		4	7.71	18.33	4.01	3.23	NA	NA	17.11	24.24
		5	4.51	11.46	3.09	2.85	NA	NA	16.7	20.73
		6	3.25	7.72	2.7	2.52	NA	NA	19.12	21.84
		7	3.05	7.67	2.61	2.47	NA	NA	21.09	24.19
		8	3.12	7.24	2.97	2.89	NA	NA	20.83	24.83
		9	4.62	8.52	2.92	3.24	NA	NA	17.8	21.36
		10	5.78	11.27	3.28	3.31	NA	NA	14.59	18.2
		11	7.34	17.76	2.95	2.58	NA	NA	12.49	17.46
		12	7.47	19.07	4.11	2.99	NA	NA	10.76	16.32
	Minimum temperature	1	8.52	18.77	17.09	7.01	-34.47	-34.47	NA	NA
		2	7.88	18.8	9.75	5.86	-29.04	-31.86	NA	NA
		3	9.37	20.53	22.98	9.73	-37.28	-37.39	NA	NA
		4	6.16	14.6	5.12	4	-19.2	-25.47	NA	NA
		5	3.73	7.52	2.78	3.08	-3.85	-6.95	NA	NA
		6	1.83	3.54	3.07	3.12	-0.01	-2.43	NA	NA
		7	1.55	3.34	2.87	3.06	3.55	1.19	NA	NA
		8	2.2	4.7	3.52	3.54	2.16	-0.61	NA	NA
		9	5.54	10.35	2.59	2.75	-1.15	-3.75	NA	NA
		10	6.2	13.57	2.84	2.68	-8.1	-12.23	NA	NA
		11	6.87	15.58	3.33	3.27	-10.72	-15.19	NA	NA
		12	7.91	18.56	8.1	5.49	-28.06	-30.26	NA	NA

Site	Parameter	Month	REDVAR variance	REMO variance	REDVAR kurtosis	REMO kurtosis	REDVAR minimum	REMO minimum	REDVAR maximum	REMO maximum
Southern	Precipitation	1	106.28	149.89	23.98	52.66	NA	NA	107.94	187.09
		2	117.01	152.95	22.81	34.75	NA	NA	104.41	136.81
		3	25.23	34.68	34	131.35	NA	NA	75.53	140.58
		4	50.42	60.3	25.22	42.74	NA	NA	92.44	123.75
		5	35.8	40.77	21.05	32.97	NA	NA	70.19	93.54
		6	18.52	21.63	22.64	33.81	NA	NA	45.02	52.54
		7	6.92	7.5	40.85	61.55	NA	NA	36.97	40.99
		8	16.61	23.41	99.73	203.74	NA	NA	87.62	126.86
		9	115.69	173.9	37.59	92.6	NA	NA	147.21	254.57
		10	125.35	152.67	18.51	24.51	NA	NA	97.33	111.54
		11	140.08	223.19	37.48	96	NA	NA	145.63	268.35
		12	102.51	138.65	33.4	58.45	NA	NA	115.13	175.76
	Maximum temperature	1	6.38	14.95	3.42	3.26	NA	NA	17.96	23.07
		2	7.9	19.97	4.93	3.56	NA	NA	19.7	26.13
		3	7.24	19.28	3.43	2.94	NA	NA	22.29	27.49
		4	7.13	18.34	2.67	2.58	NA	NA	25.18	31.12
		5	10.52	22.9	2.56	2.57	NA	NA	31.22	36.61
		6	10.48	21.89	3.01	2.76	NA	NA	35.3	40.85
		7	8.05	19.33	2.91	2.83	NA	NA	39.49	46.4
		8	9.07	19.42	2.89	2.59	NA	NA	39.64	43.18
		9	10.78	23.52	2.71	2.41	NA	NA	34.76	40.4
		10	9.47	20.95	2.62	2.67	NA	NA	28.85	34.57
		11	8.12	17.23	2.99	2.9	NA	NA	23.26	27.35
		12	6.18	14.11	3.25	3.16	NA	NA	18.13	23.84
	Minimum temperature	1	4.69	10.61	4.65	3.52	-10.9	-11.91	NA	NA
		2	4.81	10.59	8.95	5.02	-14.88	-14.88	NA	NA
		3	3.19	7.69	3.41	2.95	-6.23	-10.27	NA	NA
		4	2.75	5.87	3.02	3.08	1.37	-0.16	NA	NA
		5	4.41	8.12	2.61	2.89	4.97	2.29	NA	NA
		6	4.28	8.26	2.8	2.93	9.26	7.03	NA	NA
		7	3.23	7.28	2.83	3.15	12.52	10.48	NA	NA
		8	3.49	6.97	2.72	2.69	12.18	9.73	NA	NA
		9	4.27	8.34	2.86	2.71	7.76	5.85	NA	NA
		10	5.39	10.72	2.66	2.7	2.86	0.47	NA	NA
		11	5.83	12.12	2.72	2.72	-0.57	-2.98	NA	NA
		12	4.84	11.25	3.03	2.85	-5.04	-8.06	NA	NA

CHAPTER 7 Discussion

7.1 Introduction

Increasing CO_2 emissions are causing significant changes to the earth's climate. Temperatures are increasing, rainfall patterns are changing and extreme weather events are becoming both more frequent and more intense. These changes affect plant growth and nutritional quality. To ensure the efficiency and productivity of grassland-based livestock systems, it is important to understand these changes so that farmers know what to expect in the future and how to prepare for it.

A great deal of research has been conducted in this area, both experimentally and using models. However, this often focuses on one single climatic change without considering how different changes may interact, or it considers the issue at a global scale or else at a site-specific level. Past research also often does not consider the impacts of extreme weather events.

This thesis aimed to quantify the effects of multiple simultaneous climatic changes on the yield and N yield of grasslands at a European scale and to determine the effects of extreme weather events and the importance of considering such occurrences.

7.2 Thesis overview

Chapter two presents a meta-analysis on the effects of elevated atmospheric CO_2 concentrations, rising temperatures and changes in water availability on the yield and N concentration of European grassland plant species. It distinguishes between five geographic regions (Alpine, Atlantic, continental, northern and southern) and between four plant functional groups (shrubs, forbs, legumes and graminoids). The analysis was performed for both individual and simultaneous climatic changes. It was found that higher CO_2 concentrations increased yields but decreased N concentration. Higher temperatures increased yields in Alpine and northern areas but decreased them in continental Europe, while also reducing N concentrations. Reduced water availability led to decreased yields and increased N concentrations, while higher water availability increased yields. When multiple changes were considered simultaneously, there were usually no significant changes in yield or N concentration.

In chapter three, two different approaches were used to model grassland yield and N yield. The first was a series of regression equations; the second was the Century dynamic model applied to six sites across Europe. These approaches did not account for the effects of extreme weather events. Both approaches were found to give reasonable estimates of mean yield and N yield. It was concluded that the regression approach was applicable over large spatial scales but lacked precision, making it suitable for considering general trends. Century was more effective at a local level where more detailed and specific analysis is required.

Chapter four used the models from chapter three to make predictions about the future yield and N yield of European grasslands under two climate change scenarios. Both modelling approaches agreed that yields will increase, though probably less so in the Atlantic region, and there may be slight decreases in southern Europe. Also plant N concentration will be reduced, indicating that livestock will need to eat more to receive the same quantity of protein.

In chapter five, regression models were developed for the yield and N yield of European grasslands, accounting for the effects of extreme weather events. Two future weather datasets, one with extremes and one smoothed, were used as inputs to the models, to predict how yield and N yield will change in the future. The results showed that smoothing the weather data increased both yields and N yields, indicating that extreme weather events are detrimental to grasslands. In general, the yield of temporary grasslands decreased over time, while for permanent grasslands it increased. There was little change in N yield over time, except in northern Europe where it increased.

Chapter six also looked at the effects of extreme weather events, this time using the DailyDayCent process-based model. The model was parameterised for six sites across Europe. It was then used to predict future grassland yield and N yield for each site, using both a dataset with extreme events and another with reduced variance. Yields generally increased over time while N yields were roughly constant or else showed a small increase. Predictions using the weather dataset with extreme events were usually lower than those with the reduced variance dataset, but the difference was not statistically significant except at the Alpine and southern European sites.

This chapter discusses results from the previous five chapters, focusing on the different modelling approaches, the value of considering extreme weather events and the conclusions which can be drawn about the expected impacts of climate change on grasslands. It also includes the implications for livestock farming, adaptation options, limitations of this study and suggestions for further research.

7.3 Modelling approaches

The three approaches used in this thesis, meta-analysis, multiple regression analysis and process-based modelling, all have their benefits and limitations. The meta-analysis used data from experiments where the climate was actually changed, rather than just making predictions based on plant responses to the current climate. This is useful for understanding how plants respond to different changes, but there is also always a possibility of bias when conducting such experiments, as the methodologies used (FACE, heating lamps, etc.) will never perfectly simulate a future climate. In addition, while it was possible to consider the effects of multiple simultaneous climatic changes, the results would be more robust if more experimental data had been available. As it was, it was not possible to divide the results by region or plant functional group, which could have provided valuable insights.

The statistical models are quick to run and are applicable over wide geographic areas. There were higher correlations between observations and predictions than with the process-based models and only negligible bias. Using statistical models to estimate the effects of extreme weather events had not previously been done and involved using a novel approach to multiple regression analysis, including terms in the model specifically designed to represent the prevalence of such events. It was not possible to account for atmospheric CO_2 concentrations in the statistical models as this is generally not reported in these types of experiments. This means that these models are likely to under-predict future grassland yields as they do not account for the fertilisation effect from increasing atmospheric CO_2 concentrations. It is not clear what effect this omission has on N yield predictions as there are several conflicting effects in play, as discussed in section 1.2.2.1. The other major limitation of this type of modelling is that the models are only reliable within the confines of the experiments which contributed to their development. Using them to predict grassland yield or quality under climate conditions different from those original experiments can lead to extrapolation errors. In chapter three, this was addressed by bounding the climate change scenarios so that they did not go beyond the maximum and minimum monthly temperature and precipitation values for each region. This had little effect on predictions under the RCP4.5 scenario, but it did significantly affect yield and N yield predictions for the RCP8.5 scenario, particularly for southern Europe. This bounding approach was not possible for the analysis in chapter five, as the point was to consider extreme weather events and this would have removed most of the extremes from the data. Instead the unadjusted climate change scenario was used and it was accepted that some error due to extrapolation was inevitable.

The Century and DailyDayCent process-based models account for long-term climatic changes, including gradually increasing atmospheric CO_2 concentrations. They consider all aspects of the plant-soil ecosystem, including soil status, plant types and the fluxes of C, N and water around the system. Because the models are based on biological processes, extrapolation to a new climate is far less of an issue than with the statistical models, meaning that they can provide highly accurate predictions for a given site. Unfortunately, this high degree of complexity can also be a limitation in using these models. While they gave good estimates of mean annual yields and N yields, correlations between predicted and observed values were often quite low, particularly for the Icelandic and Swiss sites and the German site when no fertiliser was used. Generally the model struggled to capture inter-annual variation. It was hoped that switching to using the DailyDayCent model would improve the model fit, but this was not the case. This suggests that the issue was either due to some poorly estimated model inputs, or because the model itself does not provide an accurate representation of the biological processes in European grasslands. These models were developed for the US Great Plains and then adapted to other ecosystems. No other study applying these models to look at the yield and N yield of grasslands in these areas of Europe could be found, so it is not possible to see if other authors have had more success. However, Parton et al. (1993) found similar results for grasslands in Ukraine and Russia, though they found the model to be more effective in the US, Mexico and Thailand. This suggests that the models may struggle to capture variability on grassland yield and N yield in Europe, though it is also certainly possible that there were inaccuracies in the model inputs, given the huge number of input variables these models have. DailyDayCent has the advantage over Century that it uses daily rather than monthly weather data, meaning that it captures the effects of short-term extreme weather events. On the other hand, this daily time step means the model has a considerably longer run-time than Century (roughly 90-times longer), meaning that it was not possible to perform as robust parameterisation and sensitivity analysis for DailyDayCent as for Century.

