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

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10   Abstract: Meat production is increasing globally to meet the growing demand for western diets. The sustainability of this trend has been questioned, and 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 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 species identity, and changes to physiology and phenology. These relationships informed projections of future enteric cattle methane production, revealing a previously undescribed positive climate change feedback, where elevated temperatures reduced grass nutritive value and correspondingly increased methane production by 0.2 – 15%, thus creating an additional climate forcing effect. Future methane production increases were largest in parts of North America, Central and Eastern Europe, and Asia, with the geographical extent of hotspots increasing under a high emissions scenario. Nitrogen fertiliser addition, planting forage species with high nutritive value and dietary supplements could partially offset these rises but may have other negative effects. Limiting the growth of livestock farming in warmer regions and reducing ruminant meat consumption would reduce the environmental impacts of livestock and mitigate pastoral
25   greenhouse gas emissions.

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

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1. Introduction

Global meat production has increased rapidly in recent years, from 71 million tonnes in 1961 to 310 million tonnes in 2013

30   (FAOSTAT, 2016). This is due to population growth and a transition to western 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 km^2 of the Earth's surface, with an estimated 1.5 billion cattle, 1.2 billion sheep and 1

billion goats 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

35   land use change, enteric sources and manure decomposition produces approximately 7.1 gigatonnes of CO_2 and CO_2

equivalents annually (GT CO_2eq), accounting for 15% of anthropogenic greenhouse gas (GHG) emissions (FAO, 2013).

Enteric fermentation by livestock produces 2.8 GT CO_2eq 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).

40   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% of the biomass consumed by livestock was grass (Herrero *et al*., 2013). The chemical composition and

morphology of these 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

45   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). Highly nutritious forage can also 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

50   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

55   proportion of plant dry mass to fresh mass). Consequently, these grasses 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 is 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).

60 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 which 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 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

65 across many 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

70 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

75 fertiliser addition and photosynthetic pathway. Where possible, statistical models were then used to generate coarse

projections of future climate and fertiliser induced changes to forage grass nutritive value and cattle methane production.

2. Materials and methods

2.1 Data acquisition

80 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

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

85 greenhouses or field experiments that manipulated weather conditions were excluded because the prevailing growing

conditions were not representative of the location. In some cases, data obtained from experimental control plots were added

to the database if plots were not artificially manipulated for the purposes of the experiment. Experiments which manipulated

fertiliser application were included if rates of N addition were presented. Data from experimental treatments comprised 8%

90 of the database and included manipulations of inorganic fertiliser compound or combination of compounds, and harvesting and fertilization dates.

To ensure that the methods for measuring forage nutritive value were consistent across articles, data where 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

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Descriptive data were also 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

100 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 $\geq$ 18 °C), temperate (mean temperature of warmest month $\geq$ 10 °C and coldest month -3 – 18 °C) or tundra

105 (mean temperature of warmest month $\geq$ 10 °C and coldest month $\leq$ -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. 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

110 mm (MAR: 38 – 2378 mm). Rates of fertiliser application across all sites ranged from N addition of 0 to 357 kg N ha^{-1} yr^{-1}.

2.3 Gap filling

In many cases required data were obtained from the methods sections of the articles analysed, but in some cases there were gaps in the information available. Data most commonly gathered from external sources were weather and climate, which

115 were obtained from the closest weather station to each site, according to the National Centers for Environmental Prediction database (www.ncep.noaa.gov). Mean distance from weather stations to sites was 22 $\pm$ 5 km (mean $\pm$ standard error) and the mean difference in elevation was 6 $\pm$ 17 km. 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 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

120   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

(Pinheiro and Bates, 2000). Model selection was carried out by including NDF or CP as response variables with multiple

125   potential explanatory variables added as fixed effects to generate full models. Fixed effects were mean temperature during

the sampling month, total rainfall during the sampling month, elevation, rates of N addition and photosynthetic pathway. To

avoid over-fitting, grazing density, soil pH and whether the plants were grown in mono- or polyculture were shown not to

significantly relate to CP or NDF using LME models in preliminary analyses, and therefore these variables were not

included in initial full models (all $P > 0.05$).

