

Review

Evaluation of the effects of synchronising the availability of N and energy on rumen function and production responses of dairy cows – a review

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Abstract – This paper reviews the effects of synchronising the availability of N and energy on rumen function and production responses of lactating dairy cows. The paper makes a key distinction between altering the synchronicity of diets by changing dietary ingredients, or by altering the feeding frequency or the feeding patterns. Manipulating synchrony by changing dietary ingredients presents some problems, since it is not possible to discount the possibility that apparent effects of synchrony are associated with the manipulation of the ingredients (level and type) themselves. These problems can be overcome, at least partially, by altering the feeding patterns. This review shows that the evidence for the benefits of synchronising energy and N supply to the rumen is contradictory, both for efficient microbial protein synthesis and for maximising milk production responses.

dairy cow / energy / nitrogen / rumen / synchrony

Résumé – Effets de la synchronisation de la disponibilité en azote et en énergie sur la fonction ruminale et les performances de production des vaches laitières – revue. Cet article passe en revue les effets d'une synchronisation entre les disponibilités en azote et en énergie sur la fonction ruminale et les performances de production des vaches laitières. Une distinction importante est faite entre les effets d'une synchronisation obtenue en changeant les ingrédients de la ration, et celle obtenue en modifiant le schéma et la fréquence d'apport d'aliment. La première solution conduit à des difficultés d'interprétation, car il devient impossible de distinguer les effets de la synchronisation de ceux dus à la nature et au niveau des ingrédients utilisés. La deuxième solution permet, au moins

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partiellement, de pallier ce problème. L'analyse des données de la littérature est contradictoire et ne permet pas de conclure à l'avantage de synchroniser les disponibilités en azote et en énergie dans le rumen, que ce soit pour améliorer l'efficacité de la synthèse microbienne ou la maximisation des performances de production des vaches laitières.

azote / énergie / rumen / synchronisme / vache laitière

1. INTRODUCTION

Maximising the utilisation of rumen degradable protein (RDP) and its conversion into microbial protein is a key objective of protein feeding strategies. Although the importance of balancing the supply of RDP to the availability of fermentable energy on a daily basis is well recognised [14, 56], other workers have suggested that it may be important to optimise the diurnal patterns of supply of RDP and fermentable energy (the 'synchrony concept') [42, 47].

The basic assertion of the synchrony concept is that a lack of synchrony between the diurnal patterns of supply of energy and N to the microbes reduces the efficiency of microbial capture of N and results in an inefficient use of ATP for microbial growth [16]. The imbalance between N and energy availability, in asynchronous diets, can promote a considerable absorption of ammonia through the ruminal wall and the use of amino acids (AA) as an energy source [67]. Conversely, when the fermentation of the dietary carbohydrates reaches its peak, the N supply to the rumen microbes will be markedly deficient, leading to an uncoupling of ATP production and microbial protein synthesis, with fermentation occurring largely without microbial growth [67].

Therefore, synchronising energy and N availabilities in the rumen seems to have a potential to enhance the output of microbial protein from the rumen and efficiency of ruminal fermentation, thereby improving feed utilization and animal performance. It is possible to alter the synchronicity of diets, either by changing dietary ingredients, or by altering the feeding frequency or the feeding patterns. The latter approach is an extremely useful one because it allows us to

alter synchrony without altering diet ingredients. The main nutritional and practical consequences of the kinetics of feed digestion on rumen metabolism and animal responses were examined by Sauvant and Van Milgen [94]. Dijkstra et al. [32] highlighted the fact that no current rumen models attempt to describe the effects of synchrony on microbial protein supply.

This paper reviews the effects of synchronising the availability of N and energy by changing dietary ingredients, feeding pattern or feeding frequency on rumen function and production response of lactating dairy cows. The approach followed was to discuss this subject mainly focusing on studies with lactating dairy cows, including those that were not designed to evaluate the effects of synchrony, but that can be interpreted a posteriori as such, since the information obtained in production studies was considered essential to draw general conclusions for formulating diets as well as for feeding management on commercial dairy farms.

2. CHANGING DIET INGREDIENTS

Synchronising N and energy supply to the rumen can be achieved either by altering the energy source, the N source or both. Altering the diet forage/concentrate ratio can also be considered as a method of manipulating the synchronicity of diets. However, factors like the level of forage intake and its fermentation rate, composition of concentrate and its effect on the digestibility of the forage, makes it difficult to distinguish their effects from synchrony effects per se [37, 62, 86, 101, 113]. The observed effects may be more related to the amount

and fermentation rate of organic matter (OM) in the rumen than specifically to the forage/concentrate ratio [21]. Additionally, the few studies with dairy cows on the influence of diet forage/concentrate ratio on N supply to the duodenum failed to establish the optimum ratio, suggesting that simply altering the ratio in the range required to maximise milk production does not greatly affect AA supply to the duodenum [53, 85, 86], probably because both forage and concentrate composition can contribute to optimising rumen fermentation and the supply of nitrogenous compounds to the duodenum [21].

2.1. Starch sources of different degradability

Few studies have simultaneously studied effects of changing dietary energy sources on rumen function and productivity. The majority has focused on the use of starch sources of different degradabilities. The most recent work, mainly from American authors, has evaluated the following: (1) different cereal species (particularly maize and barley – which are common starchy feeds with very different degradation rates; [68]); and (2) effects of different grain processing methods.

2.1.1. Effects on rumen function

Table I presents the dietary characterisation of studies, with lactating dairy cows, that have evaluated the effects of changing starch source and grain processing on rumen pH, volatile fatty acids (VFA) and ammonia N concentrations, on sites of starch digestion and on N supply to the duodenum and on the efficiency of microbial protein synthesis. More degradable starch tends to decrease rumen pH, increase rumen VFA production and decrease rumen ammonia N concentration (Fig. 1).

The effects of rate and extent of starch digestion in the rumen on microbial (or bacterial) N supply to the duodenum and on the efficiency of microbial protein synthesis

are also presented in Figure 1. More degradable starch increased microbial N supply in two studies [75, 112] and had no effect in five studies [5, 24, 54, 70, 72]. The efficiency of microbial protein synthesis was only increased in one study [75] with more degradable starch. These generally small responses may be attributed to several factors. More degradable starch sources may, on the one hand, increase starch fermented in the rumen, but, on the other hand, lower ruminal fibre digestion for diets with more degradable starch sources can negate the beneficial effects of the higher ruminal starch digestibility, resulting in a similar amount of OM fermented in the rumen [5]. Additionally, differences among treatments within and between studies may be related to differences in dietary sources of N and energy, the amount of feed intake, solid and liquid rumen outflow rates, asynchrony between N and energy availabilities in the rumen, uncoupling fermentation and other unknown factors related to the diets [20, 69, 89].

Although the effects of starch sources on synchronisation of energy and N are mainly demonstrated by their differences in digestion rate in the rumen, the carbohydrate source per se can also have effects. That is, the effects of dietary rumen degradable carbohydrates can reflect both its 'pH effect' (determined by its rate of fermentation) and 'carbohydrate effect' [64]. This latter effect is well demonstrated in studies where the depression in fibre digestion is still observed even when the addition of buffers has prevented the decrease in rumen pH [64, 109]. The 'carbohydrate effect' of a given source is related with the microbial species that utilise it and with the interactions of these microbes with cellulolytic bacteria [16]. The information available about the 'carbohydrate effect' of different sources of rumen fermentable carbohydrates is scarce, but some evidence suggests that the effect of sugars is greater than that of starch [98]. Therefore, more research is needed to fully understand the effects of carbohydrate sources on metabolism and animal performance and

Table I. Diet descriptions for the studies used in the construction of Figures 1 and 2.