In general, process-based models such as these are ideal for consideration of a single site, but they are less useful when considering the effects of climatic changes over a large area, for which the statistical approach is better suited. On the other hand, these process-based models had lower uncertainty and (usually) smaller RMSEs than the statistical models, indicating that they tend to give more accurate predictions.

Each of these approaches has produced new insights into the effects of climate change on grasslands. Collectively, they mitigate each other's limitations and provide reliable estimates of what to expect in the future.

7.4 Consideration of extreme weather events

Statistical modelling using multiple regression analysis proved to be an effective way of estimating the impact of extreme weather events on grassland yield and N yield. Comparing the model fit results from chapters three and five, including extreme events terms led to improved model fit in terms of R^2 value, correlation and RMSE for temporary grasslands. For permanent grasslands, the fit was very slightly worse, though this may be because fewer experimental sites were included in developing the models with extreme events, due to the availability of weather data. The extreme events in the future climate dataset went far beyond the range of those in the data used for developing the regression equations. This meant that some extrapolation errors were inevitable, but it was found that some parameters were far more vulnerable to this than others. Those with a clear biological relationship to plant growth, such as 'number of days with temperature above 30°', performed well, while more abstract terms, such as 'kurtosis of mean temperatures', did not. The predicted grassland yields and N yields in chapter five were considerably more pessimistic than those in chapter three. They are not directly comparable as they use different climate change scenarios, but it is nevertheless suggestive of extreme weather events having a detrimental effect on grasslands. In chapter five, simply smoothing the dataset to reduce the most dramatic extremes had a significant positive effect on grassland yields and N yields, emphasising the importance of accounting for extreme weather events.

By using a daily time-step, the DailyDayCent model enabled the consideration of extreme weather events. However, like Century, the model struggled to capture inter-annual variation in yields and N yields, suggesting that it may not accurately represent the effects of extreme weather events. It seems likely that such events will have a greater effect than the results indicated. In general, the predictions of future grassland yield and N yield from the Century and DailyDayCent models showed comparable trends. The inclusion or exclusion of extreme weather events had little effect (except in southern Europe and in the Alpine region with low fertiliser). This suggests that if these models are to be applied in Europe, then there is little reason not to use Century in most areas, given its dramatically shorter run-time. However, it may be better to use the statistical modelling approach or, if a detailed site-specific analysis is required, to use a process-based model which more accurately captures variation in European grasslands. For example, PaSIM has produced very accurate predictions for grassland biomass in France (Pulina et al., 2018) and STICS has performed well predicting grass yields in northern Europe (Korhonen et al., 2018). Despite the limitations of the DailyDayCent predictions, this is nevertheless a useful result. It demonstrates that extreme weather events do certainly have effects in some areas, while also providing information about the model's range of applicability.

Overall, it is clearly important to consider the effects of extreme weather events. The statistical models demonstrated that they have a significant detrimental effect on grassland yield and N yield and the DailyDayCent model showed a significant effect in some areas, even though it seems very likely that the model underestimates their impact.

7.5 Expected climate change impacts

The effects of climate change on the yield and N yield of grasslands has been assessed in several different ways. Here these results are brought together to assemble a general picture of what is most likely to happen in each region in the coming decades.

7.5.1 Alpine region

The meta-analysis, statistical model, Century and DailyDayCent all indicated an increase in plant yields under climate change in this region. This is logical since growth in Alpine areas is often limited by low temperatures and warming will bring longer growing seasons. In addition, when searching for experimental grassland sites, the vast majority of those found in Alpine regions were permanent grasslands, presumably due to the difficulties of managing a crop rotation in mountainous terrain. Permanent grasslands tend to benefit more from climate change than temporary ones, as demonstrated in the statistical model results from chapters three and five. This is likely because permanent grasslands tend to have a higher degree of species richness, which is known to promote climate change resilience (Craine et al., 2012; Isbell et al., 2015; Wright et al., 2015). Century and DailyDayCent mostly suggested that there would be no change in plant N yield, though there could be a slight increase by the end of the century under certain fertiliser conditions. N yield was not assessed using the statistical models due to a lack of experimental data. There are several different relevant effects here which could explain the lack of a noticeable change in N yield. 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 (and DailyDayCent) 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 yield in mountainous areas (Dumont et al., 2015).

7.5.2 Atlantic region

The Century and DailyDayCent model results suggested small but significant increases in yields when fertiliser is used and no significant change when it is not used. The statistical models in chapter three and the meta-analysis results indicate very little change, while the statistical models considering extreme weather events in chapter five showed a small decrease in yields of temporary grasslands and a small increase for permanent grasslands. 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 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 approaches suggest very little change in N yield. Again, this is likely due to different effects cancelling one another out. In general, it seems that any changes in this region will be relatively small. This is likely because out of all the regions, this one will experience the smallest climatic changes.

7.5.3 Continental region

When extreme weather events were included, the statistical models predicted increases for permanent grassland yields and decreases for temporary grasslands. Century and DailyDayCent predicted a small increase for the permanent grassland in Germany. The meta-analysis predicts increased yields due to higher atmospheric CO_2 concentrations, but decreases due to higher temperatures. Rainfall in this region is expected to increase in the coming decades (Jacob et al., 2014), which according to the meta-analysis would increase yields. Considering that the statistical models tend to under-predict future yields by not allowing for rising atmospheric CO_2 concentrations, it seems likely that this region will see increased grassland yields in the future, especially for permanent grasslands, except in cases of extremely high temperatures. It should also be noted that 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. All methodologies agree that there will be very little change in plant N yield in this region.

7.5.4 Northern region

When extreme events were included, the statistical models predicted little change in temporary grassland yields, while without the extremes it was predicted that these yields would increase. Century and DailyDayCent predicted increases for the permanent grassland site in Iceland and the meta-analysis agreed that yields would increase in this region due to the combination of higher atmospheric CO_2 concentrations, higher temperatures and increased water availability. All methodologies also show increases in plant N yield (though this was not a significant increase in the meta-analysis). For Century and DailyDayCent, this is likely due to N increasing as C increases (Metherell et al., 1993). Wetter conditions may increase nutrient uptake from the soil (Matías et al., 2011), though elevated rainfall can also cause an increase in nutrient leaching (Metherell et al., 1993).

7.5.5 Southern region

Century and DailyDayCent predicted increases in yields at the permanent grassland site in southern France, though these increases were reduced by the inclusion of extreme weather events. The statistical models predicted decreases for temporary grasslands and the meta-analysis showed that while yields would increase due to higher atmospheric CO_2 concentrations, they would decrease due to reduced water availability. Several previous studies have predicted a reduction in plant yields for southern Europe (Rötter and Höhn, 2015; Trnka et al., 2011), making the Century and DailyDayCent results particularly surprising. Often such predictions are based on the increasing frequency of extreme weather events such as droughts and heatwaves and, as discussed in section 7.4, these models did not adequately capture the effects of such events, suggesting that they are likely to be over-estimating grassland yields. Because of this, combined with the fact that there was generally very little data available for the southern region (for both the statistical modelling and the meta-analysis), it is difficult to estimate future grassland yields here. However, decreases seem likely, especially for temporary grasslands which, as previously discussed, are especially vulnerable to the effects of climate change. In terms of N yield, Century and DailyDayCent predicted slight increases, though these are reduced when extreme events are included, while the meta-analysis results suggested there would be little change due to different effects cancelling one another out.

7.6 Implications for livestock farming and adaptation options

The Alpine, Atlantic, continental and northern regions are all likely to experience increased grassland yields. This is positive for grass-based livestock systems as there will be more for animals to eat. If they were not already at their maximum intake capacity, then this could lead to higher productivity (Morand-Fehr et al., 2007). However, with the exception of the northern region, these yield increases are not accompanied by higher plant N yields, meaning that plant N concentration will decrease. This means that livestock will need to eat more to receive the same amount of protein. If they do not receive sufficient protein then this could lead to reduced productivity and fertility, as well as increasing health problems, as described in section 1.1.3.2. For southern Europe, yields are likely to decrease, especially for temporary grasslands. Grasslands in this region are already often of poor quality (Hadjigeorgiou et al., 2005) and reductions in yield will make livestock farming harder in this region. In general, it was found that permanent grasslands perform better than temporary grasslands under climate change, suggesting that extensive livestock systems are likely to be favoured.

To address reduced plant N concentrations, farmers can use more concentrate feed, to ensure that livestock receive sufficient nutrients. Indeed, Huston et al. (1988) found that supplementing low quality feed with additional protein increased forage intake for both sheep and goats. Another option would be to increase fertiliser use. This has been found to counteract nutrient loss (Brown et al., 2016; Campbell et al., 2000), to partially offset the negative impacts of increased temperatures on the nutritive value of forage (Lee et al., 2017) and to counter reduced plant productivity under drought conditions (Carlsson et al., 2017). However, increasing fertiliser use would have major environmental consequences (Byrnes, 1990) and may be too expensive or impractical in marginal areas (Campbell et al., 2000). An alternative approach to promote grassland N yield would be to increase the proportion of legumes in grasslands so as to increase N fixation.

Increasing the number of plant species in temporary grasslands could be helpful, increasing their resilience to climate change. Careful thought should also be given to the plant species used as some are more suited for the expected future climate than others. For example, in northern Europe there will be less need for hardier species such as timothy and meadow fescue and farmers could consider switching to grasses with a higher yield, such as perennial ryegrass (Ergon et al., 2018). In Mediterranean environments, farmers currently using annual species could benefit from a switch to perennials, particularly as water shortages become more of a problem. This would require fewer system inputs, would be more efficient in terms of water-use and would mean year-round cover, thus reducing the risk of soil erosion (Ergon et al., 2018). In southern Europe it would also be beneficial to consider drought-resistant species such as tall fescue (*Lolium arundinaceum*), which is deep-rooting and has high water-use efficiency (Lelièvre et al., 2011). Through a judicious choice of plant species, farmers can maximise the potential yield and quality of their grasslands.

Using plant breeding to produce plants which are more suited to the future climate could also help to mitigate the negative effects of climate change on grasslands. Various different priorities have been identified. Soares et al. (2019) recommended focussing on preserving plant nutritional quality, which seems highly relevant given the expected reduction in plant protein content which this thesis has identified across much of Europe. Ergon et al. (2018) suggest a more regional approach, with research for northern Europe focussing on plants suitable for the longer growing season and the new temperature–photoperiod combinations; while for southern Europe they suggest breeding for plants suited to a shorter growing season, as well as those with high levels of drought resistance.

Campbell et al. (2000) suggest that the expected decrease in plant protein concentrations could necessitate a reduction in stocking densities in protein-limited areas. Some Mediterranean pastures have already been found to provide insufficient protein for grazing sheep (Silanikove, 2000) so this may become necessary in southern Europe. Ergon et al. (2018) say that farmers will need to become more flexible with stocking densities in future to minimise the risk of damage such as poaching, soil compaction, erosion, diversity loss and N leaching. Livestock grazing has major impacts on vegetation dynamics and pasture productivity and these occurrences will become more likely in future due to the increasing frequency and intensity of extreme weather events.

