

Dietary Lecithin Supplementation in Dairy Cattle

J. W. McFadden
Department of Animal Science
Cornell University

Introduction

Lecithins are sourced from animals and plants for the food, feed additive, pharmaceutical and cosmetic industries. Lecithins function as emulsifiers, fillers, viscosity regulators, carriers, wetting, anti-spattering and dispersing agents. Their amphiphilic nature (polar/hydrophilic headgroup and nonpolar/lipophilic tail) affords them properties that allow them to accumulate at the interface of oil and water, thus reducing interfacial tension and enhancing the formation of emulsions. Lecithin feeding is common practice for non-ruminants and the pre-ruminant calf; however, lecithin-based feed additives have received less attention for growing and lactating ruminants because of their susceptibility to rumen modification. This conference proceeding aims to review fundamental concepts in lipid digestion and absorption in the ruminant. The production, composition, and emulsifying properties of lecithin are summarized. The effects of phospholipids on rumen function, and the ability of lecithin or lysolecithin feeding to modulate milk production and composition is discussed. A recent comprehensive study at Cornell University that investigated the effects of dietary deoiled soy lecithin supplementation on milk production, fatty acid digestibility, and choline availability in Holstein cows fed fractionated palm fatty acids is also presented.

Definitions

Lecithin: Phospholipids (or glycerophospholipids) of animal or plant origin that contain two hydrophobic hydrocarbon tails and a hydrophilic head group. Lecithin most often exists as a mixture of phosphatidylcholine (PC), phosphatidylethanolamine (PE), and phosphatidylinositol. Phosphatidylserine, phosphatidylglycerol, and phosphatidic acid may also be present in a lesser amount.

Lysolecithin: Lysophospholipids of animal or plant origin that contain a single hydrocarbon tail and a polar head group. Lysolecithin is generally recognized as being lysophosphatidylcholine (LPC).

Crude lecithin: A mixture of triglycerides (~35%) and phospholipids (~45%) that also includes lesser amounts of glycolipids, sterols, and carbohydrates. Although variable by source, PC content is often 15 to 20%.

Deoiled lecithin: A mixture of phospholipids with triglycerides removed. Phospholipid composition varies based on origin; however, PC content is generally 20 to 30%.

Fractionated lecithin: A purified form enriched in one or more types of a specific phospholipid (e.g., >50% PC).

Modified lecithin: Lecithin with a modified structure (e.g., caused by hydrogenation or partial hydrolysis).

Lipid Digestion and Absorption in Ruminants

Esterified lipids, like dietary triglycerides, undergo extensive hydrolysis in the rumen; albeit, the magnitude of hydrolysis is influenced by rumen pH, ionophores, and level of dietary fat as reviewed by Bauman and Lock (2006). Extensive rumen hydrolysis explains why the majority of lipid that enters the small intestine exist in the free fatty acid form. Rumen lipid metabolism also involves hydrogenation of unsaturated fatty acids. Extensive biohydrogenation of 18-carbon oleic, linoleic, and linolenic acids explains why the flow of stearic acid to the duodenum is high even though stearic acid intake is low (Harvatine and Allen, 2006). Short-chain fatty acid absorption occurs in the rumen epithelium, where they serve as key energy substrate molecules for oxidative metabolism in the mature ruminant. In contrast, the absorption of long-chain fatty acids primarily occurs in the small intestine, which is due in part to their adsorption on feed particles prior to entry. The composition of long-chain fatty acids in duodenal digesta mostly reflects the rumen profile and is responsive to changes in dietary saturated and unsaturated fatty acid feeding (Harvatine and Allen, 2006).

A key feature of lipid digestion is micelle formation. Mixed micelles contain bile acids and salts, lecithin, lysolecithin, monoglycerides, cholesterol, and fatty acids that ensure lipid absorption across the unstirred water layer at the surface of the intestinal microvillus membrane. Micelle formation occurs after complex lipid digestion and emulsification. Pancreatic juice and bile aid in this capacity. Pancreatic juice is composed of digestive enzymes and bicarbonate. The digestive enzymes include proteases (i.e., trypsin and chymotrypsin), lipases, and amylase. With regard to lipid digestion, pancreatic lipase and colipase are proteins synthesized and secreted by the pancreas. Lipase catalyzes the hydrolysis of triglycerides. Colipase aids in triglyceride digestion because it is a required co-factor for pancreatic lipase. Interestingly, colipase is a cleavage product of a precursor molecule called procolipase via the actions of trypsin in the intestine. Pancreatic juice also contains pancreatic phospholipases A₁ and A₂. Phospholipase A₁ hydrolyzes the mainly saturated fatty acids located at position 1 of the phospholipid to form 2-acyl-lysolecithin. Phospholipase A₂ hydrolyzes the mainly unsaturated fatty acid in position 2. A similar product of triglyceride and phospholipid digestion is the fatty acid. Monoglyceride and lysolecithin are also formed, which have emulsifying properties and are absorbed by the intestine (the latter being more relevant in the ruminant).

