Interactions Between Energy and Protein (Amino Acids) in Lactating Dairy Cows

Bill Weiss[1]
Department of Animal Sciences
The Ohio State University

Summary

Energy is required for cows to efficiently convert amino acids (**AA**) into milk protein, and crude protein (**CP**) is needed by cows to efficiently convert gross energy into net energy for lactation (**NEL**). In early lactation when cows are in negative energy balance, milk protein yield is likely to increase when supply of the proper AA is increased independent of energy; however, in later lactation, response to AA (or CP) supplementation is dependent on energy supply. In later lactation, if energy allowable milk is approximately equal to actual milk, increasing supply of AA or CP will not greatly affect milk protein yield; however, if energy allowable milk exceeds actual milk, milk protein yield should respond to improved protein nutrition. Because of both economic and environmental reasons, lower concentrations of dietary CP in lactation diets are often encouraged, and in many situations, they have been implemented successfully. However, reducing dietary CP concentrations can reduce NEL intake via reduced digestibility and DM intake. Reducing CP via reducing rumen degradable protein (**RDP**) appears to have the greatest negative effect on digestibility, even when the resulting RDP concentration still appears adequate (e.g., ~10% of diet DM). Therefore, RDP should be maintained in lower protein diets. The negative effects of reducing dietary protein also likely depend on what nutrient or nutrients replace the CP that is being removed from the diet. If CP is replaced with forage NDF, intake often will decrease. In higher starch diets, replacing CP with starch may reduce digestibility, and in lower starch diets, replacing CP with byproduct NDF likely will reduce digestibility.

Introduction

An "interaction" between two nutrients can be defined as a non-additive response when the supply of the two nutrients is altered. For example, if you add 1 additional unit of protein to a diet, you increase milk protein yield by 1 unit and if you add 1 unit of energy you increase milk protein yield by 1 unit; however, if you add 1 unit of both nutrients, rather than getting the additive response (2 units of milk protein), you get 3 units of protein; that is an interaction. Interactions can be positive (greater response than the sum of the expected responses) or negative (lesser response than the sum of the expected response). Interactions between energy and protein would be expected because all synthetic reactions, such as milk protein production, require energy (e.g., ATP) and because enzymes are involved in essentially all biochemical reactions, AA are needed to extract energy from the diet.

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[1] Contact at 1680 Madison Ave., Wooster OH 44676. (330) 263-3622, E-mail: Weiss.6@osu.edu.

Effect of Energy on Response to Dietary Protein

Early lactation

Because of the way many (all?) mammals evolved, diet is not the only source of energy to support lactation. Dairy cows are designed to mobilize body energy reserves in early lactation to support high milk production prior to the cow's ability to consume adequate dietary energy. Because of energy mobilization and repletion, the relationships or interactions between dietary energy and protein will be different in early lactation (defined as the first ~ 4 weeks of lactation) than in mid or late lactation. A cow requires about 3.9 Mcal of metabolizable energy (**ME**) to make 1 lb of milk protein. About 2.5 Mcal of that energy is in 1 lb of milk protein and 1.4 Mcal of that energy is needed to run the reactions and is lost as heat. Conversely, if a cow mobilizes 1 lb of body protein, about 3.7 lb of fat are typically mobilized, releasing a total of 18.6 Mcal of metabolizable energy (**ME**). Because of the cow's ability to mobilize substantially more energy than protein, protein, not energy, is usually first limiting in early lactation.

