

B-VITAMIN NUTRITION IN DAIRY COWS

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INTRODUCTION

The B-vitamins include thiamin (B₁), riboflavin (B₂), niacin (B₃), pantothenic acid (B₅), the B₆ complex (pyridoxal, pyridoxamine, pyridoxine), biotin (B₈ or Vitamin H), folic acid (B₉), and B₁₂. Each of the B-vitamins plays a key role as either an enzymatic cofactor or metabolic constituent in many facets of intermediary metabolism. For example, about half of the propionate that reaches the ruminant liver is converted to glucose by a series of enzymatic reactions (Brockman, 1993); biotin, B₁₂, niacin, pantothenic acid, and riboflavin all play essential roles in these reactions. These B-vitamins, along with the others, also play other key roles in the metabolism of carbohydrates, fats, and proteins.

Ruminant B-vitamin research was quite prevalent during the mid 1940's to late 1950's, with the majority of this research being conducted in sheep, calves, and steers. This work clearly showed that even when relatively vitamin-free diets were fed the microbial population of the rumen synthesized B-vitamins. Therefore, determination of B-vitamin requirements for ruminants is difficult. Later work by Miller et al. (1986) and Zinn et al. (1987) showed that B-vitamin appearance at the small intestine exceeded that provided by feedstuffs and that when B-vitamins were supplemented (Zinn et al., 1987) many were degraded or metabolized by the rumen microbial population. The current dogma (NRC, 2001) is that since the ruminant microbial population synthesizes B-vitamins, additional supplementation to dairy cows is unnecessary. While clinical B-vitamin deficiencies are rarely observed in common feeding situations with ruminants, recent research with several B-vitamins has shown that supplementation may improve dairy cow performance (Schwab and Shaver, 2004).

This topic was extensively reviewed and discussed by the authors for the 2004 California Animal Nutrition Conference DSM Nutritional Products Technical Symposium, and therefore much of the information from that review will not be repeated herein. Readers are referred to Schwab and Shaver (2004) for that background.

RUMINAL B-VITAMIN SYNTHESIS

Santschi et al. (2004) used six ruminally-cannulated lactating Holstein cows in a cross-over design to determine the effects of forage to concentrate ratio (**F:C**) on B-vitamin concentrations in different ruminal fractions. Diets contained F:C of either 60:40 (high forage, **HF**) or 40:60 (low forage, **LF**). Ruminal fractions included solids-associated bacteria (**SAB**), liquid-associated bacteria (**LAB**), and particle-free fluid (**PFF**). Increasing dietary concentrates (HF vs. LF) increased concentrations of riboflavin ($P = 0.01$, 40.5 vs. 47.8 µg/g DM), nicotinamide ($P = 0.004$, 77.2 vs. 94.3 µg/g

DM), and pyridoxamine ($P = 0.06$, 7.5 vs. 9.1 $\mu\text{g/g DM}$) in SAB, of nicotinamide ($P = 0.03$, 86.3 vs. 123.3 $\mu\text{g/g}$) in LAB, and total niacin ($P = 0.04$, 618.8 vs. 713.6 ng/mL) in PFF. Increasing dietary concentrates (HF vs. LF) decreased concentrations of pyridoxine ($P = 0.01$, 0.95 vs. 0.63 $\mu\text{g/g DM}$) and true vitamin B₁₂ ($P = 0.01$, 4.0 vs. 3.1 $\mu\text{g/g DM}$) in SAB, true B₁₂ ($P = 0.07$, 6.34 vs. 4.75 $\mu\text{g/g DM}$) in LAB, and pyridoxine ($P = 0.03$, 98.6 vs. 57.2 ng/mL) and biotin ($P = 0.04$, 24.3 vs. 18.5 ng/mL) in PFF. Interestingly, no thiamin was detected in PFF, suggesting that it is entirely sequestered within ruminal bacteria. Overall, B-vitamin concentrations were approximately 10 – 5000 times higher in bacteria than PFF. The authors also reported that when B-vitamin concentration comparisons were made between SAB and LAB, that there were no differences between fractions for riboflavin and total B₆ concentrations but pyridoxal was higher ($P = 0.04$) in SAB than LAB. For all other vitamins, concentrations were higher ($P \leq 0.04$) in LAB than SAB, with a tendency ($P = 0.06$) for biotin. Comparing ruminal digesta concentrations versus dietary concentrations only implies ruminal B-vitamin synthesis. B-vitamin ruminal apparent synthesis (**AS**) can be estimated by subtracting B-vitamin intake from duodenal flow. However, this estimate does not reflect true B-vitamin synthesis as it ignores any potential ruminal degradation, microbial use, or absorption across the rumen wall.

