Effects of Diet on Short-Term Regulation of Feed Intake by Lactating Dairy Cattle

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ABSTRACT

Physical and chemical characteristics of dietary ingredients and their interactions can have a large effect on dry matter intake (DMI) of lactating cows. Physical limitations caused by distension of the reticulo-rumen or other compartments of the gastrointestinal tract often limit DMI of high producing cows or cows fed high forage diets. Fermentation acids also limit DMI from a combination of increased osmolality in the reticulorumen and specific effects of propionate, although the mechanisms are not clear. The specific physical and chemical characteristics of diets that can affect DMI include fiber content, ease of hydrolysis of starch and fiber, particle size, particle fragility, silage fermentation products, concentration and characteristics of fat, and the amount and ruminal degradation of protein. Site of starch digestion affects the form of metabolic fuel absorbed, which can affect DMI because absorbed propionate appears to be more hypophagic than lactate or absorbed glucose. Dry matter intake is likely determined by integration of signals in brain satiety centers. Difficulty in measurement and extensive interactions among the variables make it challenging to account for dietary effects when predicting DMI. However, a greater understanding of the mechanisms along with evaluation of animal responses to diet changes allows diet adjustments to be made to optimize DMI as well as to optimize allocation of diet ingredients to animals. This paper discusses some of the characteristics of dietary ingredients that should be considered when formulating diets for lactating dairy cows and when allocating feeds to different groups of animals on the farm. (**Key words:** dry matter intake, diet effects, lactating cows)

Abbreviation key: bm_3 = brown midrib 3, **Ca-PFA** = calcium salts of palm FA, **CCK** = cholecystokinin, **FA** = fatty acids, **LCFA** = long chain FA, **NFFS** = nonforage fiber source, **PEG** = polyethylene glycol, **RR** = reticulorumen, **TG** = triglycerides.

INTRODUCTION

Energy intake is a primary limitation on milk yield for high producing dairy cows and is determined by net energy content of the diet and DMI. The maximal productive capacity of an animal will depend on its genetic potential and will vary over the animal's lifetime according to its age, physiological status (e.g. lactating, pregnant), and climate (133). Each animal has a maximal rate at which it can utilize nutrients and metabolic fuels and unless DMI is limited by physical capacity, mechanisms must exist that balance supply with demand for nutrients.

Dry matter intake is a function of meal size and meal frequency that are determined by animal and dietary factors affecting hunger and satiety. Most research on feeding behavior of ruminants has focused on dietary characteristics affecting satiety, which determines meal length and size. Distension and hypertonicity in the reticulo-rumen (**RR**), and effects of metabolic fuels oxidized in the liver, among other factors, have been proposed as satiety factors of ruminants. Much less is known about the control of the interval between meals determined by hunger. In addition, the effects of site and temporal pattern of digestion on feeding behavior have been largely unexplored. Stimulation of receptors that transmit signals to brain satiety centers is determined by changes in concentration or flux of the stimulatory nutrient or metabolic fuel. Thus, degree of stimulation of ruminal epithelial receptors by VFA and possibly electrolytes, and hepatic receptors by propionate is determined by the rate and extent of fermentation of feeds in the RR. Feeds with a rapid rate of fermentation are expected to result in shorter meal length and size when these mechanisms are effectual.

Short-term controls that affect meal size and intermeal interval within a day can have sustained effects over weeks or months. However, homeorhetic controls probably alter thresholds of stimulation required for hunger and satiety over a lactation cycle. This review focuses on the effects of diet on short-term regulation of DMI of lactating cows and includes dietary factors that affect distension in the RR and site of starch digestion, as well as protein, fat, and conservation method of forage.

PHYSICAL REGULATION

Physical regulation of DMI occurs when feed intake is limited by the time required for chewing or by distension within the gastrointestinal tract. For lactating cows fed ad libitum, eating time is probably not a direct constraint on DMI. However, dietary factors that increase eating time could result in decreased ruminating time, increasing the filling effect of the diet. The RR is generally regarded as the site at which distension most often regulates DMI of ruminants (2, 100). Distension stimulates stretch receptors in the muscle layer in the wall of the RR (121). Brain satiety centers likely integrate these and other stimuli to signal the end of a meal (101). Because various signals to brain satiety centers probably interact to trigger meal cessation, response to distension in the RR is probably not constant across cows and across physiological states within a cow. For each cow, the threshold of stimulation by RR fill that triggers meal cessation appears to be altered by absorbed nutrients (171) and possibly hormonally.

Tension receptors and mechanoreceptors in the RR are concentrated in the reticulum and cranial rumen (160). Epithelial mechanoreceptors are excited by light mechanical and chemical stimuli, and tension receptors are stimulated by distension in the RR which provides information to the gastric centers of the medulla oblongata (159). Distension in the RR is determined by both volume and weight of digesta. This was demonstrated by an experiment with steers offered a low-quality forage diet in which DMI was reduced 112 g for each kilogram of weight and 157 g for each liter of volume that was added to the RR as inert fill (230).

The extent to which DMI of lactating dairy cows is regulated by distension in the RR depends upon the animal's energy requirement and the filling effect of the diet offered. Allen (2) reviewed experiments in which inert fill was added to the RR of lactating cows at approximately 25% of pretrial RR volume and concluded that the effects of added fill on DMI were related to energy balance. Reductions in DMI with added inert fill were observed only when cows were in negative or slightly positive energy balance. When energy balance was greater than 3.8 Mcal of NE_L per day, there was no response in DMI to addition of that amount of inert fill into the RR. Although there are multiple mechanisms regulating DMI, physical regulation probably becomes a primary factor as the animal's energy requirement and the filling effect of diets increase. In practice, reduction in the filling effect of diets can have little noticeable effect on DMI of group-housed animals, but still can increase energy intake for the group. Within a group, increased DMI of higher producing animals can be offset by reduced DMI of lower producing animals that meet their energy requirements by consuming less DM with higher energy density diets.

The threshold of stimulation by distension to trigger the end of a meal generally occurs before the RR is physically full. Dado and Allen (59) measured gaseous headspace in the RR of lactating cows limited by distension and reported that volume of contents in the RR accounted for 88% of total volume of the RR with an average of 14 L of available headspace. With the long-term addition of inert fill into the RR in that experiment, DMI as a percentage of total daily DMI was greater in the 3-h period following feeding in spite of lower daily DMI. Sensory stimuli may have altered the threshold by which brain satiety centers trigger meal cessation by distension stimuli for the first meal after feeding but not for subsequent meals, resulting in greater initial meal size after feeding but lower daily DMI (2).

Diet NDF Content

Forage NDF content was more highly related with DMI of forage by sheep compared to other chemical measures (255), and Waldo (259) suggested that NDF content is the best single chemical predictor of DMI by ruminants. Mertens (177) used NDF as the only feed characteristic to predict the filling effect and energy content of diets, with DMI positively correlated with NDF concentration when energy limits intake but negatively correlated with NDF concentration when fill limits intake. Changing the NDF content of a diet by substituting grain for forage should result in a quadratic response in DMI; DMI increases until it is no longer limited by fill and decreases when limited by an excess of metabolic fuels. Evaluation of treatment means from experiments reported in the literature in which grain was substituted for forage showed that DMI generally declined with increasing NDF and there was little evidence for the expected quadratic response (Figure 1). With few exceptions, DMI increased with decreasing NDF when NDF content of diets exceeded 25%. Although DMI will eventually decrease when grain is substituted for forage in the diet because of an excess of metabolic fuels, the extent to which this occurs in the range of diet NDF typically fed to dairy cattle appears to be small. However, when grain is substituted for forage in diets, energy intake might begin to decline at a higher dietary NDF concentration than will DMI if fiber digestibility is reduced from low ruminal pH. Differences among experiments in the decline in DMI with increasing NDF suggests that the filling effect of NDF differs among diets.

When DMI is limited by distension in the RR, the limitation results from the rate of removal of digesta
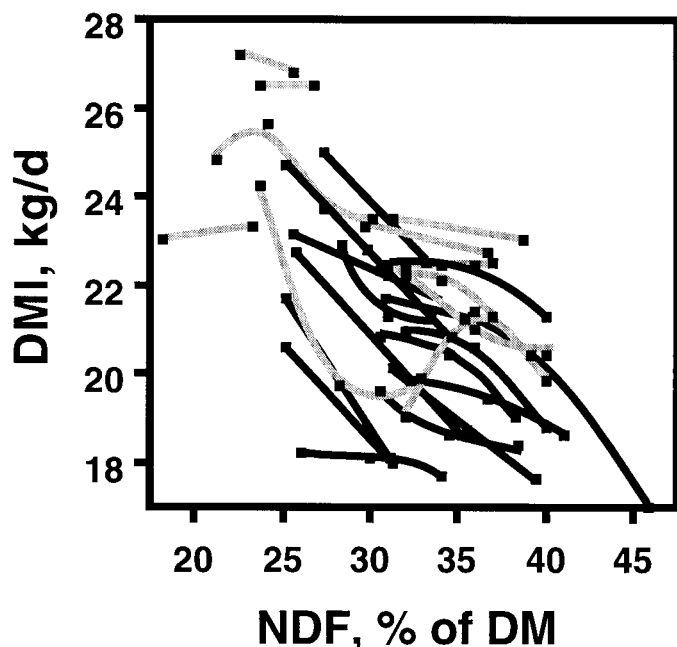
Figure 1. Relationship between diet NDF content, adjusted by altering the proportions of forage and grain, and DMI by lactating cows for experiments reported in the literature. Treatment means within a comparison are represented by smoothing splines (212) with $\lambda = 1$. Black splines signify a significant effect and gray splines signify a non-significant effect of diet NDF content on DMI within comparison. Data from 18, 19, 22, 33, 49, 59, 139, 140, 162, 179, 220, 247, 263, 264, 265.

