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Graduate Student Literature Review: System, plant, and animal factors controlling dietary pasture inclusion and its impact on ration formulation for dairy cows

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ABSTRACT

Diet formulation in a pasture-based dairy system is a challenge as the quality and quantity of available pasture, which generally constitutes the base diet, is constantly changing. The objective of this paper is to cover a more in-depth review of the nutritional characteristics of pasture-based diets, identifying potential system, plant, and animal factors that condition pasture dietary inclusion in dairy cows. In practice, there is a wide diversity of pasture-based systems with predominant to minimal use of pasture requiring a more specific classification that potentially considers the amount and time of access to pasture, access to housing, length of grazing season, seasonality of calving, and level and method of supplementation. There are important differences in the nutritional quality between pasture species and even cultivars. However, under management practices that promote maintenance of pasture in a vegetative state as well as controlling the availability of pasture, it is possible to achieve high DM intakes (~2.9–3.4% of live weight) of pasture with moderate to high diet energy density, protein supply and digestibility. The amount of pasture to include in the diet will depend on several factors, such as the type of production system, the cost of supplementary feeds, and the farmer′s objective, but inclusions of ~40–50% of the diet seems to potentially reduce costs while apparently not limiting voluntary feed intake. Considering that there seems to be a continuum of intermediate management systems, a better understanding of the factors inherent to the feed ingredients used, as well as the use of nutrients by cows, and potential interactions between animal × system should be addressed in greater depth. This requires a meta-analysis approach, but given the diversity of the pasture-based system in practice, the existing information is highly fragmented. A clear definition of "subsystems" is necessary to direct the future research and development of mechanistic models.

Key words: dairy cow, nutrient limitation, pasture-based system, ration balancing

INTRODUCTION

In temperate regions, such as northwestern Europe, New-Zealand or the southern part of Latin America, grazed pasture can be the main feed for dairy cattle (Van Vuuren and Van den Pol-van Dasselaar, 2007). These grazing systems use different species of grasses and legumes, but perennial ryegrass (*Lolium perenne* L.) is generally the predominant species used due to its high forage production and nutritional quality for grazing ruminants (Leaver, 1985).

A pasture-based system (**PBS**) is generally associated with seasonal spring-calving, in which the main feed source during the year is the pasture directly consumed by grazing (Roche et al., 2017). This system favors the use of animals of smaller size and production than in confinement systems, but it promotes production per area unit and animal robustness (the capacity to handle disturbances as changes in feed supply and quality, while maintaining their performance, reproduction, survival, among others) (Roche et al., 2018). However, a PBS can vary from those for which pasture is the primary source of nutrients to systems in which pasture is only a supplemental forage for cattle primarily fed a partial mixed ration (**PMR**) (Washburn and Mullen, 2014).

It has been reported that different dairy genetic strains (i.e., genotypes within breed from different countries) can potentially perform differently under different feeding systems (Jacobs, 2014). This phenomenon is known as genotype × environment interaction, and the physiological processes controlling these differences still need to be investigated in depth, but this suggests that there are animals that are more compatible to be

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used in each production system (Dillon, 2007; Roche et al., 2017).

Previous work has addressed some nutritional limitations when formulating diets on PBS (Kolver, 2000; Kolver, 2003), but reviews addressing the recent advances in dairy cow nutrition, as well as its interaction with the different PBS variants and animal genotypes, are lacking. Thus, understanding the particularities of dietary pasture inclusion and their subsequent impact on specific nutrients supply and limitations, the cow digestive processes, and possible differences in the nutrient partitioning in cows selected under varying grazing conditions, is a challenge that must be elucidated to specify nutrient demands and improve predictive models. The objective of this paper is to cover a more in-depth review of the nutritional characteristics of pasture-based diets, identifying potential system, plant, and animal factors that condition pasture dietary inclusion in dairy cows.

DIVERSITY OF PASTURE-BASED DAIRY PRODUCTION SYSTEMS

Traditionally, dairy production systems are mainly classified according to the feeding source — primarily the use and access to pastures (restricted or unrestricted) —, with PBS associated with animals that gather their feed directly from the paddock (grazing) and that generally spend the night in the same place (outdoor housing or open paddock). On the other hand, non-pasture diets are associated with animals that are kept in special housing generally referred to as confinement (e.g., loose housing, tie stall, and free stall barns) where the feed is delivered directly to them usually as TMR diets (Mee and Boyle, 2020). The extent of the use and access to pasture and the type of housing results in a continuum of intermediate management systems, making it difficult to establish a clear boundary between systems. For example, grazing animals can have access to temporary confinement during the day for consumption of individual supplements or in the form of PMR, or seasonally (e.g., during winter or summer drought), while confined cows can be offered pasture through cut-and-carry (zero-grazing) (Van Vuuren and Van den Pol-van Dasselaar, 2007; Mee and Boyle, 2020).

The seasonality of calving is another relevant factor when classifying dairy production systems. This comprises 2 major categories; seasonal spring-calving, and non-seasonal calving systems (Boyle and Stockdale, 2011; Mayne et al., 2011). In the former, calvings are concentrated to coincide with the onset of rapid pasture growth in the spring to ensure 7 to 9 mo of a predominantly pasture-based diet during the period when cows have the highest nutrient demand. In non-seasonal calving systems, cows calve throughout the year, since environmental conditions and feed availability can be partially controlled by using partial or total confinement during the year (Mayne et al., 2011). Seasonal fall-calving is a less common system, but it is justified in countries where milk produced in winter has a higher price. This system requires greater supplementation of conserved forages during fall and winter, but it can result in greater milk production per lactation than spring-calving, explained by greater lactational persistency. A bi-seasonal calving system can be implemented when fall allows an important growth of pastures.

Traditionally, New Zealand has been associated with PBS where approximately 80% of the DMI of dairy cows comes from pasture (grazed pasture and pasture silage), 7% from other crops, and 13% from supplements (Roche et al., 2017). A similar situation occurs in Irish dairy systems where annual pasture DMI is also 80%, with 18% from concentrates, and 2% from alternative forages (whole crop cereal silages, corn silage, and fodder beet; O′Brien et al., 2018). Many other countries in Europe, and North and South America also include pasture in the diets of their dairy cows, but in lower inclusion rates than New Zealand or Irish dairy systems, because the grazing season is shorter (e.g., less than 6 mo due to adverse climatic conditions, requiring winter housing), or due to annual variability in pasture quality together with higher milk production of the cattle used, requiring the additional use of supplements (van den Pol-van Dasselaar et al., 2020; Morales et al., 2021). Australia, Ireland, United Kingdom, and New Zealand, between other countries, have defined different feeding systems based on the timing, purpose and amount of grazing, housing, amount of feed purchased/cow, and supplementary feed used (García and Fulkerson, 2005; March et al., 2014; Ramsbottom et al., 2015). For example, Wales and Kolver (2017) described 5 different feeding systems in Australia and New Zealand, ranging from predominantly grazing and little use of supplementary feed to solely TMR rations. For a more precise characterization of productive systems, technical, economic, and social aspects can also be considered. Different efforts have been made, especially in developing countries, to categorize groups of producers according to similar realities to direct public policies as well as identifying particular technology needs. Important differences in the level of modernization among farms, with a wide margin for improvement in indicators, such as individual milk production and milk production per unit of area, stocking rate, labor efficiency, herd fertility, and milk quality have been identified (Gonzalez-Mejia et al., 2018). Thus, integrative key performance indicators are required to properly account for the diversity in dairy systems and define cluster-specific improvement strategies.

