

Nutritional limitations to increased production on pasture-based systems

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The constraints to high levels of milk production imposed by a high-quality-pasture diet, and development of feeding strategies to overcome these limitations, were examined by modelling the nutritional status of New Zealand Friesian and North American Holstein–Friesian dairy cows grazing high-quality pasture. The Cornell Net Carbohydrate and Protein System (CNCPS) was used to predict sensitivity of milk production to a 10 % change in the composition of pasture nutrients. The rate at which fibre and protein were degraded in the rumen and the value given to effective fibre and lignin content significantly affected the supply of metabolisable energy and protein, and the profile of amino acid supply. The first limiting factor in milk production when only high-quality pasture was fed was metabolisable energy supply, while specific amino acids, particularly methionine and lysine, limited milk production when >20 g/kg diet consisted of a grain supplement. Compared with cows fed a total mixed ration in confinement, North American Holstein–Friesians grazing all pasture produced less milk (29.6 v. 44.1 kg/d). Of the difference in milk production 61 % could be attributed to a lower DM intake (19 kg/d v. 23.4 kg/d). Predictions using the CNCPS indicated that supply of metabolisable energy was the first-limiting factor for milk production from high-quality pasture (251 g crude protein (N×6.25)/kg, 432 g neutral-detergent fibre/kg, 77 % *in vitro* DM digestibility), rather than metabolisable protein or amino acids. In addition, these nutritional limitations imposed by pasture diets will be greater for dairy cow genotypes that have not been selected for high performance within a pasture system.

Pasture diet: Nutrients: Dairy cow genotype: Modelling

The profitable production of milk solids from pasture-based systems is dependent on high levels of pasture production being efficiently harvested by grazing dairy cows of high genetic merit. This outcome is achieved using appropriate stocking rates, a condensed calving pattern in seasonal systems and the judicious conservation and supplementation of feeds (Holmes & Wilson, 1984). In all-pasture systems an optimum stocking rate ensures high utilisation of spring pasture without large amounts of pasture conservation, but avoids the need to purchase expensive supplements during times of the year when feed demand exceeds current pasture growth. The advantages of these feeding systems centre around the low cost of pasture compared with systems based on concentrate and forage. In a favourable economic environment a greater variety of pasture-based systems may be used, with varying levels of supplementation and year-round milk production to maximise farm profitability.

Although the nutritional constraints of pasture have been examined (Waghorn & Barry, 1986; Beever & Thorpe,

1997; Clark *et al.* 1997), there are a large number of possible interactions between the supply of dietary nutrients and the animal requirement for nutrients. The prediction of dairy cow performance across a range of different feeding regimens, production levels and climates can best be made with the use of complex models.

One such model, used widely for ration evaluation and the basis of the National Research Council (2001) recommendations, is the Cornell Net Carbohydrate and Protein System (CNCPS) model. The CNCPS is an integrated set of equations and transfer coefficients that describe physiological processes in cattle, and has been evaluated for cattle fed forage and concentrate diets in confinement (Fox *et al.* 1992; Russell *et al.* 1992; Sniffen *et al.* 1992) and for pasture-based diets (Kolver *et al.* 1998a). The model predicts the nutrient supply from digestion and absorption, nutrient requirements for metabolism and production, and nutrient excretion. It is one of a small number of models which attempts to predict the supply of, and requirements for, amino acids (AA) by dairy cows.

The feeding of supplements to grazing dairy cows has been comprehensively reviewed by Kellaway & Porta (1993) and other authors (Beever & Thorpe, 1997; Stockdale, 2000). Most of the experiments reviewed involved grazing cows with only moderate levels of production and nutrient demand. The increasing use of the North American Holstein–Friesian (NA HF) genotype, with its large requirement for nutrients, can be used as a model to identify the level of production per cow that high-quality pasture is capable of supporting. High levels of DM intake in the range 17–20 kg DM/d have been reported (Meijs & Hoekstra, 1984; Hoden *et al.* 1991; McGilloway & Mayne 1996; Bargo *et al.* 2002), but specific nutrients limiting milk production have been identified in only a few studies. Metabolisable energy (ME) is thought to limit milk production from forage diets (Kolver & Muller, 1998; National Research Council, 2001), but the supply of protein to the duodenum has also been proposed to limit milk production from high-quality pasture to approximately 25 kg milk/d (Beever & Siddons, 1986). By understanding the supply of pasture nutrients, and the order in which nutrients are first-limiting in milk production, appropriate strategies for supplemental feeding may be developed. The present paper examines this objective using a modelling approach to describe the nutrition of high-producing Holstein–Friesian dairy cows grazing high-quality pasture.

Nutrient requirements and supply

The requirements of dairy cows for specific nutrients will be driven by the level and composition of milk production, maintenance and pregnancy requirements, the extent of body tissue mobilisation and to some extent the quality of the diet.

Table 1 shows the energy, protein, AA and selected macromineral requirements for cows producing 25 or 35 kg milk, as predicted by the CNCPS for cows grazing high-quality pasture. Assuming no live-weight loss, intakes of high-quality pasture of 17.3–19.1, and 18–21.7 kg DM/cow per d were required for 550 and 650 kg cows respectively. These intakes are comparable with those calculated by

Mayne & Gordon (1995) for medium- and high-genetic-merit cows grazing pasture.