It is important to recognize that the ability of pancreatic lipase, colipase, and phospholipases to efficiently digest dietary triglycerides and phospholipids (i.e., gain access) in the ruminant requires the emulsifying and micelle-forming properties of bile salts and lysolecithin. Bile production begins in the liver. Bile is subsequently modified by

absorptive and secretory transport systems in the bile duct epithelium and concentrated in the gallbladder before delivery to the intestinal lumen. The composition of bile is complex but includes water with dissolved bile salts, lecithin, lysolecithin, and sphingomyelin (i.e., phospholipids; Figure 1A). Cholesterol, amino acids, and vitamins are also present. Pancreatic phospholipase may convert bile-derived PC to LPC. Bile salts are conjugated bile acids and products of cholesterol metabolism. Examples include cholic, taurocholic, glycocholic, chenodeoxycholic, and glycodeoxycholic acids (Karsai and Szaniszló, 1990; Washizu et al., 1991). In dairy cattle, major lecithin phospholipids of bile include PC (e.g., PC 18:0/18:2; Figure 1A), LPC (e.g., LPC 18:2), and sphingomyelin (e.g., SM 34:1). In a recycling manner, bile salts may be de-conjugated by bacteria in the small intestine to reform bile acids that may be reabsorbed in the terminal ileum to complete enterohepatic circulation.

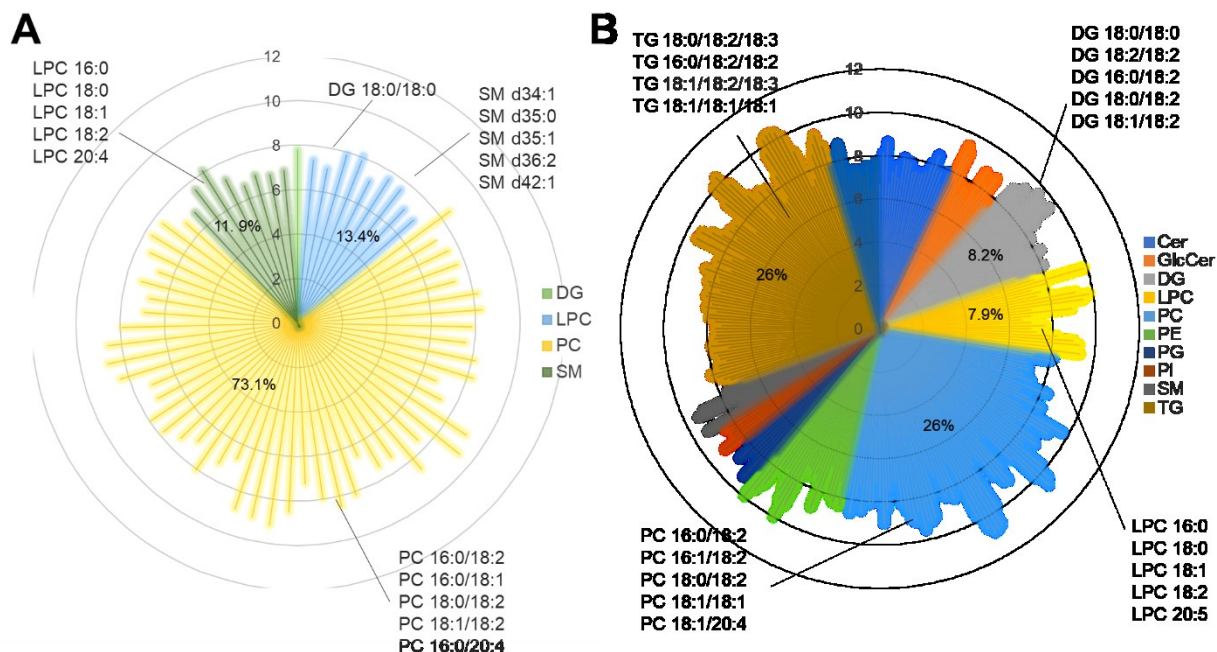


Figure 1. Lipid profiles for bovine bile (A) and deoiled soy lecithin (B). Annotated data were generated in positive mode using time-of-flight mass spectrometry. Each line represents a lipid detected with relative abundance. Examples are shown. Cer = ceramide, DG = diglyceride; GlcCer = monohexosylceramide; PG = phosphatidylglycerol; PI = phosphatidylinositol; SM = sphingomyelin; TG = triglyceride.

