Field Crops Research 324 (2025) 109791

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Trade-offs between forage nutrition and ruminant carrying capacity in response to fertiliser application – Findings from the Park Grass long-term experiment (1860–2020)

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ARTICLE INFO

Keywords:
Agriculture
Grassland
Livestock
Cattle
Animal nutrition

ABSTRACT

Context: Rothamsted Research's Park Grass Experiment, established in 1856, is the longest-running grassland study globally. Naturally regenerating grassland swards are grown in plots with varying applications of fertiliser including ammonium sulphate and sodium nitrate (at varying application rates), organic fertiliser, minerals (K, Mg, Na, P), and lime, which is mown twice a year. As the world's most widely produced crop, grass is predominantly used to feed ruminants, however, the nutritional properties and carrying capacities of these plots have not previously been quantified.
Objective: The objective of this study was to characterise the nutritional profile of forage gathered from the Park Grass plots from 1860 to 2020 and the ruminant carrying capacity that the plots would support. The study further aimed to explore the trade-offs between productivity, forage nutritional quality, and biodiversity.
Method: Dried PGE herbage samples were taken from the Rothamsted sample archive at decade intervals from 1860 to 2020, representing a range of plot treatments. Proximate analysis and XRF elemental analysis were performed, and the data was used to estimate ruminant carrying capacity of plots based on metabolisable energy and crude protein requirements for production.
Results: Fertiliser applications increased carrying capacity due to yield improvements but reduced crude protein while increasing cellulose and hemicellulose. Increased growth appeared to have a dilution effect on some essential minerals, particularly Ca, Mg, Mn, and P. Sodium nitrate produced higher carrying capacities per unit of nitrogen compared to ammonium sulphate or organic manure.
Conclusions: The findings highlight trade-offs in improved grasslands between forage quality, quantity, biodiversity, and management inputs. Results show that fertiliser applications enhance carrying capacity by increasing forage yield but potentially at the cost of reduced nutritional quality and species diversity. This study also provides the first comprehensive nutritional analysis of the Park Grass plots, revealing how historical fertiliser treatments influenced forage quality and ruminant carrying capacity over 160 years.
Significance: Studying the trade-offs and gradients within grassland systems is essential for understanding the balance between productivity and biodiversity. This study also contributes to the rich dataset available on the Park Grass Experiment, providing future opportunities and insight, whilst also highlighting the importance of long-term experimental studies in the agricultural and environmental sciences

1. Introduction

Grasslands cover up to 40 % of the Earth's surface (Bardgett et al., 2021; Blair et al., 2014), making grass the most widely produced crop in the world, widely used to support ruminant livestock production (Boval and Dixon, 2012). The benefits of grass crops are their ability to grow on

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https://doi.org/10.1016/j.fcr.2025.109791
Received 6 December 2024; Received in revised form 5 February 2025; Accepted 7 February 2025
Available online 15 February 2025

land unsuitable for other crops, enabling that land to be productive via ruminant grazing and the subsequently derived meat and dairy products (Wilkinson and Lee, 2018). Additionally, compared to housed, feedlot, and cereal-based systems, the grazing of ruminants on pasture can co-deliver other benefits for environmental sustainability, biodiversity and animal health and welfare (Cooke et al., 2023; Lee et al., 2013; Pelletier et al., 2010). Understanding how management influences the long-term productivity of grasses and their role in the environment, is therefore an important aspect of agricultural sustainability. Improving pasture productivity to reduce land use, whilst improving nutrition has the potential to improve individual animal efficiency in terms of resource use in addition to reducing methane intensity from enteric fermentation (Caicedo et al., 2023; Lee et al., 2017).

The productivity and yield of cattle systems are driven by numerous factors including animal genetics, animal health, and climate. In grazing livestock systems, pasture productivity is central to system productivity. Pasture productivity can broadly be defined as a combination of both yield and nutritional composition. It is the primary driver of the systems carrying capacity and consequently, the amount of end-product (meat and milk) that can be produced from a given area of land. The greater the quantity and quality of forage, the more animals a system can support per unit area. Forage quantity and quality can rarely be fully optimized simultaneously and can often involve a trade-off; neither factor can be entirely prioritized at the expense of the other. If forage quantity is too low, animals will not be able to meet their basic metabolic and calorific requirements and begin to lose condition and weight. If forage quality is too poor, animal performance (growth, lactation) will be poor and they may be exposed to a high risk of nutritional disorders (Allen, 1996; Allman and Hamilton, 1948). The intensification of pasture-based systems through the selection of fast-growing, sugar-rich grass varieties supported by the application of mineral fertilisers has dramatically increased the productivity of grasslands since the middle of the last century (Hopkins and Wilkins, 2006). While this has resulted in higher stocking rates and earlier and more frequent silage cuts, it has also had the negative unintended consequence of reducing species diversity as improved grasslands are now dominated by nitrophilous, competitive grass species (Walker et al., 2004). As well as contributing to the global loss of biodiversity, a reduction in the diversity of pastures may also compromise their resilience (Macholdt et al., 2023), nutritional quality (Pirhofer-Walzl et al., 2011) and support of beneficial invertebrates (Vanbergen et al., 2013).

The Park Grass Experiment (PGE) has been running continuously since 1856 at Rothamsted Research (Harpenden, UK) and is the longest-running grassland experiment in the world (Storkey et al., 2016). The original objective was to investigate how different fertiliser and, later, liming treatments drive hay yields (Jenkinson et al., 1994). In addition, the experiment has also been used more widely to study the ecology and biodiversity impacts of the treatments (Balfour et al., 2025; Crawley et al., 2005; Silvertown et al., 2010; Storkey et al., 2015) and nutrient cycling (Goulding et al., 1998; Richardson, 1938). These studies have confirmed the negative impact of fertilisers on the diversity of above (Crawley et al., 2005) and below-ground (Liang et al., 2015) biological communities with a negative trade-off between productivity and biodiversity (Storkey and Macdonald, 2022). Nevertheless, no analysis has been conducted as to the nutritional value of the plots with respect to ruminant nutrition and performance, despite this being a prime purpose of hay production. The fertiliser treatments would be expected to impact the nutritional quality of swards through the direct application of nutrients and the indirect effects of changes in plant partitioning and species composition. Given that grass crops are typically used as ruminant feed, it is important to understand the effect of the different pasture managements on the nutritional composition of the herbage harvested from the variety of Park Grass plots to test the hypothesis that **increased productivity of grasslands has been achieved at the expense of nutritional quality**. Combining nutritional data with yield data provides a more accurate measure of plot productivity and ruminant livestock carrying capacity than yield alone. Therefore, in this study, we describe the first forage nutritional data from the PGE, obtained from samples dating from 1860 until 2020 and analyse relationships with fertiliser treatments, yield and biodiversity.

