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A redundancy analysis of the relative impact of different feedstuffs on nitrogen use efficiency and excretion partitioning in beef cattle fed diets with contrasting protein concentrations

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ABSTRACT

Diet composition and intake are the main determinants of nitrogen (N) use efficiency (NUE) in beef cattle. Accounting for the interactions and comparative effects of different feedstuff types on NUE and N losses in urine and faeces can inform the development of financially and environmentally sustainable feeding protocols for beef cattle. This study aimed to assess the impact of various individual feedstuffs and feedstuff types/groups on NUE and N partitioning to faeces and urine in beef cattle, for diets with contrasting crude protein (CP) concentrations. Partial multivariate redundancy analysis (pRDA) was used to associate the influence of the intakes of individual feedstuffs and feedstuff types/groups on NUE and N partitioning by using results from 59 published trials with growing and finishing beef cattle. The data were split into three sub-sets, according to diet CP concentration (low CP, 47-120 g CP/kg DM, n=73; medium CP, 121-150 g CP/kg DM, n=90; high CP, 151-269 g CP/kg DM, n=74). In low CP diets, the main feedstuffs that improved NUE and shifted N outputs from urine to faeces were grass and legume hay, grass hay, straws, brans and pulps. In medium CP diets, the main feedstuffs that improved NUE were fresh grass and hays, fresh legumes, and straws; while legume and grass hay, straws, pulps and hulls also shifted N excretion from urine to faeces. In high CP diets, the main feedstuffs that improved NUE were grass hay, grass silages, straws, fibre-rich by-products, hulls and meals; while grass silages, straws and meals also shifted N outputs from urine to faeces. The present study highlighted that selection of feedstuffs that provide adequate digestible fibre and energy supply to rumen microbes, as well as minimizing the oversupply of CP, could be used to improve NUE and shift N outputs from urine to faeces in beef cattle; while the effectiveness of providing fibre and energy might be influenced by the overall diet CP concentration.

Keywords

nitrogen, beef, protein, urine, nitrogen partitioning, redundancy analysis

Abbreviations

ADF, acid detergent fibre; B/P/H/M, combined brans, pulps, hulls, middlings and other high-fibre feedstuffs; BR, brans; CP, crude protein; D/M, combined distillers grains with solubles and meals; DGS, distillers grains with solubles; DM, dry matter; DMI, dry matter intake; FF, fresh-cut forages; FGra, fresh-cut grass/others; FLe, fresh-cut legumes; FN/MN, faeces N output expressed per manure N output; FN/NI, faeces N output expressed per N intake; FN/UN, faeces N output expressed per urine N output; FNO, faecal N output; GHG, greenhouse gas; GR, grains; H/S, combined hays and straws; HAGra, grass hay; HALe, legume hay; HU, hulls; ME, meals; MI, miscellaneous additives; MNO, manure N output; N_2O, nitrous oxide; NCDMI, non-concentrate dry matter intake; NDF, neutral detergent fibre; NFDMI, non-forage dry matter intake; NH_3, ammonia; NI, N intake; NR, retained N; NR/NI, retained N expressed per N intake; NUE, N use efficiency; pRDA, partial redundancy analysis; PU, pulps; SICe, cereals silage; SIGra, grass silage; SIL, silages; SIMa, maize silage; ST, straws; UN/MN, urinary N output expressed per manure N output; UN/NI, urinary N output expressed per N intake; UNO, urinary N output

1. Introduction

Beef cattle are able to transform low quality dietary protein and non-protein nitrogen into high value meat suitable for human consumption, however their efficiency of dietary nitrogen (N) utilisation for growth is low (Satter et al., 2002). Typically, beef cattle only retain 5-20% of their total N intake (NI) (Koenig and Beauchemin, 2013b), with the rest being excreted in faeces and urine. As a result, farm profitability may be suboptimal due to the inefficient use of expensive dietary protein, while environmental implications also emerge from excessive N excretion (Hristov et al., 2011). For example, N losses during manure management and denitrification in the soil contribute to livestock greenhouse gas (GHG) emissions (in the form of nitrous oxide; N_2O); volatilization of ammonia (NH_3) in urine contributes to air quality pollution and terrestrial and aquatic acidification and eutrophication; while the latter is also exacerbated by nitrate (NO_3) leaching (Tamminga, 2006).

Diet crude protein (CP) concentration is a main determinant of N use efficiency (NUE) (Erickson and Klopfenstein, 2010; Koenig and Beauchemin, 2013a, b) and when requirements for rumen degradable protein and metabolisable protein are met, N excretion starts to increase proportionately with diet CP concentration (Vasconcelos et al., 2009). Furthermore, beef cattle excrete most of the non-retained N in urine, a rate that increases with increasing CP concentrations in the diet (Cole et al., 2005; Koenig and Beauchemin, 2013a, b). The most direct way to improve NUE is to reduce NI, based on the principle that as NI decreases so does N excretion (Galles et al., 2011; Waldrip et al., 2013; Dong et al., 2014). Recently, Angelidis et al. (2019) has shown that a 1g/d reduction in dietary N supply can decrease manure N excretion by 0.76 g. Additional dietary factors including diet energy level, types and inclusion rates of dietary carbohydrate and roughages, may also affect NUE in ruminants (Hristov et al., 2011) and the effect of animal diet interventions on NUE has been assessed so far by many studies using animal digestibility trials and factorial experiment designs. Digestibility trials are an excellent approach for the development of dietary interventions to improve NUE and the evaluation of their efficacy in maximum detail, however such assessments are mostly performed within the boundaries of specific combinations of dietary feedstuffs and chemical composition (and most importantly CP concentrations). There is currently limited research on the relative impact of different feedstuff types on NUE and N partitioning to urine and faeces, and whether such impact interacts with dietary CP content. To answer this question, larger datasets representing a wider spectra of dietary practices (and in particular diet CP concentrations) than those used in most single trial studies, as well as multivariate redundancy approaches, are required. The aim of the present work was therefore to (i) identify and assess the relative impact of feedstuffs which are correlated with beneficial effects on NUE and N partitioning in beef cattle, and (ii) evaluate their efficacy in diets of low CP (47-120 g CP/kg dry matter (DM)), medium CP (121-150 g CP/kg DM) and high CP (151-269 g CP/kg DM) concentration by using a redundancy analysis approach on data collected from the literature.

Materials and methods

2.1 The database

A literature search was performed using the Scopus database and the following keywords, in several combinations: (i) N, (ii) output, excretion, or balance, (iii) beef, steer, heifer, or bull, and (iv) faeces, urine or manure. Results were retained in the database for the current study only when the animals were growing for meat production and a full analysis of the total diet and diet composition was provided. A total of 59 feeding trials and N balance studies (Appendix; List of studies), conducted on growing and finishing beef cattle in several countries, included at least diet CP concentration (g CP/kg DM), DM intake (DMI) (kg/d), dietary feedstuffs and outputs of N in manure (MNO, g/d), in urine (UNO, g/d) and/or in faeces (FNO, g/d). The resulting database, comprised of 237 treatment means, included a wide range of production and animal characteristics, such as production stage (growing and finishing), bodyweight (65.5-600 kg), breed (Holstein, Angus, Hereford, Charolais, Belgian blue, Nellore, Friesian, Red Poll, Piedmontese, Bradford, Simmental, British, Schwarzbuntes Milchrind and crossbreds), type of animal (heifers, steers and bulls) and production type (dairy-bred calves or beef herds). In order to perform separate assessments according to diet CP concentration, which is known to strongly influence N outputs and NUE (Waldrip et al., 2013), the database was split into three sub-sets, based on diet CP concentration and beef feeding guidelines from the Agriculture and Horticulture Development Board (AHDB, 2016) (low CP, 47-120 g CP/kg DM, n=73; medium CP, 121-150 g CP/kg DM, n=90; high CP, 151-269 g CP/kg DM, n=74). Variation in individual variables, including mean, number of observations, standard deviation, and minimum/maximum values, for all parameters used in the current study, and related to individual feedstuffs, N outputs and efficiency parameters, are presented in Tables 1, 2 and 3, for the low, medium and high CP sub-sets, respectively.