130   Grass species were nested within experimental treatment, and treatments were nested within sites and included within LMEs

as random effects, thus accounting for measures of several species taken at the same site and/or treatment. All other variables

were treated as fixed effects. 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 explantory variables were removed from full models based on minimising Akaike's Information Criterion

135   (AIC). The relative influence of terms 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, and also to test for differences in CP

140   and NDF between bioclimatic zones. All analyses were computed using R, version 3.2.3 (R Development Core Team, 2016).

2.5 Enteric methane production modelling

Methane production projections were based on the experimentally derived relationship between NDF intake (NDFi) and

enteric methane production found in cattle (eq. 1, Kasuya & Takahashi, 2010). The majority of other methane production

145   equations for grass-fed cattle also assess nutritive value, with most including NDF and some including WSC, fat and/or

energy intakes as model parameters (Appuhamy et al., 2016). The most complex models were not used in this study because

the availability and coverage of WSC, fat and energy data were extremely low and the relationships between these

parameters and growing temperatures have not been quantified.

150 $$CH_4 \ (L \ day^{-1}) = 5.14 \ NDFi^2 - 39.30 \ NDFi + 360 \qquad (1)$$

$$NDFi = NDF \ content \ of \ forage \ (\%) \ x \ total \ forage \ intake \ (kg \ DM \ day^{-1}) \qquad (2)$$

$$NDFi = \frac{1.0T + 43.4}{100} \ x \ total \ forage \ intake \ (kg \ DM \ day^{-1}) \qquad (3)$$

$$NDFi = \frac{-0.03N + 49.4}{100} \ x \ total \ forage \ intake \ (kg \ DM \ day^{-1}) \qquad (4)$$

155 NDFi was calculated using parameters identified from the LME model outputs presented, which described the relationships between NDF and both MAT and N addition rates (see Results), multiplied by estimated daily DMI (dry matter intake) for small, medium and large cattle of 10, 15 and 20 kg, respectively (eq. 2, 3 and 4). These values are consistent with the range of daily forage intakes that have been measured for cattle (e.g. Dalley *et al.*, 1999; Ominski *et al.*, 2006; Hegarty *et al.*, 2007).

160 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 forage climate and forage-driven changes to methane production. 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).

165 Estimated increases in cattle 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-

170 driven increases in cattle methane production. Changes to methane production were also calculated for a realistic range of N addition rates (N, 0 – 300 kg N ha-1 yr-1). Regions which are unsuitable for ruminant livestock were excluded (Robinson et al., 2014).

3. Results

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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

180 NDF, with *Phleum pratense* showing the biggest range of values, from 36 – 67%

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%), over three times higher than the lowest, which was *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

185 species (8 – 36% for *Agropyron cristatum*) was also lower than for NDF.

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 outlier data were removed there was not a significant relationship between CP and DMD (t = -0.2, P > 0.05).

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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

195 a mean of 8% greater CP than grasses growing in equatorial zones (Fig. 1b). However, there were no differences between the CP contents of grasses growing in arid zones when compared with the other bioclimatic zones.

➔ Figure 1

200 ### 3.2 Environmental determinants of nutritive value

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. MAT was also positively associated with NDF, but the rate of increase

was greater than for sampling temperatures, increasing by 1% for every 1 °C increase in MAT (Table 1). 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

205   agricultural grasslands, reducing NDF by 3%. 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 =

3.6, P < 0.001) and MAT (sites = 21, t = 4.6, P < 0.001), 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

210   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 3 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. Mean CP content was 3% higher for C3 species than for C4 species, but this difference was not

215   significant (P > 0.05). None of the remaining variables were significantly related to CP (all P > 0.05).