2. Method

2.1. Site description and background

The PGE (Fig. 1) has been running continuously since 1856. It is in Harpenden (51.803812, −0.372097), 38 km north of London, United Kingdom. Average annual rainfall is 765 mm and mean temperatures range from 7°C in winter to 22°C in summer (Perryman et al., 2021). The soil type is a Luvisol (IUSS, 2022) and was uniform at the inception of the project with a pH of approximately 5.5 at a 23 cm depth. The field was in permanent pasture for at least 100 years prior to 1856 and the original classification of the vegetation was dicotyledon-rich *Cynosurus cristatus-Centaurea nigra* grassland (Dodd et al., 1994). No species have been sown but each plot now represents a naturally assembled plant community that has adapted to each of the fertiliser and liming treatments. The plots are cut in mid-June and made into hay; for the first 19 years, the regrowth was grazed by sheep penned to individual plots, but since 1875 a second cut, usually zero-grazed and removed, has been taken. The experiment predates modern statistical methods for experimental factorial design and analysis and, while there are examples of plots with the same treatments, there is no formal replication. However, the emergent gradients of system properties (including productivity and species diversity) and the long time series of data mean regression-based models can be used to explore the impact of the treatments in space and time.

2.1.1. Plot treatments

The Rothamsted sample archive contains PGE herbage samples from each plot, for each year since the start of the experiment. A subsection of these plots was selected to be used within this study (summarised in Table 1) and were chosen to cover a representative range of treatments. Specifically, plots were chosen along a gradient of nitrogen addition applied either as ammonium sulphate (AS) or sodium nitrate (SN) and compared with plots either receiving no nitrogen fertiliser (Nil) or organic manure (OR). The choice of plots also allowed the additional effects of liming (driving soil pH) and application of minerals (K, Mg, Na and P) on sward nutritional quality to be included in the models. From these plots, samples were taken from the archive at ten-year intervals from 1860 to 2020 where available, resulting in a total of 262 individual samples. The history of the PGE is long and complex and not possible to fully describe in this manuscript. For additional information, resources, and data regarding the Park Grass experiment see: www.era.rothamsted.ac.uk/experiment/rpg5. The design of Park Grass can be split into three main experimental periods:

1. 1856–1902: The original 20 plots. Split by nitrogen fertiliser type (ammonium sulphate and ammonium nitrate) at varying levels, application of organic fertiliser (farmyard manure and fish meal), and application of P & K.
2. 1903–1964: Plots were divided into two subplots, one of which received regular lime application and the other did not.
3. 1965-current: Plots were divided once again, creating four sub-plots per plot. Three sub-plots (a, b, c) receive chalk to maintain a pH of 7.0, 6.0, and 5.0 respectively. The fourth (d) receives no lime.

2.2. Nutrient analysis

Before their original archiving, all samples had been dried at 80 °C to a constant weight. Samples from before 1960 had been initially air-dried as hay and oven-dried later. Samples from 1960 onwards were harvested as grass before being oven-dried. To ensure samples were dry for ana-

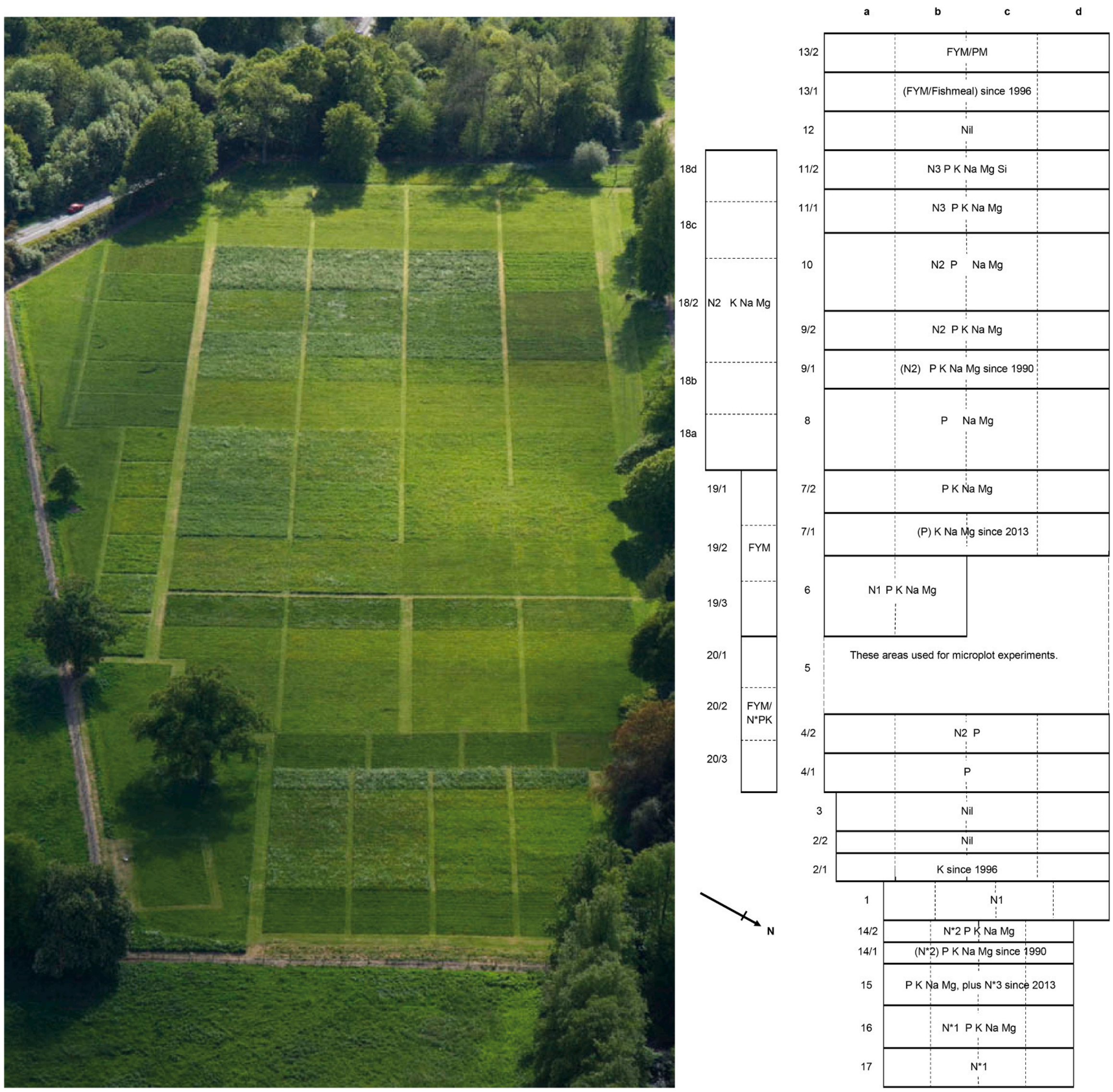

Fig. 1. Left: Arial photograph of Park Grass plots. Right: Diagram of plots including applied nutrients and plot numbers. See https://www.era.rothamsted.ac.uk/Park for more information.

