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Dear Professor Stoy,

We would like to re-submit a revised version of our article entitled “Forage quality declines with rising temperatures, with implications for livestock production and methane emissions” to your journal for review. We would like to thank both Reviewers and yourself for taking the time to read our article and provide us with detailed, thought-provoking and constructive comments. We feel that this has greatly enhanced the manuscript. We hope that it is now considered suitable for publication in Biogeosciences.

Please see our responses to your comments and both Reviewers’ comments presented below. Original comments are in blue and our responses are in black.

Yours faithfully,

mark lee

Dr Mark Lee (on behalf of all authors)

Editor comments

The recommendation instead is to use a plant physiological model to quantify the mechanisms by which temperature impacts forage quality. The challenge is that livestock are critical in the climate system and must be studied post haste, yet only basic studies of ruminant physiology oftentimes exist. (I'm running into similar challenges with bison, where it appears that only one calorimeter study on a one-year-old female cow has been published to date.)

My recommendation is to reconsider this manuscript after major revisions. It is timely and well-written, an important gap in the literature has been noted, and projections were qualified as 'coarse', which I assume to mean 'approximate'. At the same time, shifting the focus of the manuscript to important uncertainties in plant and ruminant physiology while noting that the proposed feedback exists when extrapolating the results of current understanding would result in a more conservative analysis that creates a clear path for future studies.

'Coarse' is qualitative, and I'm not sure what it means either. Using an 'if/then' framework in which global projections hold if current understanding is robust would be a more nuanced way to communicate this potentially quite important feedback to the scientific community.

Please submit a revised version of the manuscript that addresses referee comments and adjusts the tone of the manuscript to focus more on gaps in the literature and a bit less on global extrapolations and I would be happy to reconsider it for publication in Biogeosciences.

Author response

Thank you for your positive comments. We agree that this is a timely paper and we hope that it will inspire discussion as well as future work that improves the accuracy of our projections. We have now made a number of changes to the manuscript and also included several new analyses which we feel has improved the manuscript greatly. Most notably, we no longer rely on one published equation to project enteric methane production from the relationship between grass nutritive quality and rising temperatures. Instead we have re-run our analyses using six published models and present the range of possible outcomes from these models as well as a mean model, weighted by the number of contributing studies. This will give the reader additional confidence that the results are robust and that the important feedback which we have identified is likely.

We have also reduced the focus on global extrapolations and revised our projections downwards, to a more conservative set of projections based on our mean weighted model. The revised manuscript has a very small proportion of the text dedicated to geographically explicit projections or global values for increases in enteric methane production. However, we do still include one map and a small number of global projections so that the reader has a concept of the magnitude of changes that may be expected.

We have also removed all references to 'coarse' projections and focussed on an if/then approach as suggested. We feel this has greatly improved the manuscript. In particular, we focus on presenting a range of possible outcomes and discuss which outcome is the most likely given the evidence. We also discuss how future changes in the sizes and distribution of cattle and other livestock may modify the size of this feedback. We have also added a reference to other ruminants, sheep and buffalo, as there is emerging evidence that they exhibit similar enteric methane responses to reductions in forage nutritive value as cattle. Finally, we have added a detailed limitations section where we discuss the limitations of our work as well as the opportunities for future research which will improve the accuracy of our projections.

Responses to Reviewer 1

General comments: The authors present a meta-analysis of forage studies in order to ascertain any impacts of growing conditions on methane production by livestock. Overall I think this study is a valuable contribution by highlighting a positive feedback between temperature increases and methane production by livestock. The clear and succinct project raises many important questions for global methane contributions and feedbacks under future climate scenarios, but could be improved by some additional considerations and clarifications.

Response: We thank reviewer 1 for these positive comments and, in particular, that we have raised some important questions regarding global methane contributions and feedbacks.

Changes made: No changes requested by reviewer.

I did not find that the analysis of Nitrogen addition to add much value as part of the results section, and because of the limited data on this part of the study (and lack of a significant impact for the species with the most data) is too preliminary an analysis for inclusion.

Changes made: We have reduced the emphasis on nitrogen in our results and discussion. Since nitrogen fertilisers are not available to all farmers, we have also now not included nitrogen as a part of the modelling exercise. However, since information on nitrogen addition rates was present for a large proportion of the dataset (67%) and these were shown to be significant in our analysis, we have retained, a short section of results and discussion points relating to the effects of nitrogen fertilisation. We discuss the reasons why N addition may have a significant effect across all species but not when considering just one. We also highlight the size of the nitrogen dataset to prevent future misunderstanding.

Cross reference: 116, 232-234, 238, 341-349.

In addition, clarification and discussion if these results are indicative of changes within a species or between species (and relative contributions of each) is needed as this is considerable factor in the assumptions for their model.

Response: There is substantial variation between species responses to climate and nitrogen, as supported by data that we have presented. However, we were not focussed on these differences, preferring to focus on the effects of climate and fertiliser addition. We therefore included species and site as random effects in our mixed effects statistical modelling. By doing this we accounted for differences between species and between sites without making them the focus of our analysis. We also ran our analysis for the best represented species in the database, *Lolium perenne*. This allowed us to discuss the effects of physiology and phenology separately from species identity. The positive responses to both monthly temperatures and MAT imply that both compositional and physiological changes play a role in determining the observed response. We feel that our models are robust since they are based on an empirical model which includes species turnover, and well as changes to physiology and phenology.

Changes made: We have added more detail in the manuscript so that these methodological aspects are clearer. We have also discussed our results in light of this limitation.

Cross reference: 131-133, 136-142, 150, 234-238, 330-339.

Furthermore, projections related to RCP 2.6 and 8.5 and increased methane should be developed further than currently presented to clarify the relationship to livestock assumptions in these models and present the spatial variability between regions of the world in more detail.

Response: We feel that it is pragmatic not to add more detail on the spatial variability of our projections because of the concerns of both the editor and Reviewer 2.

Changes made: We have added considerable additional detail on the assumptions and limitations of our approach. We have also re-run our analyses using multiple published models, as detailed above. We have added some discussion relating to geographical variation. We also highlight the differences in our projections based on RCP 2.6 and RCP 8.5.

Cross reference: 155-181, 185-188, 276-282, 377-384.

Finally, additional clarification of other assumptions and limitations to this study are needed to generate discussion and thoughts about taking these coarse projections further. Grassland communities are complicated and although the authors show a response to general long term temperature to forage nutritive value, inter-annual and geographic variability (plus management) are additional important factors.

Response: We agree with this comment.

Changes made: We have included more detail about the assumptions and limitations of our work, including the points made regarding inter-annual and geographic variability and management.

Cross reference: 401-416.

More detailed comments on specifics sections of the manuscript follow. Specific Comments Line 42, if 48% of the biomass is grass, would be good to know what composes the other 52%. This is a big deal for methane production and would help with conclusions and discussion points.

Response: We have additional detail: "Pasture contributes 48% (2.3 billion tons) of the biomass consumed by livestock, followed by grains (1.3 billion tons, 28%). The remainder is from leaves and stalks of field crops, such as corn (maize), sorghum or soybean (Herrero et al., 2013)". We have also discussed how the trend towards feeding mixed diets, which contain a mixture of components, may also further increase methane production.

Changes made: Manuscript text updated to include this information.

Cross reference: 42-44, 374-376.

Line 51, consider talking about tundra regions here as well since you base your results on this climate type. Since these are harsh climate do they behave like arid regions (stressful) or temperate regions (cooler, so greater nutritive value)?

Response: The dataset included data from tundra zones (35 % of entries) and therefore these have informed the relationships we identified. We have also highlighted that data collected from tundra sites are consistent with the relationships generated across all sites, and we also highlight data gathered from the lowest and highest temperatures which additionally support our conclusions.

Changes made: Reference to tundra has now been included in the manuscript to make it clear that the dataset includes this biome.

Cross reference: 57-59, 114, 226-230.

Line 84, you need to talk about the size of the database here and not just percentages. It is important to know the distribution and number of species across climate types, the amount of data that your fertilizer model is based off of, etc. It is hard to determine if the results you have are from within species variability or across species variability. The two lead to different conclusions and are an important to discussing changes in methane production from cattle in the same locations (are we assuming a change in forage species?).

Response: We agree that this is essential for the reader and apologise for the lack of information presented in the manuscript.

Changes made: We have provided a great deal of further detail of how these data break down across biogeographic regions and species in the revised manuscript.

Cross reference: 110-117, 136-142, 234-238.

Line 91, a brief discussion of whether harvested time impacts DM and other variables and then later on, account for this in the analyses (i.e. on line 109 it is reported that a sample was taken at -5 degrees C).

Changes made: We now briefly discuss harvest time in the introduction and discussion. We also highlight values that will have been sampled in very low and very high temperatures.

Cross reference: 59-60, 325.

Line 143, is this for all temperature and rainfall values? Both the month of collection and mean annual values?

Response: Separate analyses were carried out for monthly and annual values.

Changes made: We have added detail to clarify this. We also now include a comparison of the results of monthly and annual temperatures and how they impact on size of the presented relationships. Since they are of similar magnitude we feel this adds confidence to our conclusions.

Cross reference: 130-133, 136-142, 150, 226-238, 330-339.

Line 167, RCP 2.6 and RCP 8.5 incorporate projections in the amount of livestock as a part of determining changes to radiative forcing. Be explicit here that you are restraining your analysis to just the projected temperature changes as determined by RCP 2.6 and then 8.5, not any changes related to projections in number of livestock in the scenarios or any assumptions about where, feed type, etc.

Changes made: The manuscript has been updated to make this point clear. We have discussed how increasing the livestock inventory may additionally increase methane production to a greater extent than we project. We also highlight that the future distribution of livestock is unknown, but the location of increases in cattle numbers are important. We have also mentioned that changes in feed composition will also change methane production.

Cross reference: 24, 281, 401-416, 420, figure 5 caption.

Line 201, consider splitting the relationship between C3 and C4 plants here as you do in the model later on. Looks like a different response but hard to tell.

Response: We have split this in the figure. We do demonstrate in the results that C3 and C4 plants differ, which is an interesting finding from our study.

Cross reference: 313, figure 1.

Line 203, please revise the table caption to better reflect the four models presented. The comparison to the results section and why the numbers of sites differ, plus the two models for NDF and CP are not clear.

Changes made: The table caption and the text have been modified to address this concern.