DMI was reduced nearly 3 kg/d when forage content was increased from 35 to 65% with diets containing the long chopped alfalfa silage, but less than 0.5 kg/d with diets containing the short chopped forage. This is one possible reason for the different responses in DMI reduction with increasing diet NDF content observed across experiments (Figure 1). However, only 3 of 20 comparisons reported in 13 articles (9, 50, 95, 112, 113, 138, 141, 181, 219, 222, 234, 265, 266) in which the same source of forage (hay or silage) was chopped at two or more lengths, reported a significant effect of forage particle length on DMI. Figure 2 shows the relationship between forage particle length represented by sieve aperture size and DMI of lactating cows for 17 of these comparisons that measured particle length and did not include long hay.

Nonforage fiber sources. Nonforage fiber sources (**NFFS**, e.g., linted cottonseeds, soyhulls, beet pulp) have a similar range of NDF content as forages but particle length is generally smaller than forages. In several experiments NFFS were substituted for forage or grain in diets and DMI was measured. When DMI is regulated by distension in the RR, substitution of NFFS for forage in diets might increase DMI and substitution for grain might decrease DMI because of differences in their relative filling effects. However, NFFS had inconsistent effects on DMI when substituted for
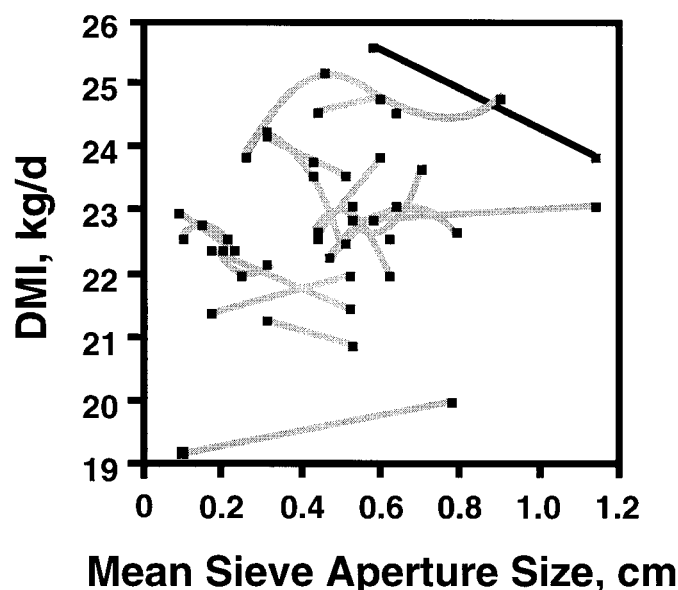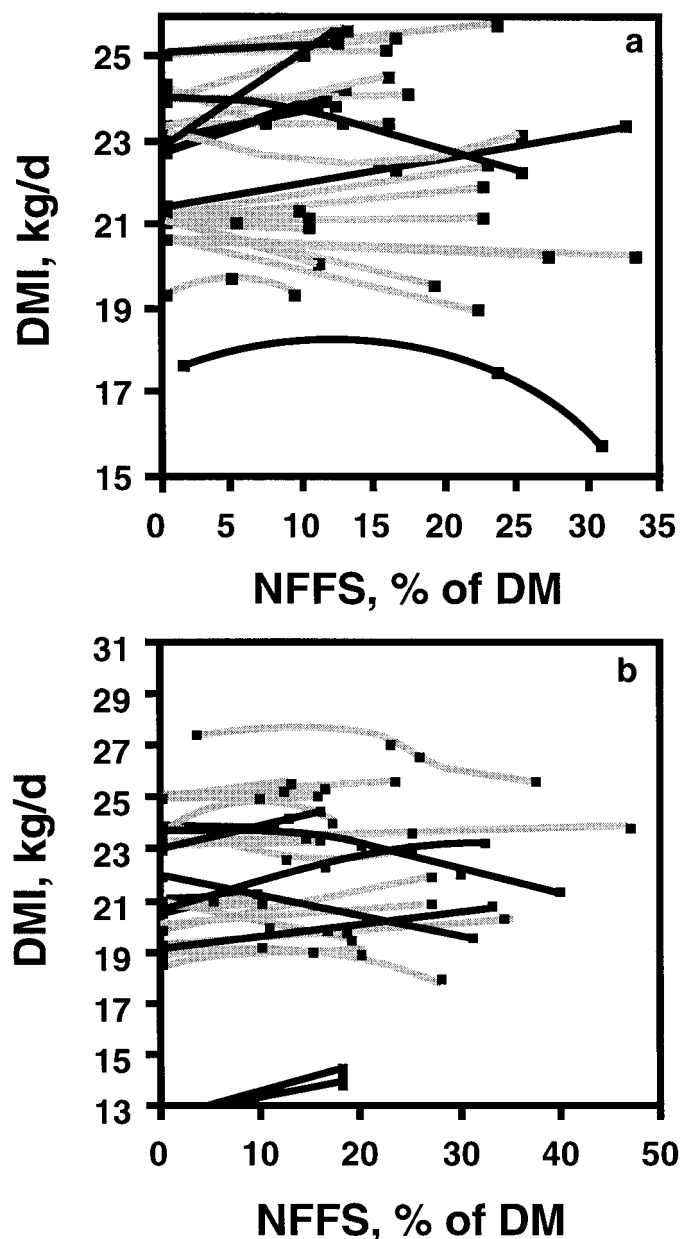
from the RR by digestion, absorption, and passage. Although initial density of feeds is somewhat related to NDF content (175), the filling effect of a diet is also highly dependent on factors affecting rate of digestion and flow from the RR. Constraints to flow from the RR were reviewed by Allen (2) and include the size and density of digesta particles, RR motility, functional characteristics of the reticulo-omasal orifice, and rate of emptying of the abomasum. The size distribution of digesta particles in the RR is dependent upon initial size that can be altered by chopping or grinding, by reduction in particle size by detrition and chewing during eating and ruminating, and rate of flow of small particles through the reticulo-omasal orifice.

Physical Form of Fibrous Feeds

Forage particle length. When distension in the RR limits DMI, decreasing forage particle size could result in increased DMI if the density of swallowed particles or the time available for rumination increases. Beauchemin et al. (21) reported an interaction ($P < 0.01$) between forage particle length (alfalfa silage chopped at 0.5 or 1.0 cm theoretical length of cut) and percentage of forage in the diet (35 or 65%). In that experiment,

Figure 2. Relationship between forage particle length, presented as mean sieve aperture size, and DMI by lactating cows for experiments reported in the literature. Treatment means within a comparison are represented by smoothing splines (212) with $\lambda = 0.0001$. Black splines signify a significant effect and gray splines signify a nonsignificant effect of forage particle length on DMI within comparison. Data from 9, 50, 112, 113, 138, 141, 181, 222, 234, 265.

either forage (Figure 3a) or grain (Figure 3b) in diets of lactating cows. When NFFS was substituted for forage, DMI increased for five and decreased for two comparisons out of a total of 31 comparisons. When NFFS was substituted for grain, DMI increased for eight and decreased for two comparisons out of a total of 33 compari-

sons. Factors other than distension in the RR likely were involved in regulation of DMI for many of these comparisons.

Digestibility of Forage NDF

Fiber is generally retained in the RR longer than other feed components and variation in NDF digestion kinetics can influence the filling effect of feeds over time. Although greater rates of digestion and passage will reduce the filling effects of NDF in the RR (4), the effect that the potentially digestible NDF fraction has on fill is not clear. While a greater fraction of potentially digestible NDF will result in increased NDF digestibility at a constant retention time, retention time of particles in the RR might also be longer because of greater buoyancy of particles over time (2).

Several experiments compared forages with different NDF digestibility but with similar NDF and CP contents to lactating dairy cows and found significant increases in DMI and milk yield with increased NDF digestibility (191). The effects of forage NDF digestibility on DMI and milk yield of dairy cows was evaluated statistically within a forage family using treatment means from the literature (191). A one-unit increase in forage NDF digestibility in vitro or in situ was associated with a 0.17-kg increase in DMI and a 0.25 kg increase in 4% FCM. Although DMI and NDF digestibility are positively related, diminishing returns for increased DMI probably applies for increases in NDF digestibility; DMI by cows will be less limited by distension in the gastrointestinal tract as NDF digestibility increases.