lyses, should they have absorbed some moisture in storage, samples were re-dried at 80 °C for 18 hrs. All samples were then ground to 1 mm (FOSS CT 293 Cyclotec) and submitted to the following analyses:

- *Ash and organic matter* were determined by loss on ignition (0.4 g at 560 °C for 8 hrs).
- *Crude protein* (CP) was determined by using the Dumas method to quantify nitrogen and multiplying by 6.25 to determine CP (Ebeling, 1968).
- *Acid Detergent Fibre (ADF), Acid Detergent Lignin (ADL), Neutral Detergent Fibre (NDF)* were quantified based on the principles of Goering and Soest (1970), utilising an Ankom 2000 fibre analyser, in line with manufacturer guidelines.
- *Cellulose* was estimated as ADF minus ADL.
- *Hemicellulose* was estimated as NDF minus ADF.
- *Ether extract (EE, crude lipids)* was not directly quantified due to the age of the samples. Instead, a value of 2.00 % was assigned to all samples, which is the weighted mean of hay and low-quality hay of multi-species forages, as reported by Glasser et al. (2013).
- *Non-fibrous carbohydrates (NFC)* were determined by calculation (Mertens, 1997):
  %NFC = 100 - %Ash - %NDF - %CP - %EE
- *Digestible energy (DE) was calculated as per* Stergiadis et al. (2015)*:*
  $DE = 2.869 + 19.02EE - 2129.0EE^2 + 39.5NDF - 47NDF^2$
- *Metabolisable energy (ME) was calculated from DE as per* Galyean et al. (2016)*:*

$ME = 0.9611DE - 0.2999$

All samples underwent X-ray fluorescence (XRF) analysis (Bruker Tracer 5i) to quantify the concentrations of essential minerals (As, Ca, Cr, Co, Cu, Fe, Mg, Mn, Mo, Na, Ni, P, K, S, and Zn) and non-nutritional minerals (Al and Pb) (Evans, 1970; Mudroch and Mudroch, 1977). Values below the limit of detection (LOD) were attributed a value half that of the lowest observed value.

2.3. Herbage yield data

Herbage yield data for each plot is taken at each harvest on a basis of metric tonnes per hectare (t ha^{-1}) using data from the first hay cut in mid-June. These data were extracted from the publicly available e-RA

Table 1
Summary of plots and their treatments chosen for this study. AS = ammonium sulphate, OR = organic by farmyard manure (FYM), SN = sodium nitrate. A dash (-) signifies no application of that fertiliser/nutrient and a plus (+) signifies application. Sub-plots labelled 'b' or 'd' receive lime with a target pH of 6 or no lime respectively. Between 1903 and 1964, subplots were labelled limed ('L') and unlimed ('U') with the former receiving occasional applications of lime without using a target pH. Before 1903, all plots were unlimed. *N application at a rate of 144 kg N ha^{-1} in the form of SN began on plot 15 in 2013. Notes: Mineral application was of K, Mg, Na, and P (all or none). Treatments represent the current treatment, not the historic treatment (which can be inferred from the aforementioned 'three periods' of the experiment).

Plot	Sub-plot	N-form	N (kg ha^{-1})	Minerals	Lime
3	b	-	-	-	+
	d	-	-	-	-
6	b	AS	48	+	+
7	b	-	-	+	+
	d	-	-	+	-
9	b	AS	96	+	+
	d	AS	96	+	-
11	b	AS	144	+	+
	d	AS	144	+	-
13	b	OR	-	-	+
	d	OR	-	-	-
14	d	SN	96	+	+
	d	SN	96	+	-
15*	b	-	-	+	+
	d	-	-	+	-
16	b	SN	48	+	+
	d	SN	48	+	-

(electronic Rothamsted Archive) which details and provides data on the institute's long-term experiments (LTEs) (Perryman and Olster, 2021). Plot yields were originally calculated by weighing the produce of the entire plot as hay. However, from 1960 onwards yields were estimated from strips cut with a forest harvester. Within the archived data, a correction factor had been applied to make yields from 1960 onwards comparable with those pre-1960 (Bowley et al., 2017).

2.4. Dry matter intake and carrying capacity estimations

As the PGE is not grazed, dry matter intake calculations were based on the theoretical grazing of the swards by a model animal; heifers of small-sized early-maturing breeds (McDonald et al., 2011) with a live weight (LW) of 400 kg, which is equivalent to 0.6 livestock units (LU), and an average daily gain of 0.75 kg (McAuliffe et al., 2018). The daily ME required for this model animal is 88 MJ ME (AFRC, 1993). Three calculations were made associated with DMI:

1. rDMI (required dry matter intake): calculated by dividing the daily ME required by the model animal by the ME content of the herbage.
2. vDMI (voluntary dry matter intake): predicted based on concentrations of CP (which has a known positive association with DMI) and ADF (which has a known negative association with DMI (Riaz et al., 2014)): vDMI/kg LW = (0.002774 × CP%) − (0.000864 × ADF%) + 0.09826 (NRC, 2000).
3. aDMI (added dry matter intake): The difference in the above two measures, calculated as aDMI = vDMI − rDMI. An aDMI value > 0 means that animals would be expected to meet their intake requirements for maintenance and growth. The greater aDMI is above 0, the greater the potential for faster growth or more animals.

To assess the carrying capacity of each sward, the indicator animal-days per ha was calculated. The total herbage DM produced per ha was divided into the rDMI to obtain the animal-days per ha based on the chosen animal (i.e., early maturing breed heifers). The resulting value was then multiplied by 0.6 to convert it into LU-days per ha (LuDha). For instance, a LuDha of 360 LU-days indicate that each ha of the sward can support 4 LU over 90 days of grazing (e.g., from turnout to pasture in mid-March until mid-June), or 6 LU over 60 days.