In chapter four, it was noted that the impact of different fertiliser levels, grassland types and geographic regions on plant yield and N yield were much greater than the impact of climate change. This is supported by the meta-analysis of Thébault et al. (2014), who found that fertilisation and defoliation were the factors having the greatest influence on grassland productivity and combinations of management practices explained considerably more of the variation in performance than either combinations of climatic changes or of interactions between management practices and climatic changes. It should be noted however that none of the studies used in their meta-analysis simulated extreme climatic events. Li et al. (2018) found a similar result in their meta-analysis, in that intensive grazing has more of an impact on both grassland productivity and species richness than climate change. These suggest that the correct management practices could make a large difference in ameliorating the negative effects of climate change on pastures.

7.7 Limitations

Each methodology used in this thesis had some specific limitations, which are detailed in chapters two to six as well as in section 7.3. In general, the main limitation was data availability. The analysis performed for southern Europe is less detailed and less robust than that for the other regions, as there were fewer data available. This is particularly concerning as this is the region which will experience the most detrimental effects of climate change and it is especially important to know how grasslands will be affected in this region.

In addition, the vast majority of data used in this thesis came from experiments where no grazing took place. This is fine if considering grasslands where grass is cut and then fed to livestock, but if considering grazed grasslands then it would be better if the models took grazing into account. Century and DailyDayCent actually do account for the effects of grazing, but the meta-analysis and statistical models do not. Grazing affects how plants grow as well as plant responses to climate change. For example, Deléglise et al. (2015) found that grazed pastures have a higher nutritive value than mowed ones and that droughts had a much greater negative impact on biomass production for a grazed grassland than a mowed one. Thornley and Cannell (1997) found that for British grasslands, grazing reduces the optimum temperature for maximising ANPP, which they attribute to the reduced leaf area index of grazed plants. This suggests that as temperatures increase, grazed plants will experience even less growth than un-grazed ones than they would under constant temperature. These emphasise the importance of considering the effects of climate change on grazed and cut grasslands separately.

Lastly, none of the methodologies accounted for plants adapting over time to the new climate. Studies have shown that plants can adapt to their circumstances (Franks et al., 2007; Matesanz and Valladares, 2014; Nicotra et al., 2010), but it would be useful to understand this phenomenon at a larger scale and to incorporate it into grassland models.

7.8 Suggestions for further research

There are many other factors which could be considered in relation to grasslands and climate change. As mentioned in section 7.7, further research in southern Europe and on grazed grasslands would be highly beneficial. It would also be valuable to investigate how plants adapt over time to changing climatic conditions and how this interacts with other factors.

This research focused on grassland yield and N yield as these are highly important for livestock farming, but also because data on these parameters are widely available. It would be useful to also consider other measures of grassland quality, such as non-structural carbohydrates and digestibility. Plant non-structural carbohydrate concentrations are expected to increase with rising atmospheric CO_2 concentrations (Dumont et al., 2015) and Campbell et al. (2000) suggest that this could enable farmers to increase stocking densities in currently energy-limited regions and that this may be relevant in some areas of Europe. It would be useful to see how this interacts with other expected climatic changes to see if increasing stocking densities could be a viable option.

Other factors affecting plant growth and nutritional quality include ozone concentrations (Fuhrer, 2009; ICP Vegetation, 2011), plant diseases (Jaggard et al., 2010), pests (Bale et al., 2002), plant phenology (Menzel et al., 2006), grassland availability (EEA, 2012; Leclère, 2012; Rounsevell et al., 2005) and grassland species composition (IFAD, 2012; Thuiller et al., 2005; Trnka et al., 2011). All these factors have been extensively researched individually, but they interact with one another, with atmospheric CO_2 concentrations and with climatic changes. There is a need for a more holistic view which brings all these factors together in order to get an accurate picture of what to expect in the future.

Bibliography

Abdalla, M., Jones, M., Yeluripati, J., Smith, P., Burke, J., Williams, M., 2010. Testing DayCent and DNDC model simulations of N2O fluxes and assessing the impacts of climate change on the gas flux and biomass production from a humid pasture. Atmos. Environ. 44, 2961–2970. doi:10.1016/J.ATMOSENV.2010.05.018

Abreu, J.P.D.M.E., Flores, I., De Abreu, F.M.G., Madeira, M. V., 1993. Nitrogen uptake in relation to water availability in wheat. Plant Soil 154, 89–96. doi:10.1007/BF00011076

ADAS, 2014. Impact of 2014 Winter Floods on Agriculture in England.

AHDB, 2014. Effects of flooding on pasture [WWW Document]. URL https://dairy.ahdb.org.uk/news/technical-article-archive/february-2014/coping-with-flooding/#.WJcGrFWLREY (accessed 2.5.17).

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

Allison, C.D., 1985. Factors Affecting Forage Intake by Range Ruminants: A Review. J. Range Manag. 38, 305–311. doi:10.2307/3899409

Andresen, L.C., Michelsen, A., Jonasson, S., Beier, C., Ambus, P., 2009. Glycine uptake in heath plants and soil microbes responds to elevated temperature, CO2 and drought. Acta Oecologica 35, 786–796. doi:10.1016/j.actao.2009.08.010

Ansquer, P., Al Haj Khaled, R., Cruz, P., Theau, J.-P., Therond, O., Duru, M., 2009. Characterizing and predicting plant phenology in species-rich grasslands. Grass Forage Sci. 64, 57–70. doi:10.1111/j.1365-2494.2008.00670.x

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. doi:10.2307/2404857

Bale, J.S., Masters, G.J., Hodkinson, I.D., Awmack, C., Bezemer, T.M., Brown, V.K., Butterfield, J., Buse, A., Coulson, J.C., Farrar, J., Good, J.E.G., Harrington, R., Hartley, S., Jones, T.H., Lindroth, R.L., Press, M.C., Symrnioudis, I., Watt, A.D., Whittaker, J.B., 2002. Herbivory in global climate change research: direct effects of rising temperature on insect herbivores. Glob. Chang. Biol. 8, 1–16. doi:10.1046/j.1365-2486.2002.00451.x

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, Ghent, Belgium, pp. 150–153.

Banik, S., Pankaj, P.K., Naskar, S., 2015. Climate change: Impacts on livestock diversity in tropical countries, in: Malik, P.K., Bhatta, R., Takahashi, J., Kohn, R.A., Prasad, C.S. (Eds.), Livestock Production and Climate Change. CABI, pp. 162–182.

Beer, C., Weber, U., Tomelleri, E., Carvalhais, N., Mahecha, M., Reichstein, M., 2014. Harmonized European long-term climate data for assessing the effect of changing temporal variability on land-atmosphere CO2 fluxes. J. Clim. 27, 4815–4834. doi:10.1175/JCLI-D-13-00543.1

Bellocchi, G., Shaoxiu, M., Köchy, M., Braunmiller, K., 2013. Identified grassland-livestock production systems and related models (D-L2.1.1).

Bellocchi, G., Villalobos, F.J., Donatelli, M., Christensen, O.B., Rojas, O., Confalonieri, R., Athanasiadis, I.N., Carpusca, I., Stöckle, C.O., 2014. Extending existing models to capture vegetation response to extreme weather events: the MODEXTREME project, in: International Conference on Environmental Modelling and Software. San Diego, California.

Bencini, R., Pulina, G., 1997. The quality of sheep milk: a review. Aust. J. Exp. Agric. 37, 485–504. doi:10.1071/EA96014

Benestad, R., Haensler, A., Hennemuth, B., Illy, T., Jacob, D., Keup-Thiel, E., Kotlarski, S., Nikulin, G., Otto, J., Rechid, D., Sieck, K., Sobolowski, S., Szabó, P., Szépszó, G., Teichmann, C., Vautard, R., Weber, T., Zsebeházi, G., 2017. Guidance for EURO-CORDEX climate projections data use. doi:10.1186/2193-2697-1-9

Bett, P.E., THornton, H.E., Clark, R.T., 2013. European wind variability over 140yr. Adv. Sci. Res. 10, 51–58.

Brookshire, E.N.J., Weaver, T., 2015. Long-term decline in grassland productivity driven by increasing dryness. Nat. Commun. 6. doi:10.1038/ncomms8148

Brown, I., Thompson, D., Bardgett, R., Berry, P., Crute, I., Morison, J., Morecroft, M., Pinnegar, J., Reeder, T., Topp, K., 2016. UK Climate Change Risk Assessment Evidence Report: Chapter 3, Natural Environment and Natural Assets. London.

Brown, L., Scholefield, D., Jewkes, E.C., Lockyer, D.R., Del Prado, A., 2005. NGAUGE: A decision support system to optimise N fertilisation of British grassland for economic and environmental goals. Agric. Ecosyst. Environ. 109, 20–39. doi:10.1016/j.agee.2005.02.021

Brunagel, M., Menez, V., Mottet, A., Chotteau, P., Ashworth, S., Brennan, P., Hadjigeorgiou, I., Paolini, S., Langreo, A., Kukovics, S., 2008. The future of the sheep and goat sector in Europe. Brussels.

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.

Byrne, K.M., Lauenroth, W.K., Adler, P.B., 2013. Contrasting Effects of Precipitation Manipulations on Production in Two Sites within the Central Grassland Region, USA. Ecosystems 16, 1039–1051. doi:10.1007/s10021-013-9666-z

Byrnes, B.H., 1990. Environmental effects of N fertilizer use - An overview. Fertil. Res. 26, 209–215. doi:10.1007/BF01048758

Cabiddu, A., Carta, G., Decandia, M., Addis, M., Piredda, G., Delogu, A., Pirisi, A., Lai, V., Cera, V., Taras, L., Lallai, C., Banni, S., 2005. Relationship between feeding regimen and content of conjugated linoleic acid in sheep milk and cheese, in: Molina Alcaide, E., Ben Salem, H., Biala, K., Morand-Fehr, P. (Eds.), Sustainable Grazing, Nutritional Utilization and Quality of Sheep and Goat Products. CIHEAM, pp. 171–175.

Campbell, B.D., Stafford Smith, D.M., GCTE Pastures and Rangelands Network, 2000. A synthesis of recent global change research on pasture and rangeland production: reduced uncertainties and their management implications. Agric. Ecosyst. Environ. 82, 39–55. doi:10.1016/S0167-8809(00)00215-2

Cantarel, A.A.M., Bloor, J.M.G., Soussana, J.-F., 2013. Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. J. Veg. Sci. 24, 113–126. doi:10.1111/j.1654-1103.2012.01452.x

Carlsson, M., Merten, M., Kayser, M., Isselstein, J., Wrage-Mönnig, N., 2017. Drought stress resistance and resilience of permanent grasslands are shaped by functional group composition and N fertilization. Agric. Ecosyst. Environ. 236, 52–60. doi:10.1016/j.agee.2016.11.009

Carter, E.B., Theodorou, M.K., Morris, P., 1999. Responses of Lotus corniculatus to environmental change. 2. Effect of elevated CO2, temperature and drought on tissue digestion in relation to condensed tannin and carbohydrate accumulation. J. Sci. Food Agric. 79, 1431–1440. doi:10.1002/(SICI)1097-0010(199908)79:11<1431::AID-JSFA384>3.0.CO;2-4

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. 6, 2165–2181. doi:10.5194/gmd-6-2165-2013

Chollet, S., Rambal, S., Fayolle, A., Hubert, D., Foulquie, D., Garnier, E., 2014. Combined effects of climate, resource availability, and plant traits on biomass produced in a Mediterranean rangeland. Ecology 95, 737–748. doi:10.1890/13-0751.1

Christensen, J.H., Kumar, K.K., Aldrian, E., An, S.-I., Cavalcanti, I.F.A., De Castro, M., Dong, W., Goswami, P., Hall, A., Kanyanga, J.K., Kitoh, A., Kossin, J., Lau, N.-C., Renwick, J., Stephenson, D.B., Xie, S.-P., Zhou, T., 2013. Climate Phenomena and their Relevance for Future Regional Climate Change, in: Stocker, T.F., Qin, D., Plattner, G.K., Tignor, M., Allen, S.K., Boschung, J., Nauels, A., Xia, Y., Bex, V., Midgley, P.M. (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. 1217–1308.