Low pasture DM intake has been identified as a major factor limiting milk production from high-producing cows under grazing conditions (Leaver, 1985; McGilloway & Mayne, 1996; Beever & Thorpe, 1997; Kolver & Muller, 1998). Mayne & Wright (1988) estimated that when no pasture quantity and quality restrictions exist, pasture DM intake by large (600 kg) high-yielding dairy cows can reach 35 g/kg live weight (21 kg DM/d). This estimate is in line with the 34 g/kg live weight (19.1 kg DM) reported by Kolver & Muller (1998) for early-lactation cows grazing high-quality pasture. Using the maximum pasture intake suggested by Mayne & Wright (1988), Beever & Thorpe (1997) calculated that if the ME density of pasture was 11.5 MJ/kg DM, this maximum intake of pasture equated to an ME intake of 235 MJ/d, with approximately 170 MJ/d available to support milk production. Assuming no substantial change in body tissue, this intake would theoretically support the production of approximately 32 kg milk of standard composition per d.

Consequently, under good grassland management practices, pasture intake is normally sufficient to meet the requirements of the medium-sized cow, but will be insufficient to meet the requirements of larger cows producing high levels of milk (Table 1). It is the greater milk production relative to intake capacity of larger animals, usually with a high proportion of North American genetics, which results in a greater energy deficit. The level of total intake on pasture is less than that which can be achieved when concentrates comprise a substantial proportion of the diet, and must be a result of physical constraints, such as the maximum amount of time available within the day to graze fresh forage, given that sufficient time must be devoted to the essential processes of rumination and resting. Equally, the rate at which ingested material is removed from the rumen by the competing processes of digestion and passage will be important, and the intake of water associated with the forage, which may approach 70–90 kg/d, must not be disregarded.

Data from grazing studies at Dairy Production Research Centre, Teagasc, Moorepark, Republic of Ireland (Stakelum, 1993) suggest that for each 1 kg increase in milk yield (over the range 15–30 kg milk/d), cows will consume an extra 0.4–0.5 kg DM/d. However, for cows yielding >30 kg milk/d the nature of this relationship is unknown, but it is speculated that because of sward and animal behaviour constraints that restrict intake, this marginal intake response will tend towards a plateau (McGilloway & Mayne, 1996). The provision of complementary concentrates with high nutrient concentrations will be a necessary component of any grazing strategy developed with high-genetic-merit high-yielding dairy cows in early lactation.

Modelling the performance of grazing dairy cows

Sensitivity of milk production to changes in nutrient supply

Understanding the sensitivity of milk production to changes in specific nutritional components of a pasture diet allows limiting nutrients to be identified, as well as opportunities to

Table 1. Nutrient requirement* and supply for cows of 550 or 650 kg live weight

Live wt (kg)	550		650	
	25	35	25	35
Milk production (kg)				
Nutrient requirements				
Metabolisable energy (MJ/d)	207	229	216	260
Metabolisable protein (g/d)	1704	1947	1730	2222
Methionine (g/d)	31	35	31	40
Lysine (g/d)	103	118	105	134
Ca (g/d)	136	155	145	184
P (g/d)	67	76	72	90
Nutrient supply				
DM intake: kg/d	17.3	19.1	18.0	21.7
g/kg live wt	31	35	30	33

*Predicted using the Cornell Net Carbohydrate and Protein System model (Cornell University, Ithaca, NY, USA). Assumes no live-weight gain or loss. Energy requirement for walking 1 km included.

improve production. Using experimental data from New Zealand and the USA, Kolver *et al.* (1998a) evaluated the CNCPS model for dairy cows fed pasture-based diets. The CNCPS was able to give a realistic prediction of ME and metabolisable protein (MP) supplies, and of subsequent milk production when cows were fed medium- to high-quality pasture (65–80 % *in vitro* DM digestibility). Using input criteria described by Kolver *et al.* (1998a), a sensitivity analysis was made of the model-predicted milk production to nutrient changes in the diet. Table 2 summarises the sensitivity of ME-, MP- and AA-allowable milk to a 10 % change in nutrient and digestion characteristics of an all-pasture diet. The base milk production indicates the predicted milk production before sensitivity changes were made, and has been reported by Carruthers *et al.* (1996).

A higher DM intake increased the supply of nutrients available for milk production; ME-, MP- and AA-allowable milk increased proportionately. The converse was true for a decrease in DM intake. A 10 % increase in pasture neutral-detergent fibre (NDF) above base-level NDF reduced ME-allowable milk by 0.7 kg/d. This outcome was probably a result of the model predicting a lower non-structural carbohydrate content and reduced synthesis of microbial protein, which also resulted in a lower AA-allowable milk production.