2.5. Biodiversity data

Plant biodiversity data, for the period 1991–2000 were available from a previous study by Crawley et al. (2005). Briefly, above-ground biomass was collected in June of each year before the first hay cut from six 50 × 25 cm quadrats in each plot and separated into species before drying overnight at 80 °C and calculating species diversity based on relative biomass. The species richness data reported by Crawley et al. (2005) were based on separate surveys of the whole plots. However, because of the variation in plot size, the species richness values used in this study are based on the standard area sampled for biomass. Species richness and composition data (relative biomass) were paired with forage nutrition data for 1990 and 2000, for the plots used in our study.

2.6. Data analysis

Linear mixed effect models (LMEs) were applied to assess the relationship of plot treatment and time with carrying capacity in the form of LuDha, yield, and forage nutrition (macronutrients and minerals). Model terms included quantity of fertiliser type, mineral application, lime application, year, and pH, with plot ID as a random factor. Because of the potential effect of variation in sample processing before and after the 1960 harvest, the analysis was split into the two periods (1860–1950 and 1960–2020) and all models run for each period separately.

The overall nutritional composition of the samples was compared by including the metrics of nutritional quality (concentrations of ash, CP, cellulose, hemicellulose, ADL and NFC) and concentrations of essential minerals in a Principal Components Analysis (PCA) for each period separately. To relate the nutritional composition data to the species composition data from Crawley (2005) directly, a third PCA was run but restricted to years 1990 and 2000.

Data analysis was conducted in R and RStudio (R Core Team, 2021; R Studio Team, 2020) except for PCA which was performed in Canoco 5 (Šmilauer and Lepš, 2014).

3. Results

The processing methodology of harvested material (which changed from the year 1960 onwards, as per Section 2.3) was a significant term in the LMEs fitted to data for yield, LuDha, and the components of nutritional quality. For clarity, data pre and post 1960 were, therefore analysed separately. The presented analysis in the main text is for the period 1960–2020. Comparable analysis for the period 1860–1960 may be found in the supplementary material.

3.1. Productivity

Nitrogen fertiliser, mineral application, and liming all significantly increased LuDha, which was strongly driven by an increase in herbage yield (Table 2). Weight for weight of N, SN fertiliser outperformed AS fertiliser, with 96 kg N ha^{-1} of SN yielding a slightly higher LuDha than 144 kg N ha^{-1} of AS (Fig. 2). Plots receiving SN had less variation in LuDha than plots receiving AS, e.g. at 96 kg N ha^{-1}, the standard deviation of LuDha for SN was 118, compared to AS at 153. aDMI was positive for all samples and there was a negative correlation between aDMI and yield (r = -0.440, $p < 0.001$) and aDMi and LuDha (r = -0.380, $p < 0.001$) (Fig. 3). Either the addition of lime or pH was a significant term in all models but there was no significant combined effect on any response variables indicating the effect of the lime on productivity was accounted for by the increase in pH. Year had a significantly negative effect on all response variables; indicating the PGE swards overall are becoming less productive. The results of the model were similar for the period 1860–1950 but *year* was not a significant term

Table 2
Linear mixed effect (LME) model results summarising the association of plot treatments, year, and pH on Livestock-Unit-days per ha (LuDha), yield, and added dry matter intake (aDMI). Values are *t*-values and cell colours correspond to those values. Superscripts signify statistical significance: 0 '***' 0.001 '**' 0.01 '*' 0.05 '^' 0.1 ' ' 1.

	AS	SN	OR	Mineral	Lime	Year	pH
LuDha	3.33**	3.99***	4.44***	5.06***	2.75**	-2.78**	0.60
Yield	4.06***	4.74***	4.67***	4.95***	2.53*	-2.44*	0.84
aDMI	-3.67**	-4.70***	-5.36***	-2.37*	1.54	-5.09***	-2.92**

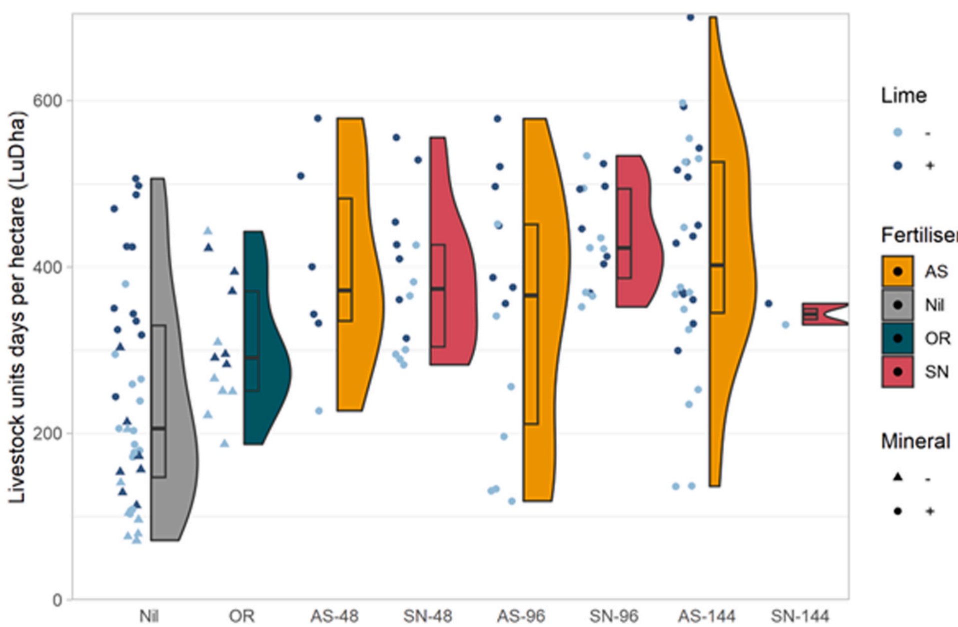

Fig. 2. Carrying capacity (LuDha) of different nitrogen fertiliser treatments. Nil = no fertiliser applied, OR = organic manure applied, AS = ammonium sulphate, SN = sodium nitrate. Numbers afterwards signify N application rate (kg N ha^{-1}). Semi-violins show distribution with medians and quartiles. Individual points represent individual samples.

(Supplementary Materials Table S2).

3.2. Nutritional composition

3.2.1. Macronutrients

Although yields increased under fertiliser treatments, this was partially at the expense of nutritive value. Fibrous components, particularly cellulose and hemicellulose increased, and NFC, CP, and ash decreased (Table 3, Table 4). Year had a similar effect in the models as the addition of fertilisers indicating overall the nutritional value of the PGE plots has been decreasing with time. Model output for the period 1860–1950 was similar in terms of the effect of fertilisers but there was no effect of year (Supplementary Materials Table S4).