Christensen, L., Coughenour, M.B., Ellis, J.E., Chen, Z.Z., 2004. Vulnerability of the Asian Typical Steppe to Grazing and Climate Change. Clim. Change 63, 351–368. doi:10.1023/B:CLIM.0000018513.60904.fe

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.

CORDEX, 2018. EUR-11i results of SMHI for daily maximum and minimum near-surface air temperature and precipitation for MOHC-HadGEM2-ES model [WWW Document]. URL https://esgf-index1.ceda.ac.uk/search/cordex-ceda/ (accessed 10.23.18).

Cotrufo, M.F., Ineson, P., Scott, A., 1998. Elevated CO2 reduces the nitrogen concentration of plant tissues. Glob. Chang. Biol. 4, 43–54. doi:10.1046/j.1365-2486.1998.00101.x

Craine, J.M., Ocheltree, T.W., Nippert, J.B., Towne, E.G., Skibbe, A.M., Kembel, S.W., Fargione, J.E., 2012. Global diversity of drought tolerance and grassland climate-change resilience. Nat. Clim. Chang. 3, 63–67. doi:10.1038/nclimate1634

Cregger, M.A., McDowell, N.G., Pangle, R.E., Pockman, W.T., Classen, A.T., 2014. The impact of precipitation change on nitrogen cycling in a semi-arid ecosystem. Funct. Ecol. 28, 1534–1544. doi:10.1111/1365-2435.12282

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. doi:10.1080/09064710.2016.1208268

De Luis, I., Irigoyen, J.J., Sanchez-Diaz, M., 1999. Elevated CO2 enhances plant growth in droughted N-2-fixing alfalfa without improving water status. Physiol. Plant. 107, 84–89. doi:10.1034/j.1399-3054.1999.100112.x

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. Change 67, 44–50. doi:10.1016/J.GLOPLACHA.2008.12.006

Del Prado, A., Van Den Pol-van Dasselaar, A., Chadwick, D., Misselbrook, T., Sandars, D., Audsley, E., Mosquera-Losada, M.R., 2014. Synergies between mitigation and adaptation to climate change in grassland-based farming systems, in: Hopkins, A., Collins, R.P., Fraser, M.D., King, V.R., Lloyd, D.C., Moorby, J.M., Robson, P.R.H. (Eds.), EGF at 50: The Future of European Grasslands. Proceedings of the 25th General Meeting of the European Grassland Federation. Aberystwyth, Wales.

Deléglise, C., Meisser, M., Mosimann, E., Spiegelberger, T., Signarbieux, C., Jeangros, B., Buttler, A., 2015. Drought-induced shifts in plants traits, yields and nutritive value under realistic grazing and mowing managements in a mountain grassland. Agric. Ecosyst. Environ. 213, 94–104. doi:10.1016/j.agee.2015.07.020

Dellar, M., Topp, C.F.E., Banos, G., Wall, E., 2019a. Modelling the impact of climate change on the yield and N content of European grasslands. Manuscript submitted for publication

Dellar, M., Topp, C.F.E., Banos, G., Wall, E., 2018. A meta-analysis on the effects of climate change on the yield and quality of European pastures. Agric. Ecosyst. Environ. doi:10.1016/j.agee.2018.06.029

Dellar, M., Topp, C.F.E., Pardo, G., del Prado, A., Fitton, N., Holmes, D., Banos, G., Wall, E., 2019b. Empirical and dynamic approaches for modelling the yield and N content of European grasslands. Environ. Model. Softw. 122, 104562. doi:https://doi.org/10.1016/j.envsoft.2019.104562

Denton, E.M., Dietrich, J.D., Smith, M.D., Knapp, A.K., 2017. Drought timing differentially affects above- and belowground productivity in a mesic grassland. Plant Ecol. 218, 317–328. doi:10.1007/s11258-016-0690-x

Devine, C.E., Graafhuis, A.E., Muir, P.D., Chrystall, B.B., 1993. The effect of growth rate and ultimate pH on meat quality of lambs. Meat Sci. 35, 63–77. doi:10.1016/0309-1740(93)90070-X

DG for Health and Food Safety, 2017. Welfare of cattle on dairy farms. Luxembourg. doi:10.2875/815860

Diaz, S., Fraser, L.H., Grime, J.P., Falczuk, V., 1998. The impact of elevated CO2 on plant-herbivore interactions: experimental evidence of moderating effects at the community level. Oecologia 117, 177–186. doi:10.1007/s004420050646

Dibari, C., Argenti, G., Catolfi, F., Moriondo, M., Staglianò, N., Bindi, M., 2015. Pastoral suitability driven by future climate change along the Apennines. Ital. J. Agron. 10, 109. doi:10.4081/ija.2015.659

Dieleman, W.I.J., Vicca, S., Dijkstra, F.A., Hagedorn, F., Hovenden, M.J., Larsen, K.S., Morgan, J.A., Volder, A., Beier, C., Dukes, J.S., King, J., Leuzinger, S., Linder, S., Luo, Y., Oren, R., De Angelis, P., Tingey, D., Hoosbeek, M.R., Janssens, I.A., 2012. Simple additive effects are rare: a quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature. Glob. Chang. Biol. 18, 2681–2693. doi:10.1111/j.1365-2486.2012.02745.x

Donath, T.W., Hölzel, N., Bissels, S., Otte, A., 2004. Perspectives for incorporating biomass from non-intensively managed temperate flood-meadows into farming systems. Agric. Ecosyst. Environ. 104, 439–451. doi:10.1016/j.agee.2004.01.039

Dubrovský, M., Žalud, Z., Šťastná, M., 2000. Sensitivity of Ceres-Maize Yields to Statistical Structure of Daily Weather Series. Clim. Change 46, 447–472. doi:10.1023/A:1005681809065

Duckworth, J.C., Bunce, R.G.H., Malloch, A.J.C., 2000. Modelling the potential effects of climate change on calcareous grasslands in Atlantic Europe. J. Biogeogr. 27, 347–358. doi:10.1046/j.1365-2699.2000.00400.x

Dumont, B., Andueza, D., Niderkorn, V., Lüscher, A., Porqueddu, C., Picon-Cochard, C., 2015. A meta-analysis of climate change effects on forage quality in grasslands: specificities of mountain and Mediterranean areas. Grass Forage Sci. 70, 239–254. doi:10.1111/gfs.12169

DWD, 2019. CDC (Climate Data Center) [WWW Document]. Dtsch. Wetterd. URL https://www.dwd.de/EN/climate_environment/cdc/cdc_node.html

EEA, 2017. Climate change, impacts and vulnerability in Europe 2016. Luxembourg.

EEA, 2016. River Floods [WWW Document]. URL http://www.eea.europa.eu/data-and-maps/indicators/river-floods-2/assessment (accessed 2.7.17).

EEA, 2012. Climate change, impacts and vulnerability in Europe 2012. Copenhagen.

Eldridge, D.J., Bowker, M.A., Maestre, F.T., Roger, E., Reynolds, J.F., Whitford, W.G., 2011. Impacts of shrub encroachment on ecosystem structure and functioning: towards a global synthesis. Ecol. Lett. 14, 709–722. doi:10.1111/j.1461-0248.2011.01630.x

Elst, E.M., De Boeck, H.J., Vanmaele, L., Verlinden, M., Dhliwayo, P., Nijs, I., 2017. Impact of climate extremes modulated by species characteristics and richness. Perspect. Plant Ecol. Evol. Syst. 24, 80–92. doi:10.1016/J.PPEES.2016.12.007

English Nature, 2006. The importance of livestock grazing for wildlife conservation. Peterborough.

Environmental Geography, 2018. Agricultural Land Use Intensity Data [WWW Document]. Inst. Environ. Stud. VU Univ. Amsterdam. URL https://www.environmentalgeography.nl/site/data-models/data/agricultural-land-use-intensity-data/ (accessed 1.18.18).

Ergon, Å., Seddaiu, G., Korhonen, P., Virkajärvi, P., Bellocchi, G., Jørgensen, M., Østrem, L., Reheul, D., Volaire, F., 2018. How can forage production in Nordic and Mediterranean Europe adapt to the challenges and opportunities arising from climate change? Eur. J. Agron. 92, 97–106. doi:10.1016/j.eja.2017.09.016

Eurostat, 2018. Agricultural production - livestock and meat [WWW Document]. Stat. Explain. URL https://ec.europa.eu/eurostat/statistics-explained/index.php?title=Agricultural_production_-_livestock_and_meat#Livestock_population (accessed 10.4.19).

Eurostat, 2017. Land cover statistics [WWW Document]. Stat. Explain. URL https://ec.europa.eu/eurostat/statistics-explained/index.php/Land_cover_statistics (accessed 9.26.19).

FAO, 2016. Climate change and food security: risks and responses.

Farfan-Vignolo, E.R., Asard, H., 2012. Effect of elevated CO2 and temperature on the oxidative stress response to drought in Lolium perenne L. and Medicago sativa L. Plant Physiol. Biochem. 59, 55–62. doi:10.1016/j.plaphy.2012.06.014

Ffoulkes, C., 2018. 2018 Heatwave: Evaluating the resilience of agri-food supply chains [WWW Document]. ADAS News. URL https://www.adas.uk/News/2018-heatwave-evaluating-the-resilience-of-agri-food-supply-chains (accessed 9.27.19).