Unsaturated fatty acids that enter the small intestine or released from triglyceride or phospholipid digestion may also aid in micelle formation. Specifically, Freeman (1969) investigated the effects of different amphiphiles on triglyceride dispersion and fatty acid solubility in a bile salt (i.e., sodium glycodeoxycholate) solution. It was confirmed that palmitic and stearic acids behave as non-polar solutes, whereas, oleic, linoleic, and lauric acids were amphiphilic. Increasing the concentration of each unsaturated fatty acid amphiphile enhanced stearic acid solubility; however, stearic acid solubility was greatest in the presence of lysolecithin, relative to oleic, linoleic, and lauric acids as well as monoglyceride. These data would suggest that lecithin hydrolysis in the small intestine

would release lysolecithin and unsaturated fatty acids (e.g., oleic or linoleic acids) and thus have an additive effect on saturated fatty acid digestibility. This uncertainty requires consideration in the cow.

At the brush border membrane of the small intestine (jejunum primarily), lipid absorption into the enterocyte occurs by simple diffusion or transporter proteins. Long-chain fatty acids and monoglycerides are utilized to re-synthesize triglyceride. Long-chain fatty acids and LPC serve as substrate for PC synthesis. Triglyceride, cholesterol, and PC are packaged with apoproteins (e.g., apo-B48) into particles called chylomicrons. Chylomicrons are then secreted from the basolateral membrane of the enterocyte into lacteals of the lymphatic system. Chylomicron-containing lymph then empties into venous blood circulation at the thoracic duct. This route of delivery ensures that triglycerides are utilized by the mammary gland, skeletal muscle, and heart prior to hepatic entry. Short- and medium-chain fatty acids are absorbed into the portal vein as free fatty acids.

Production, Composition and Emulsifying Properties of Lecithin

Derived from the Greek term 'lekithos' (i.e., egg yolk; Hensing, 2004), lecithin is a generic term to define amphiphilic phospholipids from animals or plants. The types of glycerophospholipids in lecithin include PC, PE, phosphatidylinositol, phosphatidylserine, and their lyso-phospholipid counterparts such as LPC. Lecithin distributed for commercial application is predominantly derived from soybeans but also sunflower seed and rapeseed. In addition to plant-based lecithins, animal-derived egg or milk lecithin is also available for human food applications, which includes emulsification, wetting, dispersing and texturization. To obtain lecithin from plants, processing is required. Degumming is the method of removing phosphatides from extracted crude vegetable oil with water to form a gum that contains phospholipids, triglycerides, free fatty acids, and glycolipids. Removal of water generates a liquid crude lecithin that is primarily composed of phospholipid (~45%) but still enriched in triglycerides (~35-40%). Washing the crude lecithin with acetone removes the neutral oil (i.e., the triglycerides, fatty acids, and sterols) to produce deoiled lecithin composed of phospholipids (~70-80%) and a small percentage of glycolipids (i.e., acetone insoluble compounds). Deoiled lecithin is dried by evaporation to produce a phospholipid-enriched lecithin powder. The glycerophospholipid composition of deoiled lecithin depends on the source; however, PC, PE, and phosphatidylinositols are key examples. The presence of lyso-phospholipids and triglycerides is expected to be negligible in deoiled lecithin (<5%). The fatty acid composition of crude or deoiled lecithin certainly depends on the vegetable source. A recent analysis of deoiled soy lecithin (BergaPur®; Berg+Schmidt GmbH & Co, Hamburg, Germany) by gas chromatography reported 54% C18:2, 22% C16:0, and 13% C18:1 of total fatty acids (unpublished data). A lipidomic evaluation of deoiled soy lecithin revealed an abundance of PC, LPC, and sphingomyelin (Figure 1B). Many of these lipids were enriched in linoleic and palmitic acids. Lecithin derived from sunflower seeds or rapeseed would be expected to be enriched in linoleic and oleic acids, respectively. Although more common in non-agricultural industries, deoiled lecithin may be fractionated by organic solvent extraction to separate PC from other glycerophospholipids. Moreover, purified lecithin can be chemically modified by hydroxylation, halogenation, acetylation,

hydrolysis, hydrogenation, phosphorylation, or sulfonation. For example, partial hydrolysis transforms lecithin (e.g., PC) into lysolecithin (e.g., LPC). For additional information, detailed reviews of soybean and sunflower lecithin have been prepared by List (2015) and Guiotto et al. (2015).