PARTICULARITIES OF PASTURE INCLUSION ON COWS DIETS

Seasonal PBS are usually associated with multiple economic benefits such as ease of pasture establishment, lower infrastructure requirements, low operating expenses per kilogram of milk, potential access to high-value markets because of perceived animal welfare benefits, as well as potential improvements on the nutritional quality of dairy products, and farm sustainability (Roche et al., 2017; Moscovici Joubran et al., 2021). However, in most of the countries that used pasture-based diets there is a wide variability in the feed-base throughout the year, so pasture intake is not necessarily predominant in some seasons because of environmental conditions. Variability of pasture supply have increased in recent years due to changing climatic conditions including extended winters (delaying the growth of pastures in early spring) and summer droughts, both requiring an increase in the delivery of supplementary feeds (Jacobs, 2014; Beltrán et al., 2022). Other factors that contribute to the use of supplements are exploiting the increasing genetic potential of cows, increasing out-of-season milk supply, or extending lactation, and the availability of relatively cheaper agroindustry byproducts (Jacobs, 2014). Although the factors that affect pasture intake, as well as the limitations of some macronutrients (mainly carbohydrates) on intake and energy supply, have been discussed in the past (Kolver, 2000; Kolver, 2003), the previous discussions were restricted to pasture as a predominant or sole feed rather than as a variable component of the overall diet.

Dry matter intake

Factors influencing the pasture DMI have been extensively discussed in the past (Bargo et al., 2003; Dillon, 2007; Taweel, 2007). These factors have been classified as environmental, plant factors, animal factors, and management. Environmental factors refer to climate and soil type, which condition seasonality of pasture growth, directly affecting its availability. The wide variability in annual growth rates —almost zero in winter or dry summers but exceeding 100 kg DM ha/d in spring (Ferris, 2007) — sets the first challenge; ensuring an adequate supply of quality pasture throughout the year. Strictly seasonal grazing systems have been able to deal with this problem, by using animals with low individual production (generally not exceeding 5,000 kg of milk per lactation), therefore with lower nutritional requirements which can be covered mostly with the available pasture, but favoring production per hectare. In addition, this system requires strict reproductive management, so that the cows calve every 365 d and in a short time frame (around 60 d) to avoid the dispersion of calvings and thus align the period of highest nutrient demand with the greatest pasture availability (Roche et al., 2017).

Some plant factors that maximize intake are sward structure and composition. Many pasture species are used for grazing by dairy cattle in temperate PBS, with perennial ryegrass the dominant grass species and white clover (*Trifolium repens* L.) the dominant legume. Traditionally, the use of mixed pastures of perennial ryegrass with white clover have been recommended over the use of ryegrass monocultures due to the increase in DMI and milk production, while reducing the need for synthetic N fertilization due to symbiotic nitrogen fixation (Dineen et al., 2018). However, due to the difficulty of maintaining the necessary proportions of white clover in the pasture, as well as the constant genetic improvement in ryegrass, many farmers have adopted ryegrass monoculture and synthetic N chemical fertilization. Genetic selection programs in perennial ryegrass have significantly increased annual pasture production and persistency in different seasons, nutritional quality, as well as resistance to pests and diseases (Gilliland et al., 2021). High sugar cultivars have been suggested as an option to increase DMI and milk production due their higher palatability and energy supply. However, due to a small increased in water soluble carbohydrates (**WSC**) in practice (~30 g/kg of DM), it has not translated into significant changes in grazing behavior, ruminal function and animal performance. Similarly, cultivars with higher OM digestibility and ruminal fiber degradation have been proposed, but the difficulty of the measurements as well as the lack of natural heritable variation in these traits have limited selection (Taweel, 2007). The chemical composition of commonly use pasture grasses in a vegetative state is relatively similar between species, however, the high seasonality (i.e., seed head production) in poorly selected species causes them to rapidly lignify and decrease their digestibility with respect to ryegrass. Increases in DMI using multi-species pastures have been attributed to fast digestion of the soluble fraction of legumes, and a higher rate of particle breakdown and passage through the rumen compared with grasses (Niderkorn and Baumont, 2009). Although there is plenty of information on pasture species, it has mainly focused on some species that are traditionally used. It is suggested that a more integrative approach, including traditional and non-traditional species, plant and phytochemical diversity on animal nutrition, welfare, health, and environmental impact could help to develop more sustainable and resilient systems (Distel et al., 2020).

Animal factors that drive intake capacity are BW, potential milk production, BCS, stage of lactation, state of gestation, and age (Peyraud and Delagarde, 2013). The comparison of a pasture-only diet versus TMR carried out by Kolver and Muller (1998) is generally referenced to demonstrate the difference in potential intakes among production systems. In that study, recorded DMI were 19.0 and 23.4 kg/d, and milk production were 29.6 and 44.1 kg/d, when comparing pasture-only diet versus TMR, respectively. Those values of intake and milk production on pasture-only diets, however, can only be achieved for a short period of the grazing season. Thus, considering BCS losses and loss of pasture quality, theoretical average milk production based on pasture diets is ~20 kg/d (Ferris, 2007).

Voluntary DMI can also be affected by the water content of pasture, which ranges from 70 to 88% (Estrada et al., 2004). Values around 18% DM are observed in spring pasture, which partially explains the higher intake of around 10% reported when compared with fall pastures (~14% DM) under the same management (Dillon, 2007). No effect of external water on DMI been found (Estrada et al., 2004).

Different pasture management strategies have been developed to improve the allocation of dense young and leafy pasture to cows, stimulate DMI and improve the efficiency of pasture utilization. Among the main practices are, pasture allowance (**PA**) and time of pasture allocation. The former is defined as the amount of pasture offered to the cow during one grazing day (usually measured over ground level) and expressed in kg DM/cow per day, whereas the latter corresponds to the time within a day at which the new pasture (usually grazing strip) is allocated. Other practices that can affect pasture quality and availability, and therefore modify pasture DMI, are stocking rate, feeding frequency, time of cutting (especially in zero-grazing feeding systems), and rate of fertilization (Taweel, 2007; Roche et al., 2017).

Energy

Kolver (2003) reported that under good pasture management conditions, the pasture intake achieved by a cow of medium size and production (i.e., ~550 kg BW and producing 25 kg milk/d) is sufficient to cover its requirements but in larger cows with greater production, energy would be the first limiting factor of the diet. The above was calculated using the Cornell Net Carbohydrate and Protein System model (**CNCPS**), considering a daily energy requirement of almost 50 Mcal/d of ME and a pasture DMI of 3.15% BW. Thus, the average ME concentration of the diet should be ~2.86 Mcal/kg DM. Higher milk production than previously reported can be achieved in a short period of spring grazing, where the pasture DMI can potentially reach 3.5% of BW (~19 kg pasture DM/cow/d), which would explain the almost 30 kg/d of milk production recorded by Kolver and Muller (1998). However, to sustain milk production over 35 kg/d, it is necessary to exceed 60 Mcal of ME supply, and even under a maximum pasture DMI scenario, energy concentrations of over 3.0 Mcal/kg DM of ME would be required (Kolver, 2003).

Fresh ryegrass can reach the target values of ~2.86 Mcal/kg DM during a few months in spring, but then the energy density quickly declines to values of ~2.40 Mcal/kg DM in summer. Energy values close to those of spring can also be recorded in fall, depending on pasture management (e.g., presence of dead material from summer decreases energy value), and even during winter in places where it does not snow (Fulkerson et al., 1998). High ME ryegrass cultivars have been developed in recent years, by increasing the fatty acid (**FA**) content. An increase of at least 0.25 Mcal of gross energy (**GE**)/kg DM has been suggested as the target to have a relevant impact on energy intake, however no more than +0.8–1.4% of increased FA on a DM basis has been observed, translating to increases of +0.08–0.13 Mcal of GE/kg DM (Beechey-Gradwell, 2021).