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. Nutr. Cycl. Agroecosystems 99, 119–133. doi:10.1007/s10705-014-9622-0

Forzieri, G., Feyen, L., Rojas, R., Flörke, M., Wimmer, F., Bianchi, A., 2014. Ensemble projections of future streamflow droughts in Europe. Hydrol. Earth Syst. Sci 18, 85–108. doi:10.5194/hess-18-85-2014

Franks, S.J., Sim, S., Weis, A.E., 2007. Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. Proc. Natl. Acad. Sci. U. S. A. 104, 1278–1282. doi:10.1073/pnas.0608379104

Fuhrer, J., 2009. Ozone risk for crops and pastures in present and future climates. Naturwissenschaften 96, 173–194. doi:10.1007/s00114-008-0468-7

Fuhrer, J., 2003. Agroecosystem responses to combinations of elevated CO2, ozone, and global climate change. Agric. Ecosyst. Environ. 97, 1–20. doi:10.1016/S0167-8809(03)00125-7

Gavrichkova, O., Liberati, D., Gunina, A., Guidolotti, G., de Dato, G., Calfapietra, C., De Angelis, P., Brugnoli, E., Kuzyakov, Y., 2017. Does long-term warming affect C and N allocation in a Mediterranean shrubland ecosystem? Evidence from a 13C and 15N labeling field study. Environ. Exp. Bot. 141, 170–180. doi:10.1016/J.ENVEXPBOT.2017.07.013

GERICS, 2019. The Regional Climate Model REMO [WWW Document]. GERICS Clim. Serv. Cent. Ger. URL https://remo-rcm.de/index.php.en

Giannakopoulos, C., Le Sager, P., Bindi, M., Moriondo, M., Kostopoulou, E., Goodess, C.M., 2009. Climatic changes and associated impacts in the Mediterranean resulting from a 2 °C global warming. Glob. Planet. Change 68, 209–224. doi:10.1016/j.gloplacha.2009.06.001

Golodets, C., Sternberg, M., Kigel, J., Boeken, B., Henkin, Z., Seligman, N.G., Ungar, E.D., 2015. Climate change scenarios of herbaceous production along an aridity gradient: vulnerability increases with aridity. Oecologia 177, 971–979. doi:10.1007/s00442-015-3234-5

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. doi:https://doi.org/10.1016/j.agee.2006.12.026

Goverde, M., Arnone, J.A., Erhardt, A., 2002. Species-specific reactions to elevated CO2 and nutrient availability in four grass species. Basic Appl. Ecol. 3, 221–227. doi:10.1078/1439-1791-00095

Grant, K., Kreyling, J., Beierkuhnlein, C., Jentsch, A., 2017. Importance of Seasonality for the Response of a Mesic Temperate Grassland to Increased Precipitation Variability and Warming. Ecosystems 20, 1454–1467. doi:10.1007/s10021-017-0122-3

Grant, K., Kreyling, J., Dienstbach, L.F.H., Beierkuhnlein, C., Jentsch, A., 2014a. Water stress due to increased intra-annual precipitation variability reduced forage yield but raised forage quality of a temperate grassland. Agric. Ecosyst. Environ. 186, 11–22. doi:10.1016/j.agee.2014.01.013

Grant, K., Kreyling, J., Heilmeier, H., Beierkuhnlein, C., Jentsch, A., 2014b. Extreme weather events and plant–plant interactions: shifts between competition and facilitation among grassland species in the face of drought and heavy rainfall. Ecol. Res. 29, 991–1001. doi:10.1007/s11284-014-1187-5

Graux, A.-I., Bellocchi, G., Lardy, R., Soussana, J.-F., 2013. Ensemble modelling of climate change risks and opportunities for managed grasslands in France. Agric. For. Meteorol. 170, 114–131. doi:10.1016/j.agrformet.2012.06.010

Griffiths, N., 2009. Pasture options after a coastal flood. NSW DPI Primefacts 782.

Grünzweig, J.M., Dumbur, R., 2012. Seed traits, seed-reserve utilization and offspring performance across pre-industrial to future CO2 concentrations in a Mediterranean community. Oikos 121, 579–588. doi:10.1111/j.1600-0706.2011.19770.x

Hadjigeorgiou, I., Osoro, K., Fragoso De Almeida, J.P., Molle, G., 2005. Southern European grazing lands: Production, environmental and landscape management aspects. Livest. Prod. Sci. 96, 51–59. doi:10.1016/j.livprodsci.2005.05.016

Hakala, K., Mela, T., 1996. The effects of prolonged exposure to elevated temperatures and elevated CO2 levels on the growth, yield and dry matter partitioning of field-sown meadow fescue. Agric. Food Sci. Finl. 5, 285–298.

Hall, D.O., Ojima, D.S., Parton, W.J., Scurlock, J.M.O., 1995. Response of temperate and tropical grasslands to CO2 and climate change. J. Biogeogr. 22, 537–547. doi:10.2307/2845952

Harrison, S.P., LaForgia, M.L., Latimer, A.M., 2018. Climate-driven diversity change in annual grasslands: Drought plus deluge does not equal normal. Glob. Chang. Biol. doi:10.1111/gcb.14018

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. doi:https://doi.org/10.1016/j.agee.2009.11.016

He, M., Dijkstra, F.A., 2014. Drought effect on plant nitrogen and phosphorus: A meta-analysis. New Phytol. 204, 924–931. doi:10.1111/nph.12952

Hebeisen, T., Luscher, A., Zanetti, S., Fischer, B.U., Hartwig, U.A., Frehner, M., Hendrey, G.R., Blum, H., Nosberger, J., 1997. Growth response of Trifolium repens L and Lolium perenne L as monocultures and bi-species mixture to free air CO2 enrichment and management. Glob. Chang. Biol. 3, 149–160. doi:10.1046/j.1365-2486.1997.00073.x

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.

Hedges, L. V., Gurevitch, J., Curtis, P.S., 1999. The meta-analysis of response ratios in experimental ecology. Ecology 80, 1150. doi:10.2307/177062

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: Applied Vegetation Science.

Henry, H.A.L., Abedi, M., Alados, C.L., Beard, K.H., Fraser, L.H., Jentsch, A., Kreyling, J., Kulmatiski, A., Lamb, E.G., Sun, W., Vankoughnett, M.R., Venn, S., Werner, C., Beil, I., Blindow, I., Dahlke, S., Dubbert, M., Effinger, A., Garris, H.W., Gartzia, M., Gebauer, T., Arfin Khan, M.A.S., Malyshev, A. V., Morgan, J., Nock, C., Paulson, J.P., Pueyo, Y., Stover, H.J., Yang, X., 2018. Increased Soil Frost Versus Summer Drought as Drivers of Plant Biomass Responses to Reduced Precipitation: Results from a Globally Coordinated Field Experiment. Ecosystems 21, 1432–1444. doi:10.1007/s10021-018-0231-7

Hofer, D., Suter, M., Buchmann, N., Lüscher, A., 2017. Nitrogen status of functionally different forage species explains resistance to severe drought and post-drought overcompensation. Agric. Ecosyst. Environ. 236, 312–322.

doi:10.1016/j.agee.2016.11.022

Hogan, J.P., Phillips, C.J.C., Agenäs, S., 2008. Nutrition and the welfare of sheep, in: Dwyer, C. (Ed.), The Welfare of Sheep. Springer Netherlands, Dordrecht, pp. 267–290. doi:10.1007/978-1-4020-8553-6_7

Höglind, M., Thorsen, S.M., Semenov, M.A., 2013. Assessing uncertainties in impact of climate change on grass production in Northern Europe using ensembles of global climate models. Agric. For. Meteorol. 170, 103–113. doi:10.1016/j.agrformet.2012.02.010

Hopkins, A., Del Prado, A., 2007. Implications of climate change for grassland in Europe: impacts, adaptations and mitigation options: a review. Grass Forage Sci. 62, 118–126. doi:10.1111/j.1365-2494.2007.00575.x

Hovenden, M.J., Newton, P.C.D., 2018. Variability in precipitation seasonality limits grassland biomass responses to rising CO2: historical and projected climate analyses. Clim. Change 149, 219–231. doi:10.1007/s10584-018-2227-x

Hovenden, M.J., Newton, P.C.D., Osanai, Y., 2017. Warming has a larger and more persistent effect than elevated CO2 on growing season soil nitrogen availability in a species-rich grassland. Plant Soil 421, 417–428. doi:10.1007/s11104-017-3474-8

Hovenden, M.J., Newton, P.C.D., Wills, K.E., 2014. Seasonal not annual rainfall determines grassland biomass response to carbon dioxide. Nature 511, 583–586. doi:10.1038/nature13281

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. Irish Geogr. 46, 175–201. doi:10.1080/00750778.2013.865364

Huston, J.E., Engdahl, B.S., Bales, K.W., 1988. Intake and digestibility in sheep and goats fed three forages with different levels of supplemental protein. Small Rumin. Res. 1, 81–92. doi:10.1016/0921-4488(88)90047-8

ICP Vegetation, 2011. Ozone pollution: A hidden threat to food security. Bangor, Wales.

IFAD, 2012. Livestock and climate change. Rome.

IPCC, 2013a. Annex II: Climate system scenario tables, in: Prather, M., Flato, G., Friedlingstein, P., Jones, C., Lamarque, J.-F., Liao, H., Rasch, P. (Eds.), Climate Change 2013: The Physical Science Basis. Contribution of Working Group 1 to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK and New York, USA, pp. 1395–1445.

IPCC, 2013b. 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.

Isbell, F., Craven, D., Connolly, J., Loreau, M., Schmid, B., et al., 2015. Biodiversity Increases the Resistance of Ecosystem Productivity to Climate Extremes. Nat. - Lett. 526, 574–577.

Jacob, D., Petersen, J., Eggert, B., Alias, A., Christensen, O.B., Bouwer, L.M., Braun, A., Colette, A., Déqué, M., Georgievski, G., Georgopoulou, E., Gobiet, A., Menut, L., Nikulin, G., Haensler, A., Hempelmann, N., Jones, C., Keuler, K., Kovats, S., Kröner, N., Kotlarski, S., Kriegsmann, A., Martin, E., van Meijgaard, E., Moseley, C., Pfeifer, S., Preuschmann, S., Radermacher, C., Radtke, K., Rechid, D., Rounsevell, M., Samuelsson, P., Somot, S., Soussana, J.-F., Teichmann, C., Valentini, R., Vautard, R., Weber, B., Yiou, P., 2014. EURO-CORDEX: new high-resolution climate change projections for European impact research. Reg. Environ. Chang. 14, 563–578. doi:10.1007/s10113-013-0499-2

Jaggard, K.W., Qi, A., Ober, E.S., 2010. Possible changes to arable crop yields by 2050. Philos. Trans. R. Soc. London B Biol. Sci. 365, 2835–2851. doi:10.1098/rstb.2010.0153

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. doi:10.1017/S0021859600067290

Jonasson, S., Michelsen, A., Schmidt, I.K., Nielsen, E. V, 1999. Responses in microbes and plants to changed temperature, nutrient, and light regimes in the arctic. Ecology 80, 1828–1843. doi:10.1890/0012-9658(1999)080{[}1828:RIMAPT]2.0.CO;2

Jones, E., Oliphant, E., Peterson, P., Al., E., 2001. SciPy: Open Source Scientific Tools for Python.

Jubb, I., Dix, M., 2016. Representative Concentration Pathways (RCPs). Aust. Clim. Chang. Sci. Progr. doi:10.1007/s10584-011-0156-z

Jung, V., Albert, C.H., Violle, C., Kunstler, G., Loucougaray, G., Spiegelberger, T., 2014. Intraspecific trait variability mediates the response of subalpine grassland communities to extreme drought events. J. Ecol. 102, 45–53. doi:10.1111/1365-2745.12177

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.