➔   Figure 2

➔   Table 1

220

3.3 Projected changes to methane production

The non-linear relationship between NDFi and methane production resulted in non-linear projections of cattle methane

production with rising temperatures (Fig. 3a) and N addition (Fig. 3b). Variation in NDFi was greatest for the largest cattle

and therefore temperature- and N-driven changes to methane production was also greatest for the largest cattle. Temperature-

225   driven changes were also dependent on MAT and methane production increased to the greatest extent at the highest MAT.

At a moderate N addition rate of 100 kg N ha^{-1} yr^{-1} methane production was reduced by 1 – 8%, from the smallest to largest

cattle. As N addition rates increased methane production declined and at a high N addition rate of 300 kg N ha^{-1} yr^{-1} methane

production was projected to be reduced by 2 – 20%.

230   ➜   Figure 3

When statistical models were combined with future temperature scenarios, hotspots of forage-driven increases in methane

production were identified. The low emissions scenario revealed increases in methane production for medium sized cattle by

approximately 1 - 4% in most regions; for hotpots in North America, Central and Eastern Europe, and Asia projections

235   reached 6 – 8% (Fig. 4a). 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 – 10% (Fig. 4b). Adjusting these projections for the largest cattle, consuming 20 kg DM day^{-1}, revealed

increased methane production by up to 15% in the warmest regions under the high emissions scenario.

240   ➜   Figure 4

4. Discussion

Global food consumptions patterns are shifting from traditional diets to diets rich in refined sugars, fats, oils and meats

(Tilman and Clark, 2014). Greater meat production is expected across many regions in the future, with this rise expected to

245   be particularly marked across arid, equatorial and tropical regions that historically contained a relatively small inventory of

livestock (Herrero et al., 2013). Assessments suggest that agricultural GHG emissions need to be reduced by ~1 GT CO_2eq

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. We project that future temperature-driven reductions in the nutritive value of forage grasses may increase methane

250   production by cattle by 0.2 – 15% by 2050, depending on emissions scenario, locality and cattle size, creating an additional

climate forcing effect. Our analyses generated coarse projections, because the current and future mix of cattle in the global

inventory is unknown and the effects of climate change on economic growth, technological uptake and land availability has

not been fully quantified (Audsley et al., 2014; Havlík et al., 2014). However, the potential magnitude of future decreases in

grass nutritive value and corresponding increases in methane production means that these projections cannot be ignored, and

255   are identified here as a research area requiring careful future work and refinement.

4.1 Variation in nutritive and functional traits

Forage grass nutritive value varied considerably, 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

260   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.

NDF values were generally higher and CP generally lower in warmer bioclimatic zones than in cooler zones suggesting that

ruminants across many arid, tropical and equatorial zones are currently subject to nutritional stress. Reduced nutritive value

265   in these zones is likely driven by increased abundances of plants with adaptations to prevent heat stress and avoid water loss

across warmer and drier environments; 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 (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 plant were also associated with lower

270   nutritive value. 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 strategy (Martin and Isaac, 2015; Wood et al.,

2015). Large variation within- and between-species highlights the potential for the breeding of grasses to enhance livestock

nutrition and promote resistant to environmental changes.

275   **4.2 Relationships between nutritive value, environment and management**

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 increased abundances of 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

280   tissue aging (Hirata, 1999). 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

(Dumont et al., 2015). This may be because the effect of species identity is far stronger than changes to phenology and

physiology, as evidenced by the observed greater response to long-term climate than short-term weather.

285   N fertiliser addition generally increases the productivity of grasslands, since the majority of these ecosystems are N limited

(LeBauer and Treseder, 2008; Lee et al., 2010). We present data which suggests that N addition is also generally associated

with increased grass nutritive value, due to an associated decline in NDF and an increase in CP and DMD. 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 may therefore partially offset the negative effects of

290   warmer temperatures on forage grass nutritive value.