The chemical structure of phospholipids influence their emulsifying properties. In a comparison of phospholipids, emulsion droplet size is lowest for LPC and PC, relative to phosphatidic acid, sphingomyelin, or PE (Ishii, 1992). Other work confirmed that lysolecithin forms smaller emulsion oil droplets, relative to lecithin in mock enteral preps (Shimokawa et al., 2017), and the size of mixed micelles containing lysolecithin are smaller than that of lecithin micelles when studied in comparable molar ratios (Reynier et al., 1985). Replacement of lecithin with lysolecithin has been shown to increase the solubilization of palmitic acid in an aqueous solution containing bile salts (Lough and Smith, 1976). Lysolecithin is more water soluble than lecithin. Regardless, saturation of lecithin has the potential to influence emulsification. Saturated PC with C12:0 or C14:0 produce glyceryl trioctanoate emulsion droplets of smaller size, relative to PC containing C16:0 or C18:0 (Nii and Ishii, 2004; Ishii and Nii, 2005). Interestingly, a small droplet size prepared with PC enriched in C12:0 or C14:0 is comparable to C18:1- or C18:2-linked PC (Nii and Ishii, 2004). In experiments studying egg yolk lecithin, mean droplet diameter for triglyceride emulsions tended to increase with degree of saturation of PC with 18-carbon chains (i.e., PC containing C18:2 > 18:1 > 18:0). We should consider the interaction between lecithin and the type of neutral triglyceride emulsified. As triglyceride carbon number (i.e., chain length) increases (e.g., tricaprilyn, tricaprln, trilaurin, and trimyrstin), mean diameter droplet size also increases (Nii and Ishii, 2005). This has been shown to occur more so in emulsion preps containing dipalmitoyl- or distearoyl-PC, relative to dilauroyl- or dimyristoyl-PC (Nii and Ishii, 2005). As lecithin or lysolecithin-based feed additives become commercially available for the livestock industry, the composition of phospholipid deserves consideration.

Lecithin and Lysolecithin Feeding in Ruminants

Early studies demonstrated that crude lecithin and lysolecithin are degraded to glycerylphosphorylcholine and fatty acids in ovine rumen fluid by phospholipase and lysophospholipase (Dawson, 1959; Hazlewood and Dawson, 1975; Jenkins, 1993). Subsequent work confirmed that deoiled soy lecithin is degraded in ovine rumen cultures (Jenkins et al., 1989). In sheep, supplementing crude soybean lecithin reduced energy, acid detergent fiber and nitrogen digestibility (Jenkins and Fotouhi, 1990). In vitro, lecithin from canola (deoiled/hydrolysed/acetylated) or soy (deoiled) has been shown to lower total volatile fatty acid and ammonia concentrations, and apparent ruminal degradation of organic matter and crude protein, relative to unsupplemented controls (Wettstein et al., 2000b). In beef calves, dietary supplementation of increasing amounts of a mixture containing soybean hulls, soy lecithin, and soapstock (0 to 7% supplemental fat on a DM basis; in replace of soybean hulls only) resulted in a linear decrease in the in situ rate of ruminal neutral detergent fiber (NDF) digestion with no effect on the rate of crude protein digestion (Shain et al., 1993). In lactating cows, lower apparent digestibility of dry matter, organic matter and gross energy were observed with deoiled soy lecithin feeding, relative

to animals fed calcium soaps of palm fatty acids (Wettstein et al., 2000a). This body of work would suggest that unprotected lecithin feeding modifies rumen fermentation and nutrient digestibility in ruminants.

The study of dietary lecithin supplementation on fatty acid digestibility in poultry and livestock is warranted because amphiphiles are required for the efficient absorption of saturated fat (Freeman, 1969). In broilers, dietary LPC supplementation improved total tract digestibility of palmitic, oleic, and linoleic acids (Zhang et al., 2011). In weanling pigs, lecithin (or soy oil) feeding increased fatty acid digestibility, relative to a no added fat control (Øverland et al., 1993). In similar manner, the addition of lecithin improved ether extract digestibility in weaned pigs fed tallow (Jin et al., 1998). However, lysophospholipid feeding did not modify apparent ileal digestibility of fatty acids in ileal-cannulated growing pigs (Dierick and Decuypere, 2004). The authors postulated that the reason may be related to a high ratio of unsaturated to saturated fatty acids of the animal fat source fed in the base diet. Most studies in ruminants have not observed improvements in fatty acid digestibility with unprotected lecithin feeding. In Angus steers fed hydrogenated fats that are highly saturated, dietary lecithin supplementation did not modify fatty acid digestibility (Jenkins, 1990). Replacement of dietary rumen-protected fat (calcium soaps of palm oil fatty acids) with lecithin (raw, deoiled and deoiled/partially hydrolysed soy lecithin, and raw canola lecithin) did modify total fatty acid digestibility in Brown Swiss dairy cows (Wettstein et al., 2000a). More recently, supplementing lactating Holstein cows with oleic acid with lecithin increased total and 16-carbon fatty acid digestibility, relative to cows fed a control diet containing prills of saturated fat; however, the response was not shown with lecithin alone (Shepardson and Harvatine, 2019). An exception is a study of Hampshire wethers fed soy lecithin that tended to increase fatty acid digestion in the hindgut, relative to no added fat (Jenkins and Fotouhi, 1990). It can be hypothesized that rumen phospholipid degradation may prevent their use as emulsifiers in the lower gut; however, interpreting the described studies is complicated considering that the triglyceride and phospholipid composition for phospholipid-based feed additives is often not described. Research needs to focus on the effects of the processed form (e.g., crude vs deoiled) and composition (e.g., PC content) of phospholipid feed additives on fatty acid digestibility. Of equal importance, studies need to evaluate the effects of post-ruminal lecithin delivery of intestinal 16- and 18-carbon fatty acid digestibility and absorption. The development of technologies that protect lecithin and lysolecithin from ruminal degradation are a necessity.