Kenyon, F., Sargison, N.D., Skuce, P.J., Jackson, F., 2009. Sheep helminth parasitic disease in south eastern Scotland arising as a possible consequence of climate change. Vet. Parasitol. 163, 293–297. doi:10.1016/j.vetpar.2009.03.027

Khan, M.A.S.A., Grant, K., Beierkuhnlein, C., Kreyling, J., Jentsch, A., 2014. Climatic extremes lead to species-specific legume facilitation in an experimental temperate grassland. Plant Soil 379, 161–175. doi:10.1007/s11104-014-2050-8

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. doi:10.1371/journal.pone.0174632

Kimball, B.A., Kobayashi, K., Bindi, M., 2002. Responses of Agricultural Crops to Free-Air CO2 Enrichment, in: Advances in Agronomy. pp. 293–368. doi:10.1016/S0065-2113(02)77017-X

Kipling, R.P., Virkajärvi, P., Breitsameter, L., Curnel, Y., De Swaef, T., Gustavsson, A.-M., Hennart, S., Höglind, M., Järvenranta, K., Minet, J., Nendel, C., Persson, T., Picon-Cochard, C., Rolinski, S., Sandars, D.L., Scollan, N.D., Sebek, L., Seddaiu, G., Topp, C.F.E., Twardy, S., Van Middelkoop, J., Wu, L., Bellocchi, G., 2016. Key challenges and priorities for modelling European grasslands under climate change. Sci. Total Environ. 566–567, 851–64. doi:10.1016/j.scitotenv.2016.05.144

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. doi: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. doi:10.1111/j.1365-2486.2011.02490.x

KNMI, 2019. Daggegevens van het weer in Nederland [WWW Document]. K. Ned. Meteorol. Inst. URL https://www.knmi.nl/nederland-nu/klimatologie/daggegevens

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. doi: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. F. Crop. Res. 224, 37–47. doi:10.1016/J.FCR.2018.04.014

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.

Kreyling, J., Wenigmann, M., Beierkuhnlein, C., Jentsch, A., 2008. Effects of extreme weather events on plant productivity and tissue die-back are modified by community composition. Ecosystems 11, 752–763. doi:10.1007/s10021-008-9157-9

Küchenmeister, F., Küchenmeister, K., Kayser, M., Wrage-Moennig, N., Isselstein, J., 2014. Effects of Drought Stress and Sward Botanical Composition on the Nutritive Value of Grassland Herbage. Int. J. Agric. Biol. 16, 715–722.

Kunrath, T.R., Lemaire, G., Sadras, V.O., Gastal, F., 2018. Water use efficiency in perennial forage species: Interactions between nitrogen nutrition and water deficit. F. Crop. Res. 222, 1–11. doi:10.1016/J.FCR.2018.02.031

La Pierre, K.J., Blumenthal, D.M., Brown, C.S., Klein, J.A., Smith, M.D., 2016. Drivers of Variation in Aboveground Net Primary Productivity and Plant Community Composition Differ Across a Broad Precipitation Gradient. Ecosystems 19, 521–533. doi:10.1007/s10021-015-9949-7

Landau, S., Perevolotsky, A., Bonfil, D., Barkai, D., Silanikove, N., 2000. Utilization of low quality resources by small ruminants in Mediterranean agro-pastoral systems: the case of browse and aftermath cereal stubble. Livest. Prod. Sci. 64, 39–49. doi:10.1016/S0301-6226(00)00174-3

Leakey, A.D.B., Ainsworth, E.A., Bernacchi, C.J., Rogers, A., Long, S.P., Ort, D.R., 2009. Elevated CO2 effects on plant carbon, nitrogen, and water relations: six important lessons from FACE. J. Exp. Bot. 60, 2859–2876. doi:10.1093/jxb/erp096

Leclère, D., 2012. Offre agricole Europ{é}enne et changement climatique : une exploration r{é}gionale des enjeux li{é}s aux changements d'{é}chelle par la mod{é}lisation int{é}gr{é}e. Paris Institute of Technology.

Lee, M.A., Davis, A.P., Chagunda, M.G.G., Manning, P., 2017. Forage quality declines with rising temperatures, with implications for livestock production and methane emissions. Biogeosciences 14, 1403–1417. doi:10.5194/bg-14-1403-2017

Legay, N., Piton, G., Arnoldi, C., Bernard, L., Binet, M.N., Mouhamadou, B., Pommier, T., Lavorel, S., Foulquier, A., Clément, J.C., 2018. Soil legacy effects of climatic stress, management and plant functional composition on microbial communities influence the response of Lolium perenne to a new drought event. Plant Soil 424, 233–254. doi:10.1007/s11104-017-3403-x

Lelièvre, F., Seddaiu, G., Ledda, L., Porqueddu, C., Volaire, F., 2011. Water use efficiency and drought survival in Mediterranean perennial forage grasses. F. Crop. Res. 121, 333–342. doi:10.1016/j.fcr.2010.12.023

Lesschen, J.P., Elbersen, B., Hazeu, G., van Doorn, A., Mucher, S., Velthof, G.,

2014. Final report: Task 1 - Defining and classifying grasslands in Europe. Wageningen.

Li, W., Li, X., Zhao, Y., Zheng, S., Bai, Y., 2018. Ecosystem structure, functioning and stability under climate change and grazing in grasslands: current status and future prospects. Curr. Opin. Environ. Sustain. 33, 124–135. doi:10.1016/j.cosust.2018.05.008

Lindsey, R., 2019. Climate Change: Atmospheric Carbon Dioxide [WWW Document]. NOAA. URL https://www.climate.gov/news-features/understanding-climate/climate-change-atmospheric-carbon-dioxide (accessed 10.29.19).

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

Lüscher, A., Daepp, M., Blum, H., Hartwig, U.A., Nösberger, J., 2004. Fertile temperate grassland under elevated atmospheric CO2—role of feed-back mechanisms and availability of growth resources. Eur. J. Agron. 21, 379–398. doi:10.1016/j.eja.2003.10.009

LVĢMC, 2019. Meteoroloģiskos novērojumus [WWW Document]. Latv. Vides, Ģeologijas un Meteorol. Cent. URL https://www.meteo.lv/meteorologija-datu-meklesana/?nid=461 (accessed 11.26.19).

Madakadze, I.C., Stewart, K.A., Madakadze, R.M., Smith, D.L., 2003. Base Temperatures for Seedling Growth and Their Correlation with Chilling Sensitivity for Warm-Season Grasses. Crop Sci. 43, 874. doi:10.2135/cropsci2003.8740

Madsen, H., Lawrence, D., Lang, M., Martinkova, M., Kjeldsen, T.R., 2014. Review of trend analysis and climate change projections of extreme precipitation and floods in Europe. J. Hydrol. 519, 3634–3650. doi:10.1016/j.jhydrol.2014.11.003

Malek, Ž., Verburg, P., 2017. Mediterranean land systems: Representing diversity and intensity of complex land systems in a dynamic region. Landsc. Urban Plan. 165, 102–116. doi:10.1016/J.LANDURBPLAN.2017.05.012

Marissink, M., Pettersson, R., Sindhøj, E., 2002. Above-ground plant production under elevated carbon dioxide in a Swedish semi-natural grassland, Ecosystems and Environment.

Matesanz, S., Valladares, F., 2014. Ecological and evolutionary responses of Mediterranean plants to global change. Environ. Exp. Bot. 103, 53–67. doi:10.1016/j.envexpbot.2013.09.004

Matías, L., Castro, J., Zamora, R., 2011. Soil-nutrient availability under a global-change scenario in a Mediterranean mountain ecosystem. Glob. Chang. Biol. 17, 1646–1657. doi:10.1111/j.1365-2486.2010.02338.x

McMillin, K.W., 2010. Meat production and quality, in: Solaiman, S.G. (Ed.), Goat Science and Production. Wiley.

Meng, X.-L., 1994. Posterior predictive p-values. Ann. Stat. 22, 1142–1160. doi:10.2307/2242219

Menzel, A., Sparks, T.H., Estrella, N., Koch, E., Aasa, A., Ahas, R., Alm-Kübler, K., Bissolli, P., Braslavská, O., Briede, A., Chmielewski, F.M., Crepinsek, Z., Curnel, Y., Dahl, Å., Defila, C., Donnelly, A., Filella, Y., Jatczak, K., Mâge, F., Mestre, A., Nordli, Ø., Peñuelas, J., Pirinen, P., Remišová, V., Scheifinger, H., Striz, M., Susnik, A., Van Vliet, A.J.H., Wielgolaski, F.-E., Zach, S., Zust, A., 2006. European phenological response to climate change matches the warming pattern. Glob. Chang. Biol. 12, 1969–1976. doi:10.1111/j.1365-2486.2006.01193.x

Met Office, 2019. Met Office MIDAS Open: UK Land Surface Stations Data (1853-current) [WWW Document]. Cent. Environ. Data Anal. URL http://catalogue.ceda.ac.uk/uuid/dbd451271eb04662beade68da43546e1 (accessed 9.13.19).

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

Milchunas, D.G., Mosier, A.R., Morgan, J.A., Lecain, D.R., King, J.Y., Nelson, J.A., 2005. Elevated CO 2 and defoliation effects on a shortgrass steppe: Forage quality versus quantity for ruminants. Agric. Ecosyst. Environ. 111, 166–184. doi:10.1016/j.agee.2005.06.014

Molle, G., Decandia, M., Sölter, U., Greef, J.M., Rochon, J.J., Sitzia, M., Hopkins, A., Rook, A.J., 2008. The effect of different legume-based swards on intake and performance of grazing ruminants under Mediterranean and cool temperate conditions. Grass Forage Sci. 63, 513–530. doi:10.1111/j.1365-2494.2008.00659.x

Moran, D.C., Topp, K., Wall, E., Wreford, A., Chadwick, D.R., Hall, C., Hutchings, M.R., Mitchell, M.A., Del Prado, A., Tolkamp, B., Wu, L., Davidson, R., Dwyer, C.M., Haskell, M.J., McCracken, D., McVittie, A., Sandilands, V., Shepherd, A., Sparks, N., Thompson, S., 2009. Climate change impacts on the livestock sector.

Morand-Fehr, P., Fedele, V., Decandia, M., Le Frileux, Y., 2007. Influence of farming and feeding systems on composition and quality of goat and sheep milk. Small Rumin. Res. 68, 20–34. doi:10.1016/j.smallrumres.2006.09.019

Morris, J., Hess, T., 2008. Environment, Food and Rural Affairs - Written Evidence; Memorandum FL60 [WWW Document]. URL https://www.publications.parliament.uk/pa/cm200708/cmselect/cmenvfru/49/49we56.htm (accessed 2.5.17).

Morris, J., Posthumus, H., Hess, T., 2010. Agriculture's Role in Flood Adaptation and Mitigation, in: OECD Studies on Water. Organisation for Economic Cooperation and Development (OECD), pp. 1–35. doi:10.1787/9789264083578-9-en

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.

Moss, R.H., Edmonds, J.A., Hibbard, K.A., Manning, M.R., Rose, S.K., van Vuuren, D.P., 2010. The next generation of scenarios for climate change research and assessment. Nature 463, 747–756. doi:10.1038/nature08823

MRC, 2007. WinBUGS.

Nakicenovic, N., Alcamo, J., Davis, G., de Vries, B., Fenhann, J., Gaffin, S., Gregory, K., Griibler, A., Jung, T.Y., Kram, T., La Rovere, E.L., Michaelis, L., Mori, S., Morita, T., Pepper, W., Pitcher, H., Price, L., Riahi, K., Roehrl, A., Rogner, H.H., Sankovski, A., Schlesinger, M., Shukla, P., Smith, S., Swart, R., van Rooijen, S., Victor, N., Dadi, Z., 2000. Special report on emissions scenarios. Cambridge.

Nardone, A., Ronchi, B., Lacetera, N., Ranieri, M.S., Bernabucci, U., 2010. Effects of climate changes on animal production and sustainability of livestock systems. Livest. Sci. 130, 57–69. doi:10.1016/j.livsci.2010.02.011

NASD, 2009. Salvaging crops after flooding: Recovery of alfalfa, irrigated pastures and hay [WWW Document]. URL http://nasdonline.org/2016/d001484/salvaging-crops-after-flooding-recovery-of-alfalfa-irrigated.html (accessed 2.5.17).