3.2.2. Essential minerals

Most significant associations between plot treatment and mineral concentrations were negative (Table 5). Both AS and SN application had significant negative impacts on Ca, Mg, Mn, Ni, and P concentrations. Whilst OR application also had significant negative impacts on Ca, Mg, and Ni, it had a positive impact on Mn and P. The application of minerals (P, K, Na, and Mg) was positively associated with plant concentrations of P, K and Na, but negatively associated with Mg. Whilst lime application did not have a significant impact on mineral concentrations as the aforementioned treatments, it was negatively associated with forage Mn, Na, and P concentrations, but positively associated with Zn. Except for Ca, there was no additional effect of lime after accounting for increased pH. Overall, apart from Mg, essential nutrient concentrations have reduced with time. While the effects of fertilisers on essential nutrients in the period 1860–1950 were similar (see supplementary material), concentrations appear to have generally increased over this earlier period with significant positive year effects for P, K, S and Zn. There was a negative association of As concentrations by year. Four samples exceeded 2 ppm of As (the EU threshold for processed commercial animal feeds; (European Union, 2019), but all were below the maximum tolerable thresholds (30 ppm) as per NRC (2006). As concentrations increased with time over the period 1960–2020 but there was no significant effect of year for the earlier time period (Supplementary Materials Table S6).

3.2.3. Non-nutritional minerals

There was little association of plot treatments with the concentrations of non-nutritional minerals (Al and Pb) (Table 6). There was a significant positive association of Al concentrations with OR application, however, only 16/131 samples had Al concentrations above limits of detection. Of those 16, the mean concentration was 741 ppm (s.d. = 767), with four exceeding 1000 ppm (a level at which they may be a cause for concern (Eppe et al., 2023). There was a negative association between Pb concentration and year. All concentrations were below the maximum tolerable level of 100 ppm as defined by NRC (2006), however, five samples were > 10 ppm, which is the EU limit for Pb in

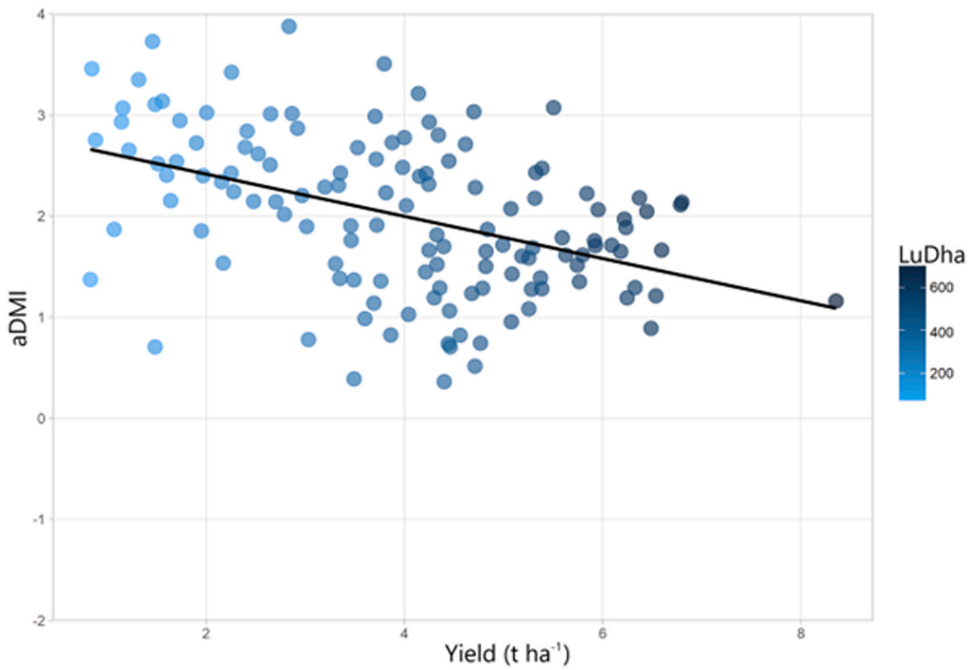

Fig. 3. Comparison of added dry matter intake (aDMI), yield, and Livestock-Unit-days per ha (LuDha) for plots samples from the period 1960–2020.

Table 3
Mean nutrient content (% DM) of samples from different fertiliser treatments (Nil = no fertiliser, OR = organic farmyard manure, SN and AS refer to sodium nitrate and ammonium sulphate respectively, at application rates of 48. 96, and 144 kg ha^{-1}). Superscript represents standard deviation (which is low for SN-144 as $n = 2$). ADL: acid detergent fibre; NFC: non-fibrous carbohydrates.

	Nil	OR	AS−48	SN−48	AS−96	SN−96	AS−144	SN−144
Ash	$8.4^{1.4}$	$8.4^{3.1}$	$7.9^{0.7}$	$8.3^{1.5}$	$7.0^{1.9}$	$7.2^{1.1}$	$7.2^{1.7}$	$5.5^{0.4}$
CP	$10.9^{1.8}$	$9.4^{1.1}$	$10.8^{1.7}$	$9.5^{1.3}$	$10.7^{2.0}$	$9.7^{1.4}$	$11.0^{1.7}$	$10.1^{0.2}$
Hemicellulose	$18.7^{3.9}$	$22.3^{2.9}$	$19.5^{0.9}$	$22.2^{3.0}$	$25.5^{2.6}$	$23.6^{2.5}$	$25.7^{2.3}$	$29.5^{0.6}$
Cellulose	$21.2^{3.1}$	$24.9^{2.8}$	$22.9^{2.1}$	$25.1^{1.7}$	$23.8^{2.4.5}$	$26.9^{1.9}$	$24.3^{2.8}$	$29.5^{0.7}$
ADL	$4.6^{1.1}$	$5.2^{1.1}$	$4.3^{0.7}$	$4.6^{1.1}$	$3.9^{0.8}$	$4.2^{0.6}$	$4.4^{1.1}$	$4.2^{0.2}$
NFC	$34.2^{5.2}$	$27.8^{4.4}$	$32.6^{1.5}$	$28.3^{3.2}$	$27.0^{3.3}$	$26.4^{4.5}$	$25.4^{4.2}$	$19.2^{0.6}$

Table 4
LME results summarising the association of plot treatments (Nil = no fertiliser, OR = organic farmyard manure, SN and AS refer to sodium nitrate and ammonium sulphate respectively, at application rates of 48. 96, and 144 kg ha^{-1}), year, and pH on macronutrients. ADL: acid detergent fibre; NFC: non-fibrous carbohydrates. Values are *t*-values and cell colours correspond to those values. Superscripts signify statistical significance: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘^’ 0.1 ‘ ’ 1.