Cross reference: 109-115, 130-133, table 2 caption

Line 223, please clarify the figure explanation, it is hard to determine where the two scenarios come from in your temperature model for each size of livestock. Also consider some clarification in the methods section where you present equations for these (line 150).

Changes made: We have removed this figure and added two additional figures. Scenarios and methods are now presented more clearly.

Cross reference: 155-181,185-188, figures 3 and 4

Line 223, I find the nitrogen addition discussion distracting and not needed for the main part of this paper. I think you could make a great point focusing on temperature and save discussion of nitrogen addition to the discussion. It complicates the methods section (data collection) and this is a small part of your database (8%), plus you find a temperature impact for the main species in your data, but not a nitrogen effect (making this a more complicated question).

Changes made: We have reduced the emphasis on nitrogen in our results and discussion. Since nitrogen fertilisers are not available to all farmers, we have also removed nitrogen from the modelling exercise. However, since nitrogen addition rates were included in a large proportion of the dataset (67%) and was shown to be significant in our analysis, we have retained, briefly, some of the results and discussion points relating to the effects of nitrogen fertilisation. We also highlight the size of the nitrogen dataset and discuss the differences between our analysis across all plant species and the best represented plant species.

Cross reference: 116, 232-234, 238, 341-349.

Line 235, I like the analyses but the figures presented could be more informative. In this case these figures mainly represent areas with larger projected temperature change. Consider some alternative presentation, such as presenting the % change by continent, or other factor. A table or figure that presents changes by geographic location for different sizes of cattle would give much more information than currently presented in the text and figure. You could even consider ramifications of increased numbers of livestock in addition to the temperature impacts (as referred to in the discussion but not presented in the results).

Response: We have not added more detail on the spatial variability of our projections because of the concerns of both the editor and Reviewer 2.

Changes made: We have re-run our projections using multiple models which represent a much larger geographic coverage than in our original article. Since these models contain data from multiple regions then we consider it inadvisable to make geographically explicit predictions. We have discussed the ramifications of increased numbers of livestock in more detail in the discussion. We have estimated the possible increase in methane production from a larger cattle inventory and discuss how this value may be modified by the relationships we have identified.

Cross reference: 276-282, 377-383, 409-414, 420-427.

Line 253, talk here a bit more about the assumptions in the model you have created (data sources, species variability vs community variability, forage type, etc.). Again, I think this is a valuable study and addition, just need to explain what additional information is needed to go beyond the “coarse projections.”

Response: We agree with this comment and thank the reviewer for their positive comments.

Changes made: We have included more information on our assumptions in the methods and also provide a discussion of these issues.

Cross reference: 23-25, 155-181, 401-416, 423.

Line 300, what is the magnitude difference of increased methane in housed cattle vs. the increase of methane from grass at warmer temperatures. Can you say your overall projection may increase?

Changes made: We have limited our analysis to climate driven changes to forage quality and methane emissions, however, the trend towards housed cattle fed mixed diets will likely further increase methane production to a greater extent than we predict. We have presented the magnitude of this difference in the revised manuscript. "Our calculations are limited to cattle which consume grass, however, the trend towards permanently housed cattle, particularly across Europe and North America, may further increase these values because the mixed diets of housed cattle increase enteric methane production by around 58 %".

Cross reference: 374-376.

Line 331, I liked the discussion overall, and think you cover a lot of good points about the conclusions of the study. Two additional factors to consider are the unknowns of the impact of increased CO₂ on NDF and CP for grass species (especially C3), how would this impact your conclusions. And secondly, consider a discussion about grazing pressure (which I know you excluded) changing community composition and species response, and those impacts to CD and NDF.

Response: Thank you for your positive and useful comments.

Changes made: We have added discussion of these two crucial points.

Cross reference: 401-416.

Responses to Reviewer 2

General comments: The study aims at investigating the relationship between forage quality, methane emissions from livestock, and projected future emissions. The topic is interesting, relevant and timely. The authors have done a good job gathering data to show the variability of forage quality for key quality parameters, plant species and across world climates. And that in itself would be useful material to be published (e.g. Fig. 1 and 2, Table 1) in a specialized forage science journal.

Response: We thank Reviewer 2 for these positive comments. We agree that we have collated a large dataset as summarised above and that the topic is interesting, relevant and timely.

Changes made: No changes requested by reviewer.

What I find less robust, is the use of statistical models derived with forage quality data, and the temperature under which the forage was sampled, to make (future) predictions of methane emissions by livestock. The analyses that would make this manuscript relevant for Biogeosciences are based on a few equations (derived from statistical analyses) which related methane emissions to the quality of the feed. Temperature is an explanatory variable that was used by other authors (Hirota Kasuya and Junichi Takahashi – see Asian-Aust. J. Anim. Sci. Vol. 23, No. 5: 563 - 566) to explain the intake of NDF, whereas methane emissions are driven by the intake of NDF. I find the extrapolation of these equations too weak to make global predictions of methane emissions.

Changes made: We have presented a detailed summary of our solution to these criticisms above, i.e. we have re-run our predictions using several other published empirical models, including those mentioned in this Reviewers' comment. These additional analyses show the overall finding of the paper are robust. However, we have discussed how these models differ in their predictions, and present a range of possible values for future methane production as a result. We have also reduced our emphasis on global predictions and highlighted the limitations to our approach. We discuss the gaps in current knowledge and call for further research which focusses on closing these knowledge gaps, thus improving future modelling efforts.

Cross reference: 155-181, 290-296, 351-376, 401-416, figures 3 and 4.

This sort of study, interesting and relevant, would be better substantiated using vegetation models that represent the physiological processes through which temperature would affect feed quality, and livestock models that would describe the effect of temperature on livestock (heat stress?) affecting the emission of methane. There are more weaknesses in the assumptions used for the study, which I describe below under specific comments. Unfortunately, I don't find this manuscript suitable for publication in Biogeosciences.

Changes made: we have added a detailed limitations section in which these points are addressed. At present there are no mechanistic models which can be applied to plant nutritive quality or enteric methane production. Empirical models are therefore the best way to make predictions for future forage-driven changes to methane production. We now highlight how several factors, including heat stress, CO₂ enrichment, grazing pressure and the frequency of extreme weather events may also influence methane production but further research is needed to quantify the direction and magnitude of these effect. Nevertheless we believe that our analyses and projections identify an important and interesting relationship between climate, forage nutritive quality and methane production.

Cross reference: 23-25, 155-181, 185-188, 401-416, 421-423.

Specific comments L108: the authors used temperature at time of sampling, mean annual temperature (MAT) and monthly rainfall (MAR) over the past 10 years. The quality of the forage is associate to the current growing

season, most like a seasonal and cumulative effect. So the use of an average long term (10 years) temperature of the temperature of the month of sampling seem inappropriate as predictors of feed quality.

Response: The use of MAT in this context allows us to link our statistical models to future climate models, which present predictions in terms of MAT. We have now added a comparison of the results from MAT and sampling temperature in the results section. Sampling temperature is a useful proxy for conditions at the time of sampling when compared with MAT which represents prevailing climatic conditions. We show how MAT and sampling temperatures are both significantly related to forage quality. We also demonstrate that MAT and sampling temperatures resulted in similar outputs and this gave us additional confidence that our conclusions are robust. We have also added detail of these comparisons to the discussion.

Cross reference: 131-133, 136-142, 150, 234-238, 330-339.

L143-148: the use of equations developed for one experiment conducted in Japan, with a limited set of feedstuff (only 4 temperate climate species) to extrapolate global methane emissions seem largely inadequate for the purpose.

Response: This comment has been addressed previously. We have now calculated our predictions using an expanded suite of models. While predictions vary between these models, the overall picture is one of support for our original conclusion.

Changes made: As above.

Cross reference: 155-181, 290-296, 351-376, 401-416, figures 3 and 4.

L192: I would have expected a species effect in the analyses of NDF. Under the same climate and soil there will be plants with largely different values of NDF, and other quality parameters simply because of genetic differences.

Response: There is substantial variation between species responses to climate and nitrogen, as supported by data that we have presented. However, we were not focussed on these differences, preferring to focus on the effects of climate and fertiliser addition. We therefore included species and site as random effects in our mixed effects statistical modelling. By doing this we accounted for differences between species and between sites without making them the focus of our analysis. We also ran our analysis for the best represented species in the database, *Lolium perenne*. This allowed us to discuss the effects of physiology and phenology separately from species identity. The positive responses to both monthly temperatures and MAT imply that both compositional and physiological changes play a role in determining the observed response. We feel that our models are robust since they are based on an empirical model which includes species turnover, and well and changes to physiology and phenology.

Changes made: We have added more detail in the manuscript so that these methodological aspects are clearer. We have also discussed our results in light of this limitation.

Cross reference: 131-133, 136-142, 150, 234-238, 330-339.

L232: the use of the selected statistical models derived from one single experiment, with future temperatures seem inappropriate to predict both future and actual methane emissions globally.

Response: This comment has been addressed previously. We have now calculated our predictions using a suite of models.

Changes made: As above.

Cross reference: 155-181, 290-296, 351-376, 401-416, figures 3 and 4.

L247: I disagree with the authors. They don't describe here a climate feedback, but an artefact of the use of statistical models and projected temperatures. The relationship between temperatures and plant quality parameters is largely known in ecology. That explains the differences between ecotypes across the globe. However, the authors extend these relationships to the calculation of methane emissions, and that seems incorrect.

Response: We do not believe this is a statistical artefact. The logic is robust at each stage and the relationships presented are supported by previous published work. If the relationship between temperatures and plant quality is largely known and the relationship between plant quality and methane production well resolved then we believe that the overarching concept we have identified is robust. As summarised in a recent review paper, elevated forage NDF has been consistently demonstrated to have a positive effect on methane production in cattle across many studies (Appuhamy et al., 2016).

Changes made: We have highlighted the consistent link between forage NDF and methane production.

Cross reference: 49, 155-181, 185-188, 312-314, 360.

L264: The differences in NDF and CP across climate doesn't mean that ruminants are under nutritional stress. Livestock keepers manage different species and breed adapted to their climate across the globe. And therefore it is not correct to use one equation derived for *Bos taurus* dry cows in Japan to predict global emissions of ruminants

Response: We have removed his reference to nutritional stress and commented simply that the nutritive value of forage grasses in warmer regions is lower. We have also discussed that there is a lack of data relating to the effects of heat stress on enteric methane production in our limitations section. Finally, we have now re-run our projections using multiple published models, as stated above. These now cover many different regions and a large number of animals.