Feeding lecithin and lysolecithin modifies lactation performance in ruminants. In Holstein dairy cattle fed isonitrogenous and isoenergetic diets, efficiency of 4% fat-corrected milk production was greatest for cows fed the same soybean hull, soy lecithin, and soapstock mixture at an intermediate feeding level (Shain et al., 1993). The abomasal infusion of soy lecithin (33% soy oil, 20% PC, 20% PE, and 21% phosphatidylinositol) increased 3.5% fat-corrected milk, and milk fat content and yield in lactating cows, relative to water or soy oil infusion; although dry matter intake was reduced by lecithin infusion, relative to water infusion (no change in milk yield). The authors postulated that abomasal lecithin infusion may have increased lipid digestion and intestinal fatty acid uptake for their utilization by the mammary gland. Increased supply of post-ruminant linoleic acid

from soy lecithin digestion could increase the incorporation of this fatty acid in milk. In support, feeding lactating cows a ration containing soy lecithin and soapstock resulted in higher milk C18:2 content, relative to cows fed a diet containing soybean oil (Abel-Caines et al., 1998). The effects of lysophospholipids on milk production have also been considered in dairy cattle. In lactating cows, lysolecithin supplementation increased milk fat concentration when lactating cows were fed a higher fiber and lower unsaturated fatty acid diet, but lowered milk fat yield when a lower fiber and higher unsaturated fatty acid diet was fed (Rico et al., 2017). In the same study, lysolecithin feeding lowered dry matter intake when cows were fed the lower fiber and higher oil diet; however, lysolecithin treatment did not appear to modify rumen biohydrogenation of unsaturated fatty acids. This may be due to a limited feeding level of lysolecithin (10 g/cow per day). In a different study, supplementation of lysophospholipids linearly increased milk yield, milk fat and protein yields, and feed efficiency to produce milk, relative to an unsupplemented control diet; however, total tract digestibility of dry matter and organic matter tended to be lower (Lee et al., 2019). In this investigation cows were fed a hydrolyzed soy lecithin-based product that included a nominal amount of lysophospholipids (6%), and the base diet contained ~33% NDF (% of ration dry matter) and hydrolyzed tallow instead of soybean oil. These findings by Rico et al. (2017) and Lee et al. (2019) suggests that feeding unprotected phospholipids is best for cows fed diets adequate in NDF with limited unsaturated fat. However, the effects of lecithin or lysolecithin supplementation at varying feeding levels, and the interactions between phospholipid feeding and the fatty acid content and composition of the base diet deserves further evaluation in dairy cattle.

Dietary Lecithin Supplementation in Dairy Cows Re-Visited

The McFadden lab recently completed a comprehensive study of dietary lecithin supplementation on milk production and composition, markers of metabolic health, plasma and milk fatty acid concentrations, and apparent fatty acid digestibility in Holstein cows fed fractionated palm fatty acids (Fontoura et al., 2019; Rico et al., 2019). In a split-plot Latin square design, sixteen Holstein cows (160 ± 7 DIM) were randomly allocated to a main plot receiving a corn silage and alfalfa haylage-based diet with palm fat containing either moderate or high palmitic acid content at 1.75% of ration DM (MPA and HPA, respectively; BergaFat® F-100 Classic or F-100 HP containing 87 or 98% PA, respectively; Berg + Schmidt, Hamburg, Germany; n = 8 per group). On each palm fat diet, deoiled soy lecithin was top-dressed at 0, 0.12, 0.24, or 0.36% of ration DM in a replicated 4×4 Latin Square design (0 to ~100 g/cow per d; BergaPur®). Following a 14 d covariate period, lecithin treatment spanned 14 d with milk and blood collected during the final 3 d of each experimental period. Milk composition was determined. Pooled serum and plasma were used to measure markers of metabolic health such as total fatty acids and liver enzymes. Milk, feed, fecal and plasma fatty acid concentrations were determined by gas chromatography. Nutrient digestibility was calculated using indigestible NDF as an internal marker. Choline-related metabolites were quantified using liquid chromatography and mass spectrometry. Untargeted lipidomics was employed for plasma lipid profiling using quadrupole time-of-flight mass spectrometry. The statistical model included the fixed effects of palm fat type, lecithin level, period, and their interactions as well as the random effect of cow.