	AS	SN	OR	Mineral	Lime	Year	pH
Ash	$-1.97^{\wedge}$	-3.75^{***}	$1.88^{\wedge}$	2.49^{*}	-0.04	-4.80^{***}	1.61
CP	-0.67	-1.16	-3.36^{**}	-1.59	-1.14	-4.65^{***}	-2.28^{*}
Hemicellulose	6.51^{***}	6.72^{***}	2.73^{**}	-0.07	0.90	4.21^{***}	-1.52
Cellulose	3.15^{**}	5.72^{***}	5.55^{***}	3.85^{***}	-0.38	2.69^{**}	$1.86^{\wedge}$
ADL	0.09	$-1.81^{\wedge}$	2.86^{**}	1.43	-0.89	0.72	2.03^{*}
NFC	-4.73^{***}	-5.44^{***}	-5.05^{***}	-2.95^{**}	0.64	-0.85	-0.46

processed commercial animal feed materials, but below the 30 ppm for forages (European Union, 2013). Pb concentrations decreased with time over the period 1960–2020 but there was no significant effect of year for the earlier time period (Supplementary Materials Table S6).

3.3. Nutritional gradients

The PCA combining the multiple components of nutritional quality discriminated between samples with high cellulose and hemicellulose and samples with high NFC and micronutrients, especially Mg and Ca, along the first axis that explained 33 % of the total variance in the data (Fig. 4a). Sample scores along this axis can be considered to represent a nutritional gradient. A similar pattern was observed when just using the data from 1990 and 2000 (Fig. 4b). There was a positive relationship between sample scores and pH (score = 0.28 × pH −1.53, $R^2 = 0.15$, $p < 0.001$); this effect was first removed by fitting this regression model and plotting the residuals against yield (Fig. 4c) and species richness (Fig. 4d). For the second analysis, only years for which there were equivalent biodiversity data were included. There was a negative relationship between sample scores and yield and a positive relationship with species richness; however, this was only observed on plots with a species richness > 14.5, indicated by the break point in a

Table 5
LME results summarising the association of plot treatments (Nil = no fertiliser, OR = organic farmyard manure, SN and AS refer to sodium nitrate and ammonium sulphate respectively, at application rates of 48. 96, and 144 kg ha^{-1}), year, and pH on essential minerals. Values are *t*-values and cell colours correspond to those values. Superscripts signify statistical significance: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1. Values were not reported for Se as all samples were below limits of detection.

	AS	SN	OR	Mineral	Lime	Year	pH
As	-1.43	-0.53	2.44*	-0.52	0.31	-6.04***	-1.44
Cr	-0.09	-1.37	3.01**	1.36	-1.26	-1.73	0.20
Co	-0.53	-0.23	-2.84**	-3.11**	0.14	0.38	0.04
Cu	-0.94	0.37	-0.99	-0.84	1.06	0.30	0.61
Fe	-0.81	-0.58	3.10**	-0.36	-0.09	-1.45	-0.78
Mg	-3.00**	-2.70**	-3.73*	-5.19*	-1.89	5.64*	-0.36
Mn	-0.83	-4.50*	1.03	2.06*	-4.34*	-0.76	-0.10
Mo	-1.14	-0.38	2.58*	1.30	1.66	-1.57	-0.85
Na	0.30	-0.44	-0.07	0.39	-2.32*	-1.60	1.84
Ni	-2.21*	-0.54	-1.85	-1.35	-1.58	1.73	-0.78
P	-3.69*	-3.07**	4.99*	10.69*	1.41	-5.37*	1.77
K	-2.78*	-3.27**	1.89	13.80*	0.66	-6.98*	1.88
S	2.58*	0.14	-5.65*	-3.69*	0.83	-5.96*	-2.59*
Zn	-1.76	-1.28	-0.11	-0.36	-1.42	-4.51*	0.94

Table 6
LME results summarising the impact of different plot treatments (Nil = no fertiliser, OR = organic farmyard manure, SN and AS refer to sodium nitrate and ammonium sulphate respectively, at application rates of 48. 96, and 144 kg ha^{-1}), year, and harvesting on non-nutritional minerals. Values are *t*-values and cell colours correspond to those values. Superscripts signify statistical significance: 0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1. Values were not reported for Se as all samples were below limits of detection.

	AS	SN	OR	Mineral	Lime	Year	pH
Al	-0.55	-0.08	2.68**	-0.77	-0.03	-1.15	-0.42
Pb	-0.85	-0.39	0.29	-2.2*	-0.21	-9.04***	0.81

split-line regression (Fig. 4d).

4. Discussion

Weight for weight, SN fertiliser outperformed AS and OR fertiliser in terms of the potential ruminant livestock carrying capacity. OR performed approximately as well as 96 kg N ha^{-1} SN and 144 kg N ha^{-1} AS. Overall, fertiliser application increased yields, however, it also led to an overall reduction in the nutritive quality of forages. The overall effect of this was an increase in carrying capacity associated with fertiliser application because the increase in yields had a greater positive impact than the negative impact of reduced forage nutrition. This was also reflected in the relationship between aDMI, CP, ADF, and LuDha. Plots of higher nutritional quality (high CP, low ADF) had greater aDMI, but a lower LuDha. Whilst the potential for greater growth rates, due to high aDMI, can be beneficial for economic and environmental efficiency (Cooke et al., 2022), the trade-off with carrying capacity will have the opposite effect and thus these factors need to be balanced. This balance will vary from system to system based on resource availability and desired outcomes. Whilst the reasons for the reduced nutritional quality (lower CP, higher ADF) are not conclusive, it may be that as plants grew, fibre concentrations increased in the lower stem to support the additional height and mass, or the proportion of less digestible species increased. Similar effects have been seen elsewhere in response to sodium and nitrogen fertilisers (Allison et al., 2012; Chiy and Phillips, 1996). Furthermore, a dilution effect may have occurred with increasing plant biomass causing some nutrients to be spread out/diluted across a greater mass of tissue, which has been observed elsewhere (Jarrell and Beverly, 1981). This could be described as an allometric dilution, of plant traits changing as their biomass increases, as described by Fernández et al. (2021). This highlights a trade-off between forage quantity and nutritional density and the complex, and not necessarily linear, relationship between fertiliser application and plant nutrition which has also been observed in long-term grassland experiments elsewhere (Hejcman et al., 2010).Changes in plant community composition may also have impacted sward quality as plant species adapted to foraging pressures; different nutrients were replaced by nitrophilous, competitive species in fertilised swards (Silvertown et al., 2006). Consequently, there appears to be a trade-off between yield and nutritional quality, which could be impactful for farm decision making in the real world when managing un-sown swards and which will be individual to each farm. Per kg of N, SN generates less greenhouse gas emissions from soil than AS, however, creates more greenhouse gasses during production (Hu et al., 2020). To support the same carrying capacity, the required application rate of SN is lower than AS, and therefore SN would yield lower transport emissions and potentially be more practical to use. The effect of the application of minerals and lime were also significant and yielded the optimum carrying capacities within any given primary fertiliser (AS, SN, OR) treatment.