Ref.	Base forage Ratio Forage/Concentrate	Starch source in the concentrate (%)
[70]	Alfalfa hay 35/65	Steam-rolled maize ₍₆₆₎ Dry-rolled sorghum ₍₆₆₎ Steam-flaked sorghum ₍₆₆₎ Dry-rolled sorghum ₍₃₃₎ + steam-flaked sorghum ₍₃₃₎
[72]	Alfalfa silage + maize silage 45/55	Maize ₍₇₂₎ Maize ₍₅₄₎ + steam-rolled barley ₍₂₂₎ Maize ₍₃₆₎ + steam-rolled barley ₍₄₅₎ Maize ₍₁₈₎ + steam-rolled barley ₍₆₇₎ Steam-rolled barley ₍₈₉₎
[75]	Alfalfa hay 43/57	Dry-rolled maize _{(0.52†)(70)} Steam-flaked maize _{(0.39†)(70)} Steam-flaked maize _{(0.32†)(70)} Steam-flaked maize _{(0.26†)(70)}
[112]	Barley silage + alfalfa hay 40/60	Steam-rolled barley ₍₈₄₎ Steam-rolled hull-less barley ₍₈₄₎ Steam-rolled maize ₍₈₃₎
[24]	Alfalfa hay 45/55	Dry-rolled maize ₍₄₉₎ Dry-rolled maize ₍₃₃₎ + steam-flaked maize ₍₁₆₎ Dry-rolled maize ₍₁₆₎ + steam-flaked maize ₍₃₃₎ Steam-flaked maize ₍₄₉₎
[54]	Wilted alfalfa silage 45/55	Dry ground maize ₍₇₇₎ Dry-rolled maize ₍₇₇₎ High moisture ground maize ₍₇₇₎ High moisture rolled maize ₍₇₇₎
[5]	Barley silage + alfalfa haylage 45/55	Steam-rolled barley ₍₈₄₎ Steam-rolled barley ₍₈₄₎ + fibrolytic enzyme Steam-rolled hull-less barley ₍₈₄₎ Steam-rolled hull-less barley ₍₈₄₎ + fibrolytic enzyme
[49]	Alfalfa hay + alfalfa silage + barley/triticale silage 40/60	Maize ₍₆₁₎ Maize ₍₅₀₎ + barley ₍₅₀₎ Barley ₍₆₁₎
[31]	Alfalfa hay + maize silage 45/55	Coarsely ground maize ₍₆₄₎ fed once a day Finely ground maize ₍₆₄₎ fed once a day Steam-flaked maize ₍₆₄₎ fed once a day Finely ground maize ₍₆₄₎ fed four times a day Steam-flaked maize ₍₆₄₎ fed four times a day
[69]	Maize silage + alfalfa silage 43/57 66/34	High-moisture corn ₍₅₆₎ Dry ground corn ₍₅₅₎ High-moisture corn ₍₃₂₎ Dry ground corn ₍₃₂₎

† Flake density.

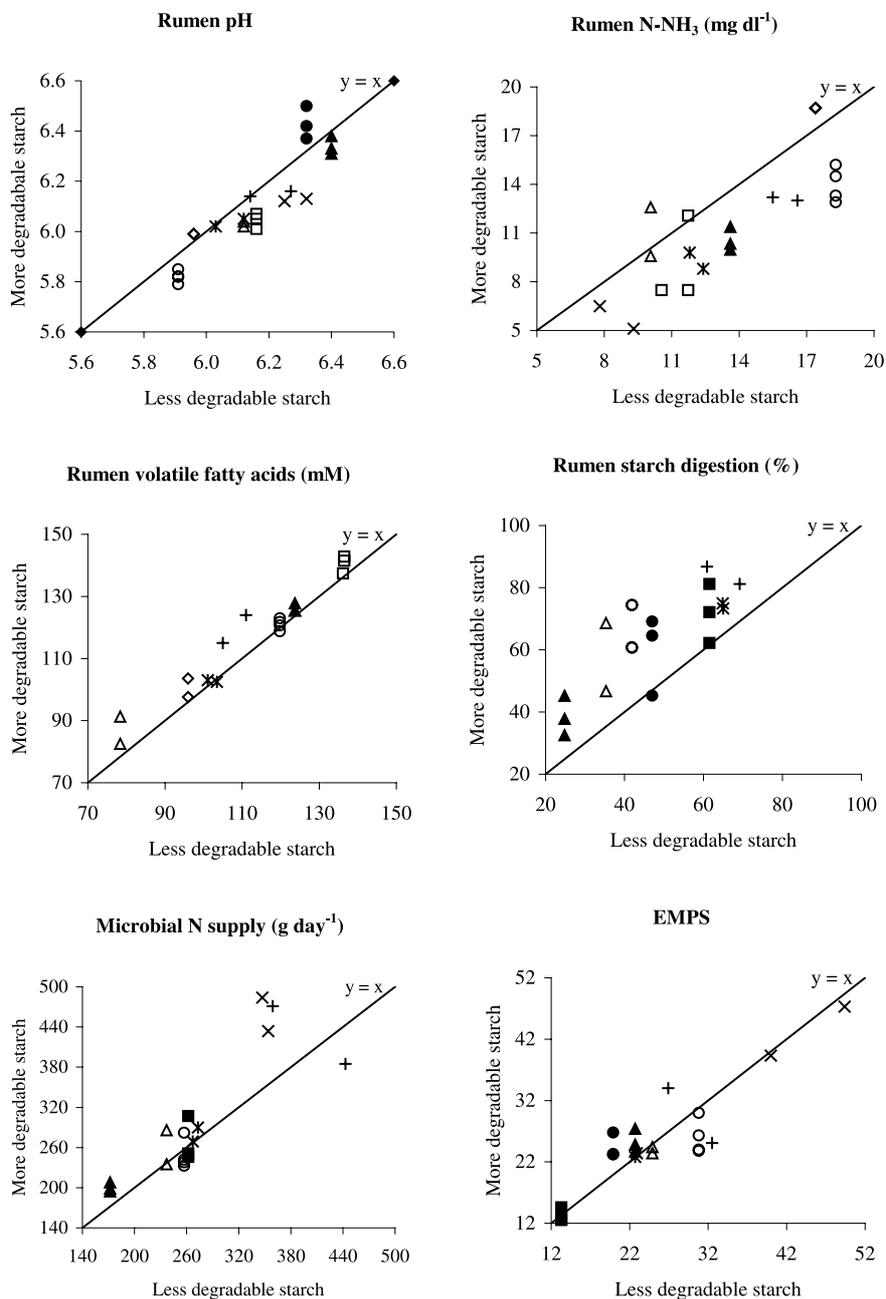


Figure 1. Effects of rumen starch degradability on rumen pH, volatile fatty acids and ammonia N concentrations, on rumen starch digestion, on microbial N supply to the duodenum and on the efficiency of microbial protein synthesis (EMPS; g microbial or bacterial N per kg rumen degradable organic matter). [70] ■; [72] ○; [75] ●; [112] △; [24] ▲; [54] +; [5] *; [49] ◇; [31] □; [69] x.