Energy density of pasture is determined by the low ether extract content (i.e., ~3% on a DM basis) and the low proportion of non-fiber carbohydrates (**NFC**). Starch content of ryegrass is low averaging 1.5% on a DM basis, while WSC ranges from 5 to 25% DM, according to plant phenological state and season (Fulkerson and Donaghy, 2001). Spring ryegrass pasture generally averages ~15% WSC on a DM basis, while fall values are around 5–10% DM (Beltrán et al., 2022). It has been suggested that high sugar ryegrass cultivars (generally ranging between 15 and 25% WSC on a DM basis) could increase milk production because of a greater DMI (due to higher palatability), and a more balanced chemical pasture composition (lower CP and NDF content) improving ruminal microbial production and digestibility, but no positive effects on DMI, milk production, and milk composition have been found (Taweel, 2007). Neutral detergent-soluble fiber (**NDSF**) generally represents a small fraction in pastures, ranging from 5 to 15% DM, but it provides a proportion of the energy supply (Morales et al., 2021). It contains pectins, β-glucans, galactans, and other organic compounds, but because it is generally calculated by difference, it is subject to large analytical measurement error (Hall, 2014). Determination of sugar content is one of the main sources of error when estimating the NDSF content, being WSC preferable instead of ethanol-soluble carbohydrate (**ESC**) determination, since the former completely extracts the fructans, avoiding overestimation on NDSF content. Dineen et al. (2020b) reported values of 12.4 and 21.6% on a DM basis using WSC or ESC determination, respectively, suggesting that a standard procedure should be used to properly compare pastures. Pasture diets generally average around 20% NFC but values can be as low as 10% in some seasons, so the main energy supply in pasture-based diets generally comes from the degradation of structural carbohydrates (Morales et al., 2021).

Protein

The recommended CP content of dairy cows diets varies between 16 and 17.5% on a DM basis, for cows producing around 30 and 50 kg/d of milk, respectively (NASEM, 2021). However, pastures have a variable CP content, ranging from 13 to 27% on a DM basis depending on the pasture species, phenological stage, fertilization, and season (Keim et al., 2013). Because of this, predominantly pasture-based diets generally contain excessive CP (~18–21%), a problem which is exacerbated when offered to medium production cows (Morales et al., 2021). The high CP content of ryegrass is partially a consequence of genetic selection, particularly by reducing the fiber content but increasing the cellular content, which has generated a forage with high digestibility but when used as the only feed source (especially during spring), it generally exceeds the nutritional protein requirements of cattle (Gilliland et al., 2021). This results in low nitrogen use efficiency (**NUE**) values in strict pasture-base diets, which are generally less than 25%, while values between 25 and 30% can be reached with pasture plus supplements (depending on the type and level of supplementation), far from values greater than 40% achieved in some systems using TMR diets (Beltrán et al., 2022).

Although the use of CP constitutes a general guide when formulating diets, the main goal in protein nutrition is to characterize feeds for their rumen-degradable protein (**RDP**) and rumen-undegradable protein (**RUP**) fractions, predict the conversion of RDP into ruminal microbial protein (**MCP**), and determine the metabolizable protein (**MP**) and metabolizable AA use efficiencies (NASEM, 2021). Unfortunately, research on these topics is less developed for PBS because its use is less frequent worldwide, but mainly because of the high variation in the quantity and quality of the species used in PBS, as well as the additional difficulty in determining feed intake.

Practical recommendations for lactating cows are 10% of RDP and ~6–7.5% of RUP on a DM basis, the latter depending on milk production (NASEM, 2021). This translates to 38–43% of RUP on a CP basis. However, protein degradation kinetics for different pasture species indicates that RDP content varies between 72 and 90% of CP depending on the season (Keim et al., 2013). Thus, ryegrass containing 25% CP with 85% RDP, will contain only 3.75% RUP on a DM basis, which is limiting for dairy cows despite the excessive CP content. An additional limitation when establishing N supply is that a single hydrolysis period (21–24 h) is routinely used to determine the AA content in a feed sample. However, this may result in incomplete recovery for some AA, so correction factors for each AA and even across different types of proteins could be used to appropriately estimate the true AA supply to dairy cows (Lapierre et al., 2019). Dineen et al. (2020b) reported that Ile and Val concentrations were underestimated when using a single 21-h HCl hydrolysis, indicating that multiple-hydrolysis time procedures are required to predict the true AA concentration of ryegrass.

Ruminal degradation of dietary CP is an important factor influencing ruminal fermentation and AA supply to dairy cattle. RDP supplies the majority of N required by ruminal microorganisms and this is composed mainly of peptides, free AA, and urea. Ruminally synthesized MCP typically supplies most of the AA passing to the small intestine (~60% of N flow to duodenum), with its synthesis affected by different factors including DMI, degradation rate (**K_d**) of diet components in the rumen, and passage rate (**Kp**) of digesta from the rumen (Kolver, 2003; NASEM, 2021). A large dependence on microbial N supply to the total flow of NAN (~82% of omasal N flow) has been reported for cows consuming fresh ryegrass-based diets, so further quantification of the specific AA contributing to this NAN flow is required (Dineen et al., 2020a). Traditionally, nutrition models use CP ruminal degradation kinetics to calculate the degradation of each individual AA (assuming that they are all degraded at the same rate in the rumen) (Van Duinkerken et al., 2011). This added to the high ruminal degradation of CP in pastures, could result in errors when estimating the degradation of some AA, potentially overestimating the supply of some AA in the diet. Protein degradation rate can be highly affected by pasture cultivar, maturity and regrowth interval, averaging 23%/h in ryegrass (Sun et al., 2010). This high rate, together with smaller Kp values derived for forages compared with concentrates (4.87 versus 5.28%/h, respectively), explain the high protein degradation of pastures (Hanigan et al., 2021).

Pastures are also characterized by having a high content of soluble protein (**SP**), which ranges from 30 to 77% in ryegrass (Sun et al., 2010; Keim et al., 2013).

Although SP is readily available for use by ruminal microorganisms, due to the high content in pastures, part of it can also escape into the intestine, providing some free AA. Values of 8% have been reported for ruminal escape of SP but this may vary for each subfraction (Volden et al., 2002). This suggests that diets excessive in N could increase the ruminal escape of AA and therefore increase MP —partially compensating for the limited MCP supply—, however, it should be considered that this will increase the blood and milk urea concentrations. This has been associated with decreased fertility, predisposition to metabolic diseases, and negative environmental impact (Raboisson et al., 2017).

It has been proposed that the synchronous availability of protein and energy in the rumen should allow a more efficient use of nutrients, thus improving the production of microbial products, increasing the supply of nutrients to the animal and potentially improving animal production performance (Sinclair et al., 1993; Hall and Huntington, 2008). Although this theory is attractive as it considers the effect of diet within the day and the interaction of the different nutrients and subfractions, no clear evidence on ruminal nutrients asynchrony has been found in practice (Hall and Huntington, 2008). A more evident asynchrony effect would be expected under the feeding patterns of a PBS, where the animal is ingesting pasture with highly degradable protein and low NFC supply for several hours a day, and supplementary feeds (generally high starch grains) are only offered at milking times (Kolver et al., 1998a). However, potential negative effects in microbial protein production caused by asynchrony of ruminal energy and N supply may be offset by the recycling of urea N, probably not affecting the whole animal N status (Hall and Huntington, 2008).

It was initially proposed by Kolver and Muller (1998) that pasture-based diets provide enough MP to sustain milk production of about 38 kg/d. However, a later study providing ad libitum or restricted pasture intake (75% of ad libitum intake) to cows producing only 21.5 and 20.9 kg milk/d, respectively, showed that several AA (arginine, methionine, and histidine) were limiting when determining intestinal supply and the apparent order of AA limiting production changed to methionine, lysine, and leucine, when intake was restricted (Kolver et al., 1999). Pacheco et al. (2003) determined the AA flux to mammary glands using the same animals as Kolver et al. (1999), and found that isoleucine, leucine, valine and lysine were the essential AA with the greatest partitioning toward the mammary gland, which could indicate a potentially limiting effect on milk protein synthesis, and the limiting of histidine was also suggested. The apparent inconsistency in order of AA limitation between studies may reflect differences in postabsorptive metabolism between individual AA (Kolver et al., 1999), which is in agreement with recent studies that contradict the single limiting AA theory, proposing that the animal response should be seen in terms of a response surface, explained by multiple combinations of available AA (NASEM, 2021; Hanigan, 2022). It is important to note that the studies of Kolver et al. (1999) and Pacheco et al. (2003), did not calculate the intestinal absorption of each AA and only estimated them using previous coefficients calculated for other feeds such as soybean (Stern et al., 1985). An in vivo stable isotope-based approach to assess the absorbed AA from feeds was proposed by Estes et al. (2018) and it was extended by Huang et al. (2021) to characterize the AA origin (MCP or from RUP). Huhtanen and Ahvenjärvi (2022) in a recent review concluded that there is scope for improving predictions of MP supply in cows diets, indicating that RUP is often overestimated compared with MCP, which can be related to underestimation of microbial MP due to underestimation of the contribution of protozoa to the protein flow. This is in agreement with Dineen et al. (2020a) who reported that protozoa NAN corresponded to 24% of microbial NAN flow from a ryegrass-based diet. Corrected and detailed information on the nitrogenous fraction of pastures, together with a comprehensive and standard methodology (e.g., the stable isotope-based approach), are required to properly assess the intestinal AA absorption from pastures, and in the future, advance with accurate data to the study of post-absorptive metabolism.