Mineral applications included P, K, Na, and Mg. Plant forage concentrations of P, K, and Na increased in response to mineral application. However, forage Mg concentrations reduced and the exact reason for

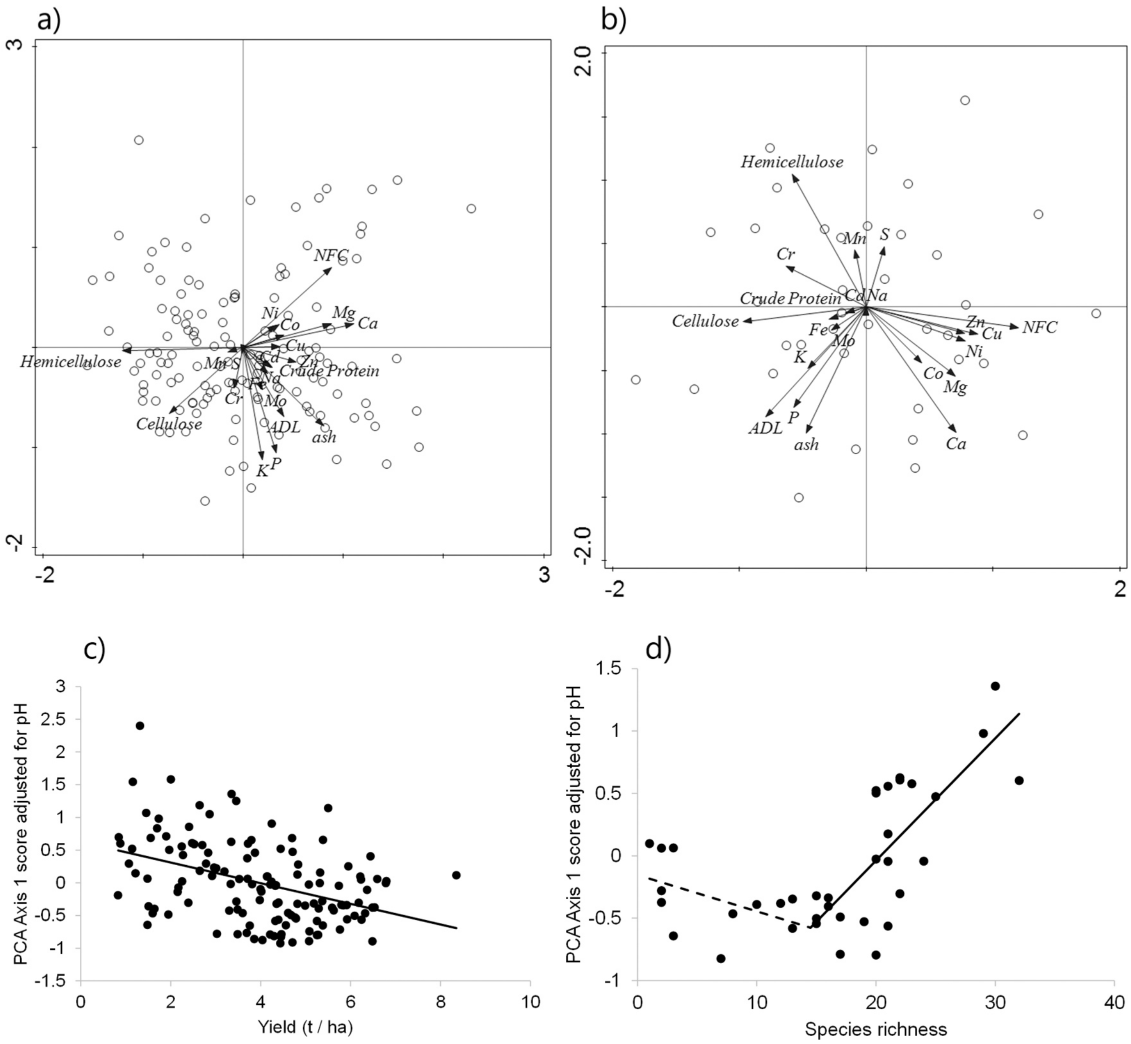

Fig. 4. (a) PCA of components of nutritional quality of herbage samples taken from selected plots on the PGE at decadal intervals between 1960 and 2020. (b) PCA of components of nutritional quality of herbage samples taken from the same plots but restricted to 1990 and 2000. (c) PCA axis 1 scores for 1960–2020, detrended for the effect of pH, plotted against yields from the first hay cut, $y = -0.158x + 0.625$, R2 = 0.17, $p < 0.001$). (d) PCA axis 1 scores for 1990 and 2000, detrended for the effect of pH, plotted against equivalent species richness data from 1991 and 2000 respectively; a split line regression has been fitted to the data with a break point of 14.5. There was no significant relationship with species richness below this point but for plots with a species richness > 14,5, there was a significant ($p < 0.001$) positive slope of 0.098.

this is unclear. One possible cause may be that the change in soil pH in response to fertiliser treatment may hinder Mg uptake by plants. Gransee and Führs (2013) reported that below pH 6 the plant availability and uptake of Mg cations is decreased. In the 1860–1950 period, 98/130 samples were from soils with pH < 6, and in the 1960–2020 period 85/131 samples had a soil pH < 6. Another possible explanation might be that cationic antagonism is occurring, with high levels of Ca, or more probably K, inhibiting Mg uptake (Xie et al., 2021). Plots that received no mineral application had lower yields than those that did. Elsewhere, in the long-term Rengen Grassland Experiment, P application was found to drive the largest differences in vegetation structure and composition, with lower sward heights in plots without P application (Hejcman et al., 2007). These results highlight the need to monitor and control P application in-line with the goals of a given system, which may be particularly important in regions where soil P or P production for fertilisers is limited (Alewell et al., 2020).