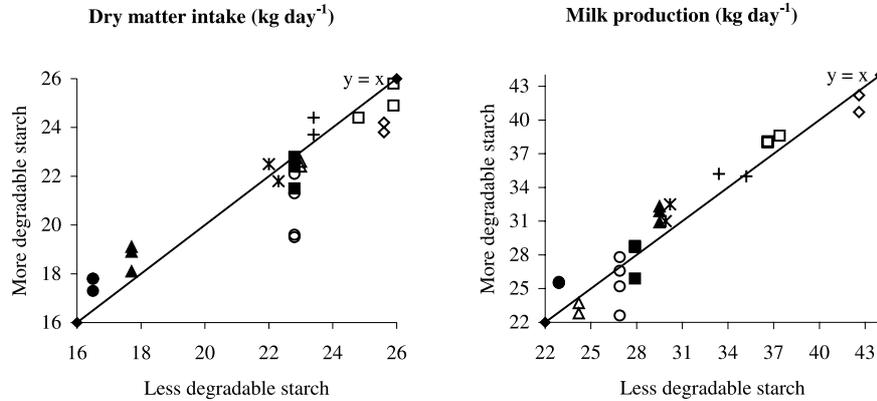


Figure 2. The effects of rumen starch degradability on dry matter intake (kg·day⁻¹) and milk production (kg·day⁻¹). [70] ■; [72] ○; [73] ●; [112] △; [24] ▲; [54] +; [5] *; [49] ◇; [31] □.

hence to make a better use of them in feeding the lactating dairy cow.

2.1.2. Effects on production response

Some of the dairy production studies described in Table I found a significant increase in DM intake and milk production with an increase in starch fermentability [5, 31, 75], others observed the opposite [72], while still others did not observe any effect [24, 54, 70, 112], (Fig. 2). Positive responses in milk production were ascribed to higher DM intake [75], higher energy intake [5], an increase in the digestibility of starch and neutral detergent fibre (NDF; [31, 75]), or higher protein supply to the duodenum [75]. In the study of Khorasani et al. [49], only primiparous cows responded to the treatment of substituting barley grain with maize, with milk production varying quadratically with increasing barley.

Studies that measured the effects of changing starch source on the production response of lactating dairy cows (not included in Tab. I) also found markedly different effects of using barley in place of other sources of lower rumen fermentable starch; some observed a reduction in milk production and DM intake with barley [6, 12, 14, 63], while in other

studies these parameters were similar or even increased with barley inclusion [13, 28, 35, 41, 85, 101]. The higher productive responses with barley may be attributed to the more rapid fermentation of barley in the rumen. Increasing starch digestion in the rumen increases the proportion of propionic acid produced [18, 76], which might result in higher net energy absorption, higher glucose synthesis in the liver, lower utilisation of amino acids [105], and hence enhanced animal performance. Additionally, rapid ruminal fermentation of barley can increase microbial protein synthesis (Fig. 1). However, when excessive fermentation of starch to VFA in the rumen occurs, the buffering and absorptive capacity of the cow may be overwhelmed, leading to a decrease in rumen pH that may decrease microbial growth and DM intake. In these situations, the substitution of barley by maize (less degradable starch source) can have positive effects on productive responses. Maize can prevent the depression in rumen pH and increases DM intake, resulting in a larger quantity of energy, amino acids, and other nutrients being provided for the synthesis of milk and milk components. The associated increase in the rate of passage from the rumen enhances microbial growth

efficiency and amino acid supply to the duodenum. The variation between experiments in the effects of barley or maize on DM intake and milk production of cows was also probably due to the dietary concentrations of maize and barley, which have distinct effects on rumen pH, to the higher starch content of maize-based diets, which increase VFA production [14], and to the higher fibre content of diets with barley [63].

Changing starch source affect the site and the end products of digestion absorbed by the animal (Fig. 1). Ruminal digestion of starch is usually higher with diets based on higher degradable starch sources (e.g., barley), whilst post ruminal digestion is higher when less degradable starch sources (e.g., maize) are used as an energy source [5, 72, 75]. This along with the effects of starch sources of different degradabilities on rumen function, with the empirical and practical rule that in diets for high producing dairy cows (with high needs for glycolytic nutrients), based on maize silage, more rumen degradable starch sources can be used in the concentrate feed. Conversely, in diets based on grass silage, a greater contribution of less degradable starch sources is advantageous, in particular for increased milk protein content.

2.2. Protein nitrogen and non protein nitrogen

Changing dietary N source also represents a method of manipulating N and energy availabilities in the rumen. In this sense, the replacement of true protein by non-protein N – often designed to reduce the cost of diets – can be considered a change in the synchronicity of diets. The studies that used this strategy have mainly focused on evaluating the possible losses in production efficiency and not their effects on the synchrony between N and energy availabilities in the rumen.

When interpreting the results of replacing true protein by non protein N we have to consider both effects of AA supply on

microbial protein synthesis and of rate of release of N. Several studies demonstrate that, although some rumen microorganisms are able to grow in the absence of true protein, some microorganisms prefer preformed AA [8, 44, 46]. The presence of AA stimulates microbial growth [1, 58, 59], growth rate [108] and growth efficiency [1, 23, 60], as well as increasing the cell wall digestion and the production of VFA [36]. Additionally, there is some evidence [1, 60] that the effects of AA supply on bacterial growth are superior with a mixture of AA than with specific AA. However, the effects *in vivo* have been less consistent [2, 19], probably due to differences in fermentation rates of carbohydrates.

To maximise the efficiency of microbial protein synthesis with non-protein N, it is considered essential to guarantee a source of quickly fermentable energy in the diet that allows the use, by rumen microbes, of the rapidly released ammonia (e.g., [45, 57, 103]). Therefore, the energy source used must be taken into account when the effects of changing N source are analysed. Indeed, carbohydrates differ greatly in terms of potential to promote the use of non-protein N sources. Cellulose seems to be the least effective carbohydrate in promoting the use of ammonia released from urea and starch the most effective, more so than sugars [38]. The observation that cellulose does not promote an effective use of urea N can be explained by the low proportion of cellulose that is rapidly hydrolysed and becomes available when bacteria needs energy to capture N [22, 78]. Sugars have been studied more extensively in relation to their positive effect on the intake of diets with urea than in relation to their effects on urea N use [38]. However, this aspect was not supported by Van Horn et al. [107] who observed that the intake of a concentrate feed with 1.9% of urea was not increased by the addition of 4.7% of molasses. Sources of quickly fermentable starch decrease rumen pH, allowing the maintenance of a greater pool of ammonia for microbial protein synthesis, since the rumen wall is more

permeable to the free form (NH_3), present with a higher rumen pH [91]. The effectiveness of starch can be increased by cooking, which making it more susceptible to microbial degradation, allows the supply of energy in a rate more closely related to that of urea N released, theoretically enabling the more efficient use of ammonia by rumen microbes, since it decreases the risk of toxicity from urea [4].

2.3. Matching energy and N sources

Some authors have evaluated the effects of changing N and energy sources in the concentrate on rumen function and dairy cow performance. These effects can be interpreted retrospectively as effects of manipulating synchrony between N and energy availabilities in the rumen (Tab. II).

2.3.1. Effects on rumen function

Mean rumen pH was not, in general, affected (Fig. 3), though VFA concentrations increased with increasing fermentable energy supply in two studies, and this was reflected in a higher utilisation of degradable N [61, 63]. It was expected that isonitrogenous diets that were more synchronised would promote a lower rumen ammonia N concentration. However, the studies analysed (Fig. 3) do not give a consistent trend, possibly due to differences in the level of RDP supply (e.g., inclusion of urea in study [12]) or differences in the pattern of rumen fluid sampling. Furthermore, rumen ammonia concentrations are not necessarily related with ammonia production, and could be related for example with changes in ruminal volumes [14] and absorption rates through the ruminal wall [12].