A reduced NDF content increased ME-allowable milk (0.5 kg/d) and AA-allowable milk (0.2 kg/d). An increase in the effective fibre of pasture increased AA-allowable milk production, largely by predicting increased microbial growth. Reducing effective fibre resulted in lower ME-, MP- and AA-allowable milk production relative to base levels. This outcome was a result of reduced rumen pH and an increased passage rate. The proportion of lignin in the diet affected predicted milk production; an increase in lignin from 60 to 66 g/kg NDF decreased ME- and AA-allowable milk by 0.3 and 0.4 kg/d respectively. A lower lignin content concomitantly increased allowable milk production, largely through more NDF being digested.

Higher crude protein (N × 6.25; CP) concentrations reduced ME-allowable milk, due primarily to a greater predicted cost of urea synthesis and excretion. Lower levels of CP resulted in the model predicting higher ME- and AA-allowable milk levels, although MP was decreased. The higher ME-allowable milk level was a reflection of a lower energy cost associated with excreting excess N, the higher AA-allowable milk level was a result of an improved AA profile from improved microbial growth with lower dietary CP and higher non-structural carbohydrate levels, and the lower MP was due to a reduction in protein intake. Changes

Table 2. Sensitivity of metabolisable energy (ME)-, metabolisable protein (MP)-, and amino acid (AA)-allowable milk production to a 10 % change in base prediction feed characteristics (Kolver *et al.* 1998a)

	Change in milk production from base prediction (kg/d)		
	ME-allowable milk production	MP-allowable milk production	AA-allowable milk production
Base prediction* (kg/d)	21.6	24.3	22.9
DMI (15.1 kg DM/d)†			
+ 10 %	+2.9	+2.8	+2.4
– 10 %	–3.0	–2.8	–2.4
NDF (460 g/kg)†			
+ 10 %	–0.7	–0.8	–0.9
– 10 %	+0.5	+0.2	+0.2
eNDF (400 g/kg NDF)†			
+ 10 %	+0.1	+0.7	+1.2
– 10 %	–0.3	–1.2	–1.8
Lignin (60 g/kg NDF)†			
+ 10 %	–0.3	–0.4	–0.4
– 10 %	+0.3	+0.3	+0.5
CP (234 g/kg)†			
+ 10 %	–0.4	+0.3	–0.7
– 10 %	+0.5	–0.4	+0.8
Soluble CP (272 g/kg CP)†			
+ 10 %	sab	–0.4	–0.2
– 10 %	sab	+0.4	+0.2
NDF rate (13 %/h)†			
+ 10 %	+0.5	+0.7	+1.0
– 10 %	–0.5	–0.8	–1.1
CP rate (22 %/h)†			
+ 10 %	sab	–0.7	–0.3
– 10 %	sab	+0.8	+0.4
Feed EAA†			
+ 10 %	sab	sab	+0.7
– 10 %	sab	sab	–0.7

DMI, DM intake; NDF, neutral-detergent fibre; eNDF, effective NDF; CP, crude protein (N × 6.25); NDF rate, B2 carbohydrate fraction; CP rate, B2 protein fraction; EAA, essential amino acids.

* Base predicted is the predicted milk production for an all-grass diet (Carruthers *et al.* 1996). When values did not change from base evaluation, same as base (sab) was entered in the table for ease of identifying the effect of the variable in question.

† Values used in base prediction.

in CP solubility from base level (272 g/kg CP) had a small effect on predicted milk production. This finding is in contrast to those of Fox *et al.* (1995), and could be a result of a comparatively lower base CP solubility. Also, a consideration is that while the synthesis and excretion of urea incurs a metabolic energy cost, the impact this factor has on the maintenance requirement of the dairy cow is not well quantified, and currently may be overestimated by the National Research Council (2001; DG Fox, Cornell University, personal communication), especially for cows that are metabolically adapted to high-protein diets.

The model was very sensitive to changes in the rate of NDF degradation (B2 carbohydrate fraction). Increasing the rate from 13 %/h to 14.3 %/h increased ME-, MP-, and AA-allowable milk production as a result of an increase in the predicted energy content of pasture. The increase in AA-allowable milk was associated with a greater predicted microbial yield. The inverse was true when NDF degradation rate was decreased. The small changes in predicted milk production when the B2 protein degradation rate was altered were largely associated with changes in the rumen N balance and subsequent excretion of urea.

A change in the composition of essential AA of undegraded pasture had little effect on ME- or MP-allowable milk, although the AA profile was altered sufficiently to change AA-allowable milk.

Targeting pasture with a lower lignin content, a higher rate of NDF degradation and, in some cases, a lower rate of protein degradation will increase energy and protein supply to the dairy cow. A key feature of high-quality pasture, compared with pasture of medium or poor quality, is the high rate of fibre degradation. Rates can be as high as 9–16 %/h (Kolver, 1997) and this level is associated with intense rumen fermentation, rumen pH between 5.8 and 6.2, and high milk yields (Kolver & de Veth, 2002).

Model application

The level of milk production predicted by the CNCPS is a reflection of the limited availability of nutrients (ME, MP and AA). This feature can be used for designing and interpreting animal experiments, and for evaluating farm rations. In the evaluation of the CNCPS (Kolver *et al.* 1998a), milk production of cows in eighteen pasture-based treatments was predicted to be limited by ME supply, while the first-limiting factor for milk production of the remaining six pasture-based treatments was the supply of AA (Table 3). AA tended to be

limiting at higher levels of concentrate supplementation and milk production, whereas ME was predicted to be the first-limiting nutrient on pasture-only diets.