4.3 Projections of methane production

Our projections suggest that cattle enteric methane production may increase by 0.2 – 3% for an initial 1 °C increase in temperature, due to a decline in grass nutritive value. This increase translates to an annual increase in methane production

295   across the global cattle inventory of approximately 0.005 – 0.06 GT CO_2eq. At a larger 5 °C increase in temperature the projected increase in cattle methane production of 2 – 15% translates to a global rise of approximately 0.03 – 0.3 GT CO_2eq. Whether overall methane production is expected to rise at the upper or lower end of the projected ranges is dependent on the proportions and location of small and large cattle across the global cattle inventory and whether these cattle are fed grasses or grains. Our calculations assumed that all cattle consume grass, however, the trend towards permanently housed cattle,

300   particularly across Europe and North America, may further increase these values because the mixed diets of housed cattle generally increase enteric methane production (March et al., 2014; O'Neill et al., 2011).

Hotspots of future increases in methane production were identified across North America, Central and Eastern Europe, and Asia using a low GHG emissions scenario with hotspots becoming more widespread, and of greater magnitude, in a high emissions scenario. At present the greatest densities of cattle can be found in parts of Asia, North and South America,

305   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 1% increase across Europe, to satisfy the growing demand (FAOSTAT, 2016). Losses in forage quality could drive farmers into more extensive farming systems across many of these regions because a larger area of land may be required for each animal. It may be beneficial to limit the growth of livestock

310   production systems in warmer and drier regions, particularly those likely to experience future warming, because the loss in livestock production efficiency and change in methane emissions across these regions could be substantial.

Cattle methane production can be reduced by N fertiliser addition, feed processing, adjusting rumen pH, increased concentrate feeding, genetic selection, and feeding methane inhibitors (Duin et al., 2016; Knapp et al., 2014). However, implementing these measures is unlikely to result in sufficient reductions in GHG emissions to meet ambitious GHG

315   reduction targets, and may also promote other negative environmental effects such as nitrous oxide emissions and pollution to air and water (Wollenberg et al., 2016). Ruminant meats (beef and lamb) produce around 250 times greater GHG emissions per gram of protein than legumes, 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, such as organic and silvopastoral systems, may reduce our reliance on intensively farmed cattle and other

320　ruminants, which may reduce the environmental impacts of agriculture, contributing to GHG emissions cuts, and with an

associated improvement in human health (Springmann et al., 2016).

The anticipated near-doubling of the global livestock inventory was not included in projections, because the social, economic

and environmental drivers of the distribution of future farming systems and uptake of technological advances are unknown.

Upscaling the GHG footprint of the current livestock inventory to the 2050 projected inventory increases annual GHG

325　emissions to around 12 GT CO_2eq. However, our projections reveal that the geographical distribution of livestock and the

interactions between nutritive values, climate and fertilisers may modify these values, both positively and negatively, by 0.2

– 20%. Expected changes to the frequency of drought, flooding and extreme weather events may further modify forage

nutritive values (Hoover et al., 2014). The incorporation of such factors, along with more detailed measures of how forage

quality changes across environmental gradients would help to refine our currently coarse estimates. Nevertheless, our

330　projections reveal 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.

5. Author contribution

M. Lee and P. Manning designed the approach and M. Lee carried out data collection and analyses. M. Lee developed

335　predictive models and maps. M. Lee prepared the manuscript with contributions from all co-authors.

6. Acknowledgements

7. Competing interests

The authors declare that they have no conflict of interest.