Navas, M.L., Sonie, L., Richarte, J., Roy, J., 1997. The influence of elevated CO2 on species phenology, growth and reproduction in a Mediterranean old-field community. Glob. Chang. Biol. 3, 523–530. doi:10.1046/j.1365-2486.1997.00092.x

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. doi:10.1016/J.ENVSOFT.2014.12.011

Nicotra, A.B., Atkin, O.K., Bonser, S.P., Davidson, A.M., Finnegan, E.J., Mathesius, U., Poot, P., Purugganan, M.D., Richards, C.L., Valladares, F., van Kleunen, M., 2010. Plant phenotypic plasticity in a changing climate. Trends Plant Sci. 15, 684–692. doi:10.1016/j.tplants.2010.09.008

Nijs, I., Roy, J., Salager, J.-L., Fabreguettes, J., 2000. Elevated CO2 alters carbon fluxes in early successional Mediterranean ecosystems. Glob. Chang. Biol. 6, 981–994. doi:10.1046/j.1365-2486.2000.00378.x

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. doi:10.1890/0012-9615(2001)071[0341:ALTFSO]2.0.CO;2

Niu, S., Luo, Y., Li, D., Cao, S., Xia, J., Li, J., Smith, M.D., 2014. Plant growth and mortality under climatic extremes: An overview. Environ. Exp. Bot. 98, 13–19. doi:10.1016/j.envexpbot.2013.10.004

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

NREL, 2012. DayCent: Daily Century Model [WWW Document]. Nat. Resour. Ecol. Lab. Color. State Univ. URL https://www2.nrel.colostate.edu/projects/daycent-home.html (accessed 10.11.19).

Ntzoufras, I., 2009. Bayesian Modelling using WinBUGS. Wiley.

Obermeier, W.A., Lehnert, L.W., Kammann, C.I., Müller, C., Grünhage, L., Luterbacher, J., Erbs, M., Moser, G., Seibert, R., Yuan, N., Bendix, J., 2017. Reduced CO2 fertilization effect in temperate C3 grasslands under more extreme weather conditions. Nat. Clim. Chang. 7, 137–141. doi:10.1038/nclimate3191

Olofsson, J., Shams, H., 2007. Determinants of plant species richness in an alpine meadow. J. Ecol. 95, 916–925. doi:10.1111/j.1365-2745.2007.01284.x

Osborne, C.P., Mitchell, P.L., Sheehy, J.E., Woodward, F.I., 2000. Modelling the recent historical impacts of atmospheric CO2 and climate change on Mediterranean vegetation. Glob. Chang. Biol. 6, 445–458. doi:10.1046/j.1365-2486.2000.00336.x

Pakeman, R.J., Hewison, R.L., Riach, D., Fisher, J.M., Hurskainen, S., Fielding, D.A., Mitchell, R.J., 2017. Long-term functional structure and functional diversity changes in Scottish grasslands. Agric. Ecosyst. Environ. 247, 352–362. doi:10.1016/j.agee.2017.06.033

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. doi: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. Global Biogeochem. Cycles 7, 785–809. doi: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 , Kiel, Germany, pp. 536–538.

Petrie, M.D., Peters, D.P.C., Yao, J., Blair, J.M., Burruss, N.D., Collins, S.L., Derner, J.D., Gherardi, L.A., Hendrickson, J.R., Sala, O.E., Starks, P.J., Steiner, J.L., 2018. Regional grassland productivity responses to precipitation during multiyear above- and below-average rainfall periods. Glob. Chang. Biol. 24, 1935–1951. doi:10.1111/gcb.14024

Pugnaire, F.I., Serrano, L., Pardos, J., 1999. Constraints by water stress on plant growth, in: Pessarakli, M. (Ed.), Handbook of Plant and Crop Stress. Marcel Dekker, New York, USA and Basel, Switzerland, pp. 271–283.

Pulina, A., Lai, R., Salis, L., Seddaiu, G., Roggero, P.P., Bellocchi, G., 2018. Modelling pasture production and soil temperature, water and carbon fluxes in Mediterranean grassland systems with the Pasture Simulation model. Grass Forage Sci. 73, 272–283. doi:10.1111/gfs.12310

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. doi: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. Modell. 297, 196–200. doi: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.

Rapacz, M., Ergon, Å., Höglind, M., Jørgensen, M., Jurczyk, B., Østrem, L., Rognli, O.A., Tronsmo, A.M., 2014. Overwintering of herbaceous plants in a changing climate. Still more questions than answers. Plant Sci. 225, 34–44. doi:10.1016/j.plantsci.2014.05.009

Reyer, C.P.O., Leuzinger, S., Rammig, A., Wolf, A., Bartholomeus, R.P., Bonfante, A., de Lorenzi, F., Dury, M., Gloning, P., Abou Jaoudé, R., Klein, T., Kuster, T.M., Martins, M., Niedrist, G., Riccardi, M., Wohlfahrt, G., de Angelis, P., de Dato, G., François, L., Menzel, A., Pereira, M., 2013. A plant's perspective of extremes: terrestrial plant responses to changing climatic variability. Glob. Chang. Biol. 19, 75–89. doi:10.1111/gcb.12023

Reyes-Fox, M., Steltzer, H., Trlica, M.J., McMaster, G.S., Andales, A.A., LeCain, D.R., Morgan, J.A., 2014. Elevated CO2 further lengthens growing season under warming conditions. Nature 510, 259–262. doi:10.1038/nature13207

Riedo, M., Grub, A., Rosset, M., Fuhrer, J., 1998. A pasture simulation model for dry matter production, and fluxes of carbon, nitrogen, water and energy. Ecol. Modell. 105, 141–183. doi:10.1016/S0304-3800(97)00110-5

Rillig, M.C., Allen, M.F., Klironomos, J.N., Chiariello, N.R., Field, C.B., 1998. Plant species-specific changes in root-inhabiting fungi in a California annual grassland: responses to elevated CO 2 and nutrients. Oecologia 113, 252–259. doi:10.1007/s004420050376

Rivest, D., Rolo, V., López-Díaz, L., Moreno, G., 2011. Shrub encroachment in Mediterranean silvopastoral systems: Retama sphaerocarpa and Cistus ladanifer induce contrasting effects on pasture and Quercus ilex production. Agric. Ecosyst. Environ. 141, 447–454. doi:10.1016/J.AGEE.2011.04.018

Rojas, R., Feyen, L., Bianchi, A., Dosio, A., 2012. Assessment of future flood hazard in Europe using a large ensemble of bias-corrected regional climate simulations. J. Geophys. Res. Atmos. 117. doi:10.1029/2012JD017461

Rose, S.K., 2014. Integrated assessment modeling of climate change adaptation in forestry and pasture land use: A review. Energy Econ. 46, 548–554. doi:10.1016/J.ENECO.2014.09.018

Rötter, R., Höhn, J., 2015. An overview of climate change impact on crop production and its variability in Europe, related uncertainties and research challenges, in: Elbehri, A. (Ed.), Climate Change and Food Systems: Global Assessments and Implications for Food Security and Trade. FAO, Rome, pp. 106–145.

Rounsevell, M.D.A., Ewert, F., Reginster, I., Leemans, R., Carter, T.R., 2005. Future scenarios of European agricultural land use II. Projecting changes in cropland and grassland. Agric. Ecosyst. Environ. 107, 117–135. doi:10.1016/j.agee.2004.12.002

Rychnovská, M., 1993. Temperate semi-natural grasslands on Eurasia, in: Coupland, R.T. (Ed.), Ecosystems of the World: 8B Natural Grasslands. Elsevier, Amsterdan, The Netherlands, pp. 125–166.

SAC, INRA, 2000. An evaluation of the common organisation of the markets in the sheep and goatmeat sector.

Saltelli, A., Aleksankina, K., Becker, W., Fennell, P., Ferretti, F., Holst, N., Li, S., Wu, Q., 2019. Why so many published sensitivity analyses are false: A systematic review of sensitivity analysis practices. Environ. Model. Softw. 114, 29–39. doi:10.1016/j.envsoft.2019.01.012

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.

Sanaullah, M., Chabbi, A., Girardin, C., Durand, J.-L., Poirier, M., Rumpel, C., 2014. Effects of drought and elevated temperature on biochemical composition of forage plants and their impact on carbon storage in grassland soil. Plant Soil 374, 767–778. doi:10.1007/s11104-013-1890-y

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. doi:10.1016/J.EJA.2016.06.006

Sañudo, C., Sanchez, A., Alfonso, M., 1998. Small ruminant production systems and factors affecting lamb meat quality. Meat Sci. 49, S29–S64. doi:10.1016/S0309-1740(98)90037-7

Sanz-Saez, A., Erice, G., Aguirreolea, J., Munoz, F., Sanchez-Diaz, M., Jose Irigoyen, J., 2012. Alfalfa forage digestibility, quality and yield under future climate change scenarios vary with Sinorhizobium meliloti strain. J. Plant Physiol. 169, 782–788. doi:10.1016/j.jplph.2012.01.010

Sardans, J., Peñuelas, J., 2013. Plant-soil interactions in Mediterranean forest and shrublands: impacts of climatic change. Plant Soil 365, 1–33. doi:10.1007/s11104-013-1591-6

Sardans, J., Penuelas, J., Estiarte, M., Prieto, P., 2008. Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. Glob. Chang. Biol. 14, 2304–2316. doi:10.1111/j.1365-2486.2008.01656.x

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

Schmid, S., Hiltbrunner, E., Spehn, E., Lüscher, A., Scherer-Lorenzen, M., 2011. Impact of experimentally induced summer drought on biomass production in alpine grassland, in: Pötsch, E., Krautzer, B., Hopkins, A. (Eds.), Grassland Farming and Land Management Systems in Mountainous Region. Organising Committee of the 16th Symposium of the European Grassland Federation 2011 and Agricultural Research and Education Centre (AREC), Raumberg-Gumpenstein, Austria, pp. 214–216.

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. doi:10.1111/j.1365-2486.2004.00803.x

Schröder, B., Schöneberger, M., Rodehutscord, M., Pfeffer, E., Breves, G., 2003. Dietary protein reduction in sheep and goats: different effects on l-alanine and l-leucine transport across the brush-border membrane of jejunal enterocytes. J. Comp. Physiol. B 173, 511–518. doi:10.1007/s00360-003-0359-3

Schuerings, J., Beierkuhnlein, C., Grant, K., Jentsch, A., Malyshev, A., Penuelas, J., Sardans, J., Kreyling, J., 2013. Absence of soil frost affects plant-soil interactions in temperate grasslands. Plant Soil 371, 559–572.

doi:10.1007/s11104-013-1724-y

Semenov, M.A., Porter, J.R., 1995. Climatic variability and the modelling of crop yields. Agric. For. Meteorol. 73, 265–283. doi:10.1016/0168-1923(94)05078-K

Sevi, A., Casamassima, D., Pulina, G., Pazzona, A., 2009. Factors of welfare reduction in dairy sheep and goats. Ital. J. Anim. Sci. 8, 81–101. doi:10.4081/ijas.2009.s1.81

Silanikove, N., 2000. Effects of heat stress on the welfare of extensively managed domestic ruminants. Livest. Prod. Sci. 67, 1–18. doi:10.1016/S0301-6226(00)00162-7

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.