To further investigate which nutrients limit milk production at different levels of supplementary feeding, the following simulation was conducted. The data of Carruthers *et al.* (1996), obtained from housed cows fed high-quality pasture (/kg DM; 234 g CP, 460 g NDF, 115 MJ ME), was adapted to a grazing scenario by adjusting ME requirements for grazing activity (National Research Council, 1989), and by increasing DM intake to 15.8 kg DM/d (35 g/kg live weight). Substitution rate was set at 0.8 kg pasture DM/kg supplement DM, and total DM intake was 15.8, 16.1, 16.5, 16.8, and 17.2 kg DM/d for pasture-based diets containing 0, 100, 200, 300 and 400 g cracked maize supplement/kg (14 MJ ME/kg DM).

The curvilinear milk response predicted by the first-limiting nutrients is similar to the response curve commonly observed when increasing levels of grain are fed (Gordon, 1984). The decreasing marginal response resulted in an overall milk response of 0.33 kg/kg supplement when the diet contained the grain supplement at 400 g/kg (6.9 kg supplement DM). This outcome is similar to the average response of 0.28 kg/kg grain DM (Grainger & Matthews, 1989) obtained from cows consuming ryegrass (*Lolium perenne*)–white clover (*Trifolium repens*) pasture of high quality and fed 3.2 kg grain.

The first limiting factor for predicted milk production from pasture diets containing up to 200 g grain/kg (3.3 kg grain DM) was the supply of ME. AA were predicted to limit milk production at supplementation rates >200 g/kg. Although all these supplemented rations had an NDF content >310 g/kg and a CP content >179 g/kg, thereby meeting National Research Council (1989) requirements, production was limited by the profile of AA supplied to the cow. Methionine and lysine were predicted to be first limiting in this modelling of maize grain supplementation. This finding may explain the reduced marginal response to concentrates as identified by Kellaway & Porter (1993), and also the inconsistent response of pasture-fed dairy cows to supplements of bypass protein (Kellaway & Porta, 1993).

Reformulation of the supplement to account for the identified nutrient deficiencies allowed potentially more milk to be produced from the same intake of pasture and supplement. The rumen pH resulting from the 400 g grain/kg ration was predicted to be 5.98. Including a fibre source as well as providing the limiting AA increased the

Table 3. Predicted order of limitation of metabolisable energy (ME)-, metabolisable protein (MP)- and amino acid (AA)-allowable milk production

Order of limitation (kg milk/d)	No. of treatments	Reference*
ME supply first-limiting factor for milk production:		
ME (19.4), MP (21.4), AA (23.2)	6	Carruthers <i>et al.</i> (1996), ES Kolver (unpublished results), Hongerholt (1995)
ME (23.1), AA (25.7), MP (28.2)	12	Carruthers <i>et al.</i> (1996), Holden <i>et al.</i> (1994), Kolver <i>et al.</i> (1998b), Mackle <i>et al.</i> (1996)
AA supply first-limiting factor for milk production:		
AA (32.6), MP (33.9), ME (35.5)	4	Holden <i>et al.</i> (1995)
AA (32.1), ME (32.7), MP (35.9)	2	Holden <i>et al.</i> (1994), Hongerholt (1995)

* Studies cited are those that were used to evaluate the Cornell Net Carbohydrate and Protein System model (Kolver *et al.* 1998a).

AA-allowable milk to the level of ME-allowable milk production. Replacing a proportion of the grain supplement with 1 kg maize silage DM, 0.1 kg soybean meal DM and 0.1 kg fishmeal DM achieved this increase without changing supplement or total DM intake. Including 0.1 kg soybean meal DM and 0.1 kg fishmeal DM in the 300 g grain/kg ration similarly increased AA-allowable milk levels to those of ME-allowable milk, without changing supplement or total DM intake. While mobilisation of body tissue will increase the supply of ME, AA appeared to be a second-limiting factor, or at best co-limiting, for milk production from high-quality pasture containing 234 g CP/kg.

The variable responses of grazing dairy cows to supplements of bypass protein reported in the literature probably reflect the changing nature of the first-limiting nutrient for a given feeding and production scenario. Under the animal, pasture and climatic conditions used in this modelling investigation, a milk response to an increased supply of AA would be likely only if additional ME was supplied either by dietary supplementation or by an increase in tissue mobilisation.

First-limiting nutrients for milk production from high-quality pasture

Comparison of pasture and total mixed rations

The comparison of pasture and total mixed ration (TMR) diets when consumed by high-producing cows (Kolver & Muller, 1998) graphically illustrates the nutrients which limit milk production, and the relative merits and nutritional problems associated with high-quality pasture. Holstein cows were fed TMR in confinement or intensively-grazed pasture with no supplements during spring. The composition of the TMR (g/kg DM; 191 CP, 330 soluble CP, 307 NDF, 190 ADF, 390 non-structural carbohydrate, 16.3 MJ net energy for lactation, 76 % *in vitro* DM digestibility) was in accordance with National Research Council (1989) recommendations for high-producing dairy cows, and the pasture was of high quality (g/kg DM; 251 CP, 306 soluble CP, 432 NDF, 228 ADF, 209 non-structural carbohydrate, 16.5 MJ net energy for lactation, 77 % *in vitro* DM digestibility).