2.2 Statistical analysis

The influence of the individual feedstuffs as well as their generic groups on NUE and N partitioning in beef cattle was assessed using partial redundancy analyses (pRDA) in CANOCO 5 (Ter Braak and Smilauer, 2012). The total variance of the dataset shows how much variation in the response variables was redundant with the variation in the explanatory variables (Ter Braak and Prentice, 1988). In addition, the effect of specific explanatory factors (e.g. unwanted variation caused by differences in various studies in the present work) on a set of response variables, was accounted for in the model by using study as a covariable (partial RDA) prior to a standard RDA (Borcard et al., 1992). The ordination score shows how much variation in the response variables was redundant with the variation in the explanatory variables (constrained variation). If, however, there is a large proportion of variation in the response matrix that is non-redundant (unconstrained variation) with the variation in the explanatory matrix, then a small amount of the variation in the response matrix is displayed and the results should be interpreted with caution (Ter Braak, 1994; Ramette, 2007). In the resulting biplots, the arrow's direction and length demonstrate the relative effects of explanatory variables (diet components) relative to the response variables (N outputs and NUE parameters; which are presented as points). The statistical significance of the relationship between the response variables and the whole set of explanatory variables was calculated by using automatic forward selection of variables and the Monte Carlo permutation test (Appendix; Tables A1, A2 and A3). The significance values determined by permutation tests are similar to those of univariate tests.

The process was as follows; firstly, DMI of individual feedstuffs were grouped to create explanatory variables that represent similar feedstuff types/groups (overall pRDA). Those included fresh-cut forages (biplot abbreviation FF; Napier grass, Leucaena leucocephala, perennial ryegrass, white clover, plantain and sugarcane), combined hays and straws (biplot abbreviation H/S; hays including bahiagrass hay, orchard hay, timothy hay, alfalfa hay, sorghum hay, brome hay, fescue hay, other grass hays and straws), silages (SIL; grass silage, maize silage, barley silage, and oats silage), grains (GR; grains including barley, maize, wheat, sorghum, pearl millet and triticale), combined DGS and meals (D/M; wheat DGS, maize DGS, soy meal, soy sauce cake, linseed meal, rapeseed meal, tapioca meal, sunflower meal, wheat meal, maize meal, maize gluten meal, coconut meal, cottonseed meal, sesame meal, and palm meal), combined brans, pulps, hulls, middlings and other high-fibre feedstuffs (B/P/H/M; wheat bran, maize bran, rice bran, sugar beet pulp, citrus pulp, soy hulls, cottonseed hulls, peanut hulls and wheat middlings) and combined miscellaneous additives in lower proportions (MI; starch, oils, urea, minerals and molasses).

Secondly, where possible, the DMI of forage feedstuffs were analysed as individual species and conservation types (forage-specific pRDA), and included fresh-cut grass/others (FGra; Napier grass, perennial ryegrass, plantain and sugarcane), grass hay (HAGra; bahiagrass hay, orchard hay, timothy hay, sorghum hay, brome hay, fescue hay and other grass hays), fresh-cut legumes (FLe; Leucaena leucocephala and white clover) legume hay (HALe; white clover and alfalfa hay), straws (ST), grass silage (SIGra), maize silage (SIMa), cereals silage (SICe; oats silage and barley silage) and non-forage DMI (NFDMI).

Thirdly, the DMI of concentrate feedstuffs were analysed as individual groups, where applicable, and the concentrate-specific biplots included grains (GR; barley, maize, wheat, sorghum, pearl millet and triticale), DGS (DGS; maize DGS, wheat DGS), brans (BR; maize bran, wheat bran and rice bran), pulps (PU, sugar beet pulp and citrus pulp), hulls (HU, soy hulls, cottonseed hulls, peanut hulls and wheat middlings), meals (ME; soy meal, soy sauce cake, linseed meal, rapeseed meal, tapioca meal, sunflower meal, wheat meal, maize meal, maize gluten meal, coconut meal, cottonseed meal, sesame meal, and palm meal), miscellaneous (biplot abbreviation MI; starch, oils, urea, minerals and molasses) and non-concentrate DMI (NCDMI).

Response variables in all three analysis groups were i) outputs of N in manure (MNO, g/d), ii) in urine (UNO, g/d) and/or iii) in faeces (FNO, g/d), as well as the following calculated NUE parameters (from the measured MNO, UNO, FNO): iv) retained N (NR), expressed per NI (NR/NI); v) UNO and vi) FNO, expressed per NI (UN/NI and FN/NI, respectively); vii) UNO and viii) FNO, expressed per MNO (UN/MN and FN/MN, respectively); and ix) FNO, expressed per UNO (FN/UN). These pRDAs were performed separately in each one of the three sub-sets, based on diet CP concentration (low CP, 47-120 g CP/kg DM, n=73; medium CP, 121-150 g CP/kg DM, n=90; high CP, 151-269 g CP/kg DM, n=74). A summary of the resulting main positive and negative correlations of the feedstuff groups with the NUE and N partitioning to faeces, are presented in Table 4.

3. Results

In this section, results for each different sub-set of CP concentration are presented separately, such that each paragraph of the results section presents three key analysis outcomes which are

i) the variation explained by axis 1 and 2, ii) the drivers that explained most of the variation and iii) the analysis of correlations.

3.1 Low CP sub-set

3.1.1 Overall pRDA

In the overall pRDA for the low CP sub-set (47-120 g CP/kg DM), drivers related to DMI of the different dietary feedstuffs explained 66.9% of the variation, of which 56.9% was explained by Axis 1 and a further 9% was explained by Axis 2 (Fig. 1a). The DGS and meals group (P = 0.002) was the most influential parameter, explaining 14.3% of the variation, followed by grains (13.5%; P = 0.004), silages (12.1%; P = 0.002), B/P/H/M (10.4%; P = 0.002), hays and straws (7.1%; P = 0.012), fresh-cut forages (6.5; P = 0.004) and miscellaneous (2.9%; P = 0.016). Manure N output and, to a lesser extent UNO and FNO, were positively associated with silages, DGS and meals group and miscellaneous additives. Ratios FN/MN, FN/NI and FN/UN were positively associated with hays and straws, fresh-cut forages and B/P/H/M. In contrast, UN/MN and UN/NI were negatively associated with the aforementioned drivers, but positively associated with grains DMI. Finally, NR/NI was positively associated to B/P/H/M and fresh forages and negatively associated to grains.

3.1.2 Forage-specific pRDA

In the forage-specific pRDA, drivers related to DMI of the forage feedstuffs and NFDMI explained 68.4% of the variation, of which 58.9% was explained by Axis 1 and a further 8.4% was explained by Axis 2 (Fig. 1b). Grass hay DMI (P = 0.002) was the most influential forage parameter, explaining 14.9% of the variation, followed by fresh legumes (9.7%; P = 0.002), maize silage (9.2%; P = 0.002), cereals silage (5.8%; P = 0.002), fresh-cut grass/others (2.2%; P = 0.018), straw (1.6%; P = 0.072) and legume hay (0.1%; P = 0.826). The NFDMI (P = 0.002) accounted for 25.0% of the total explained variation. The forage-specific pRDA identified maize silage as a positive driver of mainly MNO and FNO and cereals silage of UNO. Grass hay, fresh-cut grass/others, fresh legumes and straw were positively associated to FN/MN, FN/UN, FN/NI and NR/NI. Furthermore, UN/MN and UN/NI were negatively associated to all aforementioned parameters and positively associated to NFDMI.

3.1.3 Concentrate-specific pRDA

Similarly, in the concentrate-specific pRDA, drivers related to DMI of the concentrate feedstuffs and NCDMI explained 65.9% of the variation, of which 55.7% was explained by Axis 1 and a further 9.4% was explained by Axis 2 (Fig. 1c). Meals (P = 0.002) and grains (P = 0.004) accounted for 19.6% and 13.5% of the explained variation respectively, followed by brans (6.9%; P = 0.002), miscellaneous (3.1%; P = 0.022), hulls (2.9%; P = 0.018) and pulps (2.9%; P = 0.024). The NCDMI (P = 0.002) accounted for 16.9% of the total explained variation. In the concentrate-specific pRDA, all three N outputs were positively associated to meals and miscellaneous groups, and negatively associated to brans. Faecal N output also showed a positive association to NCDMI. Ratios FN/MN, FN/NI, FN/UN and NR/NI were positively associated with pulps and brans. In contrast, UN/MN and UN/NI were negatively associated with the aforementioned drivers, but positively associated to grains, meals and hulls.

3.2 Medium CP sub-set

3.2.1 Overall pRDA

In the overall pRDA for the medium CP sub-set (121-150 g CP/kg DM), drivers related to DMI of the different dietary feedstuffs explained 71.1% of the variation, of which 61.5% was explained by Axis 1 and a further 3.0% was explained by Axis 2 (Fig. 2a). Grains (P = 0.002) was the most significant parameter, accounting for the 19.3% of the total explained variation, followed by B/P/H/M (16.9%; P = 0.002), silages (16.5%; P = 0.002), DGS and meals group (7.6%; P = 0.002), fresh-cut forages (6.2%; P = 0.002), hays and straws (4.3%; P = 0.002) and miscellaneous (0.3%; P = 0.554). From the N outputs, FNO showed a positive association with B/P/H/M, DGS and meals group and silages, while MNO and UNO were positively associated with B/P/H/M and the DGS and meals group to a lesser extent. Furthermore, the ratios FN/MN, FN/NI and FN/UN were positively associated to hays and straws group and negatively associated to grains and fresh-cut forages. Ratios UN/NI and UN/MN, both showed a negative association with hays and straws, yet the latter was positively associated with grains. Finally, NR/NI showed a positive association to fresh-cut forages and grains and a negative to DGS and meals group, B/P/H/M and silages.