Lecithin linearly decreased dry matter intake (29.2, 28.7, 27.0 and 27.3 kg/d, $P = 0.01$). In cows fed HPA, lecithin feeding decreased milk fat content (interaction, $P < 0.01$) and tended to lower milk fat yield (interaction, $P = 0.10$). Although no changes in milk yield were observed, a quadratic reduction in 3.5% fat-corrected milk was observed with increasing lecithin supplementation ($P = 0.001$). Interestingly, lecithin linearly increased efficiency to produce energy-corrected milk in cows fed MPA ($P < 0.05$). The proportion of 16C fatty acids in milk fat decreased linearly with lecithin level, whereas 18C fatty acids increased linearly (e.g., 18:0; $P < 0.01$). The milk fat content of de novo fatty acids was lowered by lecithin ($P < 0.05$). Lecithin feeding decreased circulating milk urea nitrogen concentrations, relative to unsupplemented cows (0 vs rest, $P = 0.01$) and linearly increased total serum fatty acid concentrations ($P = 0.01$). Lecithin supplementation did not overtly modify the concentrations of individual fatty acids; plasma palmitic acid concentrations tended to be lower in cows fed HPA, relative to MPA ($P = 0.06$). Although increasing lecithin did not modify liver enzyme levels, such as sorbitol dehydrogenase, several interactions were observed between palm fat type and lecithin amount but were not of clinical concern. Because lecithin feeding decreased dry matter intake, decreased plasma milk urea nitrogen, and lowered milk de novo fatty acid content, rumen fermentation and biohydrogenation was likely modified.

Lecithin supplementation did not overtly modify total, 16-carbon, or 18-carbon fatty acid intake; however, total fatty acid intake tended to be enhanced by lecithin in cows fed HPA ($P = 0.09$). Lecithin feeding did not modify apparent dry matter, total fatty acid, or 16-carbon or 18-carbon fatty acid digestibility. An overall effect of lecithin on total, 16-carbon, or 18-carbon absorption was also not observed. Feeding HPA did modify fatty acid intake, digestibility, and absorption, relative to MPA. Specifically, cows fed HPA had greater intakes of 16-carbon and 18-carbon fatty acids ($P < 0.05$). Feeding HPA markedly reduced total fatty acid and 16-carbon fatty acid digestibility ($P < 0.001$). Consequently, total fatty acid absorption was lower in cows fed HPA ($P = 0.01$). The absorption of 16-carbon fatty acid tended to be lower in cows fed MPA ($P = 0.09$). The MPA diet did include more 18-carbon fatty acids such as oleic and stearic acids, and lower 16-carbon fatty acids, relative to HPA. The inclusion of oleic acid in prilled palm fats has been shown to improve digestibility (de Souza et al., 2018). Collectively, the data affirm that palm fat supplements that are highly enriched in palmitic acid suppressed apparent fatty acid digestibility, and feeding unprotected lecithin, which is susceptible to rumen degradation, does not enhance fatty acid digestibility or absorption in cows fed palm fat. Future research needs to evaluate whether the post-ruminal delivery of lecithin enhances fatty acid digestibility in ruminants.

Lecithin feeding is also a source of the methyl donor choline. Therefore, we explored the ability of lecithin feeding to modulate plasma choline supply. While no effects of lecithin were detected for plasma choline, methionine, or total PC, LPC, or sphingomyelin concentrations, lecithin feeding increased trimethylamine *N*-oxide and dimethyl-glycine, and linearly decreased phosphocholine concentrations ($P < 0.05$). When individual phospholipids were measured using lipidomics, plasma PC and sphingomyelin concentrations increased with lecithin feeding (e.g., PC 35:1 and SM

42:0; $P < 0.05$). Lecithin also increased the ratio of many PC to PE in plasma (e.g., PC 18:0/20:4; $P < 0.05$). These results demonstrate that lecithin-derived choline was degraded in the small intestine to form trimethylamine (to be converted to trimethylamine *N*-oxide in the liver). However, the data would also suggest that some choline may have been absorbed. The observed increase in dimethyl-glycine and individual PC concentrations, lower PC to PE ratios, and reduced phosphocholine concentrations suggests that PC synthesis was upregulated in cows fed lecithin. We cannot conclusively say that an increase in intestinal choline absorption was the cause because increased post-ruminal fatty acids from lecithin degradation could also conceivably enhance phospholipid synthesis in the cow. Nevertheless, the delivery of post-ruminal lecithin as a source of choline deserves further consideration.