Digestibility of NDF measured in vitro or in situ using a constant incubation time was a significant indicator of the filling effects of NDF, but not necessarily an index of energy content. Oba and Allen (191) reported that differences in NDF digestibility of forages measured in vivo averaged less than 40% of differences measured in vitro or in situ using a constant incubation time. Forages with higher NDF digestibility allowed greater DMI, which probably reduced retention time in the RR, decreasing differences in NDF digestibility in vivo. In addition, responses in apparent digestibility of DM of brown midrib 3 (bm_3) corn silage compared to control corn silage were negatively related to response in DMI (190). This is because NDF digestibility of bm_3 corn silage compared with the isogenic control corn silage was depressed as DMI response increased. Although the bm_3 corn silage had 9.7 percentage units higher NDF digestibility in vitro (30-h incubation time) than the isogenic control corn silage, digestibility of NDF measured in vivo ranged from 12 percentage units higher with cows for which DMI of bm_3 corn silage was

Figure 3. Relationship between nonforage fiber source (NFFS) substituted for forage (a) or grain (b) and DMI by lactating cows for experiments reported in the literature. Treatment means within a comparison are represented by smoothing splines (212) with λ = 1. Black splines signify a significant effect and gray splines signify a nonsignificant effect of diet NDF content on DMI within comparison. Data from 16, 18, 27, 47, 48, 49, 57, 65, 68, 93, 122, 164, 181, 186, 193, 197, 206, 224, 231, 245, 249, 261, 272.

2 kg/d lower than the isogenic control corn silage, to 12 percentage units lower with cows for which DMI of bm_3 corn silage was 8 kg/d higher than the isogenic control corn silage.

Another experiment in which bm_3 corn silage was compared to its isogenic control corn silage in 29 and 38% NDF diets (192), provides further support that in vitro NDF digestibility is more specifically related to the filling effects of feed than to in vivo NDF digestibility. Although 30-h in vitro NDF digestibility was 9.4 percentage units greater for the bm_3 corn silage, bm_3 corn silage resulted in greater DMI and rate of passage of NDF at both dietary NDF contents, and no differences were observed between the silages for ruminal or whole tract NDF digestibility.

High yielding cows are challenged to meet their energy requirements, and DMI of these cows is probably limited by distension in the RR to a greater extent than for lower yielding cows consuming the same diet. This is supported by an experiment that compared bm_3 corn silage to its isogenic normal corn silage with high yielding dairy cows in a crossover design (190). The corn silages had similar contents of DM, NDF, CP, and starch, but the bm_3 corn silage had 25% greater (9.7 units) in vitro NDF digestibility with a 30-h incubation time compared with the control corn silage. Dry matter intake response to the bm_3 corn silage compared to control was positively related to pretrial milk yield, with a response of 0.15 kg/kg of pretrial milk yield for cows with pretrial milk yields above 29.3 kg/d. Higher producing cows with a pretrial milk yield of 55 kg/d had a mean response of 3.9 kg DMI/d. This was a major increase in feed intake for high producing cows from increased in vitro NDF digestibility.

Interaction with diet NDF. A greater advantage might be expected for forages with high NDF digestibility when included in high NDF diets because distension in the RR is a greater limitation on DMI as NDF concentration increases. However, enhanced in vitro NDF digestibility (9.4 percentage units) of bm_3 corn silage compared to its isogenic control silage increased DMI when fed in both high fill (38% NDF) and low fill (29% NDF) diets, and no interaction was detected between treatments for their effect on DMI (192). Insight into mechanisms controlling DMI were provided by an interaction of treatments for meal size and inter-meal interval. Control corn silage compared to bm_3 corn silage resulted in smaller meal size and inter-meal interval when fed in high fill diets but larger meal size and inter-meal interval when fed in low fill diets. Corn silage with less easily hydrolyzed NDF is more filling over time, and less capacity is available in the RR leading to smaller meal size when fed in high fill diets. Because the meal size was smaller, hunger occurred sooner, resulting in a smaller inter-meal interval. More rapid fermentation of the diet containing bm_3 corn silage lowered pH in the RR, which probably increased osmolality in the RR and probably resulted in more rapid absorption of VFA, both of which might have triggered satiety sooner. More rapid clearance of VFA from the RR and blood likely resulted in hunger sooner and a shorter inter-meal interval.

Perennial grasses versus legumes. Dry matter intake of diets containing grass silage by lactating cows is lower than DMI of diets containing alfalfa silage in spite of greater DM and NDF digestibility for grass silage (125, 263). A statistical analysis across forage families (grasses and legumes) by Oba and Allen (191) found a significant interaction of NDF digestibility and forage family on DMI and FCM yield. Dry matter intake and FCM yield were positively related to NDF digestibility within a forage family but negatively related across forage families. A possible explanation is that although NDF digestibilities were often greater for grasses compared to legumes, the filling effect of legumes was less because of greater particle fragility, which decreased retention time in the RR and resulted in less distension and greater DMI. This is supported by an experiment in which fresh ryegrass decreased in size and was cleared from the RR of cows more slowly than alfalfa (258). In addition, alfalfa particles might have a shorter buoyancy period than grass particles, increasing their rate of clearance from the RR (2). Particle density depends on initial density and changes in functional density over time. Although digesta particles have a true specific gravity of 1.3 to 1.5 (238), most digesta particles in the RR are buoyant because of retained gases (248). Although some air is swallowed with the feed, most of the gas is carbon dioxide and methane produced by particle-associated microbes. The amount of gas associated with digesta particles over time is dependent on their anatomical structure and digestion kinetics that determine rate of gas production and affect the ability of particles to retain gases (142). Greater potentially digestible NDF as a proportion of total NDF and slower rate of fermentation of the potentially digestible NDF would be expected to extend the length of time particles are buoyant, reduce rate of passage, and increase the filling effect of NDF over time (2). Similar DMI observed in comparisons of alfalfa and corn silage (31, 51, 70, 111) suggests that the greater filling effects of grass NDF compared to legume NDF is limited to perennial grasses.

Other Dietary Factors Affecting Distension

Low ruminal pH from highly fermentable feeds can decrease rate of fiber digestion and increase the filling

effect of the diet, which might increase distension in the RR (4). Although low ruminal pH is generally associated with high grain diets for which distension is less likely to be a constraint on feed intake, ruminal fermentability of grains are highly variable and daily means for ruminal pH of less than 5.7 have been reported for diets with high (> 40%) NDF content (3). Fat can also inhibit fiber digestion in the RR (201) with possible effects on distension (38). Fat is a potent stimulator of cholecystokinin (**CCK**) release (161) and evidence exists that CCK contributes to satiety (211). One hypothesis is that CCK suppresses feed intake by inhibiting gastric emptying (182). High fat diets increased plasma CCK in lactating cows (38) and infusion of unsaturated long chain fatty acids (**LCFA**) inhibited motility of the RR in sheep (187). Reduction in rate of digesta passage by supplemental fat could increase distension and stimulation of tension receptors in the RR, possibly reducing DMI. Although this might be a mechanism affecting feed intake in some situations, it is not supported by experiments that evaluated the factorial effects of dietary concentrations of fat and fiber. No interactions of effects of fat and fiber level on DMI were observed in several experiments (33, 139, 149, 250) and in two others reporting a significant interaction of fat and fiber treatments, added fat decreased DMI less in high fiber diets than in low fiber diets (86, 110). While the indirect effects of fat on feed intake by increasing distension in the RR from either a reduction in fiber digestibility or digesta flow cannot be ruled out, they remain to be demonstrated for ruminants.

Biologically active peptides that exist as sequences of AA within plant and animal proteins are released during digestion and absorbed intact (108). Dietary opioid peptides are present in a variety of protein sources fed to ruminants and have been shown to affect gastrointestinal motility and passage rate in different species (108). One class of peptides released during digestion of β-casein has been reported to inhibit gastrointestinal motility and emptying rate of the stomach in rats by direct interaction with opioid receptors (60). Saliva may contain biologically active peptides, and abomasal infusion of increasing concentrations of saliva in steers over a 3-h period corresponded to a linear increase in frequency of reticular contractions and a linear decrease in RR contents (107). Although increasing the physical effectiveness of NDF in diets could increase the initial filling effect of NDF, increased secretion of saliva might increase flow from the RR, counteracting the increased filling effect. Although dietary opioid peptides have been shown to affect gastrointestinal motility, the extent of their importance in regulation of DMI is not known (108).

SITE OF STARCH DIGESTION

Site of starch digestion in ruminants is affected by type of grain fed such as barley or corn (172), by conservation method such as high moisture corn or dry corn (153, 270, 271) and by processing such as rolling, grinding, or steam flaking (153, 270, 271). Although ruminal digestibility of different forms of corn ranged from approximately 50 to 90% of starch intake, postruminal digestion ranged from 6 to 44% of starch intake, compensating for this difference, with relatively little difference across sources for whole tract starch digestibility (129). The primary fuels available to ruminants from consumed starch are propionate, acetate, butyrate, and sometimes lactate from fermentation, glucose from digestion in the small intestine, and lactate from glucose metabolism in intestinal tissues. Huntington (129) calculated that glucose absorption accounts for 28% of the total glucose supply for lactating cows, but the amount of glucose used by visceral tissues can equal or exceed this amount. Although efficiency of utilization of grain starch is highest when extensively fermented in the rumen (129), the effects of site of starch digestion on DMI of high producing dairy cows consuming high grain diets has received little attention. Decreased DMI from excessive ruminal fermentation can have a major effect on the efficiency of feed utilization and must be considered.