Cross reference: 156, 401-416, table 1.

Forage quality declines with rising temperatures, with implications for livestock production and methane emissions

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10 Abstract: Livestock numbers are increasing to supply the growing demand for meat-rich diets. The sustainability of this trend has been questioned, and future environmental changes, such as climate change, may cause some regions to become less suitable for livestock. Livestock and wild herbivores are strongly dependent on the nutritional chemistry of forage plants. Nutrition is positively linked to weight gains, milk production and reproductive success, and nutrition is also a key determinant of enteric methane production. In this meta-analysis we assessed the effects of growing conditions on forage
15 quality by compiling published measurements of grass nutritive value and combining these data with climatic, edaphic and management information. We found that forage nutritive value was reduced at higher temperatures and increased by nitrogen fertiliser addition, likely driven by a combination of species turnover, and changes to physiology and phenology. **These relationships were combined with multiple published empirical models to project forage and temperature driven changes to cattle enteric methane production. This revealed a previously undescribed positive climate change feedback, where elevated**
20 **temperatures reduced grass nutritive value and correspondingly increased methane production by 0.9% with a 1 °C temperature rise and 4.5 % with a 5 °C rise, (model average) thus creating an additional climate forcing effect.** Future methane production increases are expected to be largest in parts of North America, Central and Eastern Europe, and Asia, with the geographical extent of hotspots increasing under a high emissions scenario. These estimates require refinement and a greater knowledge of the abundance, size, feeding regime and location of cattle, and the representation of heat stress should
25 **be included in future modelling work. However, our results indicate that the cultivation of more nutritious forage plants and reduced livestock farming in warming regions will reduce this additional source of pastoral greenhouse gas emissions.**

Keywords: agriculture, cattle, climate change, fibre, grassland, greenhouse gases, nutrition, protein

1. Introduction

Global meat production has increased rapidly in recent years, from 71 million tonnes in 1961 to 318 million tonnes in 2014 (FAOSTAT, 2016). This is due to population growth and a transition to meat-rich diets across many countries (Tilman and Clark, 2014). Grazing lands have expanded to support this production, particularly across Asia and South America, and now cover 35 million km² of the Earth's surface, with an estimated 1.5 billion cattle, 1.2 billion sheep, 1 billion goats and 0.2 billion buffalo living in livestock production systems (FAOSTAT, 2016). The environmental footprint of supplying meat and dairy products has increased alongside these rises in human consumption. Livestock farming, including feed production and land use change, enteric sources and manure decomposition produces approximately 7.1 gigatonnes of CO₂ and CO₂ equivalents annually (GT CO₂eq), accounting for 15% of anthropogenic greenhouse gas (GHG) emissions (FAO, 2013). Enteric fermentation by livestock produces 2.8 GT CO₂eq of methane each year, with 77 % being produced by cattle (FAO, 2013). The upward trend in livestock production and associated GHG emissions are projected to continue in the future and global stocks of cattle, goats and sheep are expected to reach 6.3 billion by 2050 (Steinfeld et al., 2006).

Ruminants (cattle and small ruminants such as sheep and goats) consume 80 % (3.7 GT) of the plant material grown to feed livestock (Herrero et al., 2013), and grasses continue to comprise the largest proportion of livestock diets. For example, in the year 2000, 48 % (2.3 billion tons) of the biomass consumed by livestock was grass, followed by grains (1.3 billion tons). The remainder of livestock feed (0.1 billion tons) was the leaves and stalks of field crops, such as corn (maize), sorghum and soybean (Herrero et al., 2013). The chemical composition and morphology of forage grasses determines their palatability and nutritive value to livestock, thus influencing the amount of feed consumed, efficiency of rumination, rates of weight gain, the quality and volume of milk produced, and reproductive success (Herrero et al., 2015). Forage grasses generally have enhanced nutritive value for livestock if they contain a greater proportion of readily fermentable components such as sugars, organic acids and proteins, and a lower proportion of fibre (Waghorn and Clark, 2004). Furthermore, highly nutritious forage can reduce ruminant methane production, since feed moves through the digestive system more rapidly (Knapp et al., 2014).

Accordingly, regional and inter-annual variability in forage nutritive value generates corresponding variability in the production of meat and dairy products, and variability in the magnitude of ruminant methane emissions (Thornton and Herrero, 2010).

Meat and dairy production in arid, equatorial and tropical regions is often lower than production in temperate regions due to the lower nutritional quality of forage grasses, a lack of access to inorganic nitrogen (N) fertilisers, infertile soils and adverse climatic conditions (Thornton et al., 2011). Warmer regions are associated with taller, less nutritious and slow-growing grasses with low concentrations of protein, high concentrations of fibre and high plant dry matter content (DM, the proportion of plant dry mass to fresh mass) (Jégo et al., 2013; Waghorn and Clark, 2004). While extremely cold regions are also associated with grasses of low nutritive quality, cold regions are rarely suitable for ruminant livestock (Nielsen et al.,

2013). The timing of grazing and forage harvesting are also important determinants of forage quality. For example, summer harvests frequently produce grasses of lower nutritive quality than spring harvests (Kering et al., 2011). Consequently, grasses of lower forage quality have low dry matter digestibility (DMD, the proportion of plant dry mass which is digestible; high DMD is positively associated with livestock productivity) (Lavorel and Grigulis, 2012; Pontes et al., 2007a). Greater grass nutritive value has been linked to cooler temperatures and N fertiliser addition due to phenological and physiological changes towards delayed flowering, modified stem:leaf ratios, thinner cell walls and reduced lignification, and species turnover (Gardarin et al., 2014; Hirata, 1999; Kering et al., 2011).

Ruminant methane production is calculated using IPCC (2006) methodologies in GHG accounting (Tiers 1,2 and 3), and the more complex methods (Tiers 2 and 3) incorporate the effects of nutritive value (Schils et al., 2007). However, few models have been developed to predict the effects of climate change on forage nutritive value (Kipling et al., 2016), and those which include climate or management have focussed on single livestock species (Jégo et al., 2013) or regions (Graux et al., 2011). Quantifying relationships between forage grass nutritive value, growing conditions and management more broadly, and across many plant species, provides an opportunity to make general projections of future changes to livestock and associated methane production. To our knowledge such relationships have not been systematically assessed at the global scale.

We tested the following hypothesis: that increasing temperatures are associated with grasses of lower nutritive value, delivering higher concentrations of fibre, lower protein and lower DMD with N fertiliser addition having opposite effects. To quantify variation in the nutritive value of forage species growing across a range of bioclimatic zones and to understand the influence of climate and fertiliser application, data were gathered from published literature sources in which field-derived nutritive data were reported. Neutral detergent fibre (NDF, structural plant components; cellulose, lignin and hemicellulose) and crude protein (CP, approximate protein content) are presented as the most commonly reported measurements of forage nutritive value. NDF and CP are generally negatively and positively correlated with livestock productivity, respectively. These data were combined with a range of potentially modifying variables, including temperature, rainfall, rates of N fertiliser addition and photosynthetic pathway. Where possible, statistical models were then used to generate projections of future climate induced changes to forage grass nutritive value and cattle methane production.

2. Materials and methods

2.1. Data acquisition

Data were obtained from peer-reviewed journal articles. Articles were identified by systematically searching the ISI Web of Knowledge (WoK, www.wok.mimas.ac.uk). To avoid researcher bias and to maintain a consistent approach, search terms used to identify articles listed in the WoK were identified *a priori*. Articles were included within the database if nutritive

90 measurements were related to a specific grass species or hybrid that had been grown in field conditions at a defined location (hereafter termed 'site') and harvested for nutritional analyses at a stated time. Data from experiments conducted in greenhouses or field experiments, i.e. those which manipulated climatic variables, were excluded because the prevailing growing conditions were not representative of the location.

To ensure that the methods for measuring forage nutritive value were consistent across articles, data were included if NDF and CP analyses were carried out on dried samples and presented in units of g/kg DM or % DM. DMD was also recorded when available to test for relationships between NDF, CP and digestibility.

2.2. Descriptive data

Descriptive data were included in the database for each data point. These potential explanatory data described the site (latitude, longitude, elevation), experiment (degree of replication, experimental treatments and whether the grassland was a mono- or polyculture), management (fertiliser addition rate, grazing density), soil (type, pH), climate (mean annual temperature [MAT], mean annual rainfall [MAR]), weather during the month of sample collection (mean monthly temperature, total monthly rainfall) as well as data describing the plants photosynthetic pathway system (C3, C4). Data were recorded from each article from text or tables. When this was not possible, data were obtained from graphs using the digitizing software; Datathief (www.datathief.org).

Sites were allocated to a bioclimatic zone as defined by the Köppen-Geiger Climate Classification system (Kottek et al., 2006) and recorded in the database as arid ($\geq 70\%$ of precipitation falls in summer or winter), equatorial (mean temperature of coldest month ≥ 18 °C), temperate (mean temperature of warmest month ≥ 10 °C and coldest month -3 – 18 °C) or **tundra** (mean temperature of warmest month ≥ 10 °C and coldest month ≤ -3 °C). The database contained grass nutritive data collected from 32 sites in 16 countries (for detailed site descriptions see Appendix, Table A1) with NDF measurements taken from 35 grass species and CP measurements taken from 46 grass species. Overall, our dataset comprised 803 measurements of nutritive quality taken from 55 different grass species across Asia (11 % of the dataset), Australasia (6 %), Central America (11 %), Europe (34 %), the Middle East (1 %), North America (36 %) and South America (1 %). Our dataset represented arid (19 % of the dataset, 6 sites), equatorial (1 %, 1 site), temperate (46 %, 16 sites) and tundra (35 %, 9 sites) bioclimatic zones. Across all sites, temperatures at the time of sampling ranged from -5 to 36 °C (MAT: -1 – 26 °C) and monthly rainfall at the time of sampling ranged from 0.6 to 702 mm (MAR: 38 – 2378 mm yr⁻¹). Data on the rate of N addition were available for 67 % of the dataset, and these rates of fertiliser application ranged from 0 to 357 kg N ha⁻¹ yr⁻¹.

2.3 Gap filling

120 In many cases data were obtained from the articles analysed, but in some cases there were gaps in the information available. Data most commonly gathered from external sources were weather (sampling temperature and rainfall) and climate (MAT and MAR), which were obtained from the closest weather station to each site, according to the National Centers for Environmental Prediction database (www.ncep.noaa.gov). Weather data for Waimate North was not added to the database because the nearest weather station was 150 km from the site. MAT and MAR were taken as the mean temperature and
125 rainfall over the past ten years. Google Earth (www.earth.google.com) was used to obtain the elevation of the site if this was not stated in the article, based on a digital elevation model.