In theory, if the supply of needed AA is increased in early lactation, milk protein yield should increase and loss of body energy reserves should increase, resulting in a decrease in body condition score (**BCS**). On the other hand, increasing dietary energy but keeping AA supply fixed should not increase milk protein yield greatly but reduce BCS loss. This is exactly what a group of researchers from Norway found (Schei et al., 2005). They fed a control diet that contained adequate energy and protein to meet the requirements of cows during the first 4 wk of lactation. They also fed a diet that had both energy and protein reduced by about 25% compared to the control (Low/Low) and a third diet that reduced energy 25% but kept protein supply equal to control. Milk protein yield was reduced by cows fed Low/Low, but it was not reduced when only energy was reduced (Figure 1). In addition, the low energy/adequate protein diet greatly increased plasma NEFA and ketones, indicating that body fat mobilization increased. This relationship was illustrated even more dramatically in an experiment in which casein was infused into the abomasum of early lactation cows (Galindo et al., 2015; Larsen et al., 2015). In those experiments, infusing casein AA increased milk protein yield by about 0.6 and 0.7 lb/day measured at 5 and 29 days in milk. At the same times, cows infused with casein compared to control cows had calculated NEL balance about 8 Mcal more negative at 5 days in milk and about equal negative energy balance at 29 days (Figure 2). This shows that in very early lactation, if the supply of proper AA is increased, cows will mobilize body energy so that those AA can be incorporated into milk. As lactation progresses, DMI increases so that the effect of increased supply of AA on milk protein yield is maintained but mobilization of body energy is reduced. In other words, with reasonable diets and typical cows in very early lactation, yield of milk protein is mostly dependent on dietary AA supply and is almost independent of dietary energy supply.

Later lactation

The relationship between dietary energy and protein is different for cows past early lactation. In theory, at peak and later lactation, one would expect essentially no response in milk protein yield to increasing the supply of the correct AA if energy was limiting and you would expect little response to additional energy if AA were limiting. As supplies of both were increased, milk protein yield should increase with the response following the law of diminishing returns. Experimental data follow the expected pattern almost exactly. Researchers from France

(Brun-Lafleur et al., 2010) fed diets that varied in MP and NEL from deficient to excess based on the French ration formulation system. When protein was deficient, milk protein yield had almost no response to increasing energy from very deficient to excess (Figure 3). When energy was deficient, increasing MP from deficient to adequate yielded a small increase in milk protein (~0.1 lb/day) with no additional response as energy increased above requirement. When both energy and MP increased from deficient to excess, milk protein yield increased by almost 0.4 lb/day. The response to increasing MP was linear within each level of energy. However within each level of MP, response to increasing energy followed a diminishing return function; milk protein yield increased linearly as energy increased until the energy requirement was met, then no additional increasing milk protein yield was observed as energy increased. What this means is at peak and later stages of lactation, maximum response to AA supplementation or increased dietary MP requires that energy must be fed at rates equal or greater than requirement. This also means that if we want to improve our ability to estimate responses to changes in AA supply, we need to be able to accurately estimate feed energy and energy requirements.

Effects of Protein on Feed Energy Supply

Most equations used to estimate diet NEL concentrations include concentrations of standard nutrients and digestibility and efficiency coefficients, and the equations generally follow the classic net energy scheme (gross energy to digestible energy to metabolizable energy to net energy). Equations in use today do not capture all the effects protein has on energy concentrations in diets which means that estimated energy values may be erroneous when dietary protein deviates much from typical values. This may become important if we start formulating extensively for AA and that results in lower protein diets.

Dietary protein concentration may affect diet energy values because:

- Protein has 1.3 times more gross energy (**GE**) per pound than carbohydrates
- Average protein is more digestible than fiber (**NDF**) but less digestible than starch
- Increased dietary protein is associated with increased fiber digestibility
- Increasing dietary protein is associated with increased DM digestibility
- Increasing dietary protein usually increases urinary energy loss
- Increasing dietary protein usually increases heat increment

When dietary protein is increased, carbohydrate (fiber and starch) concentration usually is reduced by the same amount. Because protein has about 1.3 times as much energy per pound as carbohydrate, increasing dietary protein concentration usually increases the concentration of GE. On average (this will vary depending on the source of protein in the diet), true digestibility of protein by dairy cows is about 83%, whereas starch and NDF have average digestibilities of about 92 and 48% in lactating dairy cows. Based on differences in GE and digestibility, increasing the concentration of protein in a diet by 2 percentage units and reducing the concentration of NDF or starch by 2 units would change the digestible energy (DE) concentration of the diet by approximately 0.05 or 0.02 Mcal/lb, respectively. Those changes are equal to a 3.5 and 1.4% increase over the DE concentration of an average dairy cow diet.