345　## 8. 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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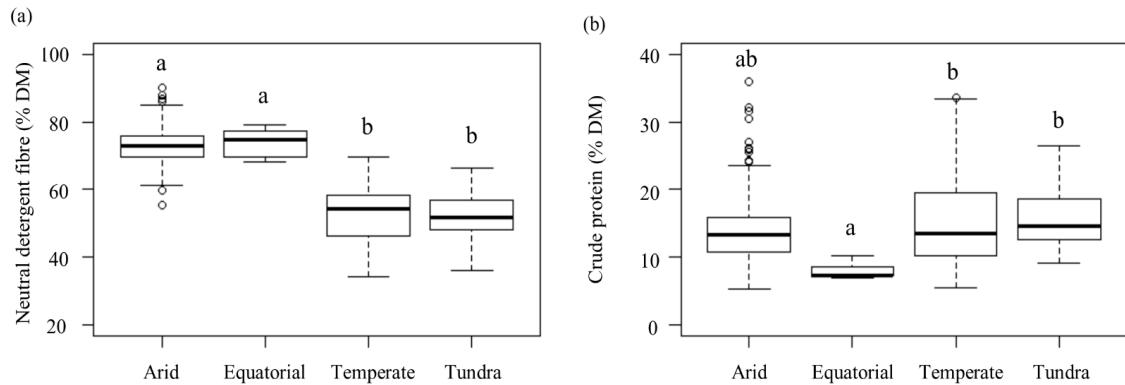
555   Figure 1: Boxplots of (a) the neutral detergent fibre (NDF) and (b) the crude protein (CP) content of grasses located in

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).
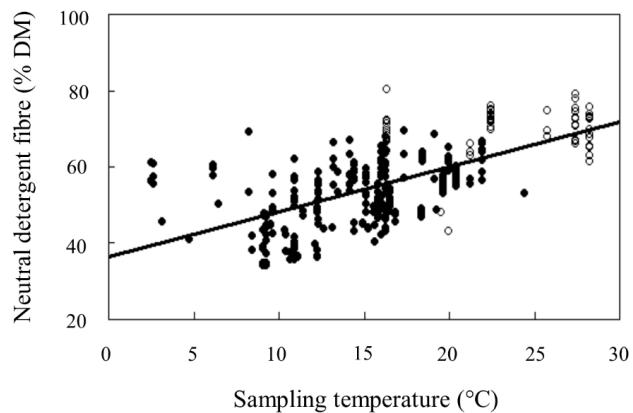
560   Figure 2: Linear relationship between forage neutral detergent fibre (NDF) content and temperature (°C) at the time of

sampling. Filled circles are C3 species and open circles are C4 species ($P < 0.05$).

Table 1: 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

565   C4 pathway.

Response	Sites	Factor	Value	SE	DF	T	P
NDF	20	Intercept	49.4	2.0	287	25.3	<0.001
		Temperature (°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

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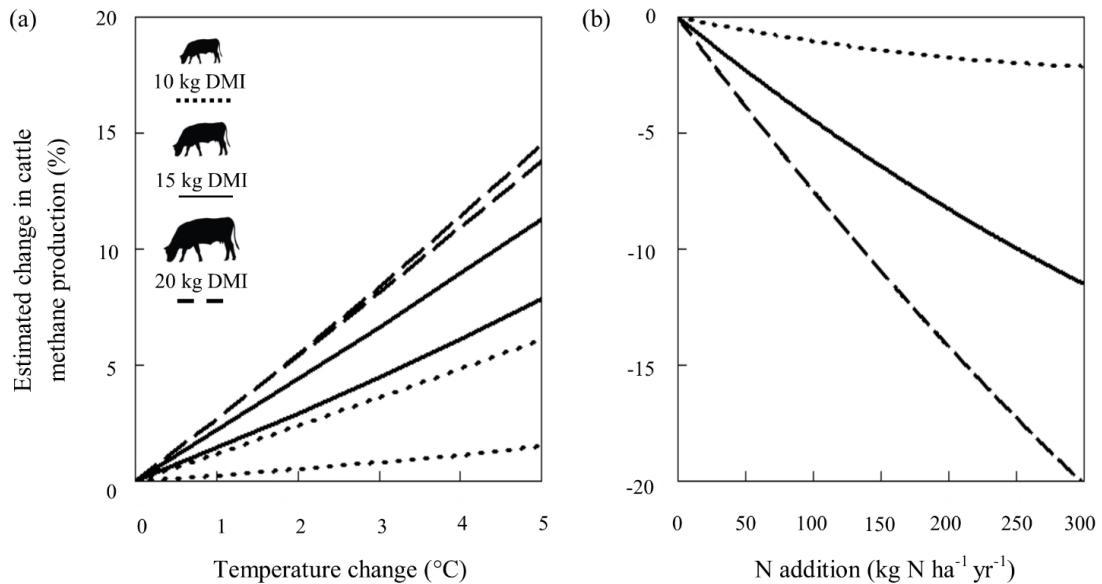
Figure 3: Estimated change in cattle methane production in response to (a) temperature driven- and (b) nitrogen (N) addition-