2.4 Statistics

Statistical analyses were carried out using weighted, restricted maximum-likelihood linear mixed-effects (LME) models
130 (Pinheiro and Bates, 2000). Model selection was carried out by including NDF or CP as response variables with multiple potential explanatory variables added as fixed effects to generate full (maximal) models. Fixed effects were mean temperature during the sampling month or MAT, total rainfall during the sampling month or MAR, elevation, rates of N addition and photosynthetic pathway. Grazing density, soil pH and whether the plants were grown in mono- or polyculture were shown not to significantly relate to CP or NDF in LME models in preliminary analyses, and therefore to avoid over-
135 fitting these variables were not included in initial full models (all $P > 0.05$).

For the random effects structure, grass species identity was nested within experimental treatment, and treatments were nested within sites and represented within LMEs, thus accounting for cases where several measurements were taken at the same site, treatment or from the same species. This accounted for differences between species and between sites without making them the focus of our analysis. Any relationships identified therefore included the effects of changes to species identity, and
140 of changes to physiology and phenology. However, a separate model was also fitted for the best represented plant species in the database (*Lolium perenne*) in order to gain an initial insight into the relative roles of physiological response and species turnover. Variation in the sample sizes used to generate treatment means was accounted for by weighting by within-site replication (Adams et al., 1997), thus making the influence of a study proportional to its degree of replication.

Non-significant explanatory variables were removed from full models as all terms were found to reduced Akaike's
145 Information Criterion (AIC). The relative influence of each term on model likelihood was assessed by comparing the AIC of the current model with that of a simplified model, with terms deleted until the AIC ceased to decline (Crawley, 2013; Richards, 2005). Temperature and rainfall could not be included together in LME models because these variables were shown to covary strongly ($P < 0.001$), so either temperature or rainfall were included in full models based on minimising AIC. LME models were also used to test for relationships between CP and NDF and climate (MAT and MAR), and DMD,
150 and also to test for differences in CP and NDF between bioclimatic zones. For comparison, separate analyses were therefore

carried out for MAT or MAR and total rainfall or mean temperature during the month of sampling. All analyses were computed using R, version 3.2.3 (R Development Core Team, 2016).

2.5 Enteric methane production modelling

155 Methane production projections were based on published, experimentally derived relationships between forage NDF content or daily NDF intake (NDFi) and enteric methane production, as measured in cattle. A suite of equations was acquired from published articles with all but one being the product of meta-analysis (Table 1). These equations summarise many measurements of cattle enteric methane production across Africa, Asia, Australasia, Europe, North America and South America, and relate the magnitude of methane production to the nutritive quality of forage and, in some cases, total feed
160 intake. In total, 303 studies were included across these meta-analyses, with methane production measured by hood, mask and whole animal calorimetry, respiration chamber and sulphur hexafluoride (SF₆) tracers. Where multiple options were available from a single article, equations were selected for inclusion in our study based on the lowest root mean square prediction error (RMSPE) when this was assessed within the article itself (Moraes et al., 2014; Patra, 2015) or based on the results of a study which compared the accuracy of multiple models in calculating methane production (Appuhamy et al.,
165 2016). These equations, when combined with relationships between forage nutritive quality and temperature identified in this study, were used to model future changes to enteric methane production.

→ Table 1

170 NDF and NDFi was calculated using parameters identified by our LME models, which described the relationship between NDF and MAT (see Results), multiplied by estimated daily feed intake or DMI (dry matter intake). Initial modelling based on equations A–E assumed that cattle DMI was 18.8 kg DMI day⁻¹, which represents mean DMI across all cattle from North America, Europe and Australasia (Appuhamy et al., 2016). For model F, which represented smaller tropical cattle, a DMI of 7.7 kg day⁻¹ was included, which was the mean value presented by Patra (2015). Some equations required values of forage
175 nutritive quality which were not included in this analysis. In these cases, nutritive values were kept constant at 2.8 % dietary fatty acid, 2.8 % ether extract, 162 MJ day⁻¹ metabolisable energy intake and 317 MJ day⁻¹ gross energy intake, values which were consistent with a range of forage nutritive quality measurements presented elsewhere (e.g. Dalley et al., 1999; Ominski et al., 2006; Hegarty et al., 2007). To present a range of possible scenarios, estimated changes to methane production were also calculated for a range of DMI values, to represent small, medium and large cattle for the maximum projections (model

180 A), minimum projections (model E) and most variable projections (model F) models. Modelled DMI ranged from 9.7 to 28.9
kg DMI day⁻¹ for models A and E (Appuhamy et al., 2016) and from 1.4 to 10.0 kg DMI day⁻¹ for model F (Patra, 2015).

Projections of temperature-driven changes to cattle methane production used the HadGEM2 (Hadley Centre Global
Environment Model version 2) family of climate models (IPCC, 2014) applying low and high representative GHG
concentration pathways (low = RCP 2.6; high = RCP 8.5) to generate geographically explicit estimates of future climate and
185 forage-driven changes to methane production. Projected temperature changes were converted to projected forage-driven
changes to enteric methane production for mean sized cattle with mean DMI (as defined above) using a weighted-average
model, with the relative contribution of the outcomes of equations A–F weighted according to the number of studies
included in each meta-analysis (Table 1). HadGEM2 has been identified as a robust model, which is valuable for predictions
across climate change scenarios and including biogeochemical feedbacks (Collins et al., 2011). Estimated increases in cattle
190 methane production was calculated as the ratio of methane production based on projected 2050 mean temperatures compared
with production based on current temperatures (Hijmans et al., 2005). HadGEM2 models based on RCP 2.6 assumed that
GHG mitigation policies are widely adopted resulting in a decline in GHG emissions after 2020. Models based on RCP 8.5
assume that GHG mitigation policies are not adopted and that GHG emissions continue to increase unabated. RCP 2.6 and
RCP 8.5 therefore represented lower and upper projections of future climate and forage-driven increases in cattle methane
195 production. Regions which are unsuitable for ruminant livestock were excluded (Robinson et al., 2014).

3. Results

200 There was a large range in mean neutral detergent fibre (NDF) across the forage grass species (for a full list of species and a
summary of each species nutritive values see Appendix, Table A2), from the lowest, *Pennisetum clandestinum* (46 %) and
Lolium multiflorum (46 %) to the highest, *Aristida longiseta* (87 %). The maximum value observed related to *Bouteloua*
gracilis (90 %) with the lowest recorded from *Lolium perenne* (34%). For some species, there was substantial variation in
NDF, with *Phleum pratense* showing the biggest range of values, from 36–67 %.

205 There was less variation between the forage grasses in crude protein (CP) (standard deviation of mean CP = 3) than the in
NDF (standard deviation of mean NDF = 10). The highest mean CP was recorded in *Pennisetum clandestinum* (23 %) and
the lowest recorded from another member of the same genus, *Pennisetum purpureum* (9 %). Maximum CP was recorded
from *Agropyron cristatum* (36 %) with the lowest recorded from *Elymus sibiricus* (5 %). The maximum variation in CP
measured within a species (8–36 % for *Agropyron cristatum*) was also lower than for NDF.

210 NDF was correlated strongly with forage dry matter digestibility (DMD), with each 1% increase in NDF linked to a 0.6 %
decline in DMD ($t = -11.3, P < 0.001$). CP was positively related to DMD, however, this significant relationship was
dependent upon data from one site. When these outliers were removed there was no significant relationship between CP and
DMD ($t = -0.2, P > 0.05$).

215 3.1 Variation between bioclimatic zones

NDF varied between bioclimatic zones, and grasses growing in cooler temperate or tundra zones had a mean 21 % lower
NDF than in warmer arid and equatorial zones (Fig. 1a), but there was no difference between NDF values recorded from arid
and equatorial zones. CP also varied between bioclimatic zones, and grasses growing in cooler temperate or tundra zones had
a mean of 8 % greater CP than grasses growing in equatorial zones (Fig. 1b). However, there were no differences between
220 the CP contents of grasses growing in arid zones when compared with the other bioclimatic zones.

→ Figure 1

3.2 Environmental determinants of nutritive value

225 Higher temperatures during the sampling month were associated with increasing NDF across the grasses (Fig. 2) and NDF
increased by 0.4 % for every 1 °C rise in temperature. A small number of samples were collected at very low temperatures (<
0°C) and had low NDF values with a mean of 50 %, whilst at very high temperatures (> 25 °C) NDF values were also high
with a mean of 72 %. These extreme values were consistent with the general trends observed. MAT, which represented
prevailing climatic conditions rather than sampling conditions, was also positively associated with NDF, but the rate of
230 increase was moderately greater than for sampling temperatures, increasing by 0.9 % for every 1 °C increase in MAT (Table
2). Rates of N addition were linked to a decline in NDF, with a 100 kg ha⁻¹ yr⁻¹ increase in the rate of N addition, a moderate
rate typical for agricultural grasslands, reducing NDF by 3 %. A very high application rate of 350 kg N ha⁻¹ yr⁻¹ was
associated with a decline in NDF of 11 %. These relationships were also tested for *Lolium perenne*, the species best
represented in the database. A positive linear relationship was found between NDF and sampling temperature (sites = 20, $t =$
235 3.6, $P < 0.001$), increasing NDF by 13 % for every 1 °C increase (over the range 9–22 °C), and between NDF and MAT
(sites = 21, $t = 4.6, P < 0.001$), increasing NDF by 23 % for every 1 °C increase (over the range 6–15 °C). However, there
was no relationship between NDF and N for this species.

NDF was also influenced by photosynthetic pathway, with the NDF content of C4 species a mean of 9 % greater than C3 species. These C4 grasses were more commonly recorded at warmer sites, and NDF content was recorded from C4 grasses growing in mean monthly temperatures greater than 15 °C and up to 28 °C whilst NDF was recorded in C3 species growing in temperatures between -5 and 25 °C.

CP was positively related to rates of N addition, with a 100 kg ha⁻¹ yr⁻¹ increase in the rate of N addition associated with a 2% increase in CP, and very high application rate of 350 kg N ha⁻¹ yr⁻¹ was associated with a 7 % increase in CP. Mean CP content was 3% higher for C3 species than for C4 species, but this difference was not significant (P > 0.05). None of the remaining variables were significantly related to CP (all P > 0.05).