From the studies summarised in Table II, only five measured microbial N supply to the duodenum and the efficiency of microbial protein synthesis (Fig. 3). The small number of studies and the difficulty of distinguishing the effects of protein and energy sources do not allow us to reach a general conclusion. Herrera-Saldana et al. [42]

showed that starch degradability affected the utilisation of nutrients in the rumen more than protein degradability. They also showed that diets synchronised for a fast release of N and energy, with barley and cottonseed meal, promoted a higher production and higher efficiency of microbial protein synthesis than the diets synchronised for a slow release of N and energy, with milo and brewers dried grains, or asynchronous diets, with barley and brewers dried grain, or milo and cottonseed meal.

When the objective is to formulate synchronised diets by changing dietary ingredients, it seems that matching the availability of N and energy in the rumen is not sufficient. Care must also be taken about the nature of N and energy sources used and their effects on rumen environment and microbial growth efficiency. Indeed, production of microbial N in the rumen is often limited by fermentable energy, but diet fermentability may also affect microbial efficiency by altering ruminal pH or rates of passage. For example, the rate of rumen starch fermentation that allows the maximal efficiency of starch use by ruminal microbes is affected by the ruminal environment and availability of N substrates required for microbial growth [49]. It is well known that bacteria fermenting non-structural carbohydrates (NSC) may decrease microbial efficiency when peptides or amino acids are insufficient [90]. The next section discusses the extent to which positive effects on rumen function achieved by synchronised diets are reflected in production responses.

2.3.2. Effects on production response

The production response to synchrony of N and energy supply to the rumen is not consistent (Fig. 4). Herrera-Saldana and Huber [41], using the same diets as in the previous study [42], showed that cows in early lactation, fed a synchronous diet for fast rumen degradation of energy and N, produced more milk than those fed slowly fermentable synchronised diets or asynchronous

Table II. Diet descriptions for the studies used in the construction of Figures 3 and 4.

Ref.	Base forage Ratio Forage/ Concentrate	Energy and N sources in concentrate (%)	Degree of synchrony considered†
[11]	MS + AH 50/50	GSM ₍₆₉₎ + SB ₍₂₉₎	+
		GSM ₍₇₅₎ + SB ₍₂₂₎ + U ₍₁₎	-
		GSM ₍₄₈₎ + SB ₍₁₈₎ + U ₍₁₎ + DWW ₍₃₀₎	+
[12]	MS + AH 50/50	GSM ₍₆₀₎ + SB ₍₃₂₎	+
		GSM ₍₆₆₎ + SB ₍₂₅₎ + U ₍₁₎	-
		BR ₍₆₇₎ + SB ₍₂₅₎	-
		BR ₍₇₃₎ + SB ₍₁₇₎ + U ₍₁₎	+
		GSM ₍₃₄₎ + DWW ₍₃₀₎ + SB ₍₂₉₎ GSM ₍₄₀₎ + DWW ₍₃₀₎ + SB ₍₂₁₎ + U ₍₁₎	- +
[63]	AGH + MS 45/55	GSM ₍₈₄₎ + FM ₍₁₃₎	-
		GSM ₍₇₉₎ + SB ₍₁₇₎	+
		SRB ₍₉₁₎ + FM ₍₆₎ SRB ₍₈₈₎ + SB ₍₈₎	- +
[13]	MS + AH 50/50	GSM ₍₆₀₎ + SB ₍₃₂₎	+
		GSM ₍₆₆₎ + SB ₍₂₅₎ + U ₍₁₎	-
		BR ₍₆₇₎ + SB ₍₂₅₎ BR ₍₇₃₎ + SB ₍₁₇₎ + U ₍₁₎	- +
[42]	AH + CH 35/65	B ₍₆₆₎ + CSM ₍₁₉₎	+
		B ₍₅₀₎ + BDG ₍₃₆₎	-
		M ₍₆₃₎ + CSM ₍₂₂₎ M ₍₄₆₎ + BDG ₍₃₉₎	- +
[10]	AHL + MS 55/45	FM ₍₁₁₎ + S ₍₂₁₎ + D ₍₇₎	-
		FM ₍₁₁₎ + U _(1.7) + S ₍₂₁₎ + D ₍₇₎	+
[61]	MS + AH + GH 52/48	GM ₍₅₉₎ + SB ₍₃₂₎	+
		GM ₍₅₄₎ + LSBM ₍₃₆₎	-
		SH ₍₆₃₎ + SB ₍₂₉₎ SH ₍₅₈₎ + LSBM ₍₃₃₎	+
[73]	GS C: 0.8% PV	BP + SB	+
		BP + FM	-
[14]	AH + MS 50/50	GSM ₍₇₈₎ + SB ₍₂₁₎	+
		GSM ₍₇₈₎ + ESBM ₍₂₁₎	-
		BR ₍₈₅₎ + SB ₍₁₄₎ BR ₍₈₅₎ + ESBM ₍₁₄₎	+
[95]	MS + AH 50/50	MR ₍₆₁₎ + SB ₍₃₃₎	+
		MDG ₍₆₂₎ + MR ₍₃₄₎	-
[93]	MS + AH + WC 62/48	17%CP:GM ₍₄₁₎ + U _(0.6)	-
		17%CP:GM ₍₂₈₎ + U _(0.6) + Sc ₍₇₎	+
		18.5%CP:GM ₍₂₉₎ + U _(1.6) + Sc ₍₇₎ 18.5%CP:GM ₍₂₈₎ + U _(0.9) + SB ₍₁₁₎ + Sc ₍₆₎	- +

†+ = more synchronised; - = less synchronised.

AGH = alfalfa-grass haylage; AH = alfalfa hay; AHL = alfalfa haylage; B = barley; BDG = brewers dried grains; BP = beet pulp; BR = barley rolled; CH = cottonseed hulls; CP = crude protein; CSM = cottonseed meal; D = dextrose; DWW = dried whole whey; ESBM = extruded soybean meal; FM = fish meal; GH = grass hay; GM = ground maize; GS = grass silage; GSM = ground shelled maize; LSBM = lignosulfonate-treated soybean meal; M = milo; MDG = wet corn distillers grains; MR = maize rolled; MS = maize silage; MZ = maize; O = oat; S = starch; SB = soybean meal; Sc = sucrose; SH = soybean hulls; SRB = steam rolled barley; U = urea; WC = whole cottonseeds.