3.2.2 Forage-specific pRDA

In the forage-specific pRDA, drivers related to DMI of the forage feedstuffs and NFDMI explained 75.0% of the variation, of which 63.7% was explained by Axis 1 and a further 4.0% was explained by Axis 2 (Fig. 2b). Straws (P = 0.002) and cereals silage (P = 0.002) both explained the majority of the variation, accounting for 12.9% and 10.2% respectively, followed by maize silage (9.6%; P = 0.002), grass silage (9.2%; P = 0.002), grass hay (3.3%; P = 0.002), fresh-cut legumes (3.0%; P = 0.008), fresh-cut grass/others (2.4%; P = 0.004) and legume hay (1.5%; P = 0.030). The NFDMI (P = 0.002) accounted for 23.0% of the total explained variation. The forage-specific pRDA identified all silages as positive drivers of FNO while straw, grass and legume hay, fresh-cut grass/others and legumes, had a negative influence on all three N outputs. Furthermore, straws and grass and legume hay were positively associated to FN/MN, FN/UN and FN/NI, with grass and legume hay also correlating positively with NR/NI, along with fresh-cut grass/others and legumes. Finally, straws and grass and legume hay, negatively affected UN/MN, UN/NI, with NFDMI affecting them positively.

3.2.3 Concentrate-specific pRDA

In the concentrate-specific pRDA, drivers related to DMI of the concentrate feedstuffs and NCDMI explained 71.3% of the variation, of which 61.5% was explained by Axis 1 and a further 3.1% was explained by Axis 2 (Fig. 2c). Meals (P = 0.002) accounted for 13.5% of the explained variation, followed by brans (13.2%; P = 0.002), grains (8.3%; P = 0.002), pulps

(3.4%; P = 0.004), hulls (3.4%; P = 0.004), DGS (1.9%; P = 0.022) and miscellaneous (0.3%; P = 0.454). The NCDMI (P = 0.002) accounted for 27.3% of the total explained variation. In the concentrate-specific pRDA, MNO, UNO as well as ratios MN/NI and UN/NI, were positively associated to brans and miscellaneous, with FNO and MN/NI also positively associated to meals. Ratios FN/MN, FN/UN and FN/NI showed a positive association with hulls and pulps and a negative association with grains. On the contrary, UN/MN seemed to be negatively affected by the two aforementioned drivers. Ratio NR/NI was positively associated to grains and DGS and negatively associated to all other variables.

3.3 High CP sub-set

3.3.1 Overall pRDA

For the high CP sub-set (151-269 g CP/kg DM), the included drivers related to DMI of the different dietary feedstuffs explained 81.9% of the variation, of which 79.4% was explained by Axis 1 and a further 1.0% by Axis 2 (Fig. 3a). The DGS and meals group (P = 0.002) was the most influential parameter, explaining 59.8% of the variation, followed by grains (6.8%; P = 0.002), hays and straws (6.2; P = 0.002), B/P/H/M (5.5; P = 0.002), silages (3.1; P = 0.030) and miscellaneous (0.4; P = 0.320). All three parameters representing N outputs showed a positive association with grains and DGS and meals. In addition, ratios UN/MN and UN/NI were positively associated to grains, DGS and meals and miscellaneous. Contrastingly, ratios FN/MN, FN/UN and FN/NI showed a negative association all three aforementioned variables. Ratio NR/NI showed a positive association only with hays and straws while being negatively associated to all other variables.

3.3.2 Forage-specific pRDA

The forage-specific pRDA drivers (DMI of the forage feedstuffs and NFDMI) explained 78.1% of the variation, of which 75.4% was explained by Axis 1 and a further 1.1% was explained by Axis 2 (Fig. 3b). Straws (P = 0.002) accounted for 12.5% of the variation, followed by cereals silage (7.9%; P = 0.002), cereals silage (9.2%; P = 0.002), grass silage (5.8%; P = 0.002), maize silage (3.9%; P = 0.006), grass hay (2.7%; P = 0.040) and legume hay (0.8%; P = 0.208). The NFDMI (P = 0.002) accounted for 44.6% of the total explained variation. All three N outputs showed a positive association to NFDMI, cereals silage and legume hay and a negative association with straws and at a lesser extent and grass silage. Ratios MN/NI, UN/MN and UN/NI were positively associated to legume hay and NFDMI and negatively associated to grass silage and straws. Ratios NR/NI, FN/MN, FN/UN and FN/NI showed a positive association to grass silage and straws and a negative association with NFDMI and legume hay.

3.3.3 Concentrate-specific pRDA

The concentrate-specific pRDA drivers (DMI of the concentrate feedstuffs and NCDMI) explained 81.5% of the variation, of which 78.5% was explained by Axis 1 and a further 1.4% was explained by Axis 2 (Fig. 3c). Distillers grains with solubles (P = 0.002) accounted for 42.2% of the explained variation, followed by meals (18.4%; P = 0.002), grains (4.3%; P = 0.010), pulps (2.1%; P = 0.016), brans (1.5%; P = 0.060), shells (0.8%; P = 0.132) and miscellaneous (0.3%; P = 0.408). The NCDMI (P = 0.002) accounted for 27.3% of the total explained variation. Ratios UN/MN, UN/NI, and UNO showed a positive association with DGS, grains and miscellaneous while being negatively associated with meals. NR/NI showed a positive association with hulls, while ratios FN/MN, FN/UN, FN/NI only showed a positive association to meals.

4. Discussion

4.1 Forages

In the overall pRDA, DMI of hays and straws showed no consistent association with NUE (as expressed by MN/NI and RN/NI), however did affect it positively in the low and high CP sub-sets. The lack of clear association with NUE across the different sub-sets could be due to the variant neutral detergent fibre (NDF) concentration (different forage species and level of maturity) and its digestibility, which is the principle factor determining the energy available for microbial protein synthesis in the rumen (NASEM, 2016) and body tissue synthesis. Conversely, the forage-specific pRDA showed a positive effect of grass hay DMI on NUE in the low and medium CP sub-set, while straws DMI showed a positive effect on NUE across all diets. This suggests that high NDF forages may play an important role in improving NUE in diets with differing concentrations of CP. For example, in low CP diets (but not lower than 70 g CP/kg DM which would impair digestibility), higher inclusion rates of high NDF forages can provide adequate energy for fermentation processes (Mathis et al., 2000). Furthermore, in high-CP diets, higher inclusion rates of NDF can slow carbohydrate digestion in the rumen leading to slower rates of volatile fatty acids production, consequently preventing significant reductions in ruminal pH (NASEM, 2016) and benefiting microbial protein synthesis (Pitt et al., 1996). The positive association between legume hay DMI and improved NUE in the medium CP sub-sets, shifted to a negative association in the high CP sub-set. In low CP diets, supplementation with a better quality hay, such as alfalfa, which typically is more nutrient dense and digestible when compared to other forages (Martin et al., 2005), was expected to improve NUE, by providing high quality rumen degradable protein as animals were not fed excessive CP. However, the change in performance between the medium and high CP sub-sets, could be attributed to the fact that alfalfa and other legumes are often high in N, therefore increasing diet CP concentration, and as legumes are typically high in concentration of rumen degradable protein, they increase rumen ammonia (NASEM, 2016); an effect which might be exacerbated when the diet CP is already high. Legume hay DMI was also a driver of N partitioning into faeces for the medium CP sub-set, probably due to the fibre digested later in the hindgut, resulting in excretion of more microbial protein in faeces (Higgs et al., 2012). This can be considered beneficial from an environmental perspective, as faecal N is less labile than urine N, and such a shift may partly reduce N_2O and NH_3 emissions (Bussink and Oenema, 1998). The forage-specific pRDA showed that all forage DMI drivers, except legume hay in the low and high CP sub-sets, beneficially influenced N partitioning and improved NUE.

Ensiled forages DMI did not show a consistent impact on NUE or N partitioning into faeces. The forage-specific pRDA showed a negative association between cereals silage DMI and NUE and N partitioning in the low CP sub-set. Similarly, cereals, grass and maize silages DMI in the medium CP sub-set negatively affected NUE. However, in the high CP sub-set, grass silage DMI showed a positive effect on NUE and N partitioning. In ensiled forages, non-structural carbohydrates are being fermented by microorganisms during the ensiling process, leading to less available energy for ruminal fermentation. As a result, ruminal microbial protein production is lower when cattle consume grass silages rather than hay (Titgemeyer and Löest, 2001) and more N may be transformed to NH_3 and urea, and be excreted in urine. Concerning the individual silages DMI associations with NUE, while theoretically N losses in urine increase with increasing proportions of grass silage in the diet (Moss et al., 1992; Browne et al., 2005), this was not noticed in the current study. Given that the effect of silage on NUE is highly relevant to its chemical composition (especially CP and NDF concentration), the high between-study variation on silage quality may be the reason for inconsistent results in literature.