→ Figure 2

→ Table 2

3.3 Projected future changes to methane production

Applying models A to F to the positive relationship between NDF and MAT resulted in a range of projections for forage and temperature-driven changes to methane production (Fig. 3). Models A to E projected increased methane production with rising temperatures assuming a mean cattle size and DMI, with model A projecting the largest increase in methane production (2.9 % for a 1 °C rise) and model E projecting the lowest increase in methane production for each unit of increased temperature (0.5 % for a 1 °C rise). Models B, C and D produced intermediate values (1.9 %, 1.2 % and 0.7 % for a 1 °C rise, respectively). However, model F projected a reduction in methane production with increased temperatures at mean cattle size (-0.3 % for a 1 °C rise). The models with intermediate predictions (B, C & D), were those based on the largest number of studies (particularly models C and D), and so contributed the most to the weighted mean.

Correspondingly, the weighted mean model also projected an intermediate increase in methane production with rising temperatures of 0.9 % for a 1 °C rise in temperatures and 4.5 % for a larger 5 °C rise in temperatures.

→ Figure 3

The effect of simulating changes to cattle size by modifying DMI had contrasting effects across the different models (Fig. 4). In the case of model A, increasing cattle size, consistent with the current global trend towards larger cattle (Herrero et al., 2013), increased the rise in projected methane production with temperature (0.8–3.7 % for a 1 °C rise, Fig. 4a) whereas

larger cattle size decreased the rise in projected methane production for model E (0.3–0.8 % for a 1 °C rise, Fig. 4b). These values represented the largest range of increases in projected methane production with rising temperatures across models A to E. Again, model F behaved differently to the other models; methane production was projected to increase with temperature for the smallest cattle (2.2 % for a 1 °C rise) but decline with temperature for the largest cattle (-1.2 % for a 1 °C rise, Fig. 4c).

→ Figure 4

When statistical models were combined with future temperature scenarios, potential hotspots of forage-driven increases in methane production were identified. The low emissions scenario predicted increases in methane production for mean sized cattle by 1–2 % across most regions, whilst hotspots in North America, Central and Eastern Europe, and Asia saw predicted increases of approximately 3–4 % (Fig. 5a). The high emissions scenario resulted in a larger area experiencing high increases in cattle methane production, with many regions across North and South America, Europe, Central and South Africa, Asia and Australasia increasing by 6–8 % (Fig. 5b). These projections represent estimated change in methane production for each animal, but do not represent anticipated increases in the global cattle inventory.

→ Figure 5

4. Discussion

Global food consumption patterns are shifting from traditional diets to diets rich in refined sugars, fats, oils and meats (Tilman and Clark, 2014). Assessments suggest that agricultural GHG emissions need to be reduced by ~1 GT CO₂eq annually in order to limit warming to 2 °C above pre-industrial levels by 2100 (Wollenberg et al., 2016). We present evidence of a previously undescribed positive climate feedback, which may affect our ability to meet these ambitious GHG emissions targets. Our models project that future temperature-driven reductions in the nutritive value of forage grasses could increase methane production considerably, depending on the emissions scenario, locality and cattle size, thus creating an additional climate forcing effect. It should be noted however, that our projections do not incorporate several important but complex factors (for a detailed discussion see Limitations to modelling approach, 4.4), including the effects of climate change on economic growth, technological uptake and land availability, which have not been fully quantified (Audsley et al., 2014; Havlík et al., 2014). Nevertheless, the potential magnitude of future decreases in grass nutritive value and

corresponding increases in methane production means that these projections cannot be ignored, and are identified here as a research area requiring careful future work and refinement.

4.1 Variation in nutritive and functional traits

300 Forage grass nutritive value varied substantially, between- and within-species, and across bioclimatic zones, with our data indicating that 34–90 % of the dry weight of the grass that livestock consume is fibre and 5–36 % is protein. These ranges are greater than those presented elsewhere, for example NDF has been shown to range from 35–67 % (O’Donovan et al., 2011) and CP from 14–24 % across several European grass species and cultivars (Pontes et al., 2007b), but these greater ranges are to be expected given the wider biogeographic coverage of our study.

305 NDF values were generally higher and CP generally lower in warmer bioclimatic zones than in cooler zones, and this is likely to be one reason why livestock productivity is lower across arid, equatorial and tropical regions. Reduced nutritive value in these zones is likely driven by increased abundances of plants with adaptations to prevent heat stress and avoid water loss; such as greater stem:leaf ratios, narrowly spaced veins, greater hair densities, thicker cell walls, a higher proportion of epidermis, bundle sheath, sclerenchyma and vascular tissues, and greater concentrations of lignin and silica

310 (Kering et al., 2011). The C4 photosynthetic pathway is also an adaptation to heat and water stress and C4 plants were more commonly recorded in warmer conditions than C3 plants, and C4 plants were also associated with lower nutritive value. This is in line with studies that have measured elevated enteric methane production in cattle consuming high fibre C4 grasses compared with those consuming C3 grasses (Ulyatt et al., 2002). Across warmer bioclimatic zones reduced forage nutritive values may be driven by increased abundances of C4 species, and of taller, slow growing species with a conservative growth

315 strategy (Martin and Isaac, 2015; Wood et al., 2015). Large variation within- and between-species highlights the potential for the cultivation and breeding of grasses to enhance livestock nutrition, which would promote resistant to future environmental changes.

4.2 Relationships between nutritive value, environment and management

320 NDF was positively related to temperatures at the time of sampling and MAT. MAT represents prevailing climatic conditions, and elevated NDF is likely driven by a shift towards grasses with heat and drought stress adaptations, and conservative functional traits associated with slow growth (Gardarin et al., 2014). The positive relationship between sampling temperature and NDF may also be linked with changes to phenology, such as advanced flowering dates and rapid tissue aging (Hirata, 1999). The timing of measurements may also have played a role in increasing NDF, since later harvests

325 generally produce grasses of lower nutritive quality (Kering et al., 2011). Temperature driven reductions in forage grass

nutritive value is consistent with mechanistic and empirical models (Barrett et al., 2005; Kipling et al., 2016). However, our results contrast with a meta-analysis of temperature manipulation experiments, which did not reveal any relationships between warming and nutritive value, although this study was across a relatively small temperature gradient (Dumont et al., 2015). The relationships between forage nutritive value and both sampling temperatures and MAT imply that compositional (i.e. turnover in species identity), phenological and physiological changes each play a role. Patterns generated by these different processes were not directly disentangled in our study. However, there were relationships between both MAT and sampling temperatures, and NDF, when measured from one species, *Lolium perenne*. This pattern will likely have been driven by changes to physiology, phenology and harvesting time, but not species turnover. The effect size when only *L.perenne* was included in our analysis was larger than for all plant species, though it was over a smaller temperature range of 6 to 15 °C. This large response indicates that phenological and physiological changes can play a significant role in driving the reduction of NDF under warming, and that changes may occur without species turnover. The positive relationships between NDF, and both MAT and sampling temperatures, across species and within an individual species, provide additional evidence that our projections are robust.

N fertiliser addition generally increases the productivity of grasslands, since the greater majority of these ecosystems are N limited (LeBauer and Treseder, 2008; Lee et al., 2010). We present data which suggests that N addition may also increase grass nutritive value, decreasing NDF by around 3–11 % (low to high fertiliser application rates), and with to an associated increase in CP by 2–7 %. Increased rates of N addition has been linked previously to increased abundances of grass species with ‘fast’ functional traits, with reduced fibre and increased protein content (Pontes et al., 2007a). N addition did not alter nutritive quality for *L.perenne* and therefore the relationship between N and NDF for all species could represent species turnover, rather than changes to physiology or phenology. N addition could partially offset the negative effects of warmer temperatures on forage grass nutritive value in polyculture (where there is species turnover), although N enrichment may also have other, potentially unwanted, ecosystem impacts (Manning, 2012).

4.3 Projections of methane production

Projections suggest that future cattle enteric methane production may change by a mean weighted value of 0.9 % (-0.3–2.9 %) for an initial 1 °C increase in temperatures, assuming no change in mean cattle size. This increase would translate to an annual change in methane production across the global cattle inventory of approximately 0.02 GT CO₂eq (-0.01–0.06 GT CO₂eq). With a larger 5 °C increase in temperatures the projected change in cattle methane production of 4.5 % (-2–14 %) translates to a global change of approximately 0.09 GT CO₂eq (-0.02–0.3 GT CO₂eq). Whether methane production will change towards the mean, upper or lower end of the projected ranges is clearly dependent on which model is correct. We postulate that the most likely models are model C, which represented North American cattle, and the mean weighted model,

as these included the largest number of studies (thus representing a large range of cattle sizes and breeds). Both gave comparable and intermediate outputs. Five of the six models were consistent with studies linking increased forage fibre with greater enteric methane production (e.g. Moraes et al., 2014), and therefore estimated increased methane production under warmer temperatures. One model (model F) projected declines in future enteric methane production with temperature. However, care must be taken in this case as the model was parameterised using data collected from smaller animals and across tropical regions. When the smallest animals were simulated with this model, as is consistent with smaller tropical breeds such as Zebu, enteric methane was also projected to rise with temperatures.

The trend towards larger cattle across many regions could also influence the magnitude of changes to enteric methane production, because larger cattle have greater feed and fibre intakes (Knapp et al., 2014). Model predictions for larger animals were more variable and therefore both the magnitude of emissions and the uncertainty surrounding these estimates increases with cattle size. The magnitude of projected change across the different models was also dependent on whether NDF or DMI was the dominant term. Furthermore, our projections are limited to cattle. However, there is emerging evidence that reductions in the nutritive value of forage also leads to increased enteric methane production from sheep (Ramin and Huhtanen, 2013) and buffalo (Patra, 2014). Together cattle, buffalo and sheep contribute >95 % of global GHG emissions from enteric fermentation (FAO, 2013) and if our projections hold across the global ruminant inventory then overall enteric methane production will increase to a greater magnitude than we predict. Our calculations are also limited to cattle that consume grass. We therefore do not account for the trend towards permanently housed cattle, particularly across Europe and North America. This may further increase emissions because the mixed diets of housed cattle increase enteric methane production by around 58 % (March et al., 2014; O'Neill et al., 2011).