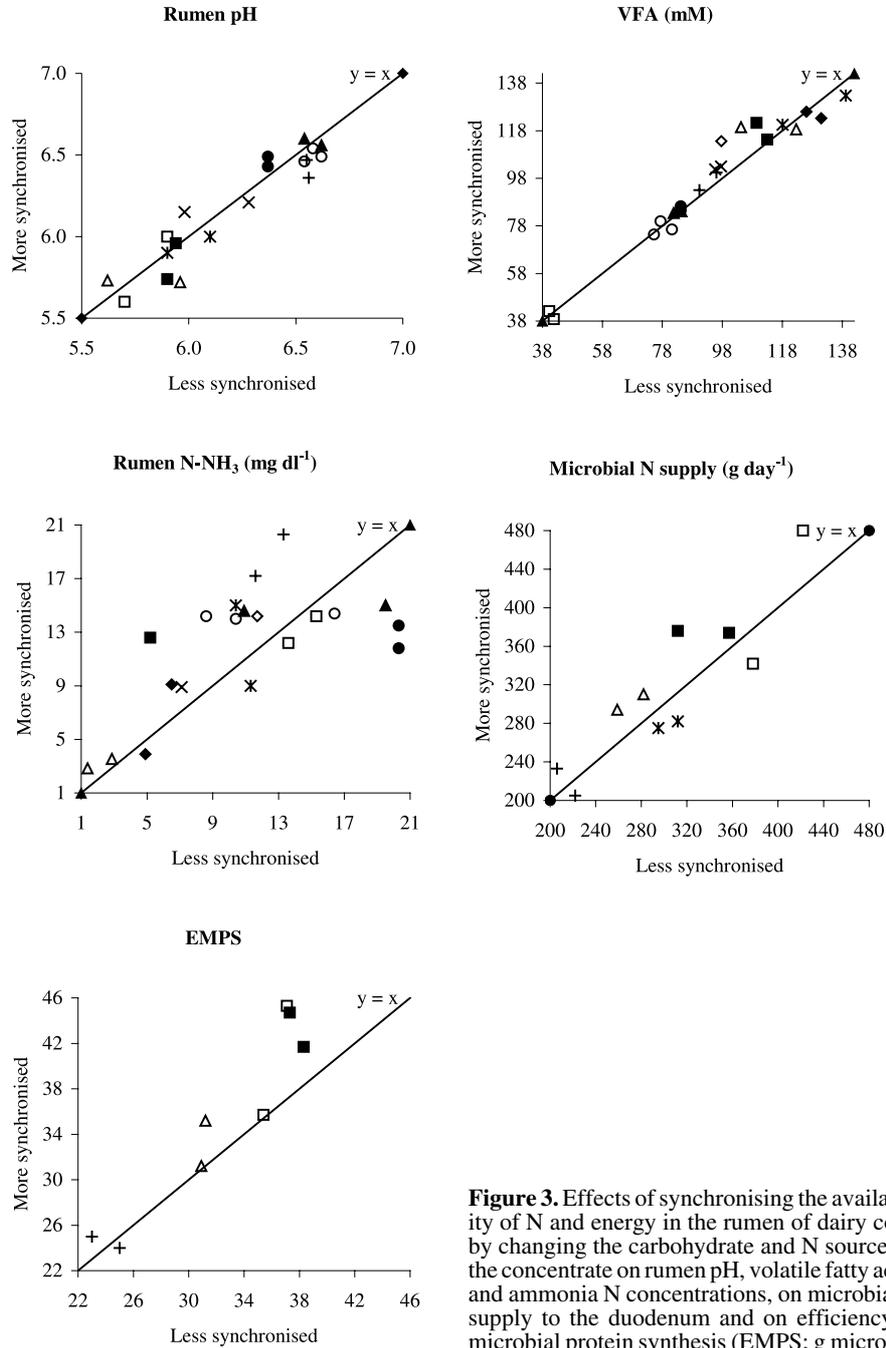


Figure 3. Effects of synchronising the availability of N and energy in the rumen of dairy cows by changing the carbohydrate and N sources in the concentrate on rumen pH, volatile fatty acids and ammonia N concentrations, on microbial N supply to the duodenum and on efficiency of microbial protein synthesis (EMPS; g microbial or bacterial N per kg rumen degradable organic matter). [11] ●; [12] ○; [63] △; [13] ▲; [42] □; [10] ■; [61] +; [73] x; [14] *; [95] ◇; [93] ◆.

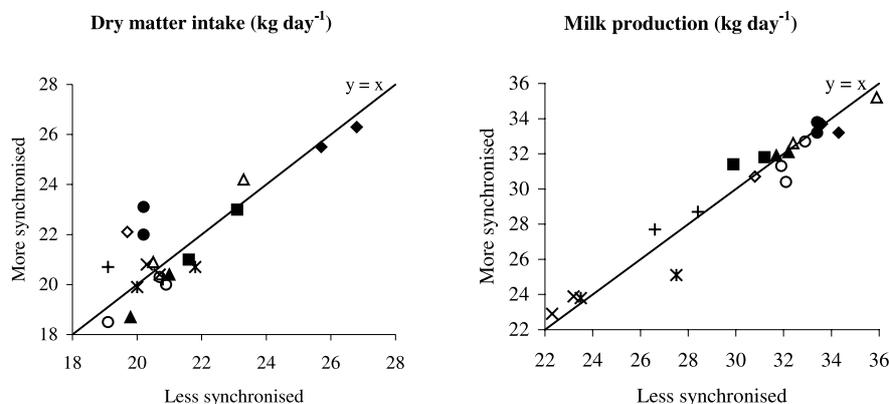


Figure 4. Effects of synchronising the availability of N and energy in the rumen of dairy cows by changing the carbohydrate and N sources in the concentrate on dry matter intake ($\text{kg}\cdot\text{day}^{-1}$) and milk production ($\text{kg}\cdot\text{day}^{-1}$). [11] ●; [12] ○; [63] △; [13] ▲; [10] ■; [61] +; [73] ×; [14] *; [95] ◇; [93] ◆.

diets, probably due to higher production of microbial protein. By contrast, other authors [10, 13, 14, 61, 73, 95] found no effects of synchronising N and energy availabilities in the rumen on milk production.

The lack of production response to synchrony between N and energy availabilities in the rumen is not clearly explained by the effects on rumen fermentation (Fig. 3). Casper and Schingoethe [12] and Casper et al. [13] state that the low milk production of cows fed diets with barley and urea could be related to the fact that degradation rates of barley and urea are incompatible, affecting DM intake. This opinion is, however, opposed to that of Blauwiel and Kincaid [7] who found greater milk production for a diet high in soluble N (barley and urea) than for a diet also based on barley, but low in soluble N. In response to these conflicting results, Casper et al. [13] suggested that differences in NSC solubility, and not in degradability, can result in different animal responses. Casper et al. [14] suggested that the minimal benefits of synchrony between NSC and RDP were due to the fact that the cows used were in the middle of lactation, with lower protein requirements.

From the foregoing discussion, it appears that the easiest practical strategy to match energy and N in the rumen is to select diet ingredients based on rumen degradability estimates (NSC and structural carbohydrates; protein and non protein N sources). Although this strategy could contribute to increased microbial protein synthesis, it could not be the more efficient or low cost one.

2.4. Synchronicity index

The studies analysed so far show that the effects of the synchrony, achieved by changing diet ingredients, between N and energy availabilities in the rumen have different effects on microbial yield and efficiency. However, those studies could have used diets which were synchronised on a wide temporal basis (e.g., day), but not synchronised over short periods (e.g., hour). Some authors examined this point in sheep. Sinclair et al. [99, 100] used in situ feed degradation data to try and to enhance the efficiency of microbial protein synthesis, through the maintenance of appropriate amounts and relations between hourly available carbohydrates and N supply. These authors

calculated a synchronicity index according to the following equation:

$$\left(25 - \sum_{1}^{24} \sqrt{(25 - N/OM \text{ hourly})^2 / 24} \right) / 25$$

where 25 = 25 g N·kg⁻¹ truly rumen digested OM, which is assumed to be the optimum relation, and where an index of 1 represents a perfect synchrony between N and energy supply during the day, while values less than 1 indicate progressively increasing asynchrony.

Using this approach, Sinclair et al. [99] conducted a study with wether sheep, which was aimed at examining the effects of hourly synchronisation of the supply of energy and N. The results suggest that the synchronised diet never promotes a deficit in ammonia for microbial growth and produces a more stable rumen microbial population, resulting in less variation in molar proportions of VFA and a greater estimated microbial protein synthesis. Conversely, the asynchronous diet resulted in a deficit in ammonia for microbial growth during 20 hours per day and a greater estimated N recycling. The carbohydrate concentration of rumen bacteria was measured to determine if microbes store excess energy and, in this sense, to serve as a synchronicity index. However, the amount of carbohydrates stored was more affected by the form and rate of degradation of carbohydrates than by the degree of synchronism between N and energy supply. Later, Sinclair et al. [100] conducted a study to examine the effects of synchronising the hourly supply of energy and N in diets with similar composition in carbohydrates, but differing in rate of release of N. The efficiency of microbial protein synthesis (g N·kg⁻¹ truly rumen degraded OM) was 11 to 20% higher in the animals fed with a synchronous diet than with an asynchronous diet.