Effects on digestibility

Protein concentration can affect digestibility of NDF and DM. Adequate RDP is needed to maximize ruminal bacterial growth which is essential for good fiber digestibility. Digestibility of NDF and DM is often reduced when RDP is deficient. For example, when RDP balance (based on the NRC, 2001) system was about 200 g/day deficient, NDF digestibility was reduced 20% compared to a diet that had 27 g/day extra RDP (Lee et al., 2011), and in another experiment (Lee et al., 2012), NDF digestibility was reduced 9% when the diet was 42 g/day deficient in RDP (Table 1). The low RDP diets had 14 to 14.9% CP and 9 or 9.6% RDP. In both experiments, diets deficient in RDP also had significantly lower DM digestibility (7 and 2% lower). Digestibility of DM is similar to energy digestibility; therefore, it is safe to assume the low RDP diets in those studies reduced DE by more than 7 and 2% when changes in GE are factored.

In those studies, RDP was deficient (based on NRC 2001), and one could argue that the response in improved digestibility is simply a result of correcting a deficiency. However, other studies have shown linear increases in NDF and DM digestibilities as CP and RDP increased at concentrations well above expected requirements (Broderick et al., 2008). In that study, diet CP increased from 14.8 to 18.6% and RDP (NRC, 2001) increased from 10.0 to 12.3%. Those increases were associated with a linear increase in NDF digestibility from about 52 to 59% and an increase in DM digestibility from about 68 to 71%. This could suggest that either the RDP requirement is underestimated or that RDP (or protein) has some stimulatory effect on bacteria or the cow even after requirements are met. An alternative possibility is that the effect was not caused by increasing protein concentrations but rather by decreasing starch concentrations. In Broderick et al. (2008), CP replaced starch so that starch concentration decreased from about 28 to 23% as protein increased (Broderick et al., 2008). Increasing dietary starch is associated with decreased NDF digestibility (Ferraretto et al., 2013). This illustrates an important concept in nutrition studies; when the concentration of one nutrient increases as least one other nutrient must decrease and we never know if the response was caused by the increase in the 'test nutrient' or the decrease in what it replaced. Regardless of the mechanism, increasing dietary CP and RDP often increases the DE concentration of diets. This needs to be considered when low protein diets are fed.

Efficiency of converting digestible to metabolizable energy

Dietary protein concentration and AA profile affects the efficiency of converting DE to ME. In an adult cow, the vast majority of AA that are not secreted in milk are eventually oxidized to provide energy. In 2 and 3 year old cows, some AA are retained in the body as growth but that amount is small (<100 g/day) relative to intake of protein. When AA are oxidized, most of the released N is excreted in urine which increases urinary energy loss. On average, each gram of urinary N is associated with about 14.3 kcal of energy. Using the OARDC digestibility database (~500 observations), for a cow that averaged 50 lb of DMI and 76 lb of milk, and fed a diet that averaged 16.5% CP, urinary N excretion averaged 182 g/day or 30% of N intake. The estimated urinary energy for that dataset is 2.6 Mcal/day or about 4% of the average DE intake. On average, for every additional gram of N consumed by a cow (equal to 6.25 g of CP), urinary N will increase by about 0.3 to 0.7 g depending on how much milk protein yield increases (greater urinary N increase when milk protein response is less). For example, if two cows had similar DMI (50 lb/day) but were fed either a 15 or 17% CP diet, intake of CP would be 1 lb greater for the cow fed the high CP diet (Table 2). This is equal to 73 g of N. If milk protein yield was not different, then the cow fed higher CP would excrete about 51 g more N in urine (73 g of N intake x 0.7g urinary N/g intake N). The 51 g of increased urinary N is equal to 0.73 Mcal of increased urinary energy. Overall, the effect on dietary ME from increasing CP is small within the range of dietary CP concentrations that are typically fed to dairy cows.