Fiber

Pregastric fermentation allows ruminants to extract much more energy from roughages than is possible by mammalian gut enzymes alone, but this evolutionary adaptation also makes them require a certain minimum amount of fiber to maintain proper rumen function. Thus, dietary fiber content can modify voluntary feed intake (mainly associated with reticulum-rumen distention), mastication and subsequent saliva production (an important ruminal buffer), fermentation and ruminal motility (affected by particle buoyancy and ruminal mat characteristics), and can even modify milk fat content (Allen, 1996; Westwood et al., 2003). Current recommendations on dietary NDF inclusion ranges between 25 and 33% on a DM basis, depending on the fiber source and dietary starch content. For example, for a diet containing 30% starch, a 25% NDF is recommended and 75% of this (19% on a DM basis) should come from forages (NASEM, 2021). The latter refers to the dietary forage NDF (**fNDF**), which recommendation ranges between 17 and 27% on a DM basis. This concept was proposed to better account for differences among forages, ruminal fill potential, and dietary risk factors compared with the use of just dietary NDF (NASEM, 2021).

Further concepts have been proposed to represent not only the fiber source but also its physical characteristics. Thus, effective NDF (**eNDF**) is defined as the effectiveness of dietary fiber to maintain milkfat percentage, values for pastures ranges between 0.17 and 0.78 (Kolver and de Veth, 2002). Physically effective NDF (**peNDF**) is the fraction of NDF that stimulates chewing activity and contributes to the floating mat of large particles in the rumen (Mertens, 1997; Westwood et al., 2003). It is important to note that the concepts and their respective recommendations mentioned above have been developed and validated mainly using information from TMR diets. However, when the diets have not been previously chopped and mixed —as is the case of pasture-based diets —, it makes practical estimations of eNDF or peNDF difficult (Westwood et al., 2003). This is associated with the fact that particle size of fresh pastures varies significantly before and after chewing, the large particles of leaf and stems are ruminally retained at different times (16.1 and 20.2 h, respectively), and that some large particles can escape to the rumen and be recovered in feces (Poppi et al., 1981; Kolver et al., 1998b). So, there is a lack of a comprehensive and standard validated method applicable to all types of diet, limiting the practical application of these concepts. Despite this, important advances have been made to better understand the NDF fraction of feeds, which does not represent a uniform fraction through rumen fermentation (Raffrenato et al., 2018). Among these, Mertens (2002) proposed a methodology to refine the determination of the NDF fraction using α-amylase and sodium sulfite and correcting for ash contamination (**aNDFom**), Raffrenato et al. (2018) developed an in vitro methodology to determine rumen undigested aNDFom (**uNDF**). These improved methodologies have resulted in a better description of the potentially digestible aNDFom fraction (Raffrenato et al., 2019). These concepts have also led to new practical recommendations, such as that the maximum uNDF intake should be 0.39–0.48% expressed as %BW (Cotanch et al., 2014), or that peuNDF dietary content (a new concept combining peNDF and uNDF) seems to better relate to DMI and energy-corrected milk (Grant et al., 2020), but they have not been tested in pasture-based diets.

Interestingly, most of the available fiber recommendations in the literature do not appear to be directly applicable to pasture-based diets, as they were derived for TMR diets (e.g., NDF and fNDF content of pasture-based diets generally exceeds the values mentioned above). Kolver (2000) recommended a minimum supply of 35% NDF in cows consuming good quality pasture diets and 17% eNDF on a DM basis, however, due to the wide variation in the NDF content of pastures, as well as in the eNDF value, the minimum dietary inclusion of fiber in practice is still unknown. It has been suggested that grazing cows can tolerate pH values close to 5.8 before OM fermentation and fiber digestibility are affected, which suggests that the required fiber content would be lower than TMR diets (de Veth and Kolver, 2001). Despite this, there are reports of subclinical acidosis in dairy herds during late winter and early spring, when pasture is fast growing and contains high concentrations of water and low concentrations of fiber (Westwood et al., 2003). A wide range for NDF ruminal degradation has been reported in the literature, between 5 and 20%/h depending on pasture species, phenological stage, cultivar, plant part, season, fertilization and pasture management, and this can also be affected by the measurement techniques used (Sun et al., 2010; Keim et al., 2013).

An upper limit for fiber recommendations is also difficult to determine. This could be associated with a potential reduction in voluntary feed intake as well as a reduction in the dietary energy supply (Allen, 1996; Kolver, 2003). NDF generally ferments and passes from the reticulorumen more slowly than other dietary constituents, because it has a greater filling effect over time than non-fibrous feed components (Allen, 1996). Kolver (2003) in a sensitivity analysis of ryegrass characteristics using the CNCPS model, reported that an increase of 10% in NDF K_d (from 13 to 14.3%/h) improved milk production allowed by dietary ME and MP supply by 0.5 and 0.7 kg/d, respectively. Temperate pasture species can have NDF values of around 30–50% (Keim et al., 2013), which explains the wide range of pasture voluntary DMI observed in the different seasons (10–20 kg DM/d) (Morales et al., 2021). Kolver (2003) also considered ryegrass chemical composition in their sensitivity analysis, showing that a 10% increase in NDF (from 36 to 46% DM) reduced milk production allowed by dietary ME supply by 0.7 kg/d, which was associated with model predictions of a lower non-structural carbohydrate content and reduced synthesis of MCP, which also resulted in a lower AA-allowable milk production. Considering that NDF corresponds to the largest chemical fraction in pastures and its degradation generally provides the main energy contribution in pasture-based diets, it is essential to define specific limits for its dietary inclusion (considering the new available methodologies and concepts), as well as to characterize in greater depth the different factors that modify the pasture content and ruminal degradation of fiber in the different pasture species of interest.

CONSIDERATIONS ON THE INCLUSION OF PASTURE IN THE DIET

Several factors can potentially limit the amount of pasture available including climatic factors (seasons, droughts, rainfall and floods, frost and snow, temperature, relative humidity, day length, sunlight, etc.), edaphic factors (fertility, organic matter, drainage, among others) and biotic factors (pests, parasites, diseases, herbivore species, etc.) (Zhao et al., 2020; Gilliland et al., 2021). Given the wide variety of factors that limit the availability of pastures during the year, it is clear that this is not enough to reach the expected voluntary intake for much of the year (Dillon, 2007). A PBS can vary from those for which pasture is used as the primary source of nutrients to systems in which pasture is only used as supplemental forage for cattle primarily fed at PMR. Due to this, factors such as supplementation level, calving seasonality, length of pasture growing season, and animal genotype, must be considered to determine the amount of feed needed and if it can be supplied by the available pasture at a given time (Washburn and Mullen, 2014).

Supplementation is the provision of additional nutrients (mainly concentrate feeds, but forages are also offered) to achieve a target milk production and/or composition (Jacobs, 2014). Positive effects on animal performance are generally observed with supplementation, but their response is variable depending on the amount of supplement offered and type of feed, as well as PA and intake, and the nutritive characteristics of pasture (Bargo et al., 2003; Jacobs, 2014). A key factor behind this response in the substitution rate (**SR**), which in PBS, is the reduction in pasture DMI/kg DM of supplement consumed (Jacobs, 2014). Reported SR ranged between 0.11 and 1.0 kg pasture/kg for concentrate, and 0.84–1.02 kg pasture/kg for pasture silage (Bargo et al., 2003). This reduction in pasture DMI has been associated with the physical limitation of ruminal filling (explaining the greater replacement generated by high-fiber feeds), changes in feeding behavior (the supply of energy feeds reduces grazing activity), and an alteration of the ruminal environment (concentrate supply can potentially reduce ruminal pH affecting fiber degradation) (Bargo et al., 2003; Jacobs, 2014).