The difference in nutrient intake between TMR- and pasture-fed dairy cows in this study (Table 4) indicates the potential nutrient intake of high-producing Holstein cows, and the extent to which intake is constrained by a grazing system based on high-quality pasture. A pasture DM intake

of 19 kg/d (Table 4) was associated with a milk production of 29.6 kg/d (Table 5). This production is similar to the 30 kg milk/d, which McGilloway & Mayne (1996) suggested as the potential milk production of high-yielding cows grazing pasture with no supplementary feeds.

The DM intake (23.4 kg/d) and milk production (44.1 kg/d) of cows fed TMR in this study indicates the potential milk production when DM intake is not limiting, and when nutrients are balanced in the ration. Intake of nutrients, rather than energy content of pasture *v.* TMR, appears to be the primary factor constraining milk production from high-quality pasture. Even after accounting for differences in live weight, grazing cows consumed DM at 33.9 g/kg live weight, compared with 39.3 g/kg live weight for cows fed TMR (Table 4).

Reasons for the reduced intake are speculative. Pasture and TMR had similarly calculated net energy of lactation contents and *in vitro* DM digestibilities, but pasture had a higher NDF content. The high *in vivo* digestibility of pasture NDF (75 %) is comparable with other reported values (Van Vuuren *et al.* 1992) and suggests that the upper limit to intake of high-quality pasture may be less related to the effect of rumen fill, and more to the constraint imposed by the grazing time and bite rate required to consume 140 kg fresh pasture/d. Using an average grazing time of 510 min/d, and a bite rate of 55 bites/min (Leaver, 1985), the grazing cows in this study would have required 0.68 g DM/bite in order to consume 19 kg DM/d. Although an average of 0.35 g DM/bite over the grazing season has been reported (Leaver, 1986), recent studies with high-producing cows have measured values ranging from 0.4 to 1.1 g DM/bite (McGilloway & Mayne, 1996). That a similar range of DM intake (17–20 kg/d) has been reported with grazing cows in The Netherlands, UK, Republic of Ireland and France (Meijs & Hoekstra, 1984; Arriaga-Jordan & Holmes, 1986; Stakelum, 1986; Hoden *et al.* 1991; McGilloway & Mayne, 1996), suggests a 'ceiling' pasture DM intake that limits milk production to approximately 30 kg/d. It must be recognised that this is an average value; in the study of Kolver & Muller (1998) the DM intake of grazing cows ranged from 16.6 to 21.6 kg/d and milk production ranged from 26 to 37.6 kg/d. In New Zealand pasture DM intakes of ≤ 45 g/kg

Table 4. Nutrient intake of Holstein cows grazing pasture or fed a total mixed ration (TMR) in confinement (Kolver & Muller, 1998)

	Pasture	TMR
Nutrient intake (kg/d)		
DM	19.0	23.4
Crude protein (N \times 6.25)	4.9	4.7
Neutral-detergent fibre	8.5	7.6
NE _L (MJ/d)	135.6	168.2
Nutrient intake (g/kg live wt)		
DM	33.9	39.3
Crude protein	8.5	7.5
Neutral-detergent fibre	14.7	12.1

NE_L, net energy of lactation.

Table 5. Production and composition of milk, live weight and body condition score of Holstein cows grazing pasture or fed a total mixed ration (TMR) in confinement (Kolver & Muller, 1998)

	Pasture	TMR
Milk production		
Milk (kg/d)	29.6	44.1
4 % FCM (kg/d)	28.3	40.5
Fat (g/kg)	37.2	34.8
Protein (g/kg)	26.1	28.0
Fat (kg/d)	1.1	1.52
Protein (kg/d)	0.77	1.22
Live wt and body condition score*		
Live wt (kg)	562	597
Body condition score	2.02	2.50

4 % FCM, $0.40 \times$ milk yield (kg/d) + $15 \times$ fat yield (kg/d).

*Five-point body condition scale (1, thin to 5, fat).

live weight have been estimated (Holmes, 1987), but quantitatively this intake is <20 kg DM/d.

Accounting for production differences between pasture and total mixed ration diets

To further understand why the cows grazing pasture in this study produced less milk than cows fed TMR, and to determine the proportion of this decrease attributable to a lower DM intake, the CNCPS model was used to simulate the grazing and TMR treatments. Observed feed and animal inputs were used, as well as inputs described by Kolver *et al.* (1998a) for high-quality pasture (B2 NDF degradation rate 13 %/h, B2 protein degradation rate 22 %/h, 400 g effective fibre/kg fibre).