Hotspots of future increases in enteric methane production were identified across North America, Central and Eastern Europe, and Asia using a low GHG emissions scenario combined with our weighted mean model. Hotspots became more widespread, and of greater magnitude, in a high GHG emissions scenario. At present the greatest densities of cattle can be found in parts of Asia, North and South America, Europe and across Australasia (FAOSTAT, 2016), and many of these regions are projected to experience the greatest forage nutrition-driven increase in cattle methane production. Added to this, meat production has increased by 3.6 % across Africa and 3.4 % across Asia over the past decade, compared with a 1 % increase across Europe (FAOSTAT, 2016), indicating greater future growth across these regions. Losses in forage quality could drive farmers into more extensive farming systems across many regions, because larger land areas will be required for each animal. Therefore, it may be necessary to limit the growth of livestock production systems in warmer and drier regions, particularly those likely to experience future warming, if significant losses in livestock production efficiency and increases in methane emissions are to be avoided.

Cattle methane production can be reduced by growing more nutritious forage plants, N fertiliser addition, feed supplements (e.g. macroalgae and fats), adjusting rumen pH, increased concentrate feeding, genetic selection, and feeding methane inhibitors (Duin et al., 2016; Machado et al., 2014). However, implementing many of these measures is not feasible at a global scale, is unlikely to result in sufficient reductions in GHG emissions to meet ambitious GHG reduction targets, and may also promote other negative environmental effects such as biodiversity loss, nitrous oxide emissions and pollution to air and water (Manning, 2012; Wollenberg et al., 2016). Ruminant meats (beef and lamb) produce around 250 times greater GHG emissions per gram of protein than legumes (crops from family Leguminosae); and eggs, seafood, aquaculture, poultry and pork all have lower emissions than ruminant meats (Tilman and Clark, 2014). A global switch in human diets and a transition to more sustainable agricultural practices, as well as a greater prevalence of organic and silvopastoral farming, may reduce our reliance on intensively farmed cattle and other ruminants. In countries with high or increasing meat consumption, these measures could reduce the environmental impacts of agriculture, contribute to GHG emissions cuts, and with an associated improvement in human health (Springmann et al., 2016).

4.4 Limitations to modelling approach

There are many uncertainties associated with modelling plant and livestock systems and all of the relevant factors could not be considered in our analysis. Future attempts to refine our predictions therefore require additional processes to be represented mechanistically and data to parameterise these processes (Hill et al., 2016). Current livestock models do not account for variation between individuals, breeds and regions, whilst mechanistic plant models do not consider nutritive quality. Recent work has addressed knowledge gaps in empirical models, such as quantifying methane produced by cattle across Africa and other tropical regions, thus improving the coverage of these models (Jaurena et al., 2015; Patra, 2015). However, there continues to be low geographic coverage of forage quality data in equatorial and tropical regions, where the nutritive quality of forage is typically lower than temperate regions (Nielsen et al., 2013). Furthermore, the effects of heat stress on enteric methane production has not been fully quantified (Kadzere et al., 2002) and the anticipated near-doubling of the global livestock inventory was also not included in our projections, because future changes in the distribution of cattle and technological advances are currently unknown (Herrero et al., 2015). If livestock numbers increase in rapidly warming regions then we predict that there will be an associated rise in enteric methane production. Increased grazing pressure may also alter plant species composition, thus changing the nutritive value and extent of grazing lands (Gardarin et al., 2014). Other global environmental changes, such as elevated CO₂ (Barbehenn et al., 2004; Roumet et al., 1999), and increased frequency of drought, flooding and extreme weather events could also affect methane production (Hoover et al., 2014).

5. Conclusions

We present evidence of future temperature-driven declines in forage nutritive quality and corresponding increases in enteric methane production. Upscaling the GHG footprint of the current livestock inventory to the 2050 projected inventory increases annual GHG emissions from enteric sources from 2.8 GT CO₂eq to 4.7 GT CO₂eq. However, our projections reveal that the geographical distribution of livestock, changes to their size and diet and the interactions between nutritive values, climate and fertilisers may modify the GHG footprint of cattle, both positively and negatively. The incorporation of a greater number of factors which were not included in our analysis, along with more detailed measures of how forage quality changes across environmental gradients would help to refine our estimates. Nevertheless, our projections reveal robust general trends and highlight a potentially important and previously unrecognised climate change feedback, with important implications for GHG emissions targets, future warming, agricultural policies and food security.

6. Author contribution

M. Lee and P. Manning designed the approach and M. Lee carried out data collection and analyses. M. Lee developed predictive models and maps. M. Lee prepared the manuscript with contributions from all co-authors.

7. Acknowledgements

This paper was produced following consultation with the members of RBG Kew Plant Nutrition and Traits Database steering committee. Thanks to Gerhard Boenisch, Jens Kattge, Charlie Marsh and Alex Papadopoulos for editorial advice and discussions on presentation and analyses.

8. Competing interests

The authors declare that they have no conflict of interest.

9. Data availability

Data can be obtained by contacting the lead author directly. Some of our data has been obtained from journals which are not open access and cannot be freely distributed.

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685 Table 1: A summary of the published equations used to model grass nutritive quality driven changes in methane production, giving details of cattle type (D = dairy, B = beef), regions covered (AF = Africa, AS = Asia, AUNZ = Australia and New Zealand, EU = Europe, NA = North America, SA = South America) and the number of studies included in each analysis. Root mean square prediction error (RMSPE) values are also presented.

Ref*	Cattle	Regions	Studies	Equation (CH ₄ =)**	RMSPE***	Model
1	D	AS	1	$5.1 \times \text{NDF}^2 - 39.3 \times \text{NDF} + 360.0$	-	A
2	D	EU, NA, AUNZ	21	$-2.8 + 3.7 \times \text{NDFi}$	18.3	B
3	D,B	NA	172	$1.6 + 0.04 \times \text{MEi} + 1.5 \times \text{NDFi}$	17.9	C
4	D,B	NA	62	$0.2 + 0.04 \times \text{GEi} + 0.1 \times \text{NDF} - 0.3 \times \text{EE}$	17.9	D
5	D	EU	12	$1.2 \times \text{DMI} - 1.5 \times \text{FA} + 0.1 \times \text{NDF}$	16.9	E
6	D,B	AF, AS, AUNZ, SA	35	$-1.0 + 0.3 \times \text{DMI} + 0.04 \times \text{DMI}^2 + 2.4 \times \text{NDFi} - 0.3 \times \text{NDFi}^2$	31.4	F

* 1. Kasuya and Takahashi, 2010, 2. Storlien et al., 2014, 3. Ellis et al., 2007, 4. Moraes et al., 2014, 5. Nielsen et al., 2013, 6. Patra, 2015

690 ** NDF = neutral detergent fibre (%DM), NDFi = neutral detergent fibre intake (kg day⁻¹), MEi = metabolisable energy intake (MJ day⁻¹), GEi = gross energy intake (MJ day⁻¹), EE = dietary ether extract (%DM), DMI = dry matter intake (kg day⁻¹) and FA = dietary fatty acid (%DM)

*** As presented by Appuhamy et al (2016) except ref 4 and 6 which were presented within the referenced article

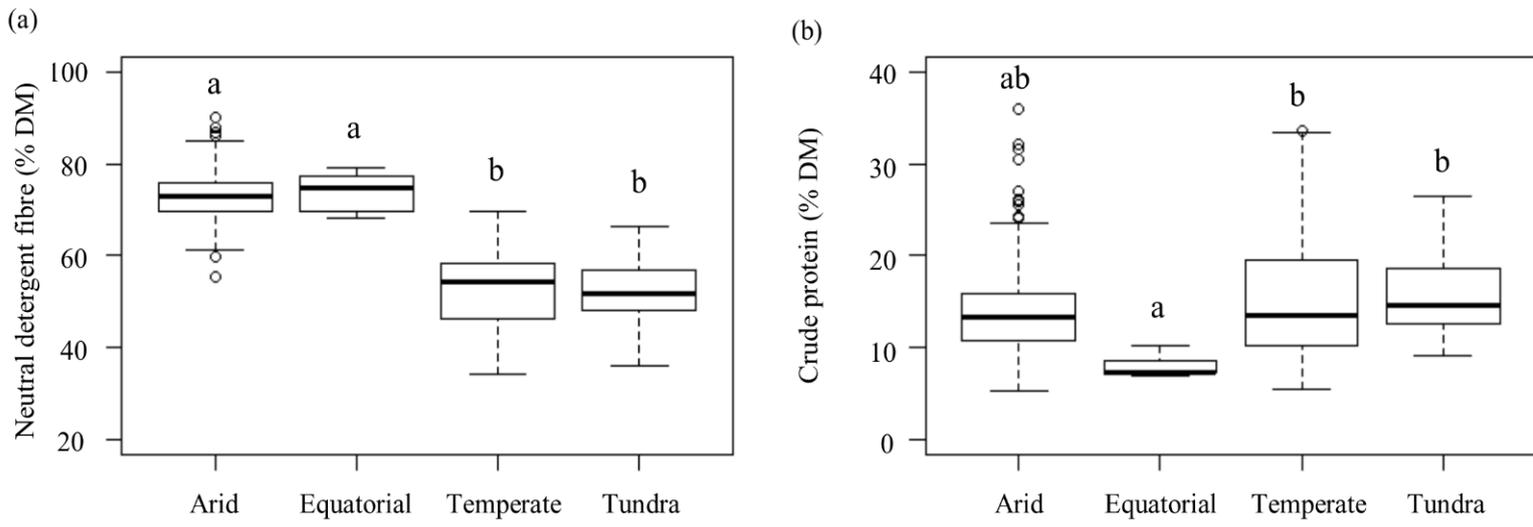
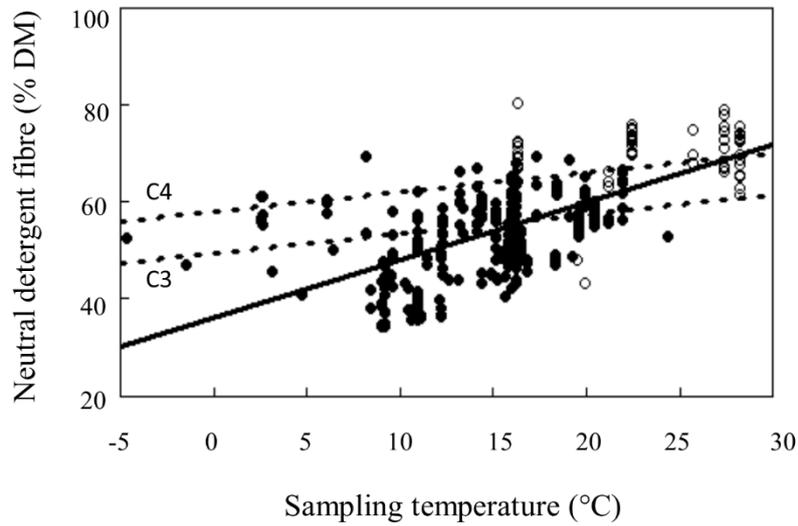


Figure 1: Boxplots of (a) the neutral detergent fibre (NDF) and (b) the crude protein (CP) content of grasses located in bioclimatic zones as described by the Köppen-Geiger Climate Classification system. Significant differences between zones, as identified by LME models, are denoted by different letters ($P < 0.05$).