NDF intake has been described as a good predictor of potential DMI intake, specifically values of 1.2 ± 0.1% of daily NDF intake expressed as %BW have been suggested using TMR diets (Mertens, 1987). Kolver and Muller (1998) reported values of 1.47 and 1.21% of NDF intake as %BW for cows consuming 19 kg DM of pasture and 23.4 kg DM TMR, respectively. Also, they reported increases in DMI from 3.39 to 3.93% (expressed as %BW) when offering unrestricted pasture or TMR diet, respectively. Similar increases in DMI were observed when comparing grazing cows versus offering a PMR or TMR (3.58, 3.99, and 4.15% of BW, respectively (Bargo et al., 2002)) or when offering a low or high PA to unsupplemented versus concentrate supplemented cows (2.91 and 3.37% versus 3.85 and 3.97% of BW, respectively (Bargo et al., 2003)). Auldist et al. (2017) tested different combinations of PA (15, 25 or 40 kg DM/cow day, measured at ground level) and supplementation (6, 10, 12 or 14 kg DM/cow day). They found that higher PA partially increased DMI but decreased pasture utilization, and there was no difference in milk production among PA levels, while increasing PMR supplementation increased total DMI but pasture substitution was observed, and milk production was only significantly different at the higher PMR level. Similarly, a moderate increase in milk production (1.08 kg milk/kg concentrate) and a SR of 0.49 kg pasture/kg concentrate were reported by Bargo et al. (2004), when offering 9 kg corn-based concentrate to cows grazing an orchardgrass/bromegrass pasture. The aforementioned studies suggest that cows can consume high values of NDF from pasture-based diets, roughly 1.3–1.8% of BW per day, but these values are importantly affected by PA and pasture quality, translating into DMI values of 2.9–3.4% of BW. Supplementation with concentrates, PMR, or TMR can reach DMI values close to 4% BW and even higher, but the milk production response to supplementation is moderate and decreasing (Bargo et al., 2002; Auldist et al., 2017). It has been suggested that in PBS, for supplementary feeding to be profitable, milk-to-feed price ratio must be approximately 1.1, 1.5, and 4.5 when post-grazing residuals are ~20, 35, or 50 mm above ground level (Roche et al., 2017). However, where DMI is sought to be optimized, it seems that pasture inclusions of ~10–14 kg DM of high-quality pasture would allow "leaving space" for supplements and reaching intakes similar to those observed in TMR diets (Auldist et al., 2017).

Under restricted grazing conditions (limited time or amount of pasture), especially in seasons other than spring, the inclusion of a smaller portion of pasture in the diet (<10 kg DM/d), has also been shown to have a positive impact. Specifically, by replacing more costly supplementary feeds but maintaining production levels, given its high digestibility (~85% DM in the vegetative stage) compared with other forages.

The amount of pasture to include in the diet will depend on several factors, such as the type of production system, the cost of supplementary feeds, and the farmer's objective, but inclusions of ~40–50% of the diet seems to potentially reduce costs while apparently not limiting voluntary feed intake

Considering that pasture is the predominant feed in a PBS, it is essential to clearly define what would be the ideal inclusion of pasture in the cows′ diet. This requires a meta-analysis approach, which includes factors such as type of production system, cow performance, total DMI, total fiber intake, cost of pasture and supplementary feeds, indicators of farm profitability, farmer′s goals, among others.

CONSIDERATIONS OF ANIMAL GENOTYPE ON NUTRITION

In previous sections, the wide diversity that exists in PBS has been discussed, as well as the factors that can modify the quality and quantity of available pasture and its intake by cows, together with their subsequent productive response. However, there is a growing amount of information supporting differences in productive responses, use of body reserves, reproductive, longevity, and health traits among and within dairy breeds, strains and even selection lines (Washburn and Mullen, 2014; Roche et al., 2017).

The development of a "specialist grazing cow" has been promoted mainly for seasonal grazing systems and with low supplementation, suggesting a robust, autonomous and "easy care" cow (Roche et al., 2017; Roche et al., 2018). Attributes of such an animal include the capability to achieve large intakes of forage (covering their nutritional requirements almost entirely from grazed pastures), producing reasonable quantities of milk (i.e., 5500–7500 kg/cow per lactation and 350–500 kg/cow of milk fat and protein per lactation), capable of walking long distances (low risk of presenting lameness), high fertility (becoming pregnant within ~80 d of calving), and longevity (high permanence in the herd and good health) (Roche et al., 2018).

Studies comparing different Holstein Friesian strains (New Zealand (**NZ-HF**) and North American (**NA-HF**)), with similar genetic merit for milk traits, have shown that under grazing conditions NZ-HF cows can eat a greater amount of pasture and produce more milk solids expressed as a percentage of their BW, and also had a lower mobilization of body reserves and better fertility than NA-HF (Baudracco et al., 2010). However, when a TMR diet was offered, NA-HF cows had a higher DMI and milk production, while the NZ-HF had a high SR, limited their DMI intake (Dillon, 2007; Baudracco et al., 2010). The existence of strain × environment interactions suggests that the most appropriate strain of cow will differ depending on the particular production system under which it is managed. Therefore, breeding plans should consider individualized system-level breeding objectives (Baudracco et al., 2010; Roche et al., 2017). The existence of heterosis effects adds an extra complexity when conducting genetic evaluations, so the potential specific breed and heterosis effects should be considered when estimating breeding values (Penasa et al., 2010).

From a nutritional standpoint, existing evidence suggests that cow genotype plays a role in determining the partitioning of nutrients, and consequently nutritional models should consider this variable to extend their predictions to different production systems and genotypes (Friggens et al., 2013). There is limited information on genetic parameters related to nutrition from grazing dairy cows mainly due to the difficulty of determining DMI. However, reported heritability for DMI (0.10–0.30), energy balance (0.06–0.29), and apparent total-tract DM digestibility (0.08–0.45) across lactations indicate that genetic variation exists and that genetic improvement is possible (Berry et al., 2007). Several factors have been suggested to explain the differences in energy use efficiency among high and low genetic merit cows, as changes in mobilization of body reserves to support production, preferential partitioning of ME intake between milk and body tissue, change in energy utilization in the rumen, change in the efficiency of utilization of ME for milk production, and differences in maintenance ME requirements. Similarly, differences in NUE have been associated to partitioning of surplus N away from urine to feces and MP efficiency (i.e., milk protein output: MP intake) (Cheng et al., 2014). Friggens et al. (2013) concluded that to properly represent the "animal′s priorities" in the use of nutrients, an explicit recognition of the role of both the genotype and the expression of this genotype through time on nutrient partitioning is required. This considers an explicit representation of how genetic factors alter the partition of nutrients according to the different physiological state, as well as the animal homeostatic capacity. This topic has been partially explored in mechanistic research models (Friggens et al., 2013), however, additional information is required, especially in PBS in which various breeds and strains are used, to develop models applicable to the field.