In the overall pRDA, DMI of fresh-cut forages was positively associated with improved NUE in the low and medium CP sub-sets, while there was no such relation in the high CP sub-set. The fresh-cut forages represented a very diverse group including Napier grass, *Leucaena leucocephala*, perennial ryegrass, white clover, plantain and sugarcane; thus being highly variant in species, as well as potentially in maturity and chemical composition. It is known that grass in grazing ruminant diets can negatively affect ruminal fermentation due to the increase in soluble protein levels and the discrepancy between the supplied CP and rumen degradable carbohydrate, thus lowering efficiency of CP utilisation and increasing NH_3-N load (Hoekstra et al., 2007). However a recent study from Du et al. (2019) has shown that the NH_3-N concentration in the rumen of crossbred Simmental cattle was lower, with a high proportion of legumes in the diet. This contrasting effect of forage species on NUE and N partitioning may have masked some of the effects of individual species when grouped together in one driver. Furthermore, the forage-specific pRDA has shown a positive association of fresh-cut grasses/others DMI with N partitioning towards faeces in the low CP sub-set. Due to the slower fermentation rates of structural carbohydrates, which are found in relatively higher amounts in forages than concentrate feedstuffs, an amount of up to 10% can reach the hindgut (Huhtanen et al., 2006), providing energy for the microbes to capture available N, thus increasing FNO (Higgs et al., 2012). This effect was also observed with DMI of fresh-cut legumes in both low and medium CP sub-sets.

The present study demonstrated that the DMI of fibrous forage feedstuffs such as hay and straw can have a beneficial effect on NUE and N partitioning leading to a lower environmental footprint. However, this observation should be interpreted in the context of individual herds and conditions as higher supply of fibrous forage (at the expense of other higher-quality feedstuffs) may have negative effects on growth rates and any such inclusion should be supported by a well-balanced total ration. The fresh-cut forages that improved NUE were mainly legumes and grasses while an increase in DMI of silages may not show a beneficial effect on NUE.

4.2 Fibre-rich by-products

The present study showed that, DMI of fibre-rich feedstuffs including brans, pulps, and hulls, had a positive association with N partitioning towards faeces in the low CP sub-set, while specific types of fibre-rich feedstuffs (hulls) had a positive association with NUE in the high CP sub-set. Pulps and brans DMI were identified, in the concentrate-specific pRDA, as positive drivers of N partitioning towards faeces in the low CP sub-set; while pulps and hulls DMI had this primary role in the medium CP sub-set. It has been well documented that an increase in diet NDF concentration may lead to a reduction in apparent N digestibility, as carbohydrates that show slower fermentation rates can end up in the hindgut and act as energy substrates for microorganisms which can capture N. Subsequently, they are excreted in faeces and hence more N is excreted in FNO than UNO (Higgs et al., 2012). Fibre-rich feedstuffs DMI had non-beneficial effects on NUE in the medium CP sub-set, while hulls DMI had a positive impact on NUE in the high CP sub-set. The concentrate-specific pRDA in the medium CP sub-set also revealed that brans DMI was the major contributor to the observed undesirable effect on NUE. A recent study by Angelidis et al. (2019) showed a positive association between diet structural carbohydrate and UNO/NI, which may explain the influence of the fibre-rich by-products in the medium CP sub-set. However, there is also a potential effect of the type of fibre, as the role of NDF, acid detergent fibre (ADF) and lignin on NUE and N partitioning may be contrasting. For example, soybean hulls consist mainly of NDF (600-700 g/kg DM), and have low lignin concentration, therefore their fibre digestibility is high (Hsu et al., 1987). As the efficiency of microbial protein synthesis is highly dependent on the supplementation of readily available energy compounds (Tas et al., 2006), energy from highly digestible fibre sources can be beneficial in animals consuming diets higher in rumen degradable protein thus improving NUE. Based on the results of the present study, the DMI of fibre-rich by-products can drive the partitioning of N excretion towards faeces across the CP inclusion range while also improving NUE in beef consuming diets of various CP concentrations, as a source of readily available energy.

4.3 Grains

Grains DMI was positively associated with NUE in medium CP diets and this effect was further supported in the concentrate-specific pRDA. Grain-based diets, which provide high amounts of non-structural carbohydrates (e.g. starch, sugars), can improve N capture by microorganisms in the rumen and therefore increase microbial protein synthesis, in comparison to cellulose-rich diets, because they increase rapidly available energy supply for microbial synthesis (Stern and Hoover, 1979). When higher amounts of N are captured in the form of microbial protein, supply of amino acids to the small intestine improves and N losses decrease (Bach et al., 2005). However, there was evidence that dietary grains DMI partitioned more N towards urine across the CP range. Results from the present study reveal that grain supplementation could be used in order to improve NUE in beef consuming medium-CP diets (e.g. at growing stage), but the same practice may also have the undesirable result of increasing the proportion of N output into urine; which may be common in beef consuming diets across the whole range of CP concentrations.

4.4 Protein-rich by-products

Dry matter intake of DGS and meals appeared to be a negative driver for both NUE and N partitioning towards faeces in the high CP sub-set. However, in the concentrate-specific pRDA for the high CP sub-set, DGS had the most notable negative effect, with meals DMI showing a positive association with NUE and N partitioning towards faeces. In contrast, meals DMI was negatively associated with NUE in both the low and medium CP sub-sets. In beef cattle, once the rumen degradable protein and metabolisable protein needs are met, excess N is excreted predominantly in urine (Vasconcelos et al., 2009), thus explaining the undesirable effect of protein-rich by-products on NUE, and the increase in the N partitioning towards urine, in diets already including high CP concentrations. In previous studies, when the wet DGS inclusion in a dry-rolled maize-based diet was increased from 0 to 60%, the N excretion also increased linearly (Spiehs and Varel, 2009; Luebbe et al., 2012). In another study, when wet DGS was added in iso-fat concentration steam-flaked maize-based diets, the N excretion was increased from 95 to 140 g/d for 0 and 45% inclusion respectively (Hales et al., 2013). In general, lower levels of DGS inclusion in beef cattle diets leads to lower CP concentration and NI, as diets containing higher proportions of DGS usually exceed beef cattle N requirements (Koenig et al., 2018). Overall, the supply of protein-rich by-products can be considered a very good source of CP in beef, but care should be taken in their inclusion rates because they can impair NUE and increase N outputs in urine when given in amounts that exceed requirements in high-CP diets.

4.5 Miscellaneous

The DMI of miscellaneous additives, including purified starch, oils, urea, minerals and molasses did not show a consistent effect on neither NUE nor N partitioning towards faeces, across the CP range. As this is a rather diverse group, particular components belonging to it could have had different or additional effects if evaluated alone. For example, starch and molasses provide rapidly available energy (Morales et al., 1989; Higgs et al., 2013), thus enhancing N capture in microbial protein and reducing NH_3-N concentration in the rumen. Oils may disrupt the rate of ruminal degradation of feedstuffs and nutrients, particularly structural carbohydrates and CP (Jenkins, 1993), and are also a good source of digestible energy for the animal (Hess et al., 2008). A review of 42 studies by Doreau and Ferlay (1995), on the effects of dietary oils on N metabolism in the rumen showed that the ruminal NH_3 concentration was generally reduced, while microbial and non-microbial N flow to the duodenum was not affected by fat supplementation. However, the low rates of inclusion in the diet along with the relatively small number of studies in the database that used these individual feedstuffs, did not allow their individual assessment as separate drivers.

5. Conclusions

The present study has revealed that key feeding strategies to improve feed efficiency in beef, and subsequently reduce N outputs in urine and subsequent N_2O and NH_3 emissions from beef cattle, are the adequate supply of digestible fibre- and energy-rich feedstuffs, as well as a reduction in the oversupply of high CP concentrate feedstuffs. The provision of hays and straws may improve N use efficiency in low CP diets and shift N partitioning from urine to faeces in low and medium CP diets (a beneficial effect from an environmental footprint point of view) mainly due to the supply of low-cost energy and the dilution of CP concentration in the diet. Similar beneficial effects could be achieved across the CP range by the higher supply of feedstuffs rich in digestible NDF, as due to their lower lignin concentration they can be valuable energy sources. In high CP diets, where the risk of excess N supply is apparent and there is a need for digestible carbohydrates, the supply of meals (e.g. soybean meal, oilseed meal etc) rather than distillers' grains, may have a beneficial effect in N partitioning towards faeces, but this is not the case in low and medium CP diets. However, distillers' grains can be valuable as a low-cost CP source in diets of medium CP concentration, where the risk of excess N inclusion is lower. Feedstuffs high in available energy, such as oils, molasses and starch may also benefit N use efficiency when used as supplements for beef diets regardless of CP concentration. In the present study 21.6-51.2% of the variation in the different N outputs and N use efficiency parameters was explained using DMI of specific feedstuffs as drivers. Although this provides a satisfactory outcome for such work and provides evidence of the important role that feedstuff choice plays on N use efficiency, it also highlights that a number of other parameters (e.g. nutrient degradability, animal factors) which were not investigated in the present study may also be highly influential to N use efficiency in beef cattle.