Site of starch digestion can have significant effects on DMI of lactating cows. This is shown by evaluation of treatments from experiments reported in the literature that compared grains varying in starch digestibility in the RR measured using duodenally cannulated cows. Figure 4 shows the effect of site of starch digestion on DMI for ruminally degraded starch as a percentage of diet DM (Figure 4a) and as a percentage of diet starch content (Figure 4b). Increased ruminal starch degradation as a percentage of DM resulted in significant depression in daily DMI of lactating cows in three out of 10 comparisons. When a significant depression in DMI from increased starch digestion in the RR occurred, the mean effect on DMI was nearly 3 kg/d, which was probably a result of increased fermentation acid production in the RR. The specific mechanism might involve effects of hypertonicity in the RR and absorbed propionate in the liver, which are discussed below. Differences in ruminally degraded starch as a percentage of total starch had no effect on DMI for seven of the 10 comparisons, and response was not related to the concentration of ruminally degraded starch in the diet (Figure 4). Different responses across experiments might be from differences in temporal pattern of absorbed metabolic fuels or changes in ruminal osmolality, differences in

clearance of metabolic fuels from the blood, or differences in response thresholds among animals and diets.

Hypertonicity of the Reticulo-Rumen

Osmolality of RR fluid is highly variable depending on the content of mineral salts and fermentability of OM in the diet. Increased osmolality is associated with various physiological responses that may affect satiety. Depression of feed intake by infusion of Na acetate into the RR was probably through its effect on osmolality because injection of the same amount of Na acetate into the jugular vein had no effect on DMI (12). Epithelial receptors in the reticulum and cranial sac of the rumen are stimulated by acids, alkali, and hypo and hyperosmotic solutions (160). Grovum (117) suggested that direct stimulation of receptors by hypertonicity of fluid in the RR triggers satiety. Although epithelial receptors in the RR responded to VFA in concentrations found in the RR, Leek and Harding (160) observed that it is unlikely that RR fluid would become so alkaline, hypo-osmotic, or hyper-osmotic to excite them under physiological conditions. Evaluation of their data suggests that the threshold for epithelial receptor response to hyperosmotic solutions by addition of NaCl is between 700 and 1700 mOsm/kg. However, undissociated VFA have been found to excite epithelial receptors in the RR with thresholds in the range of 40 to 100 mM (121). The sensitivity of these epithelial receptors to butyrate is greater than propionate and there is greater stimulation at lower pH (55). This suggests that the degree of stimulation is related to the rate of absorption of VFA. Relative rate of VFA absorption has been shown to be butyrate > propionate > acetate and rate of absorption is negatively related to pH (73). The epithelial receptors in the RR are located approximately 150 μ below the luminal surface which corresponds to the level of the basement membrane (159) and VFA would have to be absorbed for stimulation to occur. It is unlikely that osmoreceptors sensitive to physiological changes in osmolality are located within the epithelium at the basement membrane because addition of osmotic loads of polyethylene glycol (**PEG**) –200 to the RR in the physiological range resulted in faster meal termination (35), but PEG is not known to be absorbed from the gastrointestinal tract (131). Although there is consistent evidence that infusion of hyperosmotic solutions into the reticulum decreases feed intake of single meals (35, 117, 252), osmoreceptors that are sensitive to the physiological range in osmolality in the RR have not been identified (117). Yet, circumstantial evidence suggests their existence. Bergen (25) reported that feed intake decreased markedly in sheep when RR osmolality was elevated to above 400 mOsm/kg with either Na acetate
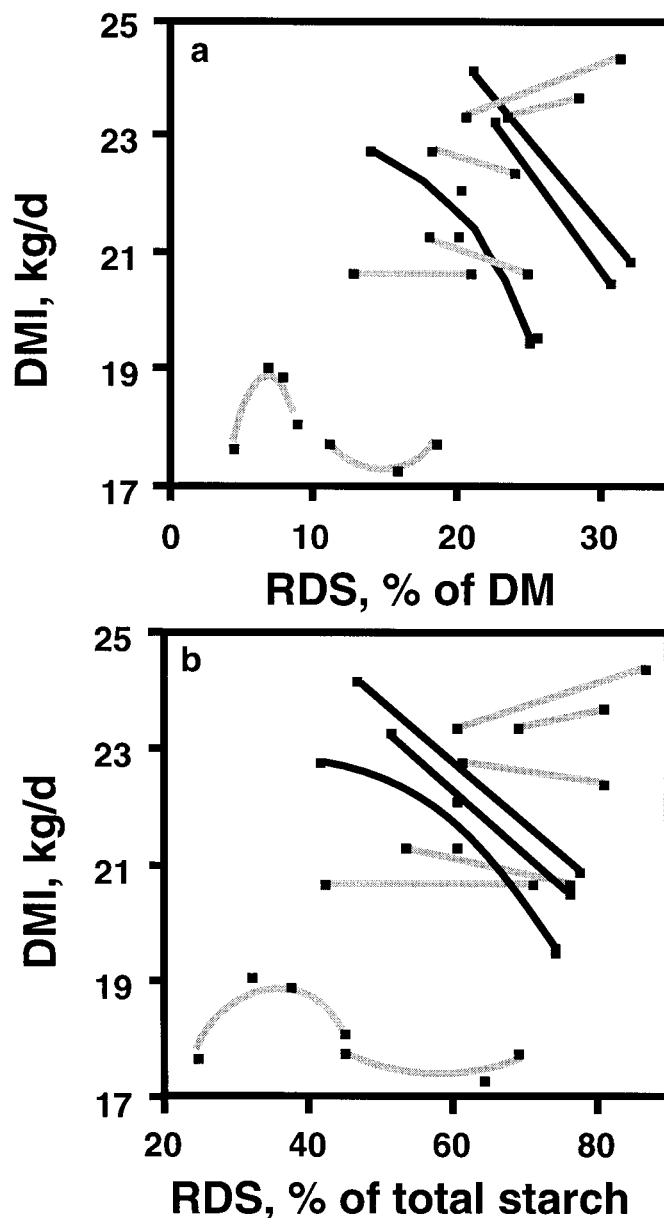
Figure 4. Relationship between ruminally degraded starch (RDS) as a percentage of DM (a) or as a percentage of total starch (b) and DMI by lactating cows for experiments reported in the literature. Treatment means within a comparison are represented by smoothing splines (212) with λ = 100. Black splines signify a significant effect and gray splines signify a nonsignificant effect of RDS on DMI within comparison. Data from 56, 153, 172, 196, 198, 207, 208.

or NaCl, and administration of a local anesthetic (carbocaine) with the osmotic load prevented the hyperosmolality induced depression in feed intake. Kato et al. (144) proposed that concentration of sodium and potassium in rumen fluid, not osmolality per se, affects feed intake because feed intake was depressed by both KCl and NaCl infusions into the RR of sheep but increased with

infusion of water and PEG (MW 3000). Because removal of sodium from extracellular fluid abolishes transmission of action potentials, Forbes and Barrio (102) suggested that effects of osmolality on stimulation of mechanoreceptors is from an increase in extracellular sodium, increasing the likelihood of transmission of an action potential rather than by direct stimulation.

The effects of hyperosmolality in the RR on meal termination are possibly mediated by stimulation of osmoreceptors located elsewhere in the gastrointestinal tract or at locations reached by the circulatory system such as the liver or the brain. Carter and Grovum (35) interpreted their series of experiments to rule out this possibility. Although osmolality in both RR fluid and in jugular plasma were significantly increased within 10 min after adding 50 g of NaCl into the RR, the authors found that feed intake of individual sheep in the 10-min period after adding NaCl to the RR was more related to change in osmolality in the RR (P = 0.053, r^2 = 0.39) than to change in osmolality of jugular plasma (P > 0.1, r^2 = 0.17). However, jugular plasma can have different osmolality than portal or carotid plasma and these correlations alone are not sufficient evidence to rule out the possibility that receptors at some sites in the circulatory system mediate meal termination. The authors (35) infused hyperosmotic solutions into both the RR and abomasum and concluded that the effects of hypertonicity following a meal were mediated by stimulation of receptors in the RR not in the abomassum or further down the gastrointestinal tract. They reported a linear decrease of 3.49 g of feed DM/g of NaCl added to the RR when intake was measured for the first 10-min period following addition of 2.37 g to 50 g of NaCl into the RR of sheep. The addition of NaCl to the abomasum had no effect on feed intake of a single meal until the levels added reached supraphysiological levels.

Meal termination associated with increased osmolality in the RR could be a result of other physiological effects rather than direct stimulation of receptors in the RR. Extracellular volume is decreased during and after a meal because of secretion of saliva during eating (251) and an influx of plasma fluids into the RR because of higher osmolality of fluid in the RR compared to plasma (260). Feed intake by ruminants is decreased by dehydration (157) and Forbes et al. (103) suggested that dehydration is likely to stimulate vasopressin which, injected intraperitoneally in goats, depressed DMI in a dose dependent manner (178). Ternouth and Beattie (252) reported that saline infused intraperitoneally beginning 30 min after the start of eating to counteract the reduction in extracellular volume following a meal, increased intake of a single meal and that intramuscular injection of a diuretic prior to a meal to

reduce extracellular volume, decreased intake of a single meal. Although osmotic loads infused into the RR have consistently reduced meal size, there might be little effect on daily feed intake which is determined by both meal size and intermeal interval. Infusion of NaCl into the RR of lactating cows at the onset of spontaneous meals decreased meal size compared with no infusion but inter-meal interval was also reduced, and DMI over the 12-h infusion period was not affected (39). This is an important observation that has been overlooked when feed intake of a single meal has been evaluated. In that experiment (39), infusion of equimolar amounts of NaCl and Na acetate had similar effects on meal size, but infusion of NaCl increased meal frequency compared with Na acetate, indicating a sustained satiety effect of VFA.