Efficiency of converting metabolizable to net energy

In addition to the energy contained in the N compounds excreted in urine, energy is required to synthesize those compounds and that energy is measured as heat production. Increased metabolic heat production decreases the efficiency of converting ME to NE. Heat production per unit of GE intake has a positive, but weak, correlation to urinary N excretion, indicating that increasing dietary CP is generally associated with increasing heat production and decreasing efficiency of converting ME to NEL. Using the example above, increasing dietary CP by 2 percentage units would increase urinary N excretion by 51 g and on average that would increase daily heat production by 0.8 Mcal/day (with a very large associated uncertainty). To put this in perspective, on average, a cow eating 50 lb of DMI and producing 75 lb of milk produces about 22 Mcal of non-maintenance heat (i.e., heat increment) per day.

Based on all these assumptions, when CP is increased and starch or NDF is reduced concomitantly, dietary NEL concentration would be reduced by 0.01 to 0.03 Mcal/lb, which is less than the accuracy of our energy estimation equations. When potential associative effects are considered (e.g., Table 1) effects of increasing dietary CP on diet NEL may actually be positive. The bottom line is that with reasonable diets, changing the concentration of CP probably has only a very minor effect on the concentration of NEL in the diet. This should not be interpreted to mean that changing dietary CP is energy neutral. Intake of NEL, not NEL concentration is what matters. On average, increasing dietary CP is associated with increasing DMI (Allen, 2000). The effect on DMI likely is related to what other nutrient changes when CP changes; however, this has not been teased out. If forage NDF is increased as dietary CP decreases, a greater negative effect on DMI would be expected than if byproduct NDF was increased. Increasing starch can have variable effects on DMI depending on stage of lactation and energy needs of the cow. Overall, formulating diets for AA rather than CP should reduce the CP concentrations of diets, but this has the distinct potential of reducing NEL intake which would result in reduced milk component yields and/or reduced body condition.

Conclusions

Interactions between dietary protein and energy and stage of lactation dictate whether cows will respond to dietary changes. In early lactation, increasing AA supply can increase milk protein yield independent of any change in energy intake, but in later lactation, milk protein yield will only respond to increased AA supply when adequate energy is available. On the other hand, energy intake is affected by dietary protein. Increasing dietary CP, especially RDP above requirement, can increase NEL intake via enhanced digestibility and DM intake. Maintaining adequate RDP concentrations and carefully considering what other nutrients (e.g., fiber or starch) will change when dietary CP concentrations change is essential to obtain good results from lower protein diets.

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Table 1. Effect of reducing dietary protein concentration on production and nutrient digestibility.

	Control	Low Protein
Experiment 1 (Lee et al., 2011)		
Diet CP, % of DM	16.7	14.8
Diet RDP, % of DM	10.6	9.8
RDP Balance (g/day)	141	-42
DMI, lb/day	54.3*	52.4
Milk, lb/day	86.5*	79.6
Milk protein, lb/day	2.46	2.49
DM digestibility, %	69.7*	68.4
NDF digestibility, %	54.0*	49.2
MUN, mg/dL	12.5*	8.3
Experiment 2 (Lee et al., 2012)		
Diet CP, % of DM	15.6	14.0
Diet RDP, % of DM	10.0	9.1
RDP Balance (g/day)	27	-203
DMI, lb/day	54.8	54.1
Milk, lb/day	86.2	83.8
Milk protein, lb/day	2.62*	2.46
DM digestibility, %	60.9*	56.6
NDF digestibility, %	42.8*	34.1
MUN, mg/dL	10.0*	8.4

*Treatment means within an experiment differ ($P < 0.05$)

Table 2. Example of how an increase in CP concentration could affect dietary digestible energy (DE) and metabolizable energy (ME) values when DM intake was 50 lb/day (no difference between diets)[1]