Summary

Phospholipids and lysophospholipids are natural emulsifiers of neutral fats. However, the presence of phospholipase and lysophospholipase in the rumen results in their hydrolysis before they can aid in post-ruminal lipid digestion. The ruminal degradation of phospholipids appears to develop with reductions in dry matter intake, modified rumen fermentation, and reduced organic matter and NDF digestibility; albeit these effects are more often observed in cows fed diets low in fiber and enriched in unsaturated oils. The ruminal hydrolytic release and biohydrogenation of unsaturated oleic, and linoleic acids are likely at play. Unfortunately, the current scientific consensus is that feeding unprotected lecithin or lysolecithin fails to improve fatty acid digestibility or absorption. Because bile is enriched in phospholipids (especially PC) and the emulsifying properties of phospholipids have been demonstrated in non-ruminants, it is logical to postulate that the post-ruminal delivery of lecithin or lysolecithin enhances saturated fatty acid digestibility and absorption in the intestine. To make this observation, we must consider the processed form, protection technologies, PC or LPC content, and feeding level of lecithin as well as potential interactions with base diet fatty acid content and composition.

References

- Abel-Caines, S. F., R. J. Grant, and M. Morrison. 1998. Effect of soybean hulls, soy lecithin, and soapstock mixtures on ruminal fermentation and milk composition in dairy cows. *J. Dairy Sci.* 81:462-470.
- Bauman, D. E. and A. L. Lock. 2006. Concepts in lipid digestion and metabolism in dairy cows. Pages 1-14. In: *Proc. Tri-State Dairy Nutr. Conf.*
- Dawson, R. M. C. 1959. Hydrolysis of lecithin and lysolecithin by rumen micro-organisms of the sheep. *Nature* 183:1822-1823.
- de Souza, J., C. L. Preseault, and A. L. Lock. 2018. Altering the ratio of dietary palmitic, stearic, and oleic acids in diets with or without whole cottonseed affects nutrient digestibility, energy partitioning, and production responses of dairy cows. *J. Dairy Sci.* 101:172-185.

- Dierick, N. and J. Decuypere. 2004. Influence of lipase and/or emulsifier addition on the ileal and faecal nutrient digestibility in growing pigs fed diets containing 4% animal fat. *J. Sci. Food Agric.* 84:1443-1450.
- Fontoura, A. B. P., J. E. Rico, K. M. Keller, A. N. Davis, W. A. Myers, J. T. Siegel, R. Gervais, and J. W. McFadden. 2019. Effects of lecithin supplementation on milk production and circulating markers of metabolic health in Holstein cows. *J. Dairy Sci.* 102(E-suppl. 1):427 (Abstract).
- Freeman, C. 1969. Properties of fatty acids in dispersions of emulsified lipid and bile salt and the significance of these properties in fat absorption in the pig and the sheep. *Br. J. Nutr.* 23:249-263.
- Guiotto, E. N., M. C. Tomás, and B. W. K. Diehl. 2015. Sunflower lecithin. Pages 57-75 in *Polar Lipids*, M. U. Ahmad and X. Xu, ed. AOCS Press, Urbana, Illinois, USA.
- Harvatine, K. J. and M. S. Allen. 2006. Fat supplements affect fractional rates of ruminal fatty acid biohydrogenation and passage in dairy cows. *J. Nutr.* 136:677-685.
- Hazlewood, G. P. and R. M. C. Dawson. 1975. Isolation and properties of a phospholipid-hydrolysing bacterium from ovine rumen fluid. *Microbiology* 89:163-174.
- Hensing, J. T. 2004. The discovery of lecithin, the first phospholipid. *Bull. Hist. Chem* 29:9-15.
- Ishii, F. 1992. Phospholipids in emulsion and dispersion systems. *J. Japan Oil Chem. Soc.* 41:787-792.
- Ishii, F. and T. Nii. 2005. Properties of various phospholipid mixtures as emulsifiers or dispersing agents in nanoparticle drug carrier preparations. *Colloids Surf. B Biointerfaces* 41:257-262.
- Jenkins, T. C. 1990. Nutrient digestion, ruminal fermentation, and plasma lipids in steers fed combinations of hydrogenated fat and lecithin. *J. Dairy Sci.* 73:2934-2939.
- Jenkins, T. C. 1993. Lipid metabolism in the rumen. *J. Dairy Sci.* 76:3851-3863.
- Jenkins, T. C. and N. Fotouhi. 1990. Effects of lecithin and corn oil on site of digestion, ruminal fermentation and microbial protein synthesis in sheep. *J. Anim. Sci.* 68:460-466.
- Jenkins, T. C., T. Gimenez, and D. L. Cross. 1989. Influence of phospholipids on ruminal fermentation in vitro and on nutrient digestion and serum lipids in sheep. *J. Anim. Sci.* 67:529-537.
- Jin, C. F., J. H. Kim, I. K. Han, H. J. Jung, and C. H. Kwon. 1998. Effects of various fat sources and lecithin on the growth performances and nutrient utilization in pigs weaned at 21 days of age. *Asian-Australas J. Anim. Sci.* 11:176-184.
- Karsai, F. and F. Szaniszló. 1990. Changes in the serum levels of primary bile acids in dairy cows. *Acta Vet. Hung.* 38:217-224.
- Lee, C., D. L. Morris, J. E. Copelin, J. M. Hettick, and I. H. Kwon. 2019. Effects of lysophospholipids on short-term production, nitrogen utilization, and rumen fermentation and bacterial population in lactating dairy cows. *J. Dairy Sci.* 102:3110-3120.
- List, G. R. 2015. Soybean lecithin: Food, industrial uses, and other applications. Pages 1-33 in *Polar Lipids*, M. U. Ahmad and X. Xu, ed. AOCS Press, Urbana, Illinois, USA.