Witt et al. [110] also used in situ degradability data to test the effect of hourly synchronisation on the productive response of ewes. They showed that the hourly synchrono-

nisation of energy and N did not significantly affect milk production, milk fat production, milk protein percentage and DM intake, but decreased plasma urea concentration during the day. They concluded that the synchrony between N and energy availabilities in the rumen does not have an important effect on the milk production of ewes and suggested that the ruminants when fed with asynchronous diets, ad libitum, have the possibility to modify their pattern of intake to achieve a more synchronised release rate of N and energy.

The previous discussion shows that manipulating synchrony by changing diet ingredients presents some problems, since it is not possible to identify whether an increase in microbial protein synthesis through feeding of different ingredients, observed in some studies, is an effect of synchrony or a factor associated with the manipulation of the ingredients (level and type) themselves, since clear effects that can be attributed to synchrony can be specific effects, for example of individual nutrients, particularly protein and energy [30].

3. CHANGING FEEDING PATTERN

The problems related to the study of synchronisation between N and energy availabilities in the rumen achieved by changing diet ingredients, can be overcome, at least partially, through the utilisation of in vitro mediums, that allows the control of the amount and supply rate of nutrients [65], or the infusion of nutrients directly in the rumen or the supply of the same ingredients to the animals according to different patterns of feeding [30].

3.1. Studies in vitro

Few studies have evaluated, in vitro, the effects of synchronisation between N and energy availabilities on microbial protein synthesis and on the efficiency of microbial protein synthesis (Tab. III). Henning et al.

Table III. Effect of synchronisation between N and energy availabilities in in vitro studies on microbial protein synthesis and on the efficiency of microbial protein synthesis.

Ref.	Nutrients added in vitro	Observations
[39]	Glucose (25 g) as pulse dose at time 0 + N in excess Glucose (25 g) as an intermediate pattern of gradually increasing, followed by gradually decreasing increments + N in excess Glucose (25 g) as 24 even increments at 0.5 h intervals + N in excess Glucose (12.5 g) as pulse dose at time 0 + N in excess Glucose (12.5 g) as an intermediate pattern of gradually increasing, followed by gradually decreasing increments + N in excess Glucose (12.5 g) as 24 even increments at 0.5 h intervals + N in excess	Synchrony decreased concentration and fluctuation of rumen ammonia, but did not affect microbial growth and efficiency of microbial protein synthesis. A single pulse dose of glucose improved the efficiency of microbial growth, being less important for acceptable levels of N supply, synchronisation between availabilities of N and energy in the rumen than the pattern of energy supply.
[39]	Glucose (12.5 g·L ⁻¹) + N (0.306 g·L ⁻¹ + 0.9 g·L ⁻¹ trypticase) Glucose and N as a pulse dose at time 0 Glucose as a pulse dose at time 0 and N in 24 even increments at 0.5 h intervals Glucose in 24 even increments at 0.5 h intervals and N as a pulse dose at time 0 Glucose and N in 24 even increments at 0.5 h intervals	
[65]	26 mg urea-N·g ⁻¹ glucose Exponential increase of 0.013 mg N·g ⁻¹ glucose from 00:00 h to 48.9 g N·g ⁻¹ glucose at 11:00 h	Bacterial population size was higher in synchrony conditions between 5 to 8 hours of incubation, but at 12 hours of incubation there were no differences. Asynchronous supply of N and energy yielding substrates only had short-term effects on bacterial growth.
[65]	Large corn particles + soybean meal Large corn particles + papaic digest soybean meal Small corn particles + soybean meal Small corn particles + papaic digest soybean meal	

[39] concluded that, for acceptable levels of N supply, synchronisation between availabilities of N and energy in the rumen is less important than the pattern of energy supply. Newbold and Rust [65] demonstrated that the asynchrony between N and energy availabilities in the rumen has only short-term effects on bacterial growth. However, the authors emphasise that these observations do not allow the conclusion that the asynchrony is unimportant in vivo. This is because of the following: (1) alterations in

N degradation rate due to changing N source can be accompanied by changing AA supply; (2) if N and energy supply rates are not synchronised, any change in rumen passage rate will decrease the efficiency of rumen utilisation of N and carbohydrates, depending on which nutrient is in excess (in fact, in this study there was no difference in the number of microorganisms between treatments, for a simulated rumen retention time of 12 hours, but if this time was shortened, N supply in relation to the energy

would be reduced and bacterial growth would be limited); and (3) the short-term effects of excess N cannot be adequately studied in simple culture mediums that do not simulate the losses of excess N through absorption by the rumen wall. Furthermore, *in vitro* studies also suffer from problems associated with the accumulation of the end products of fermentation that could affect bacterial growth [74].

3.2. Infusion of nutrients in the rumen

The results of the effects of synchronisation of N and energy availabilities in the rumen, achieved by nutrient infusion, on the synthesis and on the efficiency of microbial protein synthesis are summarised in Table IV. Due to the reduced number of studies with lactating dairy cows, studies with steers and wethers were, also included.

From the experimental evidence presented in Table IV, there were only two studies that showed positive effects of synchrony per se on microbial growth and efficiency of microbial protein synthesis [51, 88]. Although a number of earlier studies with grass silage, which is considered to be very asynchronous, have shown positive effects on microbial growth [27, 87, 88], these studies did not test the synchrony effect as the principal objective. Other factors could have an important function and had masked the effect of synchrony per se. The results obtained by Kim et al. [50, 51] (Tab. IV) are difficult to explain. Indeed, the asynchrony associated with grass silages is related to the low availability of quickly fermentable energy when the availability of peptides, AA and ammonia is high. However, Kim et al. [50] observed that in situations of asynchrony, the infusion of sucrose did not result in an improvement in microbial N supply and Kim et al. [51] found that, when they offered grass silage alone, sugar infusion had no effect on microbial protein synthesis, but when they offered grass silage and concentrates, the infusion increased microbial protein synthesis. The authors suggested that synchrony will only affect

microbial protein synthesis with diets already containing high levels of readily fermentable carbohydrates, although this is only likely if the capacity of the microbes to store starch is exceeded.

Although synchrony affected the variability of rumen ammonia N concentration in the study by Henning et al. [40] (Tab. IV), microbial N supply and efficiency of microbial protein synthesis were not affected. This observation can be explained by the fact that, although the pattern of variation of ammonia N concentration differed between treatments, the actual concentration, in relation to microbial growth resulting from the various patterns of energy supply, was never limiting. Additionally, N recycled to the rumen can partially explain the lack of response to synchronising N and energy availabilities. However, although in this study, N recycling could explain the absence of response to greater synchrony, this cannot hold true in situations of high supply of energy and N, because, in this case, excess N can be absorbed and excreted in urine and the later recycling of N to the rumen may be insufficient to match the high availability of energy [43].

In the second experiment reported by Henning et al. [40], increased synchrony resulting from a higher feed intake level did not improve the microbial protein supply, nor the efficiency of microbial synthesis. These results are in agreement with those obtained by Salter et al. [92] who did not observe a positive response to synchrony when they added tapioca and glucose (as an energy source) to the rumen of steers fed straw, provoking different levels of synchrony. It should be noted, however, that the results of Salter et al. [92] could be explained by the fact that the treatments also differed in the amounts of N and carbohydrates added to the rumen.