Schwab et al. (2004; 2005a, b) reported on B-vitamin AS in lactating dairy cows; experimental objectives were to determine intakes, duodenal flows, and ruminal AS of B-vitamins in lactating dairy cows fed diets varying in forage and non-fiber carbohydrate (**NFC**) contents. Eight ruminally- and duodenally-cannulated Holstein cows were assigned to four dietary treatments in a replicated 21-d period 4×4 Latin square design with a 2×2 factorial treatment arrangement. Diets were fed as total mixed rations and contained (DM basis) two levels of forage (35 and 60%) and two levels of NFC (30 and 40%). The forage portion of the diets contained 50% corn silage, 33% alfalfa hay, and 17% grass hay (DM basis). Soybean hulls and beet pulp (2:1 ratio) and corn meal and ground barley (2:1 ratio) were included to achieve desired NFC concentrations. No supplemental B-vitamins were fed. Dry matter and organic matter intakes were higher for cows fed the 35% forage diets and the 40% NFC diets. When averaged across diets, AS of individual B-vitamins as a percent of B-vitamin intake was: thiamin (142), riboflavin (228), total niacin (120), total B₆ (39), folic acid (137), and B₁₂ (24,276), clearly showing the importance of ruminal synthesis for most B-vitamins. B-vitamin AS results are presented in Table 1. Increasing dietary forage content decreased ruminal AS of pyridoxine, folic acid, and B₁₂. Increasing dietary NFC content increased ruminal AS of nicotinic acid, nicotinamide, niacin, pyridoxal, B₆, and folic acid, but decreased AS of B₁₂. Biotin AS values were negative for all diets, suggesting either no synthesis in the rumen or destruction by ruminal microflora greater than synthesis. Santschi et al. (2005) also reported negative biotin AS. Selected Pearson correlation coefficients from Schwab et al. (2005b) are presented in Table 2. Thiamin, riboflavin, folic acid, and B₁₂ AS were increased when intake, digestibility, microbial-N production, and ruminal VFA concentration were increased.

Table 1. B-vitamin apparent synthesis in lactating cows fed diets of 35 or 60% forage and 30 or 40% NFC^{1, 2}.

Item	Diet ³				SEM	Effect		
	3530	3540	6030	6040		Forage	NFC	INT ⁴
	mg/d					<i>P</i>		
Thiamin	60.6	47.9	43.8	50.0	5.3	0.13	0.38	0.06
Riboflavin	245.9	253.9	205.7	245.6	19.6	0.16	0.16	0.34
Nicotinic Acid	589	1015	555	771	133	0.31	0.03	0.44
Nicotinamide	-143	532	165	615	99	0.06	<0.001	0.27
Niacin	446	1547	720	1386	196	0.78	<0.001	0.28
Pyridoxal	3.4	13.0	6.0	13.9	2.3	0.42	<0.001	0.69
Pyridoxamine	41.5	41.0	37.0	39.2	3.3	0.21	0.72	0.59
Pyridoxine	-21.8	-24.2	-29.2	-26.7	2.7	0.03	0.98	0.27
B ₆	23.0	29.8	13.8	26.5	4.7	0.15	0.03	0.49
Biotin	-14.9	-10.7	-15.5	-2.6	6.3	0.56	0.19	0.50
Folic acid	16.3	20.2	13.0	16.4	2.0	0.04	0.04	0.86
B ₁₂	102.2	78.6	78.4	60.1	5.9	<0.001	<0.001	0.54

¹Schwab et al. (2004; 2005a, b).

²NFC = non-fiber carbohydrates. Calculated by difference: 100 – (CP + (NDF – NDICP) + Fat + Ash)

³DM basis: 3530 = 35% forage, 30% NFC; 3540 = 35% forage, 40% NFC; 6030 = 60% forage, 30% NFC; 6040 = 60% forage, 40% NFC.

⁴INT = interaction of dietary forage and NFC content.

Table 2. Pearson correlation coefficients^{1, 2} between B-vitamin apparent synthesis (AS) and selected intake and digestive parameters.