Although infusion of electrolytes can terminate meals, the mechanism involved is still unclear. The existence and relative importance of osmoreceptors in the RR that are sensitive to changes in osmolality in the physiological range are uncertain. Further research is needed to identify specific mechanisms involved in the effect of electrolytes in the RR on satiety. Effects of fermentation on osmolality and flux of water into the RR should be investigated for lactating cows consuming highly fermentable diets. Supplementation of electrolytes in diets beyond the requirements of the animal could be used to limit meal size of supplements, but meal frequency would have to increase to maintain DMI. Although its effect on feeding behavior is not known, addition of sodium bicarbonate to diets based on corn silage often results in a positive response in DMI (87).

Metabolic Fuels

Propionate versus acetate. Infusion of propionate into the mesenteric vein of steers reduced feed intake but acetate infused at similar rates did not (82). Baile (11) proposed that propionate receptors in the ruminal region of sheep and goats might function in the control of feed intake. This was based on experiments in which injections of propionate into the ruminal vein during spontaneous meals decreased DMI but injection of greater amounts into the jugular vein did not. At least one study found no effect of portal infusion of propionate on feeding behavior and DMI of goats, but intake was restricted to 1.5 times maintenance requirement in that experiment (62). However, there is substantial evidence that absorbed propionate affects satiety. Anil and Forbes (6) reported that infusion of propionate into the portal vein of sheep reduced feed intake over 80% compared with control, while infusion at the same rate into the jugular vein had no effect. Farningham and Whyte

(91) reported consistent, linear reductions in feed intake for sheep consuming a pelleted diet containing 50% forage when Na propionate was infused in the portal vein at rates between 0.6 and 2.5 mmol/min. Furthermore, propionate was more hypophagic than osmotically balanced infusions of acetate, mannitol, or saline. Propionate also resulted in lower DMI than acetate when infused in isocaloric amounts with long-term ruminal infusions with lactating cows (237).

Choi and Allen (39) reported that propionate (as Na propionate or propionic acid) infusions into the RR of lactating dairy cows at the onset of spontaneous meals reduced meal length and meal size to a greater extent than equimolar amounts of infused NaCl or acetate (as Na acetate or acetic acid). This indicated that meal cessation was affected specifically by propionate over its effects on osmolality. In addition, propionate infusions resulted in lower DMI over the 12-h infusion period compared with acetate infusions. The relative decrease in DMI for acetate and propionate infusions was not proportional to the energy content of the infusions; DMI was decreased 14% for acetate infusions and 33% for propionate infusions relative to control (no infusion). No differences were observed for any meal-related measurement between Na acetate and acetic acid but propionic acid resulted in smaller meal size than Na propionate, possibly from increased rate of absorption of propionic acid if pH in the RR was reduced by acid infusion.

Grovum (117) suggested that the effects of propionate infusion on reduction in DMI is from increased insulin secretion. This could explain the greater effects of propionate infusions compared to acetate infusions and of portal infusions compared to jugular infusions because 1) propionate, but not acetate, increased plasma insulin of sheep (168), 2) insulin has been reported to decrease DMI in sheep (104), and 3) propionate concentrations at the pancreas would be higher and more likely to stimulate insulin secretion when infused in the portal vein than when injected in the jugular vein. Extraction of propionate from the portal blood by the liver determines its concentration in blood reaching the pancreas, and rate of removal is probably variable and dependent on blood flow, intracellular metabolites required for propionate metabolism, and other factors (169). However, hypophagic effects have been observed for propionate infusions without an increase in insulin (91, 106), and mechanisms involving insulin do not explain the observation that depression in feed intake by infusion of propionate into the portal vein was eliminated by hepatic denervation (6). Anil and Forbes (6) reported that receptors in the liver exist that are sensitive to propionate and have afferent fibers in the hepatic plexus. Further work (7) demonstrated that the depression in feed intake by portal infusion of propionate can be elimi-

nated by splanchnic blockade with anaesthetic, splanchnotomy, and hepatic vagotomy, as well as with total liver denervation.

Elliot et al. (82) reported that the degree to which propionate infusion limited feed intake was variable and that the hypophagic effects of propionate infusion were greater for animals with higher feed intake. Animals were not fed ad libitum in this experiment (82) or in the experiment reported by De Jong et al. (62), and composition of diets differed for experiments, which helps explain the inconsistent effects of intraportal propionate administration; total propionate flux into the liver probably differed across experiment and across animals within experiment. Infusion of mixtures of VFA into the RR decreased DMI 12% for lactating cows but had little effect on DMI of dry cows (92). Further research is needed to evaluate how the dose-response relationship of portal propionate infusions on DMI of lactating cows varies with intake and fermentability of diets.

Oxidation of fuels in the liver. Although chemoreceptors sensitive to propionate might exist in the liver, they have not been specifically identified. A variety of oxidizable fuels probably have indirect effects on the same receptors in the liver. There is considerable evidence for nonruminants that oxidizable fuels in the liver affect feed intake by transmission of information to the central nervous system via hepatic vagal afferents (100). Portal glucose infusion decreased discharge rates of hepatic vagal afferents in guinea pigs (188) and portal infusion of 2-deoxy-D-glucose which reduced glucose utilization, increased the firing rate of hepatic vagal afferents, and increased feed intake in rabbits (189). Niijima (188) proposed that glucose utilization inside receptor cells in the liver reduces the firing rate of hepatic vagal afferents by activation of the energy-dependent sodium pump, increasing membrane potential. This was supported by the observation that portal infusion of ouabain, which blocks activation of the energy-dependent sodium pump, prevented effects of glucose on the firing rate of vagal hepatic afferents. Langhans et al. (156) reported hypophagic effects of subcutaneous injections of equimolar amounts of glycerol, 3-hydroxybutyrate, L-malate, L-lactate, or pyruvate in rats which were eliminated by hepatic vagotomy. Furthermore, oxidation of fuels has been reported to be the critical step for the hypophasia induced by these substances (156). Feed intake in rats was reduced by subcutaneous injection of 3-hydroxybutyrate but not by equimolar amounts of its oxidation product acetoacetate (155), and by glycerol or malate but not by equimolar amounts of their oxidation products, dihydroxyacetone or oxaloacetate (158). Langhans et al. (158) observed that feed intake by rats was reduced only by metabolites that were directly oxi-

dized by enzymes bound to the mitochondrial membrane and concluded that increased generation of reducing equivalents in the mitochondria from hepatic oxidation of metabolic fuels signals satiety. Thus, one kind of metabolic receptor in the liver might sense the oxidation of any substrate that is able to enter the cell (156).

While there is evidence that oxidation of fuels in the liver is a regulator of feed intake, some experiments have failed to demonstrate liver involvement and the extent to which the liver is involved is subject to controversy (99). In addition, effects of oxidizable fuels on rate of firing of afferent fibers of the hepatic vagus remain to be investigated for ruminants. Nonetheless, this mechanism of feed intake control is consistent with experimental observations of infusion studies with and without denervation of the liver. Ruminant hepatocytes have high activity of propionyl CoA synthetase but not acetyl CoA synthetase (64, 214). While there is extensive metabolism of propionate by ruminant liver, there appears to be little net metabolism of acetate (213), thus explaining differences in hypophagic effects of portal infusions of propionate and acetate in ruminants. Infusion of similar amounts of propionate in the portal and jugular veins result in greater propionate concentrations in the liver for the portal infusions because of greater dilution by blood for the jugular infusions. Butyrate and other 4- and 5-carbon VFA are nearly completely removed from portal blood and oxidized in the liver (213) but their hypophagic effects are not known. Lactate removal by the liver is variable and appears to be determined by carbon balance and redox state in the liver with greater removal for lactating cows and lesser removal for growing cattle (213). This could result in inconsistent hypophagic effects of lactate which might be similar to propionate at some times but not others.

Absorbed glucose. Although there is usually little net glucose absorption across the portal-drained viscera for ruminants fed a variety of carbohydrate sources (213), the effects of starch leaving the rumen which is highly digestible such as that from ground dry corn on net glucose absorption of high producing dairy cows remains to be investigated. Shifting the site of digestion of starch from the RR to the intestines will result in less fermentation and should increase net glucose absorption, decreasing the flux of propionate and increasing the flux of glucose and lactate in the portal vein. Increased glucose absorption from the gut generally results in decreased gluconeogenesis in ruminants (129). Although glucose infusion has been shown to be hypophagic in a variety of nonruminants (100), glucose infusion has generally not reduced feed intake in ruminants. Glucose had no effect on feed intake when infused intravenously in cows (74), intraperitoneally in heifers (241), intracerebroventricularly in calves (205),

abomasally in lactating cows (46, 106), or intraportally or various other locations in sheep (13). Infusion of 4.85 Mcal/d of a VFA mixture (64% acetic, 21% propionic, and 15% butyric acid) into the RR of lactating cows decreased DMI 12% but infusion of an isoenergetic amount of glucose into the abomasum had no effect (92). Baile and Della-Fera (14) concluded that "there is little evidence that glucose concentration or utilization rate has a significant role in regulation of DMI of ruminants." Differences in hypophagic effects of glucose infusion observed between ruminants and nonruminants could be because hexokinase activity is low in ruminants compared with nonruminants (15) and in mature ruminants, hepatic removal of glucose appears to be negligible (244). Stangassinger and Giesecke (244) suggested that there is a reduced hepatic capacity for glucose oxidation by both the Emden-Meyerhof and the pentose phosphate pathway as well as an increase in gluconeogenic capacity, with postnatal development of the ruminant digestive system.