However, the fact that in the *in vivo* study of Henning et al. [40] the energy supplied gradually to the rumen resulted in a high and more efficient microbial protein synthesis than the same amount of energy

Table IV. Effect of synchronization between N and energy availabilities in the rumen manipulated by nutrient infusion in the rumen on microbial protein synthesis and on the efficiency of microbial protein synthesis.

Ref.	Exp. Unity	Base diet Distribution	Infusions	Observations
[92]	Steers	Straw (60) + Concentrate (40) Straw $1 \times d^{-1}$ Concentrate $2 \times d^{-1}$	Starch and urea as a single dose (09 h) Starch as a single dose (09 h) and urea in 3 doses (09, 11 and 13 h) Glucose as a single dose (09 h) and urea in 3 doses (09, 11 and 13 h) Glucose and urea in 3 doses (09, 11 and 13 h)	Synchrony and pattern of energy supply without effect on efficiency of microbial protein synthesis.
[88]†	Cows	Grass silage $2 \times d^{-1}$	Casein ($21 \text{ g N} \cdot d^{-1} + 0.17 \text{ kg OM} \cdot d^{-1}$) Urea ($28 \text{ g N} \cdot d^{-1}$) Glucose syrup ($0.87 \text{ kg OM} \cdot d^{-1}$) Casein + Glucose syrup ($17 \text{ g N} \cdot d^{-1} + 0.93 \text{ kg OM} \cdot d^{-1}$)	Infusions of glucose increased microbial growth. The efficiency of microbial protein synthesis increased, only, by the infusion of casein and glucose syrup.
[87]	Cows	Grass silage $2 \times d^{-1}$	Sucrose† ($170 \text{ g} \cdot \text{kg}^{-1} \text{ DM of silage}$) Sucrose + Casein‡ ($23 \text{ g} \cdot \text{kg}^{-1} \text{ DM of silage}$) Sucrose + Urea‡ ($8 \text{ g} \cdot \text{kg}^{-1} \text{ DM of silage}$) Sucrose + Soybean meal‡ ($64 \text{ g} \cdot \text{kg}^{-1} \text{ DM of silage}$)	Infusion of casein increased microbial growth ($P < 0.05$) and efficiency of microbial protein synthesis (non significant effect).
[40] Exp. 1	Wethers	Wheat straw (90) + fishmeal (6) + molasses (3) + urea (0.4) $6 \times d^{-1}$	Sugars (340 g) + Urea (9.2 g) + Sodium caseinate (10.2 g) Energy and N as 12-hourly pulse-doses (08/20 h) Energy as 12-hourly pulse-doses (08/20 h) and N as a continuous infusion Energy as a continuous infusion and N as 12-hourly pulse-doses (08/20 h) Energy and N as continuous infusion	Synchrony at maintenance level (Exp. 1) or higher (Exp. 2) decreased concentration and fluctuation of ruminal ammonia, but did not affect microbial growth and efficiency of microbial protein synthesis. Continuous infusion of sugar increased efficiency of microbial growth.
[40] Exp. 2	Wethers	Wheat straw (88) + fishmeal (6) + molasses (5) + urea (0.4) $6 \times d^{-1}$	Sugars (680 g) + NH_4Cl (32.6 g) + Sodium caseinate (22.8 g) One-half of energy plus all of the N as two equal pulse-doses (08/20 h), and the remaining half of the energy as a continuous infusion	

Table IV. Continued.

Ref.	Exp. Unity	Base diet Distribution	Infusions	Observations
			One-half of the energy as two equal pulse-doses (08/20 h), and the remaining half of the energy plus the N as a continuous infusion	
			Energy as a continuous infusion and N as two equal pulse-doses (08/20 h)	
			Energy and N as a continuous infusion	
[50]	Cows	Grass silage 7.9 kg DM·d ⁻¹ 2× d ⁻¹ (10/22 h)	Without infusion Sucrose (1 kg·d ⁻¹) as continuous infusion Sucrose (1 kg·d ⁻¹) as two 6-h infusions starting at 10:00 and 22:00 h Sucrose (1 kg·d ⁻¹) as two 6-h infusions starting at 16:00 and 04:00 h	Synchronous conditions where infused sucrose did not improve microbial protein synthesis.
[51]	Cows	Grass silage + barley + peanuts meal 8 kg DM·d ⁻¹ + 4.2 kg DM·d ⁻¹ + 1.8 kg DM·d ⁻¹ 2× d ⁻¹ (10/22 h)	Without infusions 2 kg maltodextrin as continuous infusion 2 kg maltodextrin as two 6-h infusions starting at 10:00 and 22:00 h 2 kg maltodextrin as two 6-h infusions starting at 16:00 and 04:00 h	Maltodextrin infused synchronously increased microbial protein synthesis.

† Infused intraruminally at a constant rate; ‡ Fed in two equal portions.

supplied rapidly, is on the contrary to that observed in vitro by Henning et al. [39] for similar treatments. These conflicting results can be explained by the fact that in the in vitro study, pH was maintained above 6 and the values of microbial protein synthesis were only calculated until the point of depletion of energy substrates, while in the in vivo study there were periods of low pH and reduced levels of readily fermentable substrates. The results of this in vivo study also conflict with those observed by Salter et al. [92] with no significant differences in the efficiency of microbial protein synthesis, in spite of the low rumen pH (<5.5) with pulse dose supply.

As the results obtained by Henning et al. [40] suggest that the simple improvement

of synchrony of N and energy supply to the rumen do not increase microbial yield, these authors suggest that the objective, when formulating diets, should be, first, to obtain an even supply of energy and then to ensure the supply of an appropriate amount of rumen available N in relation to the amount of fermentable energy. Only then, would there be any advantage in avoiding a very quick release of N in the rumen.

3.3. Feeding frequency of total diet

Studies of feeding frequency have focused on possible effects on microbial efficiency mediated by changing metabolite patterns in the rumen, and effects on voluntary intake, resulting from changes in the degradation

rates of feeds. However, the increase in feeding frequency is, in fact, a method that allows us to overcome almost all problems of asynchrony between nutrient availability in the rumen.

Feeding frequency effects are clearly more important with housed animals, when the amount of ingested feed and feeding frequency are mainly regulated by the farmer. This is because in the wild state, ruminants can ingest feed during the day, from sunrise until sunset, or even during the night. The amount ingested and the frequency of meals are basically dependent on the desire of the animal and the availability of feed.

Offering the diet once daily can promote substantial diurnal fluctuations in rumen concentrations of ammonia [15, 96, 97], VFA [48, 81] and lactic acid [81]. These extreme conditions of metabolites can inhibit microbial growth and activity and, consequently, microbial degradation of feed [79]. Therefore, an increased frequency of feeding and decreasing metabolite fluctuations [15, 55, 71, 97, 104], can, theoretically, increase the efficiency of utilisation of nutrients in the rumen [3, 47]. However, a high frequency of feeding can decrease daily fluctuation of rumen pH [15, 71, 97, 104], but the average pH can also decrease [29, 97, 104]. Note that if the frequency of feeding results in a rumen pH variation between 5.7 and 5.9, the effect on fibre fermentation can be more negative than a low frequency of feeding that promotes a pattern of variation that decrease pH to values of 5.3, but, also, reach values of 6.7 in different parts of the day [9, 79].

The effects of frequency of feeding on digestibilities of DM, OM, CP, starch and NDF are inconsistent. In several studies, total diet digestibility [31, 77, 96] and feed intake [31, 52, 66, 96, 102] were not affected by distributing the total diet more than once per day. However, Shabi et al. [97] showed increases in post-ruminal digestibility of OM, CP and NSC with increasing feeding frequency, but did not observe effects on

synthesis and efficiency of synthesis of microbial protein.