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Figure 2: Linear relationship between forage neutral detergent fibre (NDF) content and temperature (°C) at the time of sampling. Filled circles are C3 species and open circles are C4 species ($P < 0.05$). Dotted lines represent best fit lines for C3 ($NDF = 0.4T + 49$) and C4 species ($NDF = 0.4T + 58$). The continuous line represents the best fit line for all species excluding other factors included within LME ($NDF = 1.1T + 36$).

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Table 2: Minimum adequate linear mixed effects models for forage neutral detergent fibre (NDF) and crude protein (CP). Values represent slopes except C4 pathway values which represent absolute differences between C3 pathway (Intercept) and C4 pathway. Site numbers differ between response types since temperature at the time of sampling and both NDF and CP were not always available from all articles.

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Response	Sites	Factor	Value	SE	DF	T	P
NDF	20	Intercept	49.4	2.0	287	25.3	<0.001
		Temperature at sampling (°C)	0.4	0.06	287	5.8	<0.001
		N addition (kg N ha ⁻¹ yr ⁻¹)	-0.03	0.01	287	-3.4	<0.001
		C4 pathway presence	8.7	3.2	33	2.7	<0.05
NDF	32	Intercept	43.4	3.7	300	11.6	<0.001
		MAT (°C)	1.0	0.3	19	3.8	<0.01
CP	25	Intercept	14.2	1.0	484	14.8	<0.001
		Rainfall (mm mth ⁻¹)	-0.002	0.002	484	-0.8	0.43
		N addition (kg N ha ⁻¹ yr ⁻¹)	0.02	0.006	484	3.0	<0.01
		C4 pathway presence	-2.9	1.7	46	-1.7	0.1
CP	27	Intercept	15.9	1.6	575	9.9	<0.001
		MAR (mm yr ⁻¹)	-0.001	0.001	24	-0.5	0.65

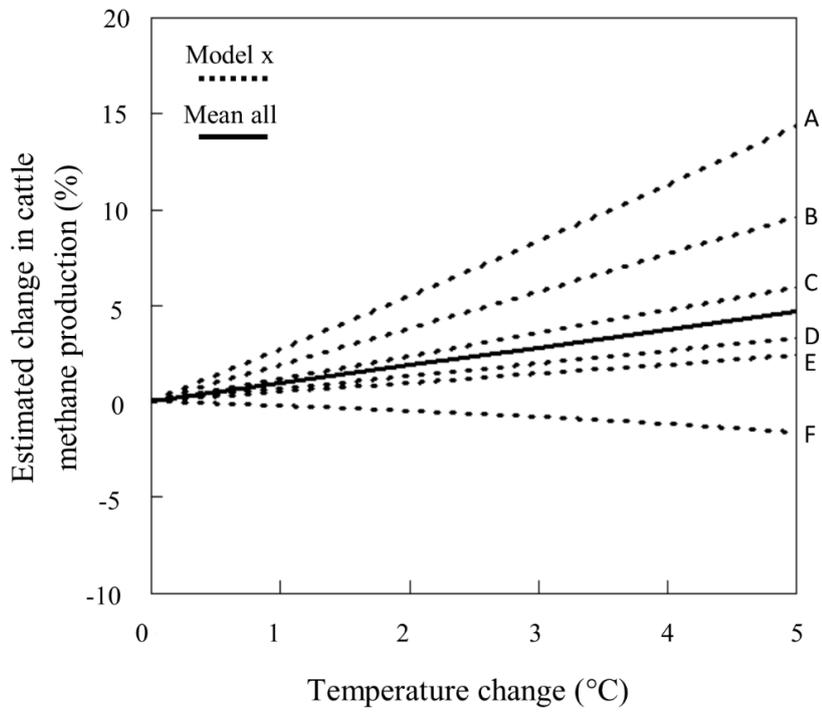
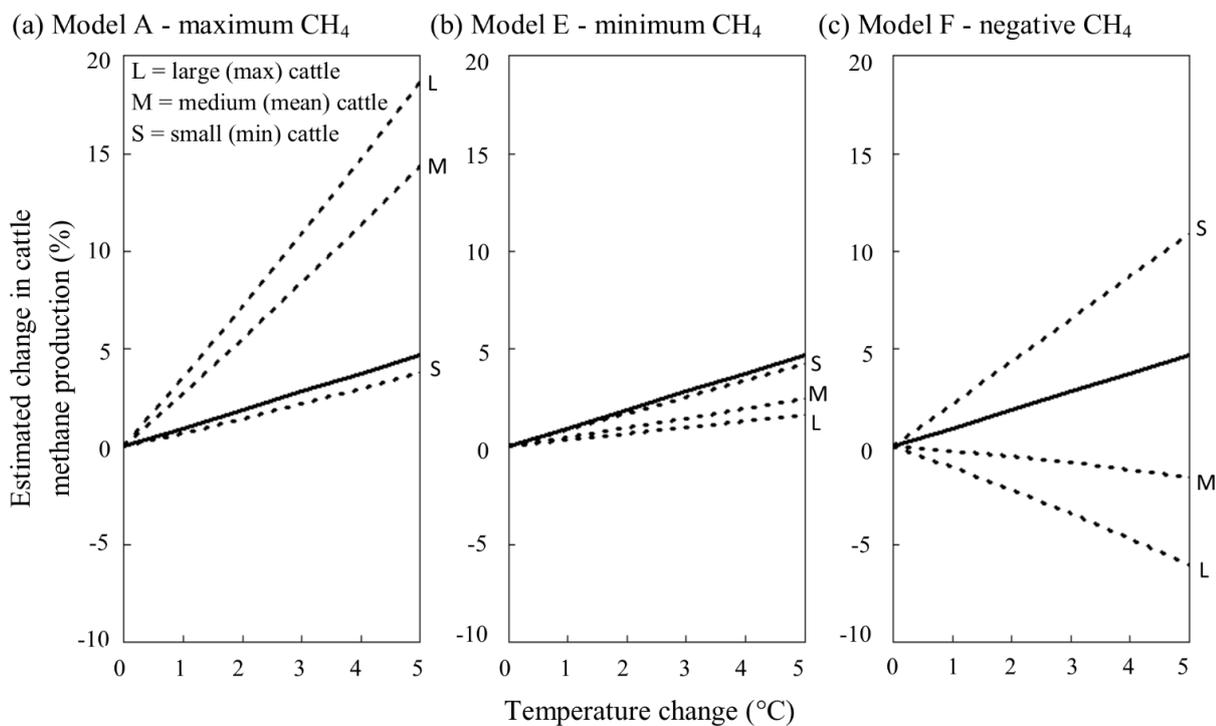


Figure 3: Estimated change in cattle methane production with temperature derived declines in grass nutritive quality. Dotted lines represent six model outputs as defined by equations A – F (defining relationships between grass nutritive quality and methane production) when combined with the inverse relationship between temperature and grass nutritive quality presented in this article. The continuous line represents mean methane production predicted by all six equations, weighted by the number of contributing datasets.

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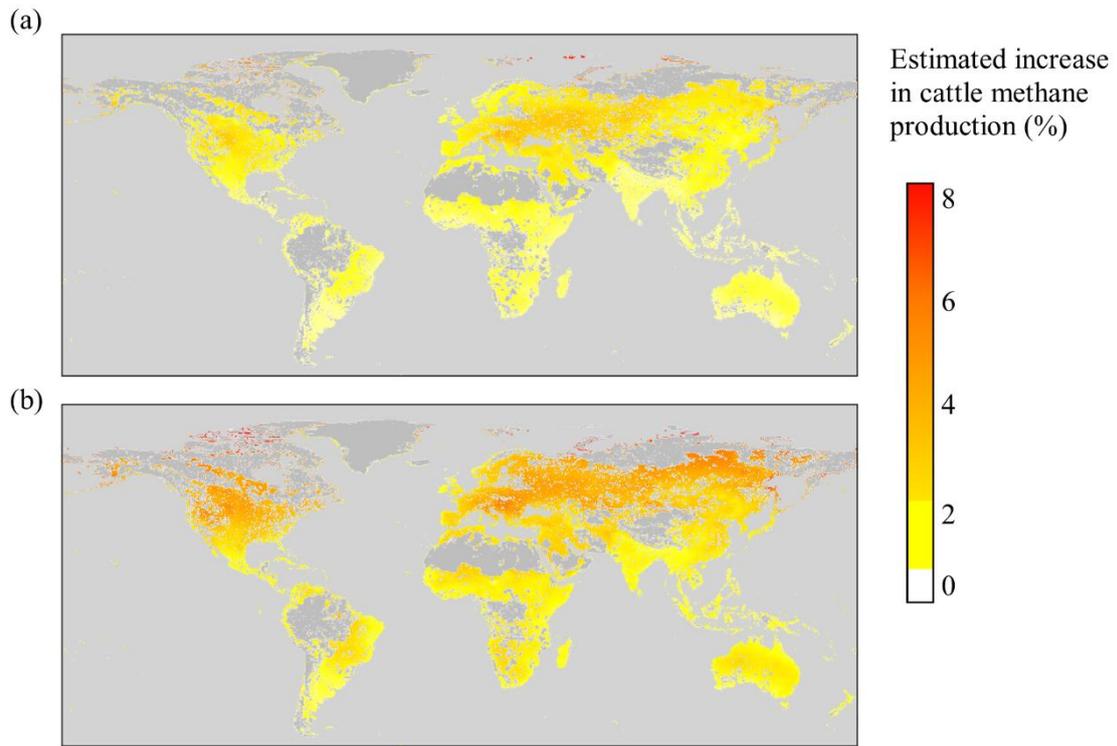
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Figure 4: Estimated change in cattle methane production with temperature change for (a) the model predicting the largest increases in methane production (maximum CH₄), (b) the model predicting the lowest increase in methane production (minimum CH₄) and (c) the model which predicts both increases and decreases in methane production (negative CH₄).