Although effects of glucose and insulin infusions cannot be separated, recent experiments with lactating cows have reported either no effect of a hyperinsulinemic-euglycemic clamp on DMI (8, 165) or a reduction in DMI to similar energy intakes after accounting for glucose infused at 2 to 3 kg/d in studies reported by McGuire et al. (174) and Grinari et al. (114). In addition, infusion of graded amounts of glucose (0 to 1500 g/d) into the duodenum of lactating cows resulted in a linear decrease in DMI, but no effect on NE_L intake when the infused glucose was included in the calculation (130). However, abomasal infusions of 1.0 to 1.6 kg of glucose/d have resulted in lower DMI (18 to 24%) of lactating cows consuming diets with 75 to 98% of DM as alfalfa silage (69, 71). This response could be a result of altered hepatic metabolism from low portal flux of propionic acid or high NPN from the high alfalfa silage, low grain diets, and should be investigated further.

Research on the effect of metabolic fuels in the liver on feed intake of ruminants is needed. Effects of oxidizable fuels on discharge rate of hepatic vagal afferents are unknown for ruminants. Dairy cows often consume highly fermentable diets that can limit DM and energy intake. Under these conditions, shifting the site of starch digestion from the RR to the intestines will alter portal concentrations of propionate and lactate and possibly glucose and might reduce the satiety effects of the diet allowing increased DMI. A better understanding of how nutrients and gut hormones interact to modify the effects of propionate on liver receptors is also needed for dairy cows.

ENSILED FORAGES

Although several studies have been conducted in which all or part of the silage in the diet was replaced

with hay, in most instances the silage and hay was from different crops and effects of conservation method were confounded with differences in NDF content, NDF digestibility, or other factors affecting DMI. Two experiments with lactating cows reported by Broderick (32) compared alfalfa silage and hay conserved from alternate windrows in diets with, or without fishmeal. Alfalfa hay diets resulted in approximately 6% higher DMI which was significantly higher in three of the four comparisons. However, DMI was calculated using the DM of the ration and orts determined by drying at 60°C for 48 h resulting in a possible underestimation of DM content and DMI for the silage-based diet compared to the hay-based diet because of volatilization of organic compounds. Although there is insufficient research to determine differences in DMI between hay and silage, fermentation products from ensiled feeds can reduce DMI.

Moisture content of silages has been reported to be negatively related to DMI (63, 253) and DMI has been decreased by addition of silage effluents and extracts to hay (45, 253). Fermentation acids, ethanol, and soluble nitrogenous compounds such as ammonia and amines are produced from fermentation of carbohydrates and protein during ensiling. Several studies have evaluated effects of specific fermentation products in silage on DMI either by evaluating differences in concentration across studies or by their direct addition to silage. These studies have been reviewed by Erdman (88), who suggested that DMI of high moisture forages is more likely limited by fermentation products than moisture content per se. Greater effects of addition of fermentation products as acids compared to salts on DMI is consistent with the observation that silage pH limits DMI (87). Dry matter intake of frozen whole-plant corn is approximately 10% higher than the same forage ensiled, and addition of hydrochloric or organic acids to fresh or frozen corn forage resulted in similar reductions in DMI as feeding ensiled corn forage (88). The addition of Na bicarbonate to partially neutralize corn silage prior to feeding increased DMI in several experiments (87, 235, 236) and the response in DMI to addition of Na bicarbonate is generally greater for corn silage than for alfalfa silage (88). Because corn silage pH is generally lower than alfalfa silage pH, Erdman (88) speculated that initial pH accounts for the differences in response to bicarbonate addition observed between corn silage and alfalfa silage. Greater effects of Na bicarbonate addition for diets containing corn silage compared with alfalfa silage is probably also from greater fermentability of corn silage. Sodium bicarbonate could reduce rate of absorption of VFA from the RR, delaying both stimulation of epithelial receptors by VFA and flux of propionate to the liver, increasing meal size and possibly DMI.

Endproducts of protein metabolism also have been reported to decrease DMI. Soluble amines produced in silages by clostridial fermentation (173) were negatively related to DMI across forages (63, 173). Clostridial growth is enhanced in high moisture (> 70%) and high pH (>5) silages (184). Ammonia also has been reported to reduce DMI although the mechanism is not known (52).

DIETARY PROTEIN

The CP content of diets is often related positively to DMI of lactating cows (195, 218). This is partly from increased RDP effects on digestibility of feeds (195). The mechanism involved is presumably a reduction in distension as fiber and DM digestibility increase. Oldham (195) reported that the marginal increase in diet DM digestibility per percentage increase in diet CP content decreased as the CP content of the diet exceeded 15%, but was still positive when diet CP content exceeded 20%. Roffler et al. (218) predicted response in DMI to increased CP content of the diet for lactating cows by evaluation of a data file developed from studies reported in the literature. They found that the increase in DMI per percentage unit of CP declined exponentially as the percentage of CP in the diet increased. Although a one unit increase in diet CP content equated to nearly a 0.9-kg increase in DMI at 12% CP in the diet, there was only a 0.04 kg/d increase in DMI with additional CP at 18% CP in the diet. Dry matter intake was positively related to diet CP content in 7 of 25 comparisons reported in 11 journal articles (Figure 5). When significant effects of CP content on DMI were detected, the range for increased DMI was 0.18 to 0.84 kg DMI/d with a mean of 0.63 kg DMI/d per percentage unit increase in diet CP content. The positive relationship between diet CP content and DMI observed in some experiments could have been from a reduction in propionate production as protein was substituted for starch in diets. As previously discussed, propionate is hypophagic and an increase in propionate production can reduce DMI. Few studies have evaluated the effects of diet CP content on DMI of high producing cows at different stages of lactation and no experiments are known that have evaluated the factorial effects of protein concentration and ruminal starch degradation.

Increased AA supply could increase rate of clearance of metabolic fuels from the blood, increasing hunger and reducing inter-meal interval. For example, increased dietary CP resulted in increased rate of clearance of acetate and propionate from the blood when injected in jugular veins of sheep (80). However, there is little evidence that improved AA supply affects DMI of lactating cows. Oldham (195) suggested that an experiment
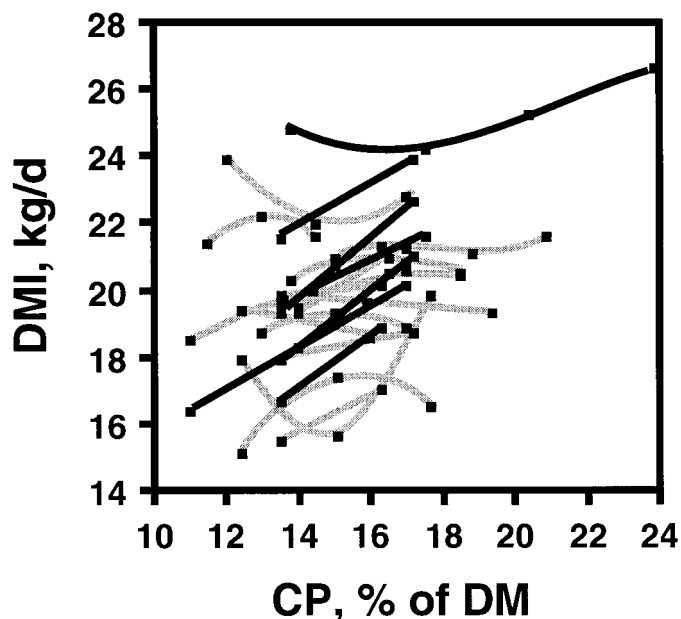
Figure 5. Relationship between CP content of diet and DMI by lactating cows for experiments reported in the literature. Treatment means within a comparison are represented by smoothing splines (212) with $\lambda = 0.01$. Black splines signify a significant effect and gray splines signify a nonsignificant effect of diet CP content on DMI within comparison. Data from 10, 54, 58, 79, 97, 115, 127, 154, 185, 217, 254.

(209) in which DMI was greater when cows consumed diets supplemented with soybean meal compared with diets supplemented with urea was evidence that DMI is increased by improved AA supply because digestibility of the diets were equal. However, the differences observed between soybean meal and urea on DMI are also consistent with hypophagic effects of urea (52). Abomasal or duodenal infusion of casein (46, 71, 114, 120) or soy protein (71) had no effect on DMI in spite of significant increases in milk yield. However, casein infusion prevented the depression in feed intake of cows subjected to a hyperinsulinemic-euglycemic clamp resulting in a significantly higher net energy balance and greater milk yield (114). Santos et al. (223) evaluated the effects of RUP on dairy cow performance and found no significant difference in DMI when soybean meal was replaced by protein sources with high RUP for 127 comparisons from 88 lactation trials. In addition, DMI was numerically lower for animal protein sources, corn gluten meal, and brewers dried grains when they replaced soybean meal. However, evaluation of 29 comparisons from 15 metabolism trials found that high RUP diets resulted in decreased microbial protein synthesis in the RR in 76% of the comparisons, and benefits of high RUP were not consistently observed for flow of AA to the duodenum (223).