The reduced fluctuation of rumen ammonia N concentration with a high feeding frequency is probably related to increased ammonia utilisation and a decrease in the amount of ammonia that is absorbed through the ruminal wall, which is reflected in a low N excretion in the urine [25]. The low frequency of feeding decreased the mean concentration of ammonia N [96, 111] and decreased microbial CP supply to the duodenum [15, 17, 96]. The increased ammonia utilisation can result from the increase in fermentable OM content, the more stable pH and the natural rumen buffering, which prevents the decrease in the number of proteolytic bacteria [79], increasing proteolysis and decreasing the amount of dietary protein that escapes fermentation [17]. In these situations, the number of protozoa tends to increase [96]. There appears to be an interaction between the energy level and frequency of feeding in relation to the apparent and true efficiency of bacterial N synthesis, suggesting that the efficiency of bacterial N synthesis can be improved when diets with moderate or high levels of concentrate feeds are offered more frequently [15].

On the basis of effects on rumen function, it is expected that the effects of frequency of feeding on rumen fermentation would be reflected in positive productive responses. However, in the 35 studies published between 1949 and 1983, reviewed by Gibson [33], and in later studies [31, 52, 66, 96], the response to the high frequency of feeding, in terms of milk production, was not always positive. Nonetheless, many producers report beneficial effects [79] and the lack of responses may reflect the greater degree of control over feeding in an experimental situation. Commercial cows are often group-fed in free stalls, with intense competition for feed space and a tendency for meals to be concentrated in the first six hours after feeding.

The interpretation of results of studies in which the feeding pattern is changed is not

always clear. This is particularly true when the diet is rich in quickly fermentable carbohydrates [16]. This is because if the frequency of feeding of a whole diet or of the compound rich in quickly fermentable carbohydrates is changed, there are generally pronounced effects on rumen pH, molar proportions of VFA, or other rumen factors that can influence microbial growth. Thus, the experimental design that offers the clearest interpretation of synchrony effect is one in which the pattern of feeding the protein component of the diet is changed, while all the others are maintained constant [16].

3.4. Changing the frequency and pattern of feeding protein supplements

The effect of changing the feeding frequency (two or five times per day) of the protein supplement (soybean meal or blood meal + maize gluten) on rumen function and on the productivity of dairy cows fed a basal diet comprising 47% alfalfa silage and timothy and 53% concentrate feed, containing barley and maize was evaluated by Robinson and McQueen [80]. Although the results do not support the benefits of a synchronised release of N and energy in the rumen on productive response, they suggest that soluble protein or peptides or both can act as a pool to supply N for microbial growth at specific times when ammonia N concentrations are too low.

The available information about rumen fermentation and passage kinetics of particles in the rumen suggests that there is a time period after feeding when the conditions of fermentation favour the passage of particles recently ingested with characteristics of an appropriate density [79]. In cows fed twice per day, rumination activity is the highest during the night [106] and rumen contents are maximal at midnight and minimal at about 7 a.m. [82]. The period between midnight and the morning feed may be the period of the day with the most rapid passage from the rumen – representing an opportunity for increased pas-

sage of undegraded dietary protein from the rumen. This passage can benefit the readily fermentable protein and starch sources that could negatively affect rumen fermentation and that are more efficiently digested in the intestine.

However, Gill and Robinson [34] and Robinson et al. [83] observed increased undegradable protein supply when the protein supplement was added in the day than when it was added in the night, suggesting that the manipulation of feeding strategies can change the synchrony of nutrient absorption. Robinson et al. [83] also observed that giving the protein supplement at night did not affect pH and rumen ammonia N concentration, but increased rumen apparent digestion of OM and CP and rumen VFA concentrations and decreased non ammonia and non bacterial N supply. Robinson et al. [84] varied the time of feeding protein supplements within the day and suggest that there is considerable diurnal variation in the patterns of bacterial protein and dietary protein that escape degradation. Although it is, generally, assumed that the feeds ingested by the dairy cow with a particle size small enough to leave the rumen will have a short rumen retention time, this study [84] showed that there was a delay (6 to 7 hours) between the ingestion of the protein supplement and changes in the AA profile in duodenal digesta. The long retention times for feeds with small particle size suggest that the amount of dietary protein that escapes rumen fermentation cannot be rigorously predicted through first-order models and that the evaluations of CP fraction, and, perhaps, of other fractions of feeds made on this basis can have little value, unless lag times of passage and digestion are included in the evaluation model.

4. CONCLUSION

Although benefits are expected when dairy cows are fed diets that provide a synchronised nutrient supply for the rumen microbes, the analysed literature shows contradictory evidence of synchronising energy

and N supply to the rumen achieved by changing dietary ingredients, the feeding frequency or the feeding patterns, on rumen fermentation, microbial protein synthesis and on productive responses of dairy cows.

Synchronising N and energy supply to the rumen by changing dietary ingredients can be achieved either by altering the energy source, the N source or both. Studies that measured the effects of changing starch source on rumen fermentation show that more degradable starch tends to decrease rumen pH, increase rumen VFA production, decrease rumen ammonia N concentration and alter the site and the end products of fermentation. The effects of more degradable starch on microbial N supply and microbial efficiency of microbial protein synthesis are generally small and production responses are not consistent. Replacing true protein with non-protein N can be considered a change in the synchronicity of diets. However, when interpreting the effects we have to consider not only the effects of rate of release of N, but also the effects of N substrates supplied – peptides, AA or ammonia – on microbial protein synthesis. The effects of changing N and energy sources on rumen fermentation are not consistent and the small number of studies that have measured microbial N supply and the efficiency of microbial protein synthesis along with the conjugated effects of protein and energy sources do not allow us to draw general conclusions. The lack of production response, using this strategy, is not clearly explained by the effects on rumen fermentation, suggesting the influence of other factors.

The above strategy for altering synchrony presents some problems, since it is not possible to identify whether the responses observed in some studies are an effect of synchrony or a factor associated with the manipulation of the ingredients (level and type) themselves. These problems could be overcome, at least partially, by supplying the same ingredients according to different patterns of feeding.

Although some *in vitro* and rumen infusion studies have observed beneficial effects of synchrony on microbial growth and efficiency of microbial protein synthesis, others suggest that asynchrony between N and energy availabilities in the rumen have only short-term effects on bacterial growth. Therefore, the objective when formulating diets, should be first, to obtain an even supply of energy, and second, to ensure the supply of an appropriate amount of available N and only then would there be any advantage in assuring a synchrony supply of energy and N.

The interpretation of the results from production studies in which the feeding pattern of a whole diet is changed is not always clear, in particular, when the diet is rich in quickly fermentable carbohydrates. This is because there are generally pronounced effects on rumen fermentation that can influence microbial growth. Thus, the experimental design most suitable for studying synchrony effects seems to be the one in which only the pattern of feeding the protein supplement is changed. Altering the time of day in which the protein supplement is supplied seems to alter microbial protein supply to the duodenum and the passage of dietary protein that escapes degradation. The studies analysed suggest that the amount of dietary protein that escapes rumen fermentation cannot be rigorously predicted through first-order models and that lag times of passage and digestion should be included in the models.

The results found in this review suggest that synchrony effects are less important *in vivo* than was theoretically expected, agreeing with the opinions of Sauvant and Van Milgen [94] and Dawson [26] that ruminants have developed some mechanisms to overcome or minimise the effects of asynchrony.

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