The model predicted that cows fed TMR would have a ME supply allowing 43 kg milk/d to be produced, which compares with 44.1 kg/d actually produced. Cows grazing pasture were predicted to have a ME supply allowing 27.6 kg milk/d, compared with 29.6 kg milk/d actually produced (Table 6), with the difference between predicted and actual production indicating the amount of energy supplied by tissue mobilisation (a loss of 1 condition score in 209 d). These estimates include an adjustment for energy associated with grazing and walking activity (National

Table 6. Predicted* production of milk yield allowed by the supply of metabolisable energy† of Holstein cows grazing pasture or fed a total mixed ration (TMR)‡

	ME-allowable milk (kg)
Cows fed TMR	43.0
Grazing cows	27.6
Difference§	15.4
Difference accounted for by:	
DMI	9.4
Energy for grazing and walking¶	3.7
Cost of urea excretion**	1.8
Milk composition††	1.1
Live weight‡‡	-0.7
Total§§	15.3

DMI, DM intake.

*Cornell Net Carbohydrate and Protein System (Cornell University, Ithaca, NY).

†Does not include change in body condition score.

‡Predictions were made of the production of grazing cows at the same DMI, activity, cost of urea excretion, milk composition, and live weight, as cows fed TMR in confinement (Kolver & Muller, 1998).

§Difference between predicted ME-allowable milk production of cows consuming pasture and that of cows fed TMR.

||Marginal increase in predicted ME-allowable milk production if cows consuming pasture had the same DMI as cows fed TMR (23.4 kg DM/d).

¶Marginal increase in predicted ME-allowable milk production if cows consuming pasture did not have to expend energy walking to the dairy (paddocks were 1.3 km from the dairy), and grazing (10 % increase in ME maintenance requirements).

**Marginal increase in predicted ME-allowable milk production if cows consuming pasture had the same cost of excreting urea as cows fed TMR (4.52 MJ/d).

††Marginal increase in predicted ME-allowable milk production if cows consuming pasture had the same milk composition as cows fed TMR (g/kg; 34.9 fat, 27.9 protein).

‡‡Marginal decrease in predicted ME-allowable milk production if cows consuming pasture had the same live weight as cows fed TMR (597 kg).

§§Total milk production associated with the marginal differences in DMI, activity, cost of excreting urea, milk composition and live weight of grazing cows v. that of cows fed TMR in confinement.

Research Council, 1989). Possible reasons for this difference in milk production between the TMR-fed and pasture-fed cows were investigated by predicting the amount of extra milk produced by the grazing cow at the same DM intake, activity, cost of synthesising and excreting urea, milk composition and live weight as cows fed TMR in confinement (Table 6). Changes were made in a non-additive manner. These five variables accounted for a total of 15.3 kg of the 15.4 kg difference in predicted ME-allowable milk. The lower DM intake of the grazing cows in this study, thus, accounted for 61 % of the decrease in milk production.

Predicted nitrogen utilisation on pasture

The impact of a high protein intake, high rate of protein degradability in the rumen and low level of non-structural carbohydrate in high-quality pasture has been discussed as contributing to a lower efficiency of N utilisation by the grazing dairy cow (Beever & Siddons, 1986; Ulyatt & Waghorn, 1993; Van Vuuren *et al.* 1993). This reduction has been attributed to an inefficient capture of rumen N as microbial protein and the metabolic cost of synthesising and excreting additional urea.

In the study of Kolver & Muller (1998) *in vivo* apparent digestibility of pasture N was high (84 %), indicating extensive digestion. In comparison with cows fed TMR grazing cows in the study of Kolver & Muller (1998) used dietary N less efficiently, captured a lower proportion of intake N as milk N and were predicted by the CNCPS to excrete more N (as indicated by a greater predicted metabolic cost of urea synthesis and blood concentrations of urea; Table 7). However, because grazing cows had a high pasture N intake (Table 4), and because the efficiency of microbial protein synthesis was predicted to be high and comparable with that of cows fed TMR (Table 7), the CNCPS predicted that AA supply from 19 kg pasture DM would allow production of 35.4 kg milk/d before specific AA would limit milk production. The efficiency of microbial protein synthesis predicted in this model was comparable with efficiency values reported for high-quality pasture (Minson, 1990; Berzaghi *et al.* 1996; Carruthers *et al.* 1996) and TMR (Clark *et al.* 1992).

Table 7. Predicted* utilization of nitrogen by Holstein cows grazing pasture or fed a total mixed ration (TMR) in confinement (Kolver & Muller, 1998)

	Pasture	TMR
Observed N intake (kg N/d)	0.79	0.75
Observed gross N efficiency (g milk N/kg dietary N)	162	273
Predicted cost of urea synthesis (MJ ME/d)	13.0	4.52
Predicted blood urea-N (mg/l)	2.6	2.2
Predicted efficiency of microbial protein synthesis (g N/kg OM truly digested in the rumen)	27.2	30.9
Predicted microbial flow (g N/d)	328	371

ME, metabolisable energy; OM, organic matter.

*Cornell Net Carbohydrate and Protein System (Cornell University, Ithaca, NY).