Item	B-vitamin AS, mg/d					
	Thiamin	Riboflavin	Niacin	B ₆	Folic acid	B ₁₂
Intake, kg/d						
DM	0.51 ^{***}	0.72 ^{****}	0.23	0.12	0.63 ^{****}	0.61 ^{****}
OM	0.51 ^{***}	0.71 ^{****}	0.23	0.12	0.63 ^{****}	0.61 ^{****}
Rumen dig., kg/d						
DM ³	0.37 ^{**}	0.51 ^{***}	0.10	0.11	0.52 ^{***}	0.52 ^{***}
OM ³	0.40 ^{**}	0.49 ^{***}	0.04	0.14	0.50 ^{***}	0.54 ^{****}
Micr. N flow, g/d	0.65 ^{****}	0.79 ^{****}	0.38 ^{**}	0.14	0.77 ^{****}	0.44 ^{***}
Total VFA, mM	0.51 ^{***}	0.46 ^{***}	0.13	0.23	0.43 ^{***}	0.54 ^{****}

¹Schwab et al. (2005b).

²* *P* < 0.10, ** *P* < 0.05, *** *P* < 0.01, **** *P* < 0.001

³Digestibility corrected for duodenal flow of microbial DM and OM.

The NRC (2001, p. 173) provided estimates of apparent ruminal B-vitamin synthesis in lactating dairy cows based on steer data of Miller et al. (1986) and Zinn et al. (1986). To investigate the validity of this approach we (Schwab et al., 2005b) adapted those data to AS measurements from our experiment by expressing the NRC (2001) estimates on a mg/kg DMI per day (NRC assumed DMI of 22.9 kg/d) basis and multiplying by our across-diet average DMI measurements. These adjusted B-vitamin AS means are compared to our measured mean, minimum, and maximum AS values in Table 3. Relative to our measured AS values, the NRC (2001) closely estimated riboflavin AS, over estimated thiamin, B₆ and biotin AS, and under estimated folic acid AS. The NRC (2001) estimates of niacin and B₁₂ AS were similar to measured maximum and minimum values, respectively. In regards to ranking B-vitamins by amounts synthesized, the two approaches were similar with niacin and riboflavin synthesis being highest, followed by thiamin, B₆, and B₁₂, with lowest values for folic acid and biotin. Due to the variation in relationships between individual B-vitamin AS and nutrient intakes, nutrient digestibility, and microbial N flow, and forage and NFC effects on AS, future prediction equations estimating B-vitamin AS will likely need to be multi-factorial and B-vitamin specific.

Table 3. Comparison of NRC (2001, p. 173) adapted and measured (Schwab et al., 2005b) B-vitamin apparent synthesis.

	B-vitamin apparent synthesis			
	NRC adapted ¹	Measured		
	Mean	Mean	Minimum	Maximum
Thiamin	127	51	44	61
Riboflavin	232	238	206	254
Niacin	1603	1025	446	1547
B ₆	85	23	14	30
Biotin	12	-11	-16	-3
Folic acid	6.2	16	13	20
B ₁₂	62	80	60	102

¹NRC (2001) ruminal synthesis (mg/kg DMI per d) adjusted to average DMI measured in Schwab et al., (2005b).

RUMINAL DEGRADATION OF SUPPLEMENTAL B-VITAMINS

To determine if supplemental B-vitamins escape ruminal degradation, Zinn et al. (1987) used three ruminally- and duodenally-cannulated beef calves (194 kg BW) in a 3 × 3 Latin square design. Diets contained 45% forage and 55% concentrate. Amounts of B-vitamins supplemented were (mg/d): zero (control), thiamin (20 and 200), riboflavin (40 and 400), niacin (200 and 2000), pyridoxine (20 and 2000), pantothenic acid (200 and 2000), folic acid (10 and 100), biotin (2 and 20), and B₁₂ (0.2 and 2). Ruminal B-vitamin escape percent was calculated as 100 × (duodenal flow of vitamin with high level of supplementation – duodenal flow of vitamin with non-supplemented diet) / (vitamin intake with high level of supplementation – vitamin intake with non-

supplemented diet). Duodenal flows of individual B-vitamins were not different ($P > 0.20$) between the control and the lower level of supplementation. At the high level of supplementation flows of thiamin, pyridoxine, pantothenic acid, and biotin were increased ($P < 0.05$). Duodenal flow of B₁₂ remained constant across treatments. Calculated ruminal escape was: thiamin, 52.3%; riboflavin, 1.2%; niacin, 6.2%; pyridoxine, 101.0%; pantothenic acid, 22.1%; biotin 132.5%; folic acid 2.7%; and B₁₂, 10%. Estimates for riboflavin, niacin, folic acid, and B₁₂ escape should be interpreted with caution since they were determined from non-significant treatment differences. Riboflavin, niacin, folic acid, and B₁₂ largely disappeared prior to the duodenum, while supplemental pyridoxine and biotin largely escaped the rumen.