CONCLUSIONS

Despite the wide variation in the inclusion of pasture in cows′ diets, farms are generally grouped under the same heading of pasture-based system. A more specific and standard classification of PBS is required to properly establish recommendations on the amount of dietary pasture inclusion; considering factors as the amount and time of access to pasture, housing, length of grazing season, seasonality of calving, and quantity and method of supplementation, between others. Pasture-based diets are assumed to consist predominantly of pasture, however, in practice, this is not really true throughout the year. Dietary pasture inclusion significantly changes due to the variability of pasture availability and nutritional quality as well as the impact of different grazing management practices, together with the wide diversity of pasture species and cultivars used. Reliable estimation of DMI remains a challenge in PBS, this is a critical point to advance to precision diets. Although there are a series of benefits associated with the use of PBS, (e.g., potential reduction on dietary costs and improvement in milk quality) it should be precise what minimum pasture inclusion would achieve these benefits. In this regard, inclusions of ~40–50% of the diet seems to potentially reduce costs while apparently not limiting voluntary feed intake, but more data analysis is needed. Future studies should delve into the characterization of the nitrogenous and carbohydrate fractions of different pastures species and supplements used, considering the new available laboratory techniques. Dietary fiber recommendations, both minimum and maximum, should be specifically defined for pasture-based diets (at least until unified into a single mechanistic explanation), since due to the greater amount of fiber inclusion and generally with a higher ruminal degradation rate, it seems that these cannot be extrapolated directly from TMR diets. It appears that cows can consume a higher amount of pasture NDF in the diet compared with TMR (~1.3–1.8% of BW/d). In general, following the guidelines of an intensive grazing system, farmers normally try to maximize the use of pasture in the cows' diet, however, this can limit DMI, generate unbalanced diets, and decrease NUE, generally resulting in a lower performance. This is more evident in intermediate systems (with pasture use plus different levels of supplementation), which use animals with moderate to high productive potential, where there seems to be an oversimplification in diet formulation. Diets tend to contain excessive N with moderate to low in non-fibrous carbohydrates. Low NUE is of particular concern in PBS, future studies should follow the advances in diet formulation used in confinement systems, and quantify in depth, the ruminal degradation of CP and AA (emphasizing the understanding of microbial N supply) as well as their intestinal absorption, and subsequent post-absorptive utilization of pasture-based diets, to create concrete strategies to face this problem. The existence of strain × environment interactions suggests that breeding plans should consider individualized system-level breeding objectives. However, the available information is very limited on this topic and is even more fragmented given the diversity of breeds used. There is scarce information on genetic parameters related to nutrition from grazing dairy cows, mainly due to the difficulty of measurements, but new phenotypes in this line could help to better understand the differences in the use of nutrients by cows as well as potential interactions between animal × system. This requires a meta-analysis approach, generating information for the development and improvement of mechanistic models, which allow to identify and quantify potential key factors that explain the phenomena mentioned above, as well as directing the development of future research.

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REFERENCES

Allen, M. S. 1996. Physical constraints on voluntary intake of forages by ruminants. J. Anim. Sci. 74:3063–3075. https://doi.org/10.2527/1996.74123063x.

Auldist, M. J., M. M. Wright, L. C. Marett, J. L. Jacobs, and W. J. Wales. 2017. Effects of pasture allowance on milk production of dairy cows offered increasing amounts of partial mixed rations in spring. Anim. Prod. Sci. 57:1305–1310. https://doi.org/10.1071/AN16544.

Bargo, F., J. E. Delahoy, and L. D. Muller. 2004. Milk production of dairy cows fed total mixed rations after a grazing period. Prof. Anim. Sci. 20:270–277. https://doi.org/10.15232/S1080-7446(15)31310-3.

Bargo, F., L. D. Muller, J. E. Delahoy, and T. W. Cassidy. 2002. Performance of high producing dairy cows with three different feeding systems combining pasture and total mixed rations. J. Dairy Sci. 85:2948–2963. https://doi.org/10.3168/jds.S0022-0302(02)74381-6.

Bargo, F., L. D. Muller, E. S. Kolver, and J. E. Delahoy. 2003. Invited Review: production and digestion of supplemented dairy cows on pasture. J. Dairy Sci. 86:1–42. https://doi.org/10.3168/jds.S0022-0302(03)73581-4.

Baudracco, J., N. Lopez-Villalobos, C. W. Holmes, and K. A. Macdonald. 2010. Effects of stocking rate, supplementation, genotype and their interactions on grazing dairy systems: a review. N. Z. J. Agric. Res. 53:109–133. https://doi.org/10.1080/00288231003777665.

Beechey-Gradwell, Z. 2021. Progress towards delivering high metabolisable energy ryegrass. J. N. Z. Grasslands 83:99–106. https://doi.org/10.33584/jnzg.2021.83.3493.

Beltrán, I. E., I. Calvache, R. Cofre, F. Salazar, J. P. Keim, A. Morales, R. G. Pulido, and M. Alfaro. 2022. Nitrogen intake and its partition on urine, dung and products of dairy and beef cattle in Chile. Agronomy (Basel) 12:15. https://doi.org/10.3390/agronomy12010015.

Berry, D. P., B. Horan, M. O'Donovan, F. Buckley, E. Kennedy, M. McEvoy, and P. Dillon. 2007. Genetics of grass dry matter intake, energy balance, and digestibility in grazing Irish dairy cows. J. Dairy Sci. 90:4835–4845. https://doi.org/10.3168/jds.2007-0116.

Boyle, P. T., and C. R. Stockdale. 2011. Dairy farm management systems: Seasonal, pasture-based, dairy cow breeds. Pages 29–37 in Encyclopaedia of Dairy Sciences. Vol. 2. J. W. Fuquay, P. F. Fox, and P. L. H. McSweeney, ed. Academic Press: Amsterdam, The Netherlands.

Cheng, L., S. L. Woodward, R. J. Dewhurst, H. Zhou, and G. R. Edwards. 2014. Nitrogen partitioning, energy use efficiency and isotopic fractionation measurements from cows differing in genetic merit fed low-quality pasture in late lactation. Anim. Prod. Sci. 54:1651–1656. https://doi.org/10.1071/AN14171.

Cotanch, K. W., R. J. Grant, M. E. Van Amburgh, A. Zontini, M. Fustini, A. Palmonari, and A. Formigoni. 2014. Applications of UNDF in ration modeling and formulation. Pages 114–131 in Proc. Cornell Nutrition Conference. Department of Animal Science—Cornell University, Ithaca, NY, USA.

de Veth, M. J., and E. S. Kolver. 2001. Digestion of ryegrass pasture in response to change in pH in continuous culture. J. Dairy Sci. 84:1449–1457. https://doi.org/10.3168/jds.S0022-0302(01)70178-6.

Dillon, P. 2007. Achieving high dry-matter intake from pasture with grazing dairy cows. Pages 1–26 in Fresh herbage for dairy cattle. The key to a sustainable food chain. A. Elgersma, J. Dijkstra, and S. Tamminga, ed. Springer, Dordrecht, The Netherlands.

Dineen, M., L. Delaby, T. Gilliland, and B. McCarthy. 2018. Meta-analysis of the effect of white clover inclusion in perennial ryegrass swards on milk production. J. Dairy Sci. 101:1804–1816. https://doi.org/10.3168/jds.2017-12586.

Dineen, M., B. McCarthy, P. Dillon, P. A. LaPierre, S. Fessenden, C. Matthews, N. Galvin, and M. E. Van Amburgh. 2020a. Rumen metabolism, omasal flow of nutrients, and microbial dynamics in lactating dairy cows fed fresh perennial ryegrass (Lolium perenne L.) not supplemented or supplemented with rolled barley grain. J. Dairy Sci. 103:11332–11348. https://doi.org/10.3168/jds.2020-18437.

Dineen, M., B. McCarthy, D. Ross, A. Ortega, P. Dillon, and M. E. Van Amburgh. 2020b. Characterization of the nutritive value of perennial ryegrass (Lolium perenne L.) dominated pastures using updated chemical methods with application for the Cornell Net Carbohydrate and Protein System. Anim. Feed Sci. Technol. 114752. https://doi.org/10.1016/j.anifeedsci.2020.114752.

Distel, R. A., J. I. Arroquy, S. Lagrange, and J. J. Villalba. 2020. Designing diverse agricultural pastures for Iimproving ruminant production systems. Front. Sustain. Food Syst. 4:1–18. https://doi.org/10.3389/fsufs.2020.596869.

Estes, K. A., R. R. White, P. S. Yoder, T. Pilonero, H. Schramm, H. Lapierre, and M. D. Hanigan. 2018. An in vivo stable isotope-based approach for assessment of absorbed amino acids from individual feed ingredients within complete diets. J. Dairy Sci. 101:7040–7060. https://doi.org/10.3168/jds.2017-13447.