The model predicted that digestion of the pasture diet would supply essential AA in the following amounts (as a percentage of requirement): methionine 119.1, lysine 121.7, arginine 160.4, threonine 166.1, leucine 127, isoleucine 132.2, valine 141.3, histidine 112.1, phenylalanine 164.9, tryptophan 368.6. Methionine, lysine and histidine were predicted to be the most limiting amino acids for milk production. There are few reports of the AA that are absorbed by lactating cows fed fresh pasture. The studies of Kolver *et al.* (1999), van Vuuren *et al.* (1992, 1993) and Younge (1997) have all reported similar flows of individual amino acids, once flow was adjusted for differences in DM intake. Relative to published AA requirements (Wu *et al.* 1997), data presented by Kolver *et al.* (1999) and calculations based on the data of van Vuuren *et al.* (1992, 1993) show methionine to be limiting, but not lysine. Younge (1997) reported that methionine and lysine were adequate. Arginine and histidine also appeared to be potentially limiting (Kolver *et al.* 1999). These amino acid limitations will only affect production if there are no other first-limiting nutrients.

The model predicted that for cows fed pasture or TMR, bacterial N would account for 63 and 60 % of the N flow to the duodenum respectively. Van Vuuren *et al.* (1992) suggested that maximal duodenal supply of non-NH₃-N was achieved at a dietary N:organic matter value of 38 g/kg when fresh pasture was fed to dairy cows. The corresponding value in the study of Kolver & Muller (1998) was about 36 g N/kg organic matter, which suggests that >35 % of dietary N was lost in the reticulo-rumen. In this modelling scenario, however, when grazing cows were assigned the same DM intake as TMR-fed cows (23.4 kg DM/d), flow of bacterial N to the duodenum was 395.6 g N/d, compared with 370.9 g N/d predicted for the TMR diet. This finding suggests that synthesis of microbial protein from high-quality pasture can be efficient relative to a TMR.

The lower milk protein content of grazing cows in the study of Kolver & Muller (1998) may have resulted from an inefficient utilisation of ingested N. Milk synthesis, however, did not appear to be limited by the supply or profile of AA, which suggests that a larger proportion of AA were partitioned towards gluconeogenesis in the grazing cow. The model predicted that the supply of MP would not become limiting until a milk production of 38 kg/d was reached. Since ME was the first-limiting nutrient in milk production in this simulation, supplementation of high-quality pasture would first need to correct the deficiency in energy rather than AA supply, which might explain the inconsistent milk response of cows consuming high-quality pasture and fed supplemental rumen-undegradable protein (Kellaway & Porta, 1993; Minson, 1990). The generally poor milk response to supplemental methionine and lysine of cows grazing high-quality pasture (Pacheco-Rios *et al.* 1997; Rusdi & van Houtert, 1997) would also tend to support this result.

Predicted improvements in milk production from pasture

The comparison of pasture and TMR (Kolver & Muller, 1998) indicated that high-quality pasture would need to be supplemented with an energy source that supplied sufficient

ME and AA to produce 35 kg milk/d. In this modelling scenario this level of milk production was achieved by supplying the grazing cows in the present study with 4.8 kg cracked maize DM/d (including associated minerals; 230 g/kg DM intake), assuming a substitution rate of 0.7 kg pasture DM/kg concentrate DM (Kellaway & Porta, 1993).

Previous studies have reported that DM intakes for supplemented cows grazing high-quality pasture and cows in confinement were comparable (Muller *et al.* 1995). When grazing cows in the Kolver & Muller (1998) study were assigned the same DM intake as cows fed TMR (23.4 kg DM/d), and supplemented at 400 g/kg DM intake, the CNCPS predicted that 40 kg milk/d could be produced in early lactation. In this scenario a supplement of 9.4 kg DM/d was required for cows consuming 14 kg pasture DM/d. The supplement mix included (kg DM): 5 cracked maize, 3.4 maize silage, 0.5 soybean meal, 0.1 Ren Plus (a bypass protein product; Mopac, Soderton, PA, USA), with 0.4 kg vitamins and minerals.

These levels of supplementation resulted in a higher marginal milk response (1.1 kg milk/kg supplement DM) than might be expected from studies with grazing dairy cows with a lower yield of milk (Stakelum, 1986; Kellaway & Porta, 1993). Heavy dairy cows producing >30 kg milk/d, however, are unlikely to receive sufficient nutrients from pasture alone to maintain production. Studies with these types of cows (Hoden *et al.* 1991; Muller *et al.* 1995; McGilloway & Mayne, 1996) have reported a greater milk response to supplementation than that from lower-producing cows.