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Figure captions

Fig. 1 Biplots derived from the redundancy analysis using the low CP sub-set, showing the relationship between either a) distiller's grains with solubles (DGS)/meals (D/M), silages (SIL), brans/pulps/hulls/middlings (B/P/H/M), grains (GR), fresh-cut forages (FF), hays/straws (H/S), miscellaneous additives (MI), b) non-forage dry matter intake (DMI) (NFDMI), grass hay (HAGra), fresh legumes (FLe), maize silage (SIMa), cereals silage (SICe), fresh grass (FGra), straws (ST), legume hay (HALe), and c) meals (ME), non-concentrate DMI (NCDMI), brans (BR), GR, hulls (HU), pulps (PU), miscellaneous additives (MI) and i) manure N output (MNO), ii) urine N output (UNO), iii) faeces N output (FNO), iv) retained N (NR) and v) MNO, expressed per N intake (NI); vi) UNO and vii) FNO expressed per NI; viii) UNO and ix) FNO, expressed per MNO; and x) FNO, expressed per UNO (shown as dots; abbreviated as i) MNO, ii) UNO, iii) FNO, iv) NR/NI, v) MN/NI, vi) UN/NI, vii) FN/NI, viii) UN/MN, ix) FN/MN, x) FN/UN). Continuous variables (shown as arrows) were a) D/M ($P = 0.002$), SIL ($P = 0.002$), B/P/H/M ($P = 0.002$), GR ($P = 0.004$), FF ($P = 0.004$), H/S ($P = 0.012$) and MI ($P = 0.016$), b) NFDMI ($P = 0.002$), HAGra ($P = 0.002$), FLe ($P = 0.002$), SIMa ($P = 0.002$), SICe ($P = 0.002$), FGra ($P = 0.018$), ST ($P = 0.072$) and HALe ($P = 0.826$), and c) ME ($P = 0.002$), NCDMI ($P = 0.002$), BR ($P = 0.002$), GR ($P = 0.004$), HU ($P = 0.018$), MI ($P = 0.022$) and PU ($P = 0.024$); Axis 1 explained a) 56.9%, b) 58.9% and c) 55.7% of the variation and axis 2 a further a) 9%, b) 8.4% and c) 9.4%, for the three biplots respectively.

Fig. 2 Biplots derived from the redundancy analysis using the medium CP sub-set, showing the relationship between either a) grains (GR), brans/pulps/hulls/middlings (B/P/H/M), silages (SIL), distiller's grains with solubles (DGS)/meals (D/M), hays/straws (H/S), fresh-cut forages (FF), miscellaneous additives (MI), b) non-forage dry matter intake (DMI) (NFDMI), straws (ST), cereals silage (SICe), maize silage (SIMa), grass silage (SIGra), grass hay (HAGra), fresh-cut grass/others (FGra), fresh legumes (FLeg) and legume hay (HALe), and c) non-concentrate DMI (NCDMI), meals (ME), brans (BR), GR, hulls (HU), pulps (PU), DGS and MI and i) manure N output (MNO), ii) urine N output (UNO), iii) faeces N output (FNO), iv) retained N (NR) and v) MNO, expressed per N intake (NI); vi) UNO and vii) FNO expressed per NI; viii) UNO and ix) FNO, expressed per MNO; and x) FNO, expressed per UNO (shown as dots; abbreviated as i) MNO, ii) UNO, iii) FNO, iv) NR/NI, v) MN/NI, vi) UN/NI, vii) FN/NI, viii) UN/MN, ix) FN/MN, x) FN/UN). Continuous variables (shown as arrows) were a) GR ($P = 0.002$), B/P/H/M ($P = 0.002$), SIL ($P = 0.002$), D/M ($P = 0.002$), H/S ($P = 0.002$), FF ($P = 0.002$) and MI ($P = 0.554$), b) NFDMI ($P = 0.002$), ST ($P = 0.002$), SICe ($P = 0.002$), SIMa ($P = 0.002$), SIGra ($P = 0.002$), HAGra ($P = 0.002$), FGra ($P = 0.004$), FLe ($P = 0.008$) and HALe ($P = 0.030$), and c) NCDMI ($P = 0.002$), ME ($P = 0.002$), BR ($P = 0.002$), GR ($P = 0.002$), HU ($P = 0.004$), PU ($P = 0.004$), DGS ($P = 0.022$) and MI ($P = 0.454$); Axis 1 explained a) 61.5%, b) 63.7% and c) 61.5% of the variation and axis 2 a further a) 3%, b) 4% and c) 3.1%, for the three biplots respectively.

Fig. 3 Biplots derived from the redundancy analysis using the high CP sub-set, showing the relationship between either a) distiller's grains with solubles (DGS)/meals (D/M), grains (GR), hays/straws (H/S), brans/pulps/hulls/middlings (B/P/H/M), silages (SIL) and miscellaneous additives (MI), b) non-forage dry matter intake (DMI) (NFDMI), straws (ST), cereals silage (SICe), grass silage (SIGra), maize silage (SIMa), grass hay (HAGra) and legume hay (HALe), and c) DGS, meals (ME), non-concentrate DMI, GR, pulps (PU), hulls (HU) and MI and i) manure N output (MNO), ii) urine N output (UNO), iii) faeces N output (FNO), iv) retained N (NR) and v) MNO, expressed per N intake (NI); vi) UNO and vii) FNO expressed per NI; viii) UNO and ix) FNO, expressed per MNO; and x) FNO, expressed per UNO (shown as dots; abbreviated as i) MNO, ii) UNO, iii) FNO, iv) NR/NI, v) MN/NI, vi) UN/NI, vii) FN/NI, viii) UN/MN, ix) FN/MN, x) FN/UN). Continuous variables (shown as arrows) were a) D/M ($P = 0.002$), GR ($P = 0.002$), H/S ($P = 0.002$), B/P/H/M ($P = 0.002$), SIL ($P = 0.030$) and MI ($P = 0.320$), b) NFDMI ($P = 0.002$), ST ($P = 0.002$), SICe ($P = 0.002$), SIGra ($P = 0.002$), SIMa ($P = 0.006$), HAGra ($P = 0.040$) and HALe ($P = 0.208$), and c) DGS ($P = 0.002$), ME ($P = 0.002$), NCDMI ($P = 0.002$), GR ($P = 0.002$), PU ($P = 0.002$), HU ($P = 0.132$) and MI ($P = 0.408$); Axis 1 explained a) 79.4%, b) 75.4% and c) 78.5% of the variation and axis 2 a further a) 1%, b) 1.1% and c) 1.4%, for the three biplots respectively.

Tables

Table 1 Description of data collected from 59 published studies, used to conduct multivariate redundancy analysis, including forage proportion, dietary feedstuffs, N outputs and N use efficiency parameters; in beef (n=73) fed diets with low CP concentration (47-120 g CP/kg DM)