Although AA imbalances can depress DMI of nonruminants (123), imbalances are less likely to exist in ruminants because the majority of AA absorbed are from microbial protein produced in the RR and AA profile of microbial protein is relatively consistent (210). Supplementation of ruminally protected lysine and methionine, AA commonly limiting for milk production, showed no consistent effects on DMI in a summary of studies reported by Robinson et al. (215). However, analysis of the reported treatment means by paired t-test showed that AA supplementation tended ($P = 0.10$) to increase DMI with a mean increase of 0.32 kg of DMI/d. Increasing the CP content of diets can increase DMI of lactating cows, particularly when the CP content of diets is low. However, differences in CP or RUP content of diets within the range typically fed to high producing lactating cows can be expected to have relatively minor effects on DMI.

SUPPLEMENTAL FAT

Supplemental fat increases energy density of diets and can increase energy intake by dairy cattle (53, 201). While added fat has improved energy intake and milk yield in many experiments, the results have been inconsistent. In some studies, added fat depressed DM digestibility (201) and DMI (38, 227) of lactating cows. Sanchez et al. (221) suggested that insufficient metabolizable protein is responsible for the depression in DMI commonly observed when feeding supplemental fat. If decreased DMI is from insufficient metabolizable protein, a significant interaction of protein and supplemental fat would be expected for DMI in individual experiments. However, no interaction has been detected for several experiments that have evaluated factorial effects of protein (concentration or degradability) and fat for DMI of dairy cows using different fat sources (5, 26, 37, 90, 109, 126, 146, 200, 202, 216, 262). The mechanisms by which supplemental fat sometimes depresses feed intake are not clear but could involve effects of fat on ruminal fermentation and gut motility previously mentioned, acceptability of diets containing added fat, release of gut hormones, and oxidation of fat in the liver. Fat sources have been reported to vary in acceptability (119) and this will be discussed in a later section.

Dry matter intake was decreased, and postprandial plasma concentrations of insulin and CCK were decreased and increased, respectively, by feeding fat to lactating cows (38). Also, intravenous injection of exogenous CCK depressed feed intake of sheep (116). Choi et al. (40) reported that injection of MK-329, a nonpeptide CCK_A receptor antagonist, increased DMI by 92% in heifers fed a high fat diet during the first 2-h postinjection. Hypophagic effects of CCK are considered to be

from direct action of brain CCK on brain satiety centers, or peripheral action of gut CCK (211). Reidelberger (211) suggested that peripheral action of gut CCK includes inhibition of gastric emptying and increased distention, activation of vagal or splanchnic afferent neurons that inhibit the brain satiety centers, or increased absorption of nutrients by stimulation of pancreatic enzyme secretion and gallbladder contraction which stimulate hepatic satiety mechanisms.

Rate of oxidation of fatty acids (**FA**) in the liver alters signals generated by hepatic vagal afferent nerves to brain centers signaling satiety (225). Inhibition of beta oxidation of FA by mercaptoacetate, an inhibitor of acyl CoA dehydrogenases, increased DMI of rats fed a diet containing 18% fat but did not affect DMI of rats fed a 3.3% fat diet (225). Feeding supplemental fat can increase plasma NEFA concentration, increasing hepatic uptake and oxidation of NEFA in lactating cows (41). Mercaptoacetate injection decreased DMI by heifers (41), and effects of prevention of FA oxidation in the liver on hypophagic effects of supplemental fat have not been shown for ruminants. Effects of oxidation of FA on signals generated by hepatic vagal afferent nerves might be directly from generation of reducing equivalents or generation of ATP and its effect on the ATP dependent sodium pump as previously mentioned.

Effects of fat on satiety appear to be relatively rapid but the satiety effect does not appear to be sustained. Addition of animal-vegetable fat blend or tallow as 10% of the grain mix decreased the weight of the first meal after feeding but did not affect the weight of spontaneous meals (which were much smaller), or on total grain consumed in two experiments with lactating cows (124). Lack of fat effects on grain intake appeared to have been from an increase (not significant) in number of spontaneous meals. Although meal length of the first meal was not decreased in experiment 1, meal length in experiment 2 was reduced from 9.5 to 6.1 min for animal-vegetable fat and to 7.5 min for tallow. No differences in meal paterns were observed between the fat sources. Although injection of CCK reduced feed intake 39% by sheep during the first 10 min of feeding (116), plasma CCK concentrations were not significantly higher for lactating cows consuming diets containing fat compared to control until 3-h postfeeding (40). Evaluation of effects of dietary fat on temporal effects of CCK release, rate of absorption, and oxidation of FA in the liver in relation to meals will help elucidate mechanisms involved in the hypophagic effects of fat.

Comparison of Fat Sources

Insight into potential mechanisms of the hypophagic effects of fat can be gained by evaluation of effects of different sources of supplemental fat on DMI and animal performance. Fat sources used in experiments with lactating cows include oils, extruded and whole oilseeds, yellow grease, hydrogenated yellow grease, tallow, partially hydrogenated tallow, prilled tallow, prilled FA, and calcium salts of palm FA (**Ca-PFA**). These fat sources vary in physical and chemical characteristics that affect their digestibility as well as associative effects on diet DM digestibility, and possibly DMI. Fat sources fed to dairy cows vary in chain length (primarily C_{16} and C_{18}), degree of saturation, and degree of esterification.

The effects of added fat on feed intake were evaluated statistically for several categories of supplemental fat. A data file was developed containing treatment means from published experiments with lactating cows that compared fat sources or that evaluated animal response to different concentrations of added fat in the diet. All experiments included supplemental fat in TMR. Fat supplements were initially classified into the following categories: vegetable oil, whole oilseeds, extruded oilseeds, grease, tallow, Ca-PFA, protected (prilled or hydrogenated) tallow, and prilled FA. Treatment means that included multiple sources of added fat were eliminated from the data file, as were those for vegetable oil which were too few to evaluate. Categories consolidated after regression analysis showed no difference for effects of similar fat sources on DMI (results not shown). The following four categories of fat were evaluated for effects on DMI: oilseeds (extruded and whole), unprocessed animal fat (grease and tallow), hydrogenated FA and triglycerides (**TG**), and Ca-PFA. The measure of fat content of diets varied by study with some reporting total FA and others reporting values for ether extract. Equation 1 was developed with treatment means of diets reported in the literature (36, 75, 85, 86, 147) and used to predict total FA content from ether extract content of diets ($r^2 = 0.87$; $P < 0.0001$; RMSE = 0.71; n = 18).

$$FA = -0.98 + 1.03 \times EE \qquad [1]$$

where FA = fatty acid content of the diet (% of DM), and EE = ether extract content of the diet (% of DM). Besides glycerol, EE includes various amounts of wax, galactolipids, steroids, and phospholipids that are not measured as FA. Therefore, accuracy of prediction of FA from EE will vary by diet and dietary ingredient. Variation in added FA and total FA content of diets, DMI, and milk yield were similar for the four categories of fat in the data file and each category contained at least 26 treatment means (Table 1). The relationship between dietary FA content and DMI by lactating cows is shown in Figure 6 for each category of fat. Significant

Table 1. Simple statistics for the data file used to evaluate effects of fatty acids (FA) on DMI.

Item	Fat category	n[1]	Minimum	Maximum	Median	Mean	SD
Added FA (% of DM)	Oilseeds	33	0.9	5.0	2.5	2.8	2.2
	Unprocessed animal fat	26	1.8	5.8	3.6	3.9	2.7
	Hydrogenated fat	29	1.2	5.7	3.2	3.0	2.1
	Ca-PFA[2]	28	1.6	6.2	2.8	2.9	1.5
Contol diet FA (% of DM)	Oilseeds	33	1.1	3.2	2.3	2.5	1.3
	Unprocessed animal fat	26	0.6	4.2	2.5	2.6	1.5
	Hydrogenated fat	29	1.2	4.5	2.9	2.7	1.4
	Ca-PFA	28	1.5	4.9	2.7	2.8	2.0
Diet FA (% of DM)	Oilseeds	33	2.8	7.0	5.0	5.2	2.7
	Unprocessed animal fat	26	3.8	8.6	6.1	6.4	3.1
	Hydrogenated fat	29	3.0	9.0	6.2	5.7	2.9
	Ca-PFA	28	4.3	8.8	6.0	5.6	2.0
DMI for control diet (kg/d)	Oilseeds	33	14.2	28.2	21.1	22.8	5.4
	Unprocessed animal fat	26	17.3	27.1	22.4	20.3	4.6
	Hydrogenated fat	29	17.6	28.9	21.2	20.5	3.2
	Ca-PFA	28	17.1	25.5	22.0	21.8	4.9
Milk yield for control diet (kg/d)	Oilseeds	33	15.1	38.5	30.9	32.4	8.5
	Unprocessed animal fat	26	23.4	37.8	30.8	31.3	7.1
	Hydrogenated fat	29	20.0	44.4	28.2	27.9	7.8
	Ca-PFA	28	20.0	39.3	31.9	30.5	9.9
Dietary CP (% of DM)	Oilseeds	33	15.7	20.2	17.5	17.6	3.0
	Unprocessed animal fat	26	13.9	20.1	17.8	15.9	5.3
	Hydrogenated fat	29	14.5	25.5	17.3	17.3	2.0
	Ca-PFA	28	15.6	20.8	17.7	17.3	3.0

[1]n = Number of treatment means from the literature (5, 26, 33, 34, 36, 37, 38, 44, 65, 66, 67, 72, 75, 77, 78, 84, 85, 86, 89, 90, 109, 110, 118, 128, 136, 137, 139, 143, 145, 146, 147, 149, 150, 151, 152, 163, 166, 167, 170, 194, 199, 200, 202, 203, 204, 216, 226, 227, 228, 229, 232, 233, 239, 240, 243, 250, 256, 262, 267, 268).