Estrada, J. I. C., R. Delagarde, P. Faverdin, and J. L. Peyraud. 2004. Dry matter intake and eating rate of grass by dairy cows is restricted by internal, but not external water. Anim. Feed Sci. Technol. 114:59–74. https://doi.org/10.1016/j.anifeedsci.2003.11.013.

Ferris, C. P. 2007. Sustainable pasture based dairy systems – meeting the challenges. Can. J. Plant Sci. 87:723–738. https://doi.org/10.4141/CJPS06011.

Friggens, N. C., L. Brun-Lafleur, P. Faverdin, D. Sauvant, and O. Martin. 2013. Advances in predicting nutrient partitioning in the dairy cow: recognizing the central role of genotype and its expression through time. Animal 7:89–101. https://doi.org/10.1017/S1751731111001820.

Fulkerson, W. J., and D. J. Donaghy. 2001. Plant-soluble carbohydrate reserves and senescence - key criteria for developing an effective grazing management system for ryegrass-based pastures: a review. Aust. J. Exp. Agric. 41:261–275. https://doi.org/10.1071/EA00062.

Fulkerson, W. J., K. Slack, D. W. Hennessy, and G. M. Hough. 1998. Nutrients in ryegrass (Lolium spp.), white clover (Trifolium repens) and kikuyu (Pennisetum clandestinum) pastures in relation to season and stage of regrowth in a subtropical environment. Aust. J. Exp. Agric. 38:227–240. https://doi.org/10.1071/EA97161.

García, S. C., and W. J. Fulkerson. 2005. Opportunities for future Australian dairy systems: a review. Aust. J. Exp. Agric. 45:1041–1055. https://doi.org/10.1071/EA04143.

Gilliland, T. J., T. Ball, and D. Hennessy. 2021. Opportunities and challenges for breeding perennial ryegrass cultivars with improved livestock production potential. Ir. J. Agric. Food Res. 59:233–245. https://doi.org/10.15212/ijafr-2020-0111.

Gonzalez-Mejia, A., D. Styles, P. Wilson, and J. Gibbons. 2018. Metrics and methods for characterizing dairy farm intensification using farm survey data. PLoS One 13:e0195286. https://doi.org/10.1371/journal.pone.0195286.

Grant, R., W. Smith, and M. Miller. 2020. Relationships between fibre digestibility and particle size for lactating dairy cows. Pages 47–57 in Proc. Western Canadian Dairy Seminar, Advances in Dairy Technology. Department of Agricultural, Food and Nutritional Science—University of Alberta, Edmonton, Alberta, Canada.

Hall, M. B. 2014. Feed analyses and their interpretation. Vet. Clin. North Am. Food Anim. Pract. 30:487–505. https://doi.org/10.1016/j.cvfa.2014.07.001.

Hall, M. B., and G. B. Huntington. 2008. Nutrient synchrony: Sound in theory, elusive in practice. J. Anim. Sci. 86(suppl_14):E287–E292. https://doi.org/10.2527/jas.2007-0516.

Hanigan, M. D. 2022. What's new in the NRC for how we formulate for protein in diets for dairy cattle? in Proc. 2022 Tri-State Dairy Conference, Columbus, Ohio.

Hanigan, M. D., V. C. Souza, R. Martineau, V. L. Daley, and P. Kononoff. 2021. Predicting ruminally undegraded and microbial protein flows from the rumen. J. Dairy Sci. 104:8685–8707. https://doi.org/10.3168/jds.2020-19672.

Huang, X., P. S. Yoder, L. Campos, E. Huang, and M. D. Hanigan. 2021. A method of assessing essential amino acid availability from microbial and ruminally undegraded protein in lactating dairy cows. J. Dairy Sci. 104:1777–1793. https://doi.org/10.3168/jds.2020-18248.

Huhtanen, P., and S. Ahvenjärvi. 2022. Review: Problems in determining metabolisable protein value of dairy cow diets and the impact on protein feeding. Animal 16:100539. https://doi.org/10.1016/j.animal.2022.100539.

Jacobs, J. L. 2014. Challenges in ration formulation in pasture-based milk production systems. Anim. Prod. Sci. 54:1130–1140. https://doi.org/10.1071/AN14463.

Keim, J. P., X. Valderrama, D. Alomar, and I. F. López. 2013. In situ rumen degradation kinetics as affected by type of pasture and date of harvest. Sci. Agric. 70:405–414. https://doi.org/10.1590/S0103-90162013000600005.

Kolver, E. 2000. Nutrition guidelines for the high producing dairy cow. Pages 17–28 in Proc. Proceedings of the 52nd Ruakura Dairy Farmers' Conference. Dairying Reseach Corporation, Hamilton, NZ.

Kolver, E., V. Carruthers, P. Neil, M. de Veth, E. Jansen, and D. Phipps. 1999. Amino acid supply to the small intestine of dairy cows fed pasture. Pages 180–183 in Proceedings of the New Zealand Society of Animal Production. Vol. 59. New Zealand Society of Animal Production.

Kolver, E., L. D. Muller, G. A. Varga, and T. J. Cassidy. 1998a. Synchronization of ruminal degradation of supplemental carbohydrate with pasture nitrogen in lactating dairy cows. J. Dairy Sci. 81:2017–2028. https://doi.org/10.3168/jds.S0022-0302(98)75776-5.

Kolver, E. S. 2003. Nutritional limitations to increased production on pasture-based systems. Proc. Nutr. Soc. 62:291–300. https://doi.org/10.1079/PNS2002200.

Kolver, E. S., and M. J. de Veth. 2002. Prediction of ruminal pH from pasture-based diets. J. Dairy Sci. 85:1255–1266. https://doi.org/10.3168/jds.S0022-0302(02)74190-8.

Kolver, E. S., and L. D. Muller. 1998. Performance and nutrient intake of high producing Holstein cows consuming pasture or a total mixed ration. J. Dairy Sci. 81:1403–1411. https://doi.org/10.3168/jds.S0022-0302(98)75704-2.

Kolver, E. S., L. D. Muller, M. C. Barry, and J. W. Penno. 1998b. Evaluation and application of the Cornell Net Carbohydrate and Protein System for dairy cows fed diets based on pasture. J. Dairy Sci. 81:2029–2039. https://doi.org/10.3168/jds.S0022-0302(98)75777-7.

Lapierre, H., S. Binggeli, M. Sok, D. Pellerin, and D. R. Ouellet. 2019. Estimation of correction factors to determine the true amino acid concentration of protein after a 24-hour hydrolysis. J. Dairy Sci. 102:1205–1212. https://doi.org/10.3168/jds.2018-15392.

Leaver, J. D. 1985. Milk production from grazed temperate grassland. J. Dairy Res. 52:313–344. https://doi.org/10.1017/S0022029900024201.

March, M. D., M. J. Haskell, M. G. G. Chagunda, F. M. Langford, and D. J. Roberts. 2014. Current trends in British dairy management regimens. J. Dairy Sci. 97:7985–7994. https://doi.org/10.3168/jds.2014-8265.

Mayne, S., J. McCaughey, and C. Ferris. 2011. Dairy farm management systems: Non-seasonal, pasture-based milk production systems in Western Europe. Pages 44–52 in Encyclopaedia of Dairy Sciences. Vol. 2. 2nd ed. J. W. Fuquay, P. F. Fox, and P. L. H. McSweeney, ed. Academic Press: Amsterdam, The Netherlands.

Mee, J. F., and L. A. Boyle. 2020. Assessing whether dairy cow welfare is "better" in pasture-based than in confinement-based management systems. N. Z. Vet. J. 68:168–177. https://doi.org/10.1080/00480169.2020.1721034.

Mertens, D. R. 1987. Predicting intake and digestibility using mathematical models of ruminal function. J. Anim. Sci. 64:1548–1558. https://doi.org/10.2527/jas1987.6451548x.

Mertens, D. R. 1997. Creating a system for meeting the fiber requirements of dairy cows. J. Dairy Sci. 80:1463–1481. https://doi.org/10.3168/jds.S0022-0302(97)76075-2.