- Lough, A. and A. Smith. 1976. Influence of the products of phospholipolysis of phosphatidylcholine on micellar solubilization of fatty acids in the presence of bile salts. *Br. J. Nutr.* 35:89-96.
- Nii, T. and F. Ishii. 2004. Properties of various phosphatidylcholines as emulsifiers or dispersing agents in microparticle preparations for drug carriers. *Colloids Surf. B Biointerfaces* 39:57-63.
- Nii, T. and F. Ishii. 2005. Dialkylphosphatidylcholine and egg yolk lecithin for emulsification of various triglycerides. *Colloids Surf. B Biointerfaces* 41:305-311.
- Øverland, M., M. D. Tokach, S. G. Cornelius, J. E. Pettigrew, and J. W. Rust. 1993. Lecithin in swine diets: I. Weanling pigs. *J. Anim. Sci.* 71:1187-1193.
- Reynier, M. O., H. Lafont, C. Crotte, P. Sauve, and A. Gerolami. 1985. Intestinal cholesterol uptake: Comparison between mixed micelles containing lecithin or lysolecithin. *Lipids* 20:145-150.
- Rico, D. E., Y. Ying, and K. J. Harvatine. 2017. Short communication: Effects of lysolecithin on milk fat synthesis and milk fatty acid profile of cows fed diets differing in fiber and unsaturated fatty acid concentration. *J. Dairy Sci.* 100:9042-9047.
- Rico, J. E., A. B. P. Fontoura, B. N. Tate, and J. W. McFadden. 2019. Effects of soy lecithin on circulating choline metabolite concentrations and phosphatidylcholine profile in Holstein cows. *J. Dairy Sci.* 102(E-suppl. 1):385 (Abstract).
- Shain, D. H., M. H. Sindt, R. J. Grant, T. J. Klopfenstein, and R. A. Stock. 1993. Effect of a soybean hull:soy lecithin:soapstock mixture on ruminal digestion and performance of growing beef calves and lactating dairy cattle. *J. Anim. Sci.* 71:1266-1275.
- Shepardson, R. and K. J. Harvatine. 2019. Effect of oleic acid and lecithin in saturated fatty acid supplements on production and nutrient digestibility in lactating dairy cows. *J. Dairy Sci.* 102(E-suppl. 1):317 (Abstract).
- Shimokawa, K.-I., Y. Nagasaka, M. Sawa, Y. Wada, and F. Ishii. 2017. Physicochemical properties and stability of the emulsion prepared with various emulsifiers for enteral nutrition preparations. *J. Disp. Sci. Tech.* 38:1221-1226.
- Washizu, T., I. Tomoda, and J. J. Kaneko. 1991. Serum bile acid composition of the dog, cow, horse and human. *J. Vet. Med. Sci.* 53:81-86.
- Wettstein, H.-R., M. G. Quarella Forni, M. Kreuzer, and F. Sutter. 2000a. Influence of plant lecithin partly replacing rumen-protected fat on digestion, metabolic traits and performance of dairy cows. *J. Anim. Physiol. Anim. Nutr.* 84:165-177.
- Wettstein, H. R., A. Machmüller, and M. Kreuzer. 2000b. Effects of raw and modified canola lecithins compared to canola oil, canola seed and soy lecithin on ruminal fermentation measured with rumen simulation technique. *Anim. Feed Sci. Tech.* 85:153-169.
- Zhang, B., L. Haitao, D. Zhao, Y. Guo, and A. Barri. 2011. Effect of fat type and lysophosphatidylcholine addition to broiler diets on performance, apparent digestibility of fatty acids, and apparent metabolizable energy content. *Anim. Feed Sci. Tech.* 163:177-184.