	15% CP	17% CP
CP intake, lb/day	7.50	8.50
CP GE intake, Mcal/day	19.3	21.8
CP-DE intake, Mcal/day	12.5	14.2
Change in CP-DE intake, Mcal/day	0	1.7
If starch was replaced as CP increased		
Change in starch intake, lb/day	0	1.0
Change in starch DE intake, Mcal/day	0	-1.8
Net change in DE, Mcal/day	0	-0.1
If NDF was replaced as CP increased		
Change in NDF intake, lb/day	0	1.0
Change in NDF DE intake, Mcal/day	0	-0.9
Net change in DE, Mcal/day	0	0.8
Change in urinary N, g/day	0	51
Change in urinary N energy, Mcal/day	0	0.73
Net change in ME intake		
When starch is replaced, Mcal/day	0	-0.83
When NDF is replaced, Mcal/day	0	+0.07

[1] Assumed apparent digestibility of CP, starch, and NDF as 65, 92, and 48% (OARDC digestibility database) and no negative or positive associative effects were applied. The energy content of CP was assumed to be 2.57 Mcal/lb and 1.91 Mcal/lb for starch and NDF, respectively.

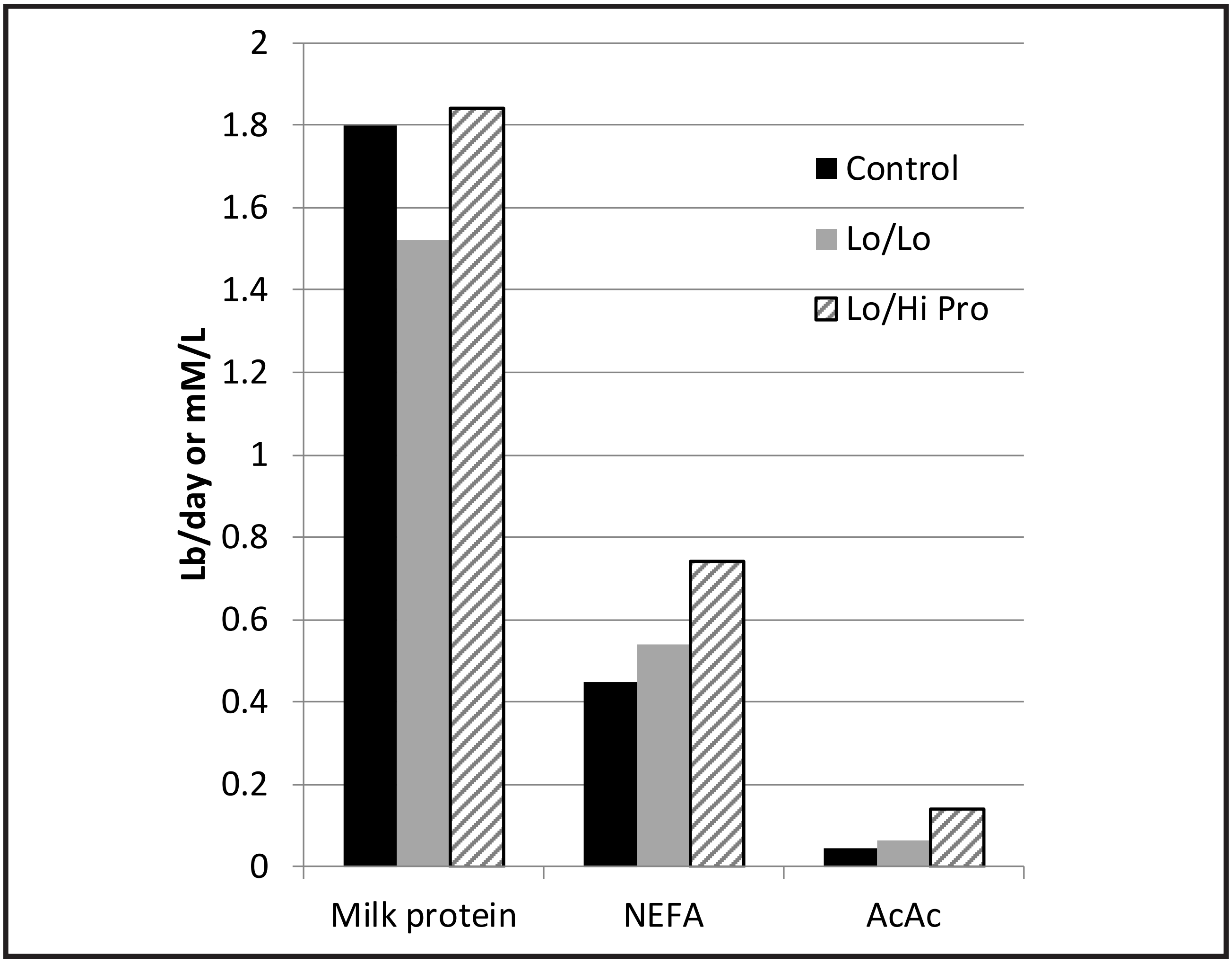

Figure 1. Effect of diets that were adequate in energy and protein (Control), deficient in both energy and protein (Lo/Lo), or deficient in energy but adequate in protein (Lo/Hi Pro) on milk protein yield (lb/day), plasma non-esterified fatty acids (NEFA) and plasma acetoacetate (AcAc). Diets were fed the

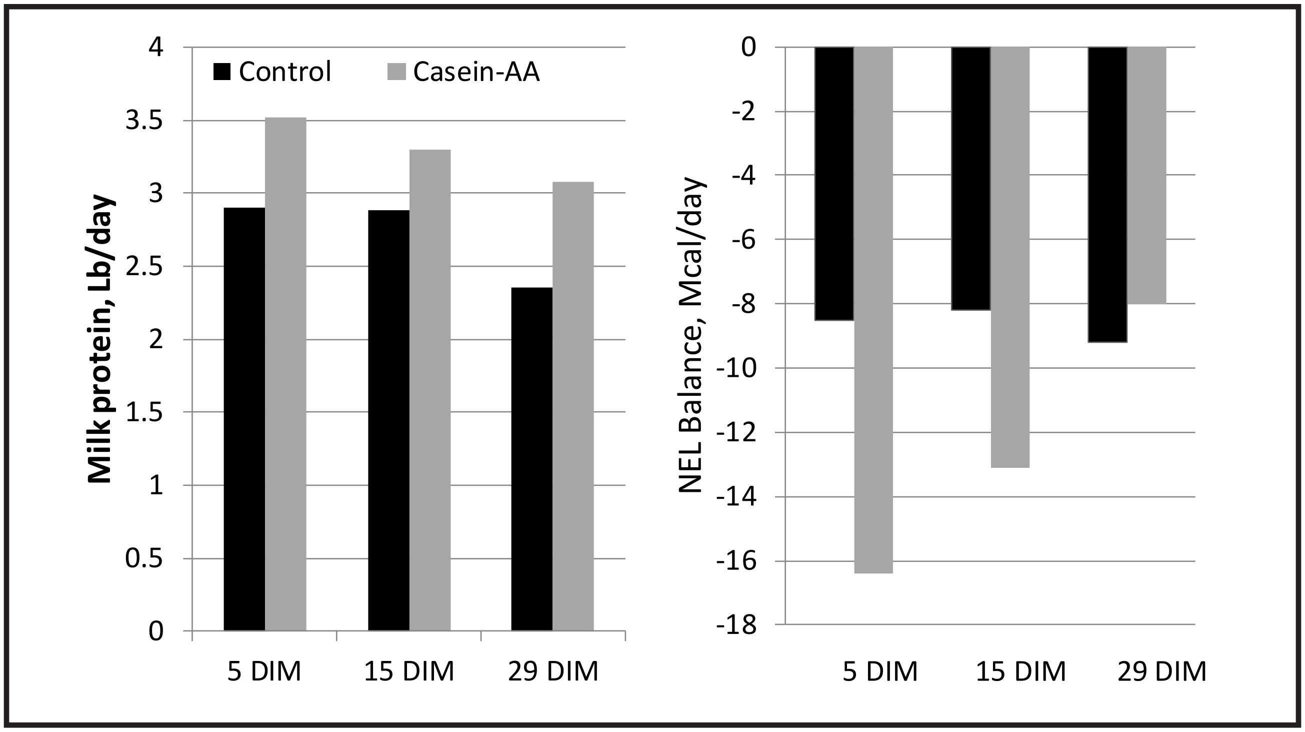

Figure 2. Effect of infusing casein amino acids (Casein-AA) into the abomasum of early lactation cows. The infusion greatly increased milk protein yield but also greatly increased mobilization of body energy (Larsen et al., 2015; Galindo et al., 2015).