Mertens, D. R. 2002. Gravimetric determination of amylase-treated neutral detergent fiber in feeds with refluxing in beakers or crucibles: collaborative study. J. AOAC Int. 85:1217–1240. https://doi.org/10.1093/jaoac/85.6.1217.

Morales, A. G., R. E. Vibart, M. M. Li, A. Jonker, D. Pacheco, and M. D. Hanigan. 2021. Evaluation of Molly model predictions of ruminal fermentation, nutrient digestion, and performance by dairy cows consuming ryegrass-based diets. J. Dairy Sci. 104:9676–9702. https://doi.org/10.3168/jds.2020-19740.

Moscovici Joubran, A., K. M. Pierce, N. Garvey, L. Shalloo, and T. F. O'Callaghan. 2021. Invited review: A 2020 perspective on pasture-based dairy systems and products. J. Dairy Sci. 104:7364–7382. https://doi.org/10.3168/jds.2020-19776.

NASEM. 2021. Nutrient requirements of dairy cattle: Eighth revised edition. The National Academies Press, Washington, DC.

Niderkorn, V., and R. Baumont. 2009. Associative effects between forages on feed intake and digestion in ruminants. Animal 3:951–960. https://doi.org/10.1017/S1751731109004261.

O'Brien, D., B. Moran, and L. Shalloo. 2018. A national methodology to quantify the diet of grazing dairy cows. J. Dairy Sci. 101:8595–8604. https://doi.org/10.3168/jds.2017-13604.

Pacheco, D., M. H. Tavendale, G. W. Reynolds, T. N. Barry, J. Lee, and W. C. McNabb. 2003. Whole-body fluxes and partitioning of amino acids to the mammary gland of cows fed fresh pasture at two levels of intake during early lactation. Br. J. Nutr. 90:271–281. https://doi.org/10.1079/BJN2003886.

Penasa, M., N. López-Villalobos, R. D. Evans, A. R. Cromie, R. Dal Zotto, and M. Cassandro. 2010. Crossbreeding effects on milk yield traits and calving interval in spring-calving dairy cows. J. Anim. Breed. Genet. 127:300–307. https://doi.org/10.1111/j.1439-0388.2009.00840.x.

Peyraud, J. L., and R. Delagarde. 2013. Managing variations in dairy cow nutrient supply under grazing. Animal 7(S1):57–67. https://doi.org/10.1017/S1751731111002394.

Poppi, D., D. Minson, and J. Ternouth. 1981. Studies of cattle and sheep eating leaf and stem fractions of grasses. 3. The retention time in the rumen of large feed particles. Aust. J. Agric. Res. 32:123–137. https://doi.org/10.1071/AR9810123.

Raboisson, D., A. Albaaj, G. Nonne, and G. Foucras. 2017. High urea and pregnancy or conception in dairy cows: A meta-analysis to define the appropriate urea threshold. J. Dairy Sci. 100:7581–7587. https://doi.org/10.3168/jds.2016-12009.

Raffrenato, E., C. F. Nicholson, and M. E. Van Amburgh. 2019. Development of a mathematical model to predict pool sizes and rates of digestion of 2 pools of digestible neutral detergent fiber and an undigested neutral detergent fiber fraction within various forages. J. Dairy Sci. 102:351–364. https://doi.org/10.3168/jds.2018-15102.

Raffrenato, E., D. A. Ross, and M. E. Van Amburgh. 2018. Development of an in vitro method to determine rumen undigested aNDFom for use in feed evaluation. J. Dairy Sci. 101:9888–9900. https://doi.org/10.3168/jds.2018-15101.

Ramsbottom, G., B. Horan, D. P. Berry, and J. R. Roche. 2015. Factors associated with the financial performance of spring-calving, pasture-based dairy farms. J. Dairy Sci. 98:3526–3540. https://doi.org/10.3168/jds.2014-8516.

Roche, J. R., D. P. Berry, A. M. Bryant, C. R. Burke, S. T. Butler, P. G. Dillon, D. J. Donaghy, B. Horan, K. A. Macdonald, and K. L. Macmillan. 2017. A 100-Year Review: A century of change in temperate grazing dairy systems. J. Dairy Sci. 100:10189–10233. https://doi.org/10.3168/jds.2017-13182.

Roche, J. R., D. P. Berry, L. Delaby, P. G. Dillon, B. Horan, K. A. Macdonald, and M. Neal. 2018. Review: New considerations to refine breeding objectives of dairy cows for increasing robustness and sustainability of grass-based milk production systems. Animal 12(s2):s350–s362. https://doi.org/10.1017/S1751731118002471.

Sinclair, L. A., P. C. Garnsworth, J. R. Newbold, and P. J. Buttery. 1993. Effect of synchronizing the rate of dietary energy and nitrogen release on rumen fermentation and microbial protein synthesis in sheep. J. Agric. Sci. 120:251–263. https://doi.org/10.1017/S002185960007430X.

Stern, M. O., K. A. Santos, and L. D. Satter. 1985. Protein degradation in rumen and amino acid absorption in small intestine of lactating dairy cattle fed heat-treated whole soybeans. J. Dairy Sci. 68:45–56. https://doi.org/10.3168/jds.S0022-0302(85)80796-7.

Sun, X. Z., G. C. Waghorn, and H. Clark. 2010. Cultivar and age of regrowth effects on physical, chemical and in sacco degradation kinetics of vegetative perennial ryegrass (Lolium perenne L.). Anim. Feed Sci. Technol. 155:172–185. https://doi.org/10.1016/j.anifeedsci.2009.12.004.

Taweel, H. 2007. Improving dry-matter intake of perennial-ryegrass pasture by dairy cows. Pages 159–174 in Fresh herbage for dairy cattle. The key to a sustainable food chain. A. Elgersma, J. Dijkstra, and S. Tamminga, ed. Springer, Dordrecht, The Netherlands.

van den Pol-van Dasselaar, A., D. Hennessy, and J. Isselstein. 2020. Grazing of dairy cows in Europe—An in-depth analysis based on the perception of grassland experts. Sustainability (Basel) 12:1098. https://doi.org/10.3390/su12031098.

Van Duinkerken, G., M. C. Blok, A. Bannink, J. W. Cone, J. Dijkstra, A. M. Van Vuuren, and S. Tamminga. 2011. Update of the Dutch protein evaluation system for ruminants: the DVE/OEB2010 system. J. Agric. Sci. 149:351–367. https://doi.org/10.1017/S0021859610000912.

Van Vuuren, A. M. and A. Van den Pol-van Dasselaar. 2007. Grazing systems and feed supplementation. Pages 85–101 in Fresh herbage for dairy cattle. The key to a sustainable food chain. A. Elgersma, J. Dijkstra, and S. Tamminga, ed. Springer, Dordrecht, The Netherlands.

Volden, H., L. T. Mydland, and V. Olaisen. 2002. Apparent ruminal degradation and rumen escape of soluble nitrogen fractions in grass and grass silage administered intraruminally to lactating dairy cows. J. Anim. Sci. 80:2704–2716. https://doi.org/10.2527/2002.80102704x.

Wales, W. J., and E. S. Kolver. 2017. Challenges of feeding dairy cows in Australia and New Zealand. Anim. Prod. Sci. 57:1366–1383. https://doi.org/10.1071/AN16828.

Washburn, S. P., and K. A. E. Mullen. 2014. Invited review: Genetic considerations for various pasture-based dairy systems. J. Dairy Sci. 97:5923–5938. https://doi.org/10.3168/jds.2014-7925.

Westwood, C. T., E. Bramley, and I. J. Lean. 2003. Review of the relationship between nutrition and lameness in pasture-fed dairy cattle. N. Z. Vet. J. 51:208–218. https://doi.org/10.1080/00480169.2003.36369.

Zhao, X., X. Xu, F. Wang, I. Greenberg, M. Liu, R. Che, L. Zhang, and X. Cui. 2020. Climatic, edaphic and biotic controls over soil δ13C and δ15N in temperate grasslands. Forests 11:433. https://doi.org/10.3390/f11040433.

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