Dotted lines represent predictions for minimum sized (small, S), mean sized (medium, M) and maximum sized (large, L)

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cattle. S, M and L cattle were defined as cattle consuming 9.7, 18.8 and 28.9 kg DMI day⁻¹, respectively, for model A and E. S, M and L cattle were defined as consuming 1.4, 7.7 and 10 kg DMI day⁻¹, respectively, for model F which represents less productive tropical regions.



730 Figure 5: Predictions of climate and forage-driven increases in cattle methane production (%) under 2050 predicted
 temperatures using (a) a low estimate of future temperature changes (RCP 2.6) and (b) a high estimate of future temperature
 changes (RCP 8.5). Regions in dark grey are currently unsuitable for ruminant livestock. Values do not include projected
 increases in the global cattle inventory. Projections are based on HADGEM2 climate projections combined with our mean
 weighted model defining the negative relationship between forage nutritive quality and rising temperatures, as applied to
 735 mean sized cattle.

Appendix

Table A1: Sites included in the database, detailing latitude, longitude, Mean Annual Temperature (MAT, °C), Mean Annual Rainfall (MAR, mm) and altitude (m). The site with no climatic data is indicated by an em-rule (–). Some sites did not contribute both NDF and CP values.

Site	Country	Latitude	Longitude	MAT	MAR	Altitude
Calden ¹	Argentina	-38.450	-63.750	15.0	400.0	95
Buenos Aires ²	Argentina	-37.183	-62.133	15.9	602.7	181
Mutdapily ³	Australia	-27.767	152.667	19.9	815.0	40
Pernambuco ⁴	Brazil	-8.014	-34.951	25.7	2310.3	23
Lacombe ⁵	Canada	52.467	-113.733	2.4	466.0	855
Melfort ⁵	Canada	52.817	-104.600	0.7	439.0	483
Alberta ⁶	Canada	53.756	-113.339	3.0	455.8	674
Fredericton ⁷	Canada	45.917	-66.604	5.6	1065.0	26
Gansu ⁸	China	37.667	103.533	-1.0	385.7	3000
Fodder Research ⁹	Czech Republic	49.517	15.967	6.9	617.0	560
Grange ^{10,11,12,13}	Ireland	53.500	-6.670	6.3	877.3	83
Moorepark ¹⁴	Ireland	52.163	-8.260	10.0	1040.0	70
Tohoku ¹⁵	Japan	39.733	141.133	9.3	1180.0	110
Ohda ¹⁶	Japan	35.167	132.500	15.9	1603.9	53
Sumiyoshi ¹⁷	Japan	31.983	131.467	17.3	2378.0	11
Nuevo Leon ¹⁸	Mexico	25.717	-100.033	22.0	500.0	393
Sauces Ranch ¹⁹	Mexico	25.407	-99.776	22.0	360.0	272
Chifeng ²⁰	Mongolia	42.261	118.931	4.5	380.0	900
Wageningen ²¹	Netherlands	51.967	5.667	9.3	771.4	7
Lincoln ²²	New Zealand	-43.633	172.467	11.5	581.2	22
Waimate North ²³	New Zealand	-35.300	173.900	–	–	83
Quassim ²⁴	Saudi Arabia	26.308	43.767	24.7	160.6	652
Alpine region ²⁵	Slovenia	46.050	14.467	10.8	914.8	300
Atatürk ²⁶	Turkey	39.917	41.267	4.4	37.9	1850
Black Sea ²⁷	Turkey	41.244	36.510	14.6	709.3	4
Erzurum ²⁸	Turkey	39.906	41.271	5.7	409.4	1905
Aberystwyth ²⁹	United Kingdom	52.367	-4.083	10.0	1174.0	100
Ty Gwyn ³⁰	United Kingdom	52.267	-4.083	10.0	1823.8	257
Fort Keogh ³¹	United States	46.367	-105.083	8.2	498.3	719
Ithaca ³²	United States	42.440	-76.500	8.4	963.9	120
Logan ³³	United States	41.767	-111.817	9.1	509.6	1406
Mount Pleasant ³²	United States	41.110	-73.810	11.5	1327.0	100

¹ Distel et al., 2005, ² Catanese et al., 2009, ³ Callow et al., 2003, ⁴ dos Santos et al., 2003, ⁵ McCartney et al., 2008,

⁶ Suleiman et al., 1999, ⁷ Bélanger and Mcqueen, 1997, ⁸ Dong et al., 2003, ⁹ Skladanka et al., 2010, ¹⁰ Conaghan et al.,

2008¹¹ Keating and O’Kiely, 2000, ¹² King et al., 2012, ¹³ Mceniry et al., 2014, ¹⁴ Beecher et al., 2015, ¹⁵ Nashiki et al., 2005,

¹⁶ Kobayashi et al., 2008, ¹⁷ Hirata et al., 2008, ^{18,19} Ramirez, 2007, ²⁰ Zhao et al., 2012, ²¹ Smit et al., 2005, ²² Bryant et al.,

2012, ²³Ulyatt et al., 2002, ²⁴Al-Ghumaiz and Motawei, 2011, ²⁵Çop et al., 2009, ²⁶Akgun et al., 2008, ²⁷Surmen et al., 2013, ²⁸Sahin et al., 2012, ²⁹Lee et al., 2001, ³⁰Weller and Cooper, 2001, ³¹Haferkamp and Grings, 2002, ³²Cherney and Cherney, 1997, ³³Griggs et al., 2007

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Table A2: Species included in the database showing NDF (% DM) and CP (%DM) mean, standard deviation (SD), maximum (Max) and minimum (Min) values. Hybridised species are denoted by a multiplication sign (x). The site with no climatic data is indicated by an em-rule (-).

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	NDF (% DM)				CP (% DM)			
	Mean	SD	Max	Min	Mean	SD	Max	Min
<i>Agropyron cristatum</i>	-	-	-	-	17	7	36	8
<i>Agropyron intermedium</i>	-	-	-	-	16	5	26	9
<i>Agropyron riparium</i>	-	-	-	-	16	3	23	11
<i>Agropyron trachycaulum</i>	-	-	-	-	15	5	25	10
<i>Agropyron trichophorum</i>	-	-	-	-	16	5	27	11
<i>Alopecurus pratensis</i>	58	9	70	39	15	4	24	8
<i>Aristida longiseta</i>	87	1	88	85	-	-	-	-
<i>Arrhenatherum elatius</i>	61	1	61	60	8	1	9	7
<i>Bouteloua curtipendula</i>	74	3	79	72	11	3	14	8
<i>Bouteloua gracilis</i>	83	5	90	77	-	-	-	-
<i>Bouteloua trifida</i>	74	3	76	70	11	4	15	8
<i>Brachiaria brizantha</i>	75	-	75	75	7	-	7	7
<i>Brachiaria fasciculata</i>	64	5	72	60	14	4	18	10
<i>Bromus inermis</i>	-	-	-	-	16	6	26	7
<i>Cenchrus ciliaris</i>	76	2	78	74	-	-	-	-
<i>Cenchrus incertus</i>	77	3	80	74	-	-	-	-
<i>Chloris ciliata</i>	70	3	72	65	13	3	18	10
<i>Dactylis glomerata</i>	58	5	64	43	14	4	26	9
<i>Digitaria insularis</i>	72	2	75	70	11	3	13	7
<i>Echinochloa crusgalli</i>	64	2	66	63	11	1	12	10
<i>Elymus nutans</i>	-	-	-	-	14	1	15	13
<i>Elymus sibiricus</i>	-	-	-	-	14	8	26	5
<i>Elytrigia intermedia</i>	-	-	-	-	20	9	32	6
<i>Eremochloa ophiuroides</i>	-	-	-	-	12	3	20	8
<i>Festuca arundinacea</i>	57	3	60	53	15	4	23	9
<i>Festuca arundinacea</i> x <i>Lolium multiflorum</i>	58	2	61	56	8	1	9	8
<i>Festuca pratensis</i>	-	-	-	-	11	1	12	11
<i>Festuca rubra</i>	-	-	-	-	17	3	21	11
<i>Hilaria belangeri</i>	79	4	83	75	-	-	-	-
<i>Holcus lanatus</i>	54	9	65	39	11	4	19	5
<i>Hordeum brevisubulatum</i>	-	-	-	-	14	1	15	13
<i>Leptochloa filiformis</i>	70	4	75	67	12	2	15	10
<i>Lolium multiflorum</i>	46	6	56	36	15	5	28	6

<i>Lolium multiflorum</i> × <i>Festuca pratensis</i>	–	–	–	–	12	1	13	12
<i>Lolium perenne</i>	50	8	62	34	18	8	34	7
<i>Lolium perenne</i> × <i>Festuca pratensis</i>	–	–	–	–	11	0	11	10
<i>Panicum hallii</i>	71	3	76	67	13	5	18	8
<i>Panicum obtusum</i>	65	8	74	55	14	2	17	12
<i>Pascopyrum smithii</i>	–	–	–	–	18	6	26	7
<i>Paspalum notatum</i>	–	–	–	–	12	3	19	9
<i>Paspalum unispicatum</i>	68	2	70	64	11	3	13	9
<i>Pennisetum clandestinum</i>	46	4	48	43	23	1	23	22
<i>Pennisetum maximum</i>	78	1	79	77	7	0	7	7
<i>Pennisetum purpureum</i>	69	1	70	68	9	1	10	9
<i>Phalaris arundinacea</i>	58	5	67	52	–	–	–	–
<i>Phleum pratense</i>	51	8	67	36	15	4	23	9
<i>Poa crymophila</i>	–	–	–	–	13	5	20	8
<i>Rhynchelytrum repens</i>	72	2	74	69	10	2	11	7
<i>Roegneria turczaninonii</i>	–	–	–	–	15	1	16	14
<i>Setaria grisebachii</i>	72	8	81	61	14	4	17	9
<i>Setaria macrostachya</i>	74	7	86	63	13	2	16	11
<i>Stipa clarazii</i>	55	2	57	54	16	6	22	11
<i>Stipa eriostachya</i>	66	6	69	59	10	5	16	7
<i>Tridens eragrostoides</i>	73	2	76	71	13	2	17	11
<i>Tridens muticus</i>	75	3	78	72	11	4	16	8