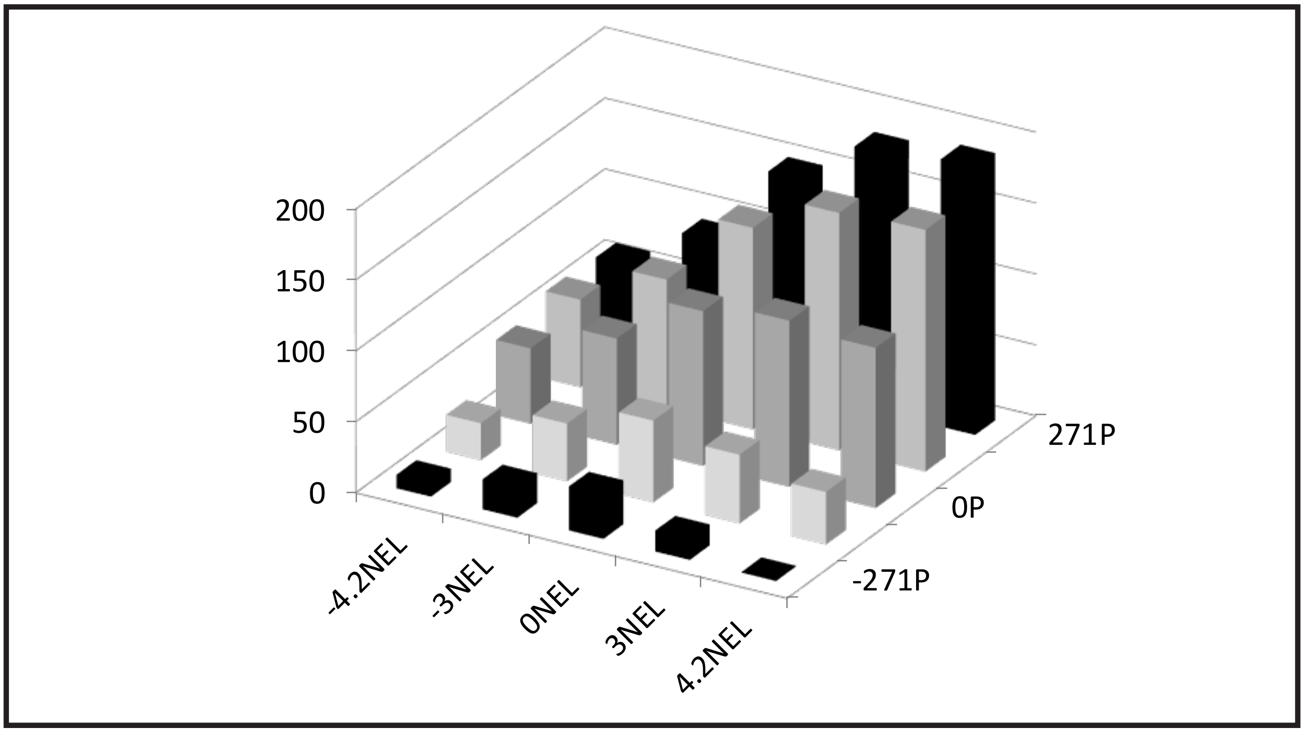

Figure 3. Response to changes in intake of NEL and metabolizable protein (MP) in midlactation dairy cows. Energy and protein were calculated using the French system (Brun-Lafleur et al., 2010). When protein was deficient, essentially no response was observed with increasing NEL, and when NEL was deficient, response to protein was muted.