Parameters assessed	Mean[a] ±SD	Min[b]	Max	CV	n[c]
Intakes					
DMI (kg/d)	6.7 ±1.77	3.6	10.6	0.27	73
NI (g/d)	111.4 ±39.50	35.9	205.4	0.36	73
Animal diet (g/kg DM)					
Total forage	538 ±325.3	0	1000	0.60	73 (66)
Silage	154 ±253.0	0	800	1.64	73 (25)
Maize	145 ±250.1	0	800	1.73	73 (23)
Cereals[1]	9 ±64.5	0	536	6.86	73 (02)
Hay	264 ±314.6	0	1000	1.19	73 (39)
Grass	263 ±315.5	0	1000	1.20	73 (38)
Legumes[2]	1 ±11.6	0	100	8.49	73 (01)
Fresh-cut	41 ±198.5	0	1000	4.83	73 (03)
Grass	25 ±123.6	0	800	5.01	73 (03)
Legumes[3]	16 ±86.0	0	600	5.23	73 (03)
Straw	79 ±239.3	0	1000	3.03	73 (12)
Grains	231 ±309.9	0	852	1.34	73 (41)
Maize	175 ±269.2	0	825	1.54	73 (37)
Cereals[4]	56 ±158.8	0	828	2.83	73 (12)
Brans	44 ±134.1	0	500	3.04	73 (08)
Cereals[5]	44 ±134.1	0	500	3.04	73 (08)
Pulps	39 ±107.4	0	400	2.77	73 (09)
Hulls	34 ±67.6	0	300	2.01	73 (19)
Meals	69 ±142.8	0	761	2.06	73 (40)
Soybean	26 ±32.6	0	130	1.28	73 (34)
Oilseed[6]	1 ±6.1	0	52	7.77	73 (02)
Other[7]	43 ±133.0	0	719	3.17	73 (13)
Miscellaneous	44 ±79.6	0	501	1.81	73 (62)
Starch	11 ±60.7	0	489	5.61	73 (04)
Oils	1 ±0.9	0	8	7.44	73 (02)
Urea	2 ±4.0	0	20	2.08	73 (18)
Minerals	11 ±10.6	0	35	0.93	73 (46)
Molasses	20 ±55.4	0	365	2.73	73 (24)
N output and retention (g/d)					
Manure N output	87.2 ±32.02	41.5	177.9	0.37	62
Urine N output	43.1 ±27.84	13.7	149.9	0.65	62
Faeces N output	43.7 ±11.74	19.2	75.8	0.27	73
Retained N	31.5 ±16.12	4.2	72.5	0.51	62
N use efficiency parameters (kg/kg)					
Manure N : NI	0.735 ±0.1081	0.508	0.949	0.13	62
Urine N : NI	0.348 ±0.1196	0.129	0.743	0.35	62
Faeces N : NI	0.413 ±0.1002	0.138	0.755	0.25	73
Retained N : NI	0.265 ±0.1027	0.049	0.492	0.37	62
Urine N : Manure N	0.466 ±0.1201	0.254	0.843	0.25	62
Faeces N : Manure N	0.534 ±0.1196	0.157	0.746	0.22	62
Faeces N : Urine N	1.275 ±0.4579	0.187	2.944	0.42	62

N = nitrogen; CP = crude protein; DM = dry matter; SD = standard deviation; Min = minimum value observed; Max = maximum value observed; CV = coefficient of variation; n = number of observations; DMI = dry matter intake; NI = N intake

[a] The column represents the mean of measurements with a value higher or equal to zero. [b] This represents the minimum value observed in studies where the feedstuff was offered to the animals. In case that the feedstuff was not offered (no intake) the analysis considered that the contribution of this feedstuff to the diet was 0 kg/kg DM. [c] Number of observations in the parentheses represent the number of data points with values higher than zero.

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[1]barley, oats; [2]white clover, alfalfa; [3]*Leucaena leucocephala*, white clover; [4]barley, maize, wheat, sorghum, pearl millet, triticale; [5]wheat, rice; [6]linseed, rapeseed, sunflower, sesame, palm; [7]tapioca, wheat, maize, maize gluten, coconut, cottonseed

Table 2 Description of data collected from 59 published studies, used to conduct multivariate redundancy analysis, including forage proportion, dietary feedstuffs, N outputs and N use efficiency parameters; in beef (n=90) fed diets with medium CP concentration (121-150 g CP/kg DM)

Parameters assessed	Mean[a] ±SD	Min[b]	Max	CV	n[c]
Intakes					
DMI (kg/d)	7.9 ±2.11	3.9	11.8	0.27	90
NI (g/d)	171.7 ±49.69	80.5	299.2	0.29	90
Animal diet (g/kg DM)					
Total forage	337 ±281.0	0	1000	0.83	90 (86)
Silage	197 ±250.4	0	884	1.27	90 (50)
Grass	22 ±112.9	0	750	5.13	90 (05)
Maize	123 ±218.7	0	884	1.78	90 (33)
Cereals[1]	52 ±147.7	0	550	2.87	90 (14)
Hay	99 ±134.2	0	900	1.93	90 (38)
Grass	66 ±185.2	0	900	2.80	90 (19)
Legumes[2]	33 ±74.0	0	350	2.29	90 (22)
Fresh-cut	33 ±163.3	0	1000	4.90	90 (04)
Grass	24 ±128.5	0	1000	9.43	90 (04)
Legumes[3]	9 ±83.9	0	800	5.23	90 (01)
Straw	8 ±33.7	0	200	4.17	90 (06)
Grains	465 ±295.9	0	917	0.64	90 (84)
Maize	323 ±316.1	0	907	0.98	90 (62)
Cereals[4]	142 ±258.9	0	917	1.82	90 (32)
DGS	15 ±66.9	0	400	4.46	90 (05)
Maize	13 ±65.3	0	400	4.90	90 (04)
Cereals[5]	2 ±15.7	0	150	9.43	90 (01)
Brans	21 ±78.6	0	450	3.70	90 (07)
Maize	18 ±76.9	0	450	4.19	90 (05)
Cereals[6]	3 ±19.2	0	130	6.63	90 (02)
Pulps	13 ±47.6	0	294	3.66	90 (08)
Hulls	15 ±52.6	0	225	3.56	90 (09)
Meals	84 ±126.7	0	551	1.52	90 (58)
Soybean	37 ±66.2	0	315	1.80	90 (40)
Oilseed[7]	14 ±37.7	0	209	2.68	90 (15)
Other[8]	33 ±95.4	0	551	2.92	90 (24)
Miscellaneous	51 ±34.9	0	187	0.69	90 (85)
Starch	5 ±25.2	0	162	5.07	90 (04)
Oils	3 ±9.0	0	35	2.72	90 (18)
Urea	5 ±6.4	0	30	1.21	90 (51)
Minerals	24 ±15.0	0	60	0.62	90 (83)
Molasses	13 ±20.9	0	97	1.62	90 (39)
Nitrogen output and retention (g/d)					
Manure N output	128.7 ±50.42	36.7	259.5	0.39	83
Urine N output	75.2 ±37.70	20.4	186.4	0.50	78
Faeces N output	50.6 ±16.47	21.1	82.8	0.33	83
Retained N	43.3 ±17.15	7.9	97.4	0.40	81
Nitrogen use efficiency parameters (kg/kg)					
Manure N : NI	0.730 ±0.1142	0.330	0.924	0.16	83
Urine N : NI	0.422 ±0.1015	0.202	0.758	0.24	78
Faeces N : NI	0.301 ±0.0723	0.131	0.444	0.24	83
Retained N : NI	0.261 ±0.0981	0.077	0.497	0.38	81
Urine N : Manure N	0.570 ±0.0939	0.363	0.853	0.16	77
Faeces N : Manure N	0.427 ±0.0910	0.147	0.625	0.21	77
Faeces N : Urine N	0.791 ±0.2875	0.173	1.667	0.36	77

N = nitrogen; CP = crude protein; DM = dry matter; SD = standard deviation; Min = minimum value observed; Max = maximum value observed; CV = coefficient of variation; n = number of observations; DGS = distillers grains with solubles; DMI = dry matter intake; NI = N intake

[a] The column represents the mean of measurements with a value higher or equal to zero. [b] This represents the minimum value observed in studies where the feedstuff was offered to the animals. In case that the feedstuff was not offered (no intake) the analysis considered that the contribution of this feedstuff to the diet was 0 kg/kg DM. [c] Number of observations in the parentheses represent the number of data points with values higher than zero.

[1] barley, oats; [2] white clover, alfalfa; [3] *Leucaena leucocephala*, white clover; [4] barley, maize, wheat, sorghum, pearl millet, triticale; [5] wheat; [6] wheat, rice; [7] linseed, rapeseed, sunflower, sesame, palm; [8] tapioca, wheat, maize, maize gluten, coconut, cottonseed

Table 3 Description of data collected from 59 published studies, used to conduct multivariate redundancy analysis, including forage proportion, dietary feedstuffs, N outputs and N use efficiency parameters; in beef (n=74) fed diets with high CP concentration (151-269 g CP/kg DM)