The positive relationships of pH with liming and SN, and the negative relationship with AS, are all effects widely observed elsewhere (Chien et al., 2008; Johnston et al., 1986; Li et al., 2019). These effects highlight the ability to control soil pH by altering fertiliser use to increase/decrease pH as and when necessary, which has been successfully used to enhance yields of various crops (Holland et al., 2019) There is a potential trade off here also, as P fertiliser has been found to significantly reduce the critical pH of some crops.

Aluminium and toxicity thresholds for ruminants are not well understood, but concentrations > 500 ppm might be considered high, certainly > 1000 ppm (Eppe et al., 2023). At the higher levels observed, this could influence nutrient utilisation, in particular the utilisation of P (Allen, 1984). Although there was a positive association of OR with Al concentrations, this is most likely because the two plots with the highest Al content were OR plots, by chance. Notably, 16/17 samples with detectable Al were taken from 1960 onwards, despite those samples making up 50.3 % of total sample numbers. This timing broadly coincides with a dramatic increase in global Al production (United States Geological Survey, 2024). This may increase the potential Al available or the likelihood of contamination from external sources. Concentrations of Pb were highest in the period 1960–1980 and gradually declined from then. This timing coincides with the phasing out of Pb in fuel, paints, and other materials, reducing Pb in the environment, such as seen by Levin et al. (2008) in the USA. Results for Al and Pb highlight the potential vulnerability of agricultural systems to the secondary impacts of industrial processes, but also their ability to recover, given time.

Species richness was lowest in the AS plots, followed by SN, OR and Nil fertiliser plots. Liming appeared to enable greater species richness and yields for any given treatment. Overall, a negative relationship was found between plot species richness and carrying capacity, which is primarily driven by yield. These results further support the findings of Crawley et al. (2005) who found that increasing biomass was associated with lower plot biodiversity. The trend is likely caused by a small number of, or individual, species that are best able to utilise and respond to fertiliser availability to achieve dominance. This is not dissimilar to how and why monoculture pastures, such as perennial ryegrass, have gained popularity. However, increased grassland biodiversity can yield a variety of benefits such as encouraging invertebrate biodiversity, improving system resilience, enhancing soil microbial activity, carbon stocks, soil stability, mineral bioavailability through different root profiles and exudates, and providing livestock with a varied diet (Hopkins, 2004; Sanderson et al., 2007; Woodcock et al., 2007; Yang et al., 2019). Long-term grassland experiments elsewhere have similarly shown shifts in plant species composition due to fertilisation effects (Hejcman et al., 2007). Below ground and soil biology were not investigated within this study, however, microbial activity has previously been explored in PGE, with acidic soil (i.e., not limed) having lower microbial activity (Silvertown et al., 2006). There is, therefore, a balance to be struck between biomass production and biodiversity.

The temporal trends and fluctuation in carrying capacities from year to year highlight the importance of LTEs such as Park Grass. LTEs allow for slow or subtle changes to be observed, which may otherwise be inapparent or masked by 'noise' from confounding variables. Furthermore, they allow for more reflective data-led historical comparisons than may otherwise be possible. Understanding year-on-year variation is also important to understand system resilience and potential. Our analysis has highlighted negative effects of environmental change on sward productivity and nutritional quality, particularly since 1960. This is supported by a separate analyses of the impact of climate change on PGE biomass production (Addy et al., 2022) and the implications for grassland function in the future warrants further investigation.

4.1. Limitations

It was only possible to analyse a subset of the thousands of archived Park Grass samples that are available. Expansion of this data set, both retrospectively and into the future, would enable all projects on Park Grass to be contextualised with regard to livestock productivity and possibly discover more subtle trends.

Plots were harvested, not grazed. It is known that the presence and pressures of grazing can impact factors such as biodiversity, nutrient turnover, and soil properties, as well as the livestock to actively select species (Lai and Kumar, 2020; Škornik et al., 2010; Tallowin et al., 2005). Therefore, the presence of grazing livestock on these plots may affect the factors explored within this study.

Due to their differing ages, samples had been in storage for varying lengths of time. The effect that this has had on sample composition is unquantifiable and possibly amplified by the changes in technology and storage over that time. Therefore, any temporal conclusions from this study should be considered with that in mind. Plot differences should be less affected by this; however, it may be the case that temporal changes in archived samples vary by their composition.

5. Conclusion

Increases in pasture carrying capacity are predominantly driven by increasing overall biomass yield but at the cost of decreasing forage nutritional value. Ensuring balanced nutritional intakes is key in all ruminant systems, but potentially more so in those that utilise high fertiliser inputs. Greater carrying capacities were generally associated with lower biodiversity, though liming appeared to facilitate this. Nevertheless, trade-offs between carrying capacity and biodiversity are important considerations within grazing systems. This study is the first to characterise the Park Grass dataset in terms of animal nutrition, building upon over 160 years of ongoing experimental research and adding to a rich body of evidence and data. Results highlight the importance of LTEs in agricultural science.

Funding statement

The work was part of Rothamsted Research's Institute Strategic Programme Soil to Nutrition, funded by the UK Research and Innovation – Biotechnology and Biological Sciences Research Council (UKRI-BBSRC) (BBS/E/C/000I0320). The PGE and its datasets in the electronic Rothamsted Archive (e-RA) are part of the Rothamsted Long-Term Experiments - National Bioscience Research Infrastructure (RLTE-NBRI) supported by UKRI-BBSRC (BBS/E/RH/23NB0007) and the Lawes Agricultural Trust. This work was also funded by UKRI Grant NE/W005050/1 AgZero+ : Towards sustainable, climate-neutral farming. AgZero+ is jointly supported by the UKRI-Natural Environment Research Council (UKRI-NERC) and UKRI-BBSRC.

CRediT authorship contribution statement

A.S. Cooke: Conceptualization, Methodology Formal analysis, Investigation, Resources, Data curation, Writing – original draft, Writing – review & editing, Visualization, Project administration. **J. Storkey:** Conceptualization, Methodology, Formal analysis, Investigation, Writing – original draft, Writing – review & editing, Visualization, Funding acquisition. **G. Acquah:** Methodology, Investigation, Resources, Writing – original draft. **M. R. F. Lee:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition. **M. J. Rivero:** Conceptualization, Methodology, Writing – original draft, Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

Thanks are extended to Margaret Glendining, Andy Gregory, and Steve Freeman for their assistance with this research. Rothamsted Research, Harper Adams University and Andrew S. Cooke are members of the Global Farm Platform initiative (www.globalfarmplatform.org) collaboratively working towards sustainable ruminant livestock production systems.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2025.109791.

Data Availability

Data will be made available on request.

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