Santschi et al. (2005) studied ruminal disappearance of supplemental B-vitamins in lactating dairy cows. Four ruminally-, duodenally-, and ileally-cannulated cows were fed a 58% forage (mixed grass/alfalfa silage-based) supplemented with the following B-vitamins (mg/d): thiamin (300), riboflavin (1600), nicotinamide (12000), pyridoxine (800), biotin (20), folic acid (2600), and B₁₂ (500). Chromic oxide was included as the digesta flow marker. Digesta was collected for 4 d prior to and 4 d during B-vitamin addition. Disappearance prior to the small intestine was calculated with the following equation: $100 - (100 \times [(duodenal\ flow\ supplemented - duodenal\ flow\ control)/supplemented\ amount])$. B-vitamin disappearance prior to the small intestine was: thiamin (67.8%), riboflavin (99.3%), nicotinamide (98.5%), pyridoxine (41.0%), biotin (45.2%), folic acid (97.0%), and B₁₂ (62.9%). Similar to the results of Zinn et al. (1987), ruminal disappearance was greatest for riboflavin, niacin, and folic acid and the majority of supplemental pyridoxine and biotin escaped the rumen.

While the results of Zinn et al. (1987) and Santschi et al. (2005) generally agree, large discrepancies exist between the two reports for pyridoxine, biotin, and B₁₂. Greater emphasis should be placed on the more recent report due to the significant progress made in B-vitamin analytical techniques. Techniques used by Zinn et al. (1987) were largely microbial and less vitamer-specific, whereas Santschi et al. (2005) used advanced techniques such as HPLC and vitamer-specific radio-assay. Clearly, the biotin ruminal escape value of 132.5% given by Zinn et al. (1987) is suspect, unless an unknown recycling mechanism (i.e. salivary) exists for this B-vitamin. While far from conclusive, these results indicate that if ruminants are to be supplemented with B-vitamins via the diet, most would need to be supplied in large amounts or in forms resistant to ruminal degradation.

ABSORPTION OF B-VITAMINS

Ruminal

Limited data indicate that there is no appreciable ruminal B-vitamin absorption in fed-ruminants (Rerat et al 1958a, b; Hoeller et al., 1977; Girard et al., 2001; Girard and Remond, 2003). Rérat et al. (1958a) observed no ruminal B-vitamin absorption in fed sheep but did observe ruminal absorption when B-vitamins were infused into an

evacuated rumen (Rérat et al. 1958b). The authors concluded that B-vitamins could be absorbed through the rumen wall, but in fed-conditions B-vitamins are associated with the ruminal microbial population and therefore are not available for absorption. In vitro data of Hoeller et al. (1977) showed that the rumen wall is largely impermeable to thiamin. Erickson et al. (1991), using lactating dairy cows with evacuated rumens, showed that niacin, primarily as nicotinamide, could be absorbed through the rumen wall. Using lactating dairy cows with catheters placed in the right ruminal vein and auricular artery, Girard et al. (2001) calculated that 0.015 and 4×10^{-6} % of infused doses of folic acid and vitamin B12, respectively, passed the rumen wall within 60 minutes following ruminal infusion. Later work in sheep (Girard and Remond, 2003) confirmed that absorption and passage of folic acid and vitamin B12 into the blood stream through the rumen wall is minimal. These reports along with that of Santschi et al. (2004) which indicated that B-vitamins are primarily sequestered within ruminal bacteria, suggest that the rumen is not a primary site of B-vitamin absorption. Clearly more research is needed to support this premise.

Intestinal

In general, the small intestine is considered to be the primary site of B-vitamin absorption; hence it plays an important role in maintaining and regulating body homeostasis of these nutrients. The intestine receives B-vitamins from the diet that escape ruminal degradation and those produced ruminally or intestinally by bacteria. B-vitamins entering the intestine can be in free or protein/peptide associated forms; protein/peptide associated B-vitamins must be liberated by digestive enzymes for intestinal absorption to occur.

Experiments utilizing steers (Miller et al., 1986; Zinn et al., 1987), sheep (Girard and Remond, 2003), and lactating dairy cows (Santschi et al, 2005), have reported appreciable small-intestinal B-vitamin absorption. Except Girard and Remond (2003), which used venously catheterized sheep, the other reports utilized animals fitted with ruminal-, duodenal-, and ileal- cannulae. In these studies, intestinal absorption of B-vitamins can be estimated as the difference between duodenal and ileal flows; though this estimate may be confounded by potential intestinal B-vitamin synthesis. Table 4 shows intestinal disappearance (percent of duodenal flow) of B-vitamins from the three studies, calculated with the following equation: intestinal disappearance (%) = $100 \times ((\text{duodenal flow} - \text{ileal flow})/\text{duodenal flow})$. Percent intestinal disappearance of thiamin, riboflavin, niacin, and B₆ were similar across studies and averaged 71, 28, 77, and 76%, respectively.