Parameters assessed	Mean[a] ±SD	Min[b]	Max	CV	n[c]
Intakes					
DMI (kg/d)	7.6 ±2.62	3.1	13.1	0.35	74
NI (g/d)	207.8 ±80.4	72	353	0.39	74
Animal diet (g/kg DM)					
Total forage	281 ±257.3	0	1000	0.91	74 (72)
Silage	156 ±234.5	0	770	1.50	74 (34)
Grass	34 ±133.8	0	700	3.91	74 (06)
Maize	66 ±159.4	0	600	2.43	74 (13)
Cereals[1]	56 ±165.6	0	770	2.94	74 (15)
Hay	88 ±170.8	0	900	1.93	74 (16)
Grass	69 ±173.8	0	900	2.50	74 (15)
Legumes[2]	19 ±37.8	0	106	2.01	74 (16)
Fresh-cut	13 ±115.5	0	1000	8.54	74 (01)
Grass	12 ±103.9	0	900	8.54	74 (01)
Legumes[3]	1 ±11.5	0	100	8.54	74 (01)
Straw	23 ±52.5	0	200	2.24	74 (16)
Grains	367 ±233.0	0	730	0.63	74 (65)
Maize	239 ±240.4	0	730	1.01	74 (50)
Cereals[4]	129 ±208.8	0	717	1.62	74 (29)
DGS	176 ±190.8	0	600	1.08	74 (38)
Maize	80 ±160.9	0	600	2.00	74 (17)
Cereals[5]	96 ±160.9	0	600	1.68	74 (21)
Brans	20 ±75.0	0	450	3.74	74 (07)
Maize	6 ±51.9	0	450	8.27	74 (03)
Cereals[6]	14 ±55.6	0	250	4.03	74 (06)
Pulps	23 ±55.3	0	241	2.45	74 (13)
Hulls	10 ±40.2	0	300	3.97	74 (07)
Meals	81 ±108.6	0	410	1.35	74 (37)
Soybean	53 ±77.8	0	259	1.46	74 (28)
Oilseed[7]	8 ±19.9	0	70	2.52	74 (13)
Other[8]	20 ±48.8	0	172	2.48	74 (11)
Miscellaneous	42 ±35.4	0	178	0.85	74 (67)
Starch	4 ±25.4	0	158	6.00	74 (02)
Oils	2 ±6.6	0	35	3.05	74 (09)
Urea	2 ±3.4	0	12	2.17	74 (15)
Minerals	22 ±16.8	0	60	0.78	74 (61)
Molasses	12 ±24.6	0	95	2.01	74 (28)
Nitrogen output and retention (g/d)					
Manure N output	159.3 ±73.55	23.8	303.0	0.46	71
Urine N output	92.1 ±52.33	9.4	201.0	0.57	62
Faeces N output	53.1 ±19.59	14.4	101.9	0.37	63
Retained N	51.0 ±23.31	4.0	123.0	0.46	68
Nitrogen use efficiency parameters (kg/kg)					
Manure N : NI	0.737 ±0.1092	0.506	0.964	0.15	71

Urine N : NI	0.439 ±0.1101	0.198	0.618	0.25	62
Faeces N : NI	0.277 ±0.0452	0.173	0.410	0.16	63
Retained N : NI	0.263 ±0.1118	0.036	0.494	0.43	68
Urine N : Manure N	0.604 ±0.0906	0.391	0.782	0.15	61
Faeces N : Manure N	0.400 ±0.0935	0.218	0.609	0.23	61
Faeces N : Urine N	0.700 ±0.3034	0.279	1.556	0.43	61

N = nitrogen; CP = crude protein; DM = dry matter; SD = standard deviation; Min = minimum value observed; Max = maximum value observed; CV = coefficient of variation; n = number of observations; DGS = distillers grains with solubles; DMI = dry matter intake; NI = N intake

[a]The column represents the mean of measurements with a value higher or equal to zero. [b]This represents the minimum value observed in studies where the feedstuff was offered to the animals. In case that the feedstuff was not offered (no intake) the analysis considered that the contribution of this feedstuff to the diet was 0 kg/kg DM. [c]Number of observations in the parentheses represent the number of data points with values higher than zero

[1]barley, oats; [2]white clover, alfalfa; [3]*Leucaena leucocephala*, white clover; [4]barley, maize, wheat, sorghum, pearl millet, triticale; [5]wheat; [6]wheat, rice; [7]linseed, rapeseed, sunflower, sesame, palm; [8]tapioca, wheat, maize, maize gluten, coconut, cottonseed

Table 4 Summary of correlation between DMI of individual feedstuffs and NUE and N partitioning to faeces, for diets with contrasting CP concentrations

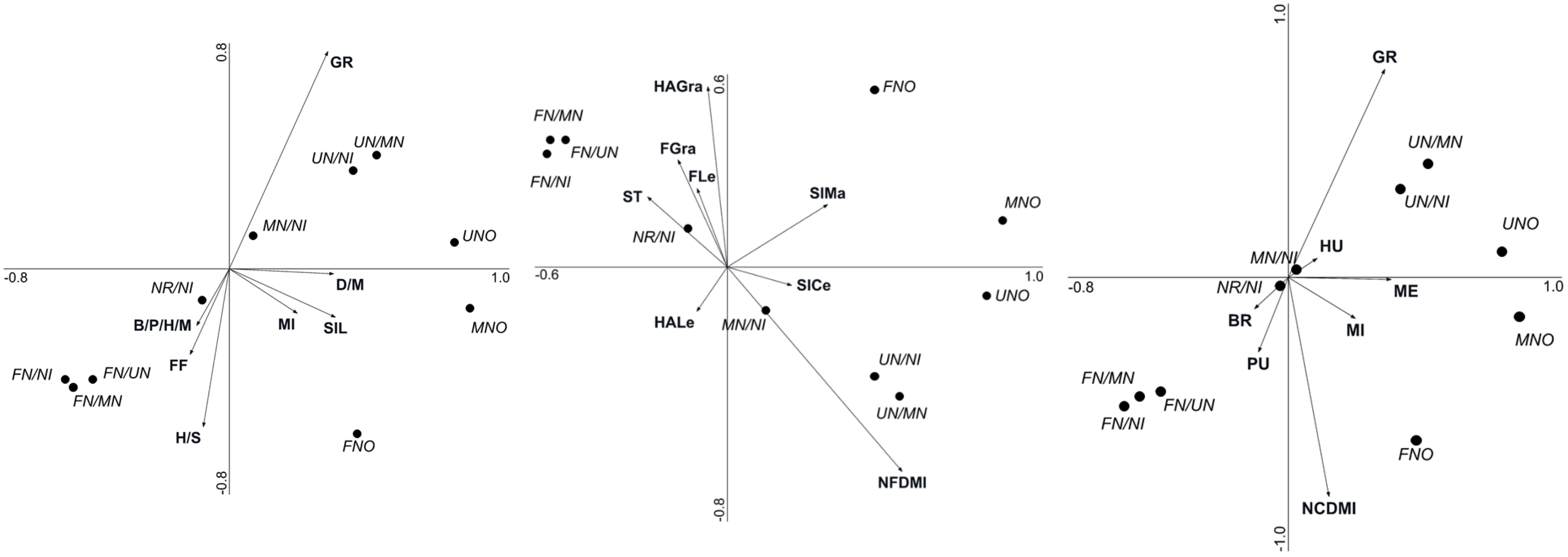
	Low CP sub-set		Medium CP sub-set		High CP sub-set	
Feedstuff groups	NUE	Npart	NUE	Npart	NUE	Npart
Hays/straw	+	+	•	+	+	•
Silages	•	•	-	•	-	•
Fresh-cut forages	+	+	+	•	•	•
Fibre-rich by-products	+	+	-	•	•	•
Grains	-	-	+	-	•	-
Protein-rich by-products	•	•	-	•	-	-
Additives	•	•	•	-	•	•

DMI = dry matter intake; NUE = nitrogen use efficiency; Npart = nitrogen partitioning to faeces; CP = crude protein; + = positive; - = negative; • = no clear relationship/not enough data

Highlights

1. Data from 59 studies was analysed to assess feeds impact on N use efficiency (NUE)
2. Protein-rich by-products adversely affected NUE in high crude protein (CP) diets
3. Adequate fibre inclusion was a key factor for better NUE in high CP diets
4. In low CP diets hays and straws improved NUE and N partitioning to faeces
5. Fibre-rich by-products were beneficial for N partitioning to faeces in low CP diets

Figure 1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(a) (b) (c)