SMHI, 2019. SMHI: Data [WWW Document]. Sveriges Meteorol. och Hydrol. Inst. URL https://www.smhi.se/data

Smit, H.J., Metzger, M.J., Ewert, F., 2008. Spatial distribution of grassland productivity and land use in Europe. Agric. Syst. 98, 208–219. doi:10.1016/J.AGSY.2008.07.004

Soares, J.C., Santos, C.S., Carvalho, S.M.P., Pintado, M.M., Vasconcelos, M.W., 2019. Preserving the nutritional quality of crop plants under a changing climate: importance and strategies. Plant Soil 443, 1–26. doi:10.1007/s11104-019-04229-0

Sotiraki, S., Stefanakis, A., Hoste, H., Maurer, V., Butler, G., Leifert, C., 2013. The role of biotic and abiotic stress factors on sheep welfare: The example of parasites and climatic changes in European countries, in: Ben Salem, H., López-Francos, A. (Eds.), Feeding and Management Strategies to Improve Livestock Productivity, Welfare and Product Quality under Climate Change. CIHEAM, pp. 159–169.

Squintu, A.A., van der Schrier, G., van den Besselaar, E.J.M., 2019. EUSTACE / ECA&D: European land station daily air temperature measurements, homogenised. European Climate Assessment & Dataset [WWW Document].

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.

Stampfli, A., Bloor, J.M.G., Fischer, M., Zeiter, M., 2018. High land-use intensity exacerbates shifts in grassland vegetation composition after severe experimental drought. Glob. Chang. Biol. 24, 2021–2034.

doi:10.1111/gcb.14046

Stevnbak, K., Scherber, C., Gladbach, D.J., Beier, C., Mikkelsen, T.N., Christensen, S., 2012. Interactions between above- and belowground organisms modified in climate change experiments. Nat. Clim. Chang. 2, 805–808. doi:10.1038/NCLIMATE1544

Stuart-Haëntjens, E., De Boeck, H.J., Lemoine, N.P., Mänd, P., Kröel-Dulay, G., Schmidt, I.K., Jentsch, A., Stampfli, A., Anderegg, W.R.L., Bahn, M., Kreyling, J., Wohlgemuth, T., Lloret, F., Classen, A.T., Gough, C.M., Smith, M.D., 2018. Mean annual precipitation predicts primary production resistance and resilience to extreme drought. Sci. Total Environ. 636, 360–366. doi:10.1016/J.SCITOTENV.2018.04.290

Thébault, A., Mariotte, P., Lortie, C.J., MacDougall, A.S., Thebault, A., Mariotte, P., Lortie, C.J., MacDougall, A.S., 2014. Land management trumps the effects of climate change and elevated CO2 on grassland functioning. J. Ecol. 102, 896–904. doi:10.1111/1365-2745.12236

Thornley, J.H.M., Cannell, M.G.R., 1997. Temperate Grassland Responses to Climate Change : an Analysis using the Hurley Pasture Model. Ann. Bot. 80, 205–221.

Thornton, P.K., Herrero, M., Thornton, P.K., Herrero, M., 2009. The inter-linkages between rapid growth in livestock production, climate change, and the impacts on water resources, land use, and deforestation. World Dev. Rep. 2010.

Thorsen, S.M., Höglind, M., 2010. Assessing winter survival of forage grasses in Norway under future climate scenarios by simulating potential frost tolerance in combination with simple agroclimatic indices. Agric. For. Meteorol. 150, 1272–1282. doi:10.1016/j.agrformet.2010.05.010

Thuiller, W., Lavorel, S., Araújo, M.B., Sykes, M.T., Prentice, I.C., 2005. Climate change threats to plant diversity in Europe. Proc. Natl. Acad. Sci. U. S. A. 102, 8245–50. doi:10.1073/pnas.0409902102

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, Kiel, Germany, pp. 90–92.

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., Bartošová, L., Schaumberger, A., Ruget, F., Eitzinger, J., Formayer, H., Seguin, B., Olesen, J.E., 2011. Climate change and impact on European grasslands, in: Pötsch, E., Krautzer, B., Hopkins, A. (Eds.), 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, Austria, pp. 39–51.

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. doi:10.1111/j.1365-2494.2006.00530.x

Tubiello, F.N., Soussana, J.-F., Howden, S.M., 2007. Crop and pasture response to climate change. Proc. Natl. Acad. Sci. U. S. A. 104, 19686–19690. doi:10.1073/pnas.0701728104

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 (Jan. 1901- Dec. 2016) [WWW Document]. Cent. Environ. Data Anal. doi:10.5285/58a8802721c94c66ae45c3baa4d814d0

Vanuytrecht, E., Thorburn, P.J., 2017. Responses to atmospheric CO2 concentrations in crop simulation models: a review of current simple and semicomplex representations and options for model development. Glob. Chang. Biol. 23, 1806–1820. doi:10.1111/gcb.13600

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.

Velthof, G.L., Lesschen, J.P., Schils, R.L.M., Smit, A., Elbersen, B.S., Hazeu, G.W., Mucher, C.A., Oenema, O., 2014. Grassland areas, production and use. Wageningen.

Vital, J.-A., Gaurut, M., Lardy, R., Viovy, N., Sousanna, J.-F., Bellocchi, G., Martin, R., 2013. High-performance computing for climate change impact studies with the Pasture Simulation model. Comput. Electron. Agric. 98, 131–135. doi:10.1016/J.COMPAG.2013.08.004

Volaire, F., Norton, M.R., Lelièvre, F., 2009. Summer drought survival strategies and sustainability of perennial temperate forage grasses in Mediterranean areas. Crop Sci. 49, 2386–2392. doi:10.2135/cropsci2009.06.0317

VSNi, 2013. GenStat.

Walter, J., Hein, R., Auge, H., Beierkuhnlein, C., Löffler, S., Reifenrath, K., Schädler, M., Weber, M., Jentsch, A., 2012. How do extreme drought and plant community composition affect host plant metabolites and herbivore performance? Arthropod. Plant. Interact. 6, 15–25. doi:10.1007/s11829-011-9157-0

Walter, J., Jentsch, A., Beierkuhnlein, C., Kreyling, J., 2013. Ecological stress memory and cross stress tolerance in plants in the face of climate extremes. Environ. Exp. Bot. 94, 3–8. doi:10.1016/j.envexpbot.2012.02.009

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

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. Modell. 259, 16–23. doi:10.1016/j.ecolmodel.2013.03.008

Wang, X., 2007. Effects of species richness and elevated carbon dioxide on biomass accumulation: a synthesis using meta-analysis. Oecologia 152, 595–605. doi:10.1007/s00442-007-0691-5

Watson, R.T., Zinyowera, M.C., Moss, R.H., 1997. The Regional Impacts of Climate Change. Cambridge University Press.

Wellstein, C., Poschlod, P., Gohlke, A., Chelli, S., Campetella, G., Rosbakh, S., Canullo, R., Kreyling, J., Jentsch, A., Beierkuhnlein, C., 2017. Effects of extreme drought on specific leaf area of grassland species: a meta-analysis of experimental studies in temperate and sub-Mediterranean systems. Glob. Chang. Biol. Accepted. doi:10.1111/gcb.13662

Wilcox, K.R., Shi, Z., Gherardi, L.A., Lemoine, N.P., Koerner, S.E., Hoover, D.L., Bork, E., Byrne, K.M., Cahill, J., Collins, S.L., Evans, S., Gilgen, A.K., Holub, P., Jiang, L., Knapp, A.K., LeCain, D., Liang, J., Garcia-Palacios, P., Peñuelas, J., Pockman, W.T., Smith, M.D., Sun, S., White, S.R., Yahdjian, L., Zhu, K., Luo, Y., 2017. Asymmetric responses of primary productivity to precipitation extremes: A synthesis of grassland precipitation manipulation experiments. Glob. Chang. Biol. doi:10.1111/gcb.13706

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

Wright, A.J., Ebeling, A., de Kroon, H., Roscher, C., Weigelt, A., Buchmann, N., Buchmann, T., Fischer, C., Hacker, N., Hildebrandt, A., Leimer, S., Mommer, L., Oelmann, Y., Scheu, S., Steinauer, K., Strecker, T., Weisser, W., Wilcke, W., Eisenhauer, N., Tilman, D., Reich, P.B., Knops, J.M.H., Loreau, M., Behera, N., Tilman, D., Downing, J.A., Yachi, S., Loreau, M., Pfisterer, A.B., Schmid, B., McNaughton, S.J., Ives, A.R., Carpenter, S.R., Steiner, C.F., Long, Z.T., Krumins, J.A., Morin, P.J., Zhang, Q.G., Zhang, D.Y., Hautier, Y., Vogel, A., Scherer–Lorenzen, M., Weigelt, A., Svenning, J.C., Sandel, B., Connell, J., Ojima, D.S., Schimel, D.S., Parton, W.J., Owensby, C.E., Reich, P., Lauenroth, W.K., Dodd, J.L., Sims, P.L., Tilman, D., Wedin, D., Knops, J., Blöschl, G., Nester, T., Komma, J., Parajka, J., Perdigão, R.A.P., Voesenek, L., Bailey–Serres, J., Mommer, L., Lenssen, J.P.M., Huber, H., Visser, E.J.W., Kroon, H. De, Paine, R., Tegner, M., Johnson, E., Caldeira, M.C., Hector, A., Loreau, M., Pereira, J.S., Jongman, B., Roscher, C., Marquard, E., Scheu, S., 2015. Flooding disturbances increase resource availability and productivity but reduce stability in diverse plant communities. Nat. Commun. 6, 6092. doi:10.1038/ncomms7092

Wu, X., Liu, H., Li, X., Ciais, P., Babst, F., Guo, W., Zhang, C., Magliulo, V., Pavelka, M., Liu, S., Huang, Y., Wang, P., Shi, C., Ma, Y., 2018. Differentiating drought legacy effects on vegetation growth over the temperate Northern Hemisphere. Glob. Chang. Biol. 24, 504–516. doi:10.1111/gcb.13920

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. doi: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. Modell. 213, 365–380. doi:10.1016/J.ECOLMODEL.2008.01.005

Zanetti, S., Hartwig, U.A., vanKessel, C., Luscher, A., Hebeisen, T., Frehner, M., Fischer, B.U., Hendrey, G.R., Blum, H., Nosberger, J., 1997. Does nitrogen nutrition restrict the CO2 response of fertile grassland lacking legumes? Oecologia 112, 17–25. doi:10.1007/s004420050278

Zavalloni, C., Vicca, S., Buscher, M., de la Providencia, I.E., de Boulois, H.D., Declerck, S., Nijs, I., Ceulemans, R., 2012. Exposure to warming and CO2 enrichment promotes greater above-ground biomass, nitrogen, phosphorus and arbuscular mycorrhizal colonization in newly established grasslands. Plant Soil 359, 121–136. doi:10.1007/s11104-012-1190-y

Zeeman, M.J., Mauder, M., Steinbrecher, R., Heidbach, K., Eckart, E., Schmid, H.P., 2017. Reduced snow cover affects productivity of upland temperate grasslands. Agric. For. Meteorol. 232, 514–526. doi:10.1016/J.AGRFORMET.2016.09.002

Zwicke, M., Alessio, G.A., Thiery, L., Falcimagne, R., Baumont, R., Rossignol, N., Soussana, J.-F., Picon-Cochard, C., 2013. Lasting effects of climate disturbance on perennial grassland above-ground biomass production under two cutting frequencies. Glob. Chang. Biol. 19, 3435–3448. doi:10.1111/gcb.12317