Table 4. Disappearance of B-vitamins from the small intestine (% duodenal flow).

	Miller et al., 1986 ¹	Zinn et al., 1987 ¹	Santschi et al., 2005 ²
Thiamin	63	75	75
Riboflavin	23	24	36
Niacin	67	80	84
Pyridoxine	--	813	71
Biotin	-142	--	37
Folic Acid	--	--	Negative
B ₁₂	--	48 (15) ³	11

¹ Calculated from across-treatment averages.

² Calculated from across-study control averages.

³ Parenthetical value adjusted for assay type.

The intestinal disappearance value of -142% for biotin calculated from the Miller et al. (1986) data occurred as ileal biotin flow was greater than duodenal flow. The authors speculated that this was due to intestinal biotin synthesis. While data contradicting this theory are unavailable, a more plausible explanation may be that the microbiological assay used by Miller et al. (1986) resulted in an underestimation of duodenal and ileal biotin flow. Pancreatic biotinidase liberates protein-bound biotin (see following discussion), and Miller et al. (1986) did not specify whether biotinidase or pancreatic extract were included in the assay. In duodenal digesta, approximately 93% of total biotin is protein-bound (Schwab, Girard, and Shaver, unpublished results). Therefore, duodenal samples taken by Miller et al. (1986) may not have been exposed to biotinidase if the cannulae were placed distally to the pancreatic duct. While it is likely that the ileal samples taken by Miller et al. (1986) were exposed to pancreatic biotinidase, it is unlikely that the enzyme is able to completely liberate all protein-bound biotin.

Using lactating dairy cows, Santschi et al. (2005) reported negative intestinal folate disappearance, which they attributed to duodenal cannulae placement. Folate is absorbed in the proximal small intestine (Girard and Remond, 2003), and Santschi et al. (2005) placed the duodenal cannulae approximately 30 cm from the pylorus.

Intestinal B₁₂ disappearance estimates were similar and averaged 13% across studies when the Zinn et al. (1987) data were corrected for differences in microbiological assays. Zinn et al. (1987) used *Lactobacillus leichmannii* cultures to assay B₁₂. Smith and Marston (1970) reported that estimates of B₁₂ activity using *Ochromonas* were 32% of those determined using *L. leichmannii*.

Santschi et al. (2005) post-ruminally infused thiamin (10 mg/d), riboflavin (2 mg/d), nicotinamide (1173 mg/d), pyridoxine (34 mg/d), biotin (0.02 mg/d), folic acid (111 mg/d), and B₁₂ (0.4 mg/d) and observed no significant ($P > 0.05$) changes in intestinal B-vitamin disappearance relative to controls. This suggests that B-vitamin absorption

was increased and that the absorptive capacity of the small intestine was not maximized.

ATTEMPTS TO DEFINE B-VITAMIN REQUIREMENTS

The NRC (2001, p 173) attempted to estimate dairy cow B-vitamin requirements. Tissue requirements were calculated from those of a 175-kg lactating sow (NRC, 1998) and adjusted to a 650-kg lactating cow. Requirements for 35 kg/d per cow of milk production were adapted from Jenness (1985). Based on these estimates of B-vitamin requirements and ruminal B-vitamin AS (calculated from steer data of Miller et al., 1986 and Zinn et al., 1987) and escape (calculated from Zinn et al., 1987), only folic acid and pantothenic acid appeared to be limiting relative to calculated requirements. The conclusions from NRC (2001) calculations should be interpreted with caution as ruminal B-vitamin AS derived from young steers fed grain-based diets may or may not be accurate (Table 3; Schwab et al., 2005) and B-vitamin requirements extrapolated from lactating sows may or may not be accurate for lactating dairy cows.

While B-vitamin requirements have been determined for milk-fed calves (NRC, 2001), it appears unlikely that definitive requirements – in terms of amounts required to avoid a clinical deficiency – for ruminating cattle can be determined due to rumen microbial synthesis. Clinical symptoms of B-vitamin deficiency are rarely observed in mature dairy cattle (NRC, 2001). However, current research does suggest that lactating dairy cows could benefit from supplementation of specific B-vitamins in certain situations (Schwab and Shaver, 2004).

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