Figure 2

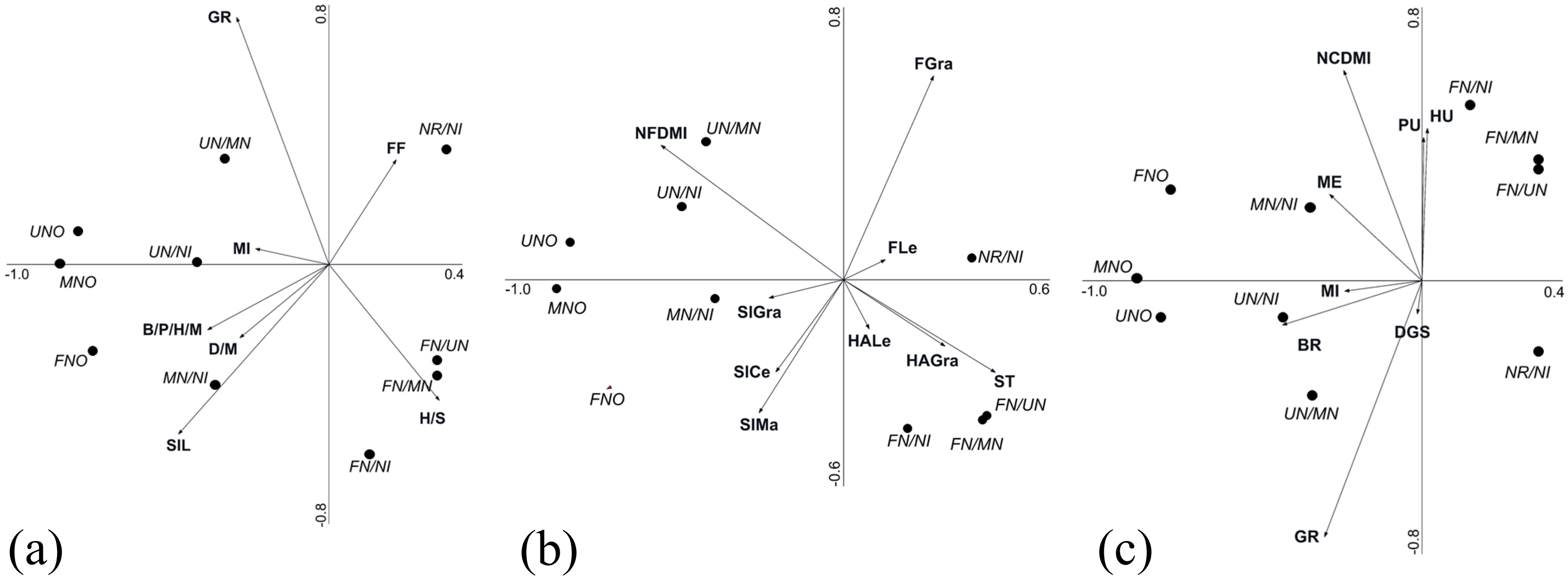
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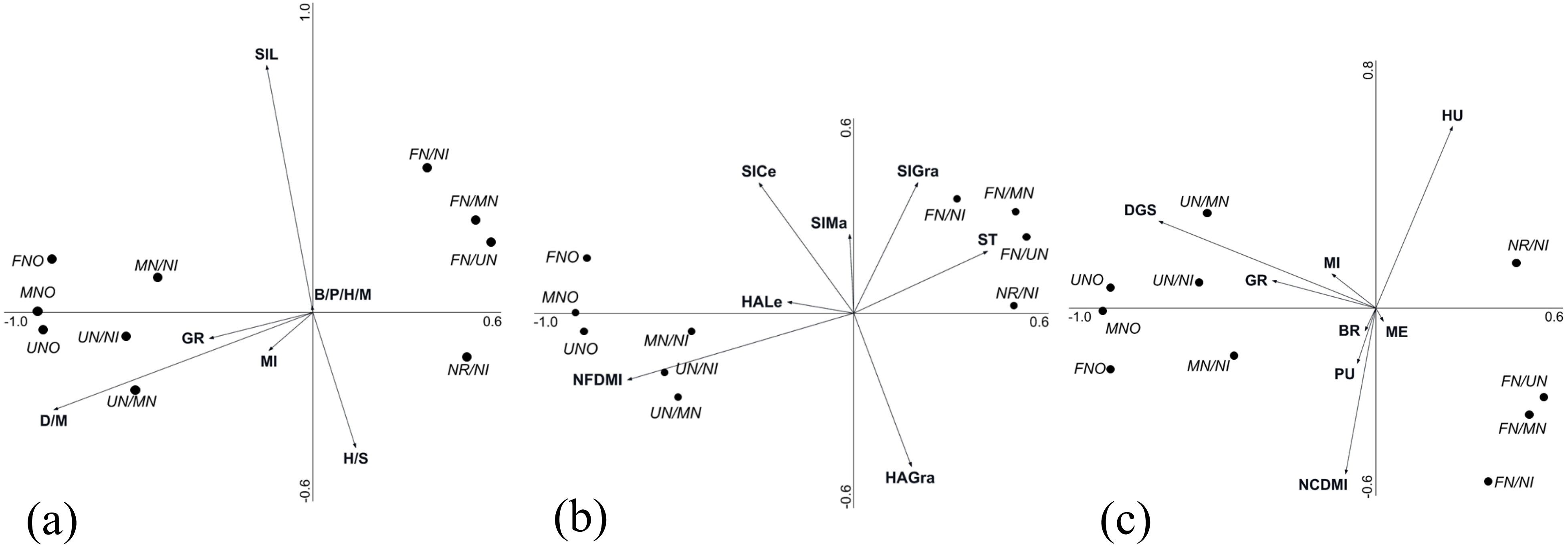
Figure 3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GR
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MNO
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ME
FNO
MN/NI
PU
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NCDMI
FN/NI
-0.6
(c)

Appendix

Table A1 Description of the redundancy analysis results for beef (n=73) fed diets with low CP concentration (47-120 g/kg DM)

	Feedstuff group	Explained variation	pseudo-F	P-value
Full diet	Distiller's grains/meals	14.3	11.5	0.002
	Silages	12.1	12.8	0.002
	Brans/pulps/hulls/mid.	10.4	15.6	0.002
	Grains	13.5	9.2	0.004
	Fresh-cut forages	6.5	7.8	0.004
	Hays/straws	7.1	6.2	0.012
	Miscellaneous	2.9	4.6	0.016
Forages	Non-forage DMI	25.0	19.7	0.002
	Grass hay	14.9	16.6	0.002
	Fresh legumes	9.7	13.2	0.002
	Maize silage	9.2	8.1	0.002
	Cereals silage	5.8	9.0	0.002
	Fresh grass	2.2	3.5	0.018
	Straws	1.6	2.6	0.072
	Legumes hay	0.1	0.2	0.826
Concentrates	Meals	19.6	22.4	0.002
	Non-concentrate DMI	16.9	14.1	0.002
	Brans	6.9	9.0	0.002
	Grains	13.5	9.2	0.004
	Hulls	2.9	4.3	0.018
	Miscellaneous	3.1	4.2	0.022
	Pulps	2.9	4.6	0.024

Table A2 Description of the redundancy analysis results for beef (n=90) fed diets with medium CP concentration (121-150 g/kg DM)

	Feedstuff group	Explained variation	pseudo-F	P-value
Full diet	Grains	19.3	22.0	0.002
	Brans/pulps/hulls/mid.	16.9	25.7	0.002
	Silages	16.5	14.6	0.002
	Distiller's grains/meals	7.6	13.6	0.002
	Hays/straws	4.3	8.5	0.002
	Fresh-cut forages	6.2	14.7	0.002
	Miscellaneous	0.3	0.6	0.554
Forages	Non-forage DMI	23.0	22.1	0.002
	Straws	12.9	14.7	0.002
	Cereals silage	10.2	20.4	0.002
	Maize silage	9.6	12.6	0.002
	Grass silage	9.2	14.4	0.002
	Grass hay	3.3	7.1	0.002
	Fresh grass	2.4	6.0	0.004
	Fresh legumes	3.0	7.2	0.008
	Legumes hay	1.5	3.9	0.030
Concentrates	Non-concentrate DMI	27.3	38.4	0.002
	Meals	13.5	25.3	0.002
	Brans	13.2	11.3	0.002
	Grains	8.3	7.7	0.002
	Hulls	3.4	7.5	0.004
	Pulps	3.4	6.9	0.004
	Distiller's grains	1.9	4.5	0.022
	Miscellaneous	0.3	0.7	0.454

Table A3 Description of the redundancy analysis results for beef (n=74) fed diets with high CP concentration (151-269 g/kg DM)

	Feedstuff group	Explained variation	pseudo-F	P-value
Full diet	Distiller's grains/meals	59.8	81.9	0.002
	Grains	6.8	12.0	0.002
	Hays/straws	6.2	13.5	0.002
	Brans/pulps/hulls/mid.	5.5	15.2	0.002
	Silage	3.1	4.6	0.030
	Miscellaneous	0.4	1.0	0.320
Forages	Non-forage DMI	44.6	44.2	0.002
	Straws	12.5	15.7	0.002
	Cereals silage	7.9	12.0	0.002
	Grass silage	5.8	12.7	0.002
	Maize silage	3.9	7.0	0.006
	Grass hay	2.7	4.3	0.040
	Legumes hay	0.8	1.7	0.208
Concentrates	Distiller's grains	42.2	40.2	0.002
	Meals	18.4	25.3	0.002
	Non-concentrate DMI	11.8	26.5	0.002
	Grains	4.3	6.5	0.002
	Pulps	2.1	5.4	0.016
	Hulls	0.8	2.1	0.132
	Miscellaneous	0.3	0.7	0.408

List of studies

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