570   driven changes to forage quality. Upper and lower ranges for temperature change are based on maximum and minimum

MAT of 0 – 30 °C. Cattle size was modelled according to estimated dry matter intakes (DMI).

(a) RCP 2.6 (2050)
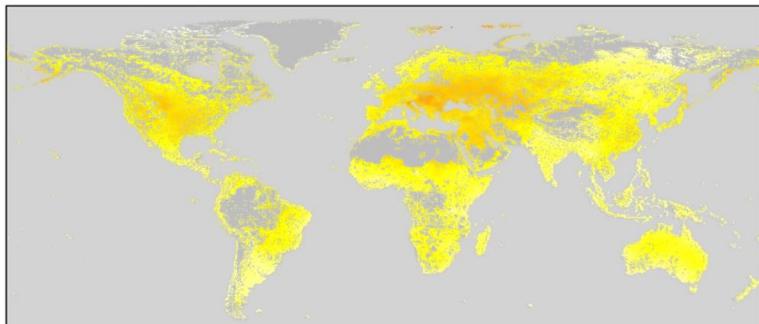
(b) RCP 8.5 (2050)

Estimated increase in cattle methane production (%)
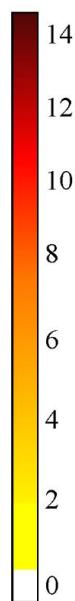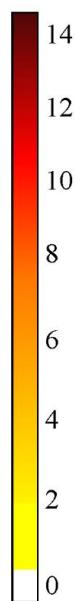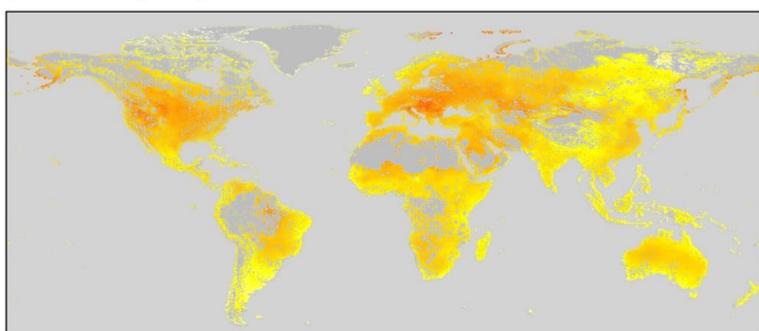
Figure 4: Coarse predictions of climate and forage-driven increases in cattle methane production (%) under 2050 predicted temperatures using (a) a low estimate of future temperatures (RCP 2.6) and (b) a high estimate of future temperatures (RCP 8.5). Regions in dark grey are unsuitable for ruminant livestock. Values do not include projected increases in the global cattle inventory. Projections are for medium sized cattle (DMI = 15 kg DM day^{-1}).

Appendix

580   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 indicted by -. 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

585   [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.,

2008[11] 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, [23]Ulyatt et al., 2002, [24]Al-Ghumaiz and Motawei, 2011, [25]Čop et al., 2009, [26]Akgun et al., 2008, [27] Surmen et al.,

590   2013, [28]Sahin et al., 2012, [29]Lee et al., 2001, [30]Weller and Cooper, 2001, [31]Haferkamp and Grings, 2002, [32]Cherney and

Cherney, 1997, [33]Griggs et al., 2007

Table A2: Species included in the database showing NDF (% DM) and CP (%DM) mean, standard deviation (SD),

595   maximum (Max) and minimum (Min) values. Hybridised species are denoted by x.

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

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

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