Genotype × diet interactions

A growing body of evidence indicates the existence of an interaction between various environmental factors (principally nutrition) and genotype. Studies during the last 15 years have demonstrated that NA HF will be constrained by the limitations of pasture, and pasture systems, to a greater extent than the Friesian genotype which has been selected for high performance on pasture diets. Evidence of genotype × environment interactions for pasture systems have been discussed by Harris & Kolver (2001), Holmes (1995) and Mayne & Gordon (1995). Some of this evidence came from a joint Canadian and New Zealand study in which daughters of Canadian and NZ sires were farmed in both Canadian and New Zealand management systems. There was a re-ranking of sires for yield traits between the two countries (Peterson, 1991). When farmed in the New Zealand environment, daughters of Canadian sires had lower survival rates, while daughters of New Zealand sires had higher culling rates than their Canadian contemporaries in the Canadian farming system (Mwansa & Peterson, 1998). A recent analysis of 100 000 first-lactation cows from sire-proving herds in New Zealand from 1987 to 1999 (Harris & Winkelmann, 2000) measured the main differences between 2-year-old New Zealand Holstein-Friesian (NZ HF) and NA HF. Those cows with a high proportion of NA HF genetics were: heavier (+43 kg); produced the same fat yield but more protein (8 kg) and more milk (390 litres); were less likely to produce a calf by artificial insemination during a seasonal breeding programme (47 % v. 61 %), a measure of the

Table 8. Effect of genotype \times diet interaction in New Zealand (NZ HF) and North American Holstein–Friesians (NA HF) grazing pasture with no supplements or fed a total mixed ration (TMR) for an entire 300 d lactation in a seasonal calving system (Kolver *et al.* 2002)

Genotype	NZ HF		NA HF	
	Grass	TMR	Grass	TMR
Annual production				
Milk yield (kg/cow)	5300	7304	5882	10097
Milk fat (g/kg)	50.3	46.0	42.8	36.2
Milk protein (g/kg)	37.4	36.5	35.0	35.4
Milk solids (MS; kg/cow)	465	602	459	720
Efficiency (kg MS/kg LW)	0.94	1.08	0.81	1.14
Mean LW (kg/cow)	495	556	565	634
Gain during lactation (g/kg LW)	88.9	165.5	35.4	121.5
Not-in-calf rate (%)	7	14	62	29
Intake (g/kg LW)				
Early lactation (spring)	36	40	33	41
Mid lactation (summer)	32	33	33	34
Late lactation (autumn)	30	30	29	33

LW, live weight.

combined ability to show oestrus, conceive and have a successful pregnancy; had lower survival rates from first to second lactation (78 % *v.* 89 %), and from first to fifth lactation (33 % *v.* 60 %).

An economic farm model used to calculate the effects of all these differences between the NZ HF and the NA HF on farm profitability (Harris & Kolver, 2001) showed that the NZ HF produced a higher economic farm surplus, by 12 %. The study also reported that longevity declined by 2.6 d for every 1 % increase in the percentage NA HF ancestry.

These genotype \times diet differences are a function of the 12-month seasonal calving nature of all-pasture systems in New Zealand, and also a reflection of the inadequacy of nutrient supply to NA HF from pasture diets.

A graphic example of the production and survival response of genotype to a pasture diet has been provided by comparing NZ HF and NA HF genetics, both with similar initial genetic merit (breeding worth) values (Kolver *et al.* 2002). On an all-pasture diet, stocked at approximately 80 kg live weight/t DM, NA HF were less likely to get in calf, lost more body condition during spring, gained less live weight during lactation, produced less milk solids per kg live weight than NZ HF (Table 8). In marked contrast, when fed TMR, NA HF had similar fertility, gained live weight at similar rates during mid and late lactation, produced more milk solids and produced more milk solids per kg live weight compared with NZ HF (Table 8).

On pasture, the poorer performance of NA HF seems to be the result of an inability of these animals to consume the extra pasture required to meet their additional energy costs for maintenance and milk production. For example, in spring NA HF had a DM intake of 33 g/kg live weight, compared with the DM intake of 36 g/kg live weight for NZ HF (Table 8). Three possible explanations for this lower intake are that: the NA HF are not 'good grazers'; the limitations on intake imposed by grazing are more severe for larger cattle; the NA HF lack some metabolic adaptation that is present in the NZ HF.

Conversely, with intensive TMR feeding NA HF had a higher intake than NZ HF, especially in late lactation

(33 g/kg live weight *v.* 30 g/kg live weight), and were more efficient producers of milk solids.

Conclusions

The ability to identify specific limiting nutrients, and understand the biological reasons for these limitations, can allow milk production from high-quality pasture to be increased. For animals with large nutrient requirements, such as NA HF, most of this production increase is associated with supplementary feed and is simply a result of increased DM (and thereby ME) intake. The predicted benefits of providing a balanced supply of nutrients arise principally from the reduction in energy costs associated with urea excretion and avoiding the nutrient deficits induced when a large amount of supplement is fed. As the result of an efficient synthesis of microbial protein coupled with the high protein content (> 220 g/kg DM) of pasture, the quantity and profile of AA available for absorption do not appear to be first-limiting in milk production despite (or perhaps because of) the highly-degradable nature of pasture protein. Production can be limited by specific AA, notably methionine and lysine, when a grain supplement is fed in some cases, even at recommended National Research Council (1989) levels of CP and NDF.

The potential for herd milk yields greater than approximately 30 kg/d is dependent on either the provision of supplemental ME or overcoming constraints to *ad libitum* pasture intake. Alternately, dairy cow genotypes that are better suited to diets of grazed pasture could be used to improve the whole-farm profitability of pastoral dairying systems.

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