[2]Ca-PFA = Calcium salts of palm FA.

decreases in DMI were observed for Ca-PFA for 11 of 24 comparisons (Figure 6d). In addition Ca-PFA resulted in a numerical decrease in DMI in 22 of the 24 comparisons. Other sources of fat had less consistent effects on DMI and there were few significant decreases in DMI by added FA for each category of fat (Figure 6a, b, and c).

Linear and quadratic effects of added FA from the four fat sources were evaluated by linear regression using a common intercept, separate slopes model (Equation 2). Crude protein content of diets and FA content of control diets were included as covariates. Data were weighted by the reciprocal of the variance of treatment means (n/s^2) to account for unequal statistical power from differences in experimental design and replication across studies (246).

$$Y_{ijklmno} = \beta_0 + \beta_1 O_i + \beta_2 O_i^2 + \beta_3 U_j + \beta_4 U_j^2 + \beta_5 H_k + \beta_6 H_k^2 \quad [2]$$
$$+ \beta_7 S_l + \beta_8 S_l^2 + \beta_9 P_m + \beta_{10} F_n + e_{ijklmno}$$

where $Y_{ijklmno}$ = DMI (% of control treatment with no supplemental fat), O_i = added FA for oilseeds (% of DM), U_j = added FA for unprocessed animal fat (% of DM), H_k = added FA for hydrogenated fat (% of DM), S_l = added FA for Ca-PFA (% of DM), P_m = CP content of diet (% of DM), F_n = FA content of control diet (% of DM), $\beta_{0 \text{ to } 10}$ = regression coefficients, and $e_{ijklmno}$ = residual error.

Effects of added FA on DMI varied by category of fat (Table 2, Figure 7a). Quadratic effects were removed from the model when not significant ($P > 0.10$). Also, the FA content of control diets was not significant ($P > 0.10$) and was removed from the model. The significant effect of dietary CP content as a covariate suggests that hypophagic effects of fat is reduced with greater metabolizable protein as suggested by Sanchez et al. (221). However, the effect is relatively small for the range in CP concentration normally observed for diets of high producing dairy cows (~2 percentage units) and not sufficient to eliminate the hypophagic effects of added fat when they exist. No effect of added FA on DMI was observed for hydrogenated fat. Addition of FA from oilseeds resulted in a quadratic effect on DMI with a minimum at approximately 2% added FA. The reason for the quadratic effect observed for oilseeds is not clear. Negative linear effects were observed for unprocessed animal fat and Ca-PFA. Dry matter intake was depressed approximately 2.5% for each percentage unit of added Ca-PFA in the diet over control. This was approximately twice the depression for each percentage unit of added FA observed for unprocessed animal fat.

The maximum amount of added FA ranged from 5.0 to 6.2% of diet DM for the different categories of fat in this data file (Table 1). Because this is in addition to the FA content of the control diets, the maximum FA content of diets in this data file ranges from 7.0 to 9.0% of diet DM for the different categories of fat, which is greater than the maximum typically included in diets of lactating dairy cows (approximately 5.5 to 6% total FA). Although the FA concentration of the control diet as a covariate was not significant and the depressions in DMI for Ca-PFA and unprocessed animal fat were linear, higher than recommended concentrations of total FA in diets could have affected the regression coefficients obtained. To examine this further, a subset of the data file described in Table 1 containing 72 treatment means for which the total FA content of diets were less than or equal to 6% of DM was evaluated using the same regression model (Equation 2). Quadratic effects of added FA were removed from the model when not significant ($P < 0.10$). Unlike the regression analysis using the complete data file, the effect of CP content

of control diet was not significant ($P > 0.10$) and was removed from the model. The significant regression coefficient for FA content of the control diet (-1.38, $P = 0.06$) suggests that response in DMI to added FA depends on the FA content of the initial diet. While this might be expected, it was not significant for the regression analysis using the complete data file, which included data with greater concentrations of dietary FA. Addition of FA from hydrogenated fat and from oilseeds resulted in a quadratic effect on DMI with a minimum at approximately 2.3 and 3.0% added FA, respectively. The reason for the quadratic effect is again not clear. Negative linear effects were observed for both unprocessed animal fat and Ca-PFA and the effect for Ca-PFA was again greater than that for unprocessed animal fat (Table 2). This analysis demonstrates definite differences among fat sources for effects of added FA on DMI.

Although digestible fat has over twice the energy per unit of mass than digestible carbohydrate, FA digestibility and effects of added fat on digestibility of diet DM varies by fat source. Saturation of TG can greatly
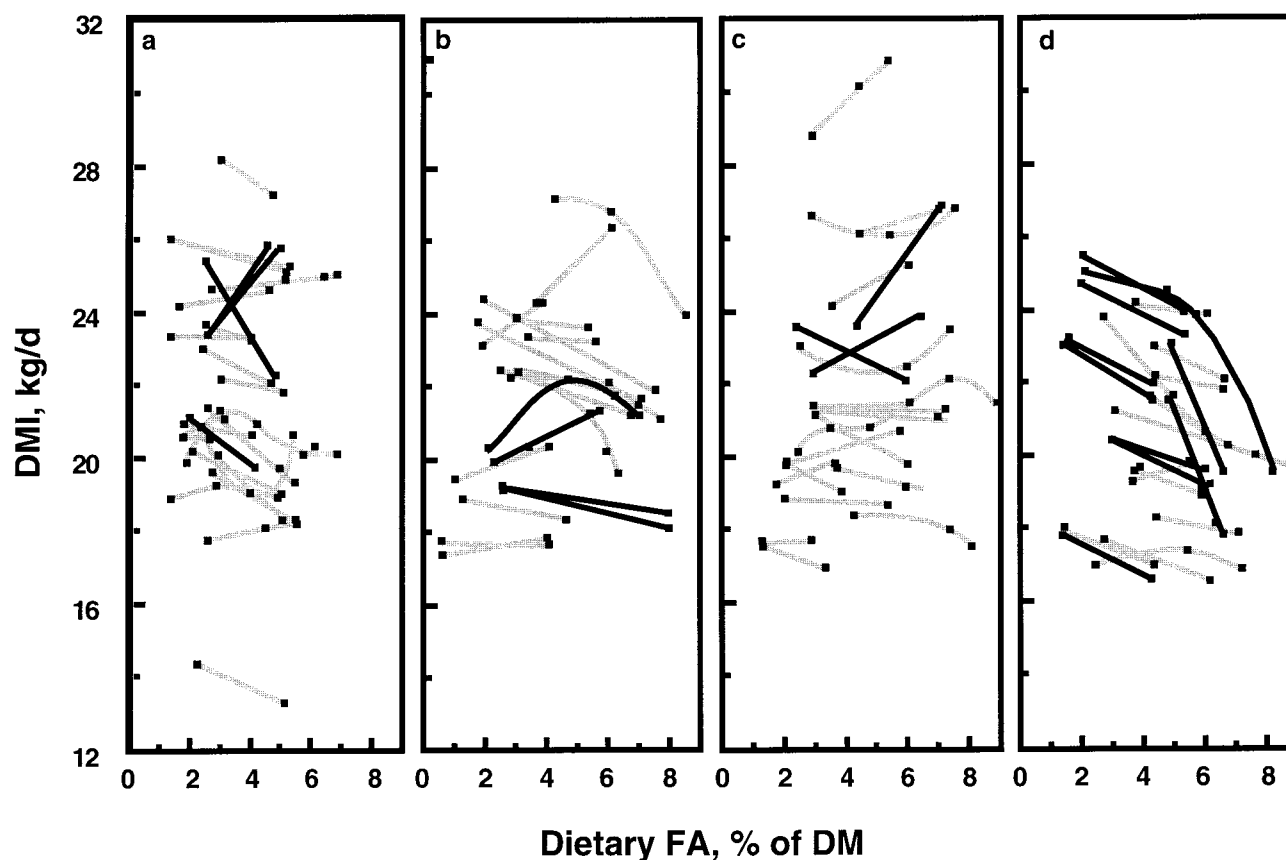
Figure 6. Relationship between fatty acid (FA) content of diet and DMI by lactating cows for four categories of fat in the data file described in Table 1. Categories of fat include oilseeds (a), unprocessed animal fat (b), hydrogenated triglycerides and FA (c), and calcium salts of palm FA (d). Treatment means within a comparison are represented by smoothing splines (212) with $\lambda = 0.01$. Black splines signify a significant effect and gray splines signify a nonsignificant effect of FA on DMI within comparison.

Table 2. Results for regression of added fatty acids (FA) from four categories of fat (% of DM) on DMI (% of control) using the data file described in Table 1 (complete data file) and a subset of the data file which includes only treatment means with dietary FA content of 6% of DM or less (restricted data file).

Factor	Order	Estimate	SE	95% Confidence interval		P
Complete data file						
Mean		94.8	4.3	86.2 to	103.4	<0.0001
Oilseeds	L[1]	−2.84	1.27	−5.38 to	−0.30	0.03
	Q[2]	0.59	0.29	0.01 to	1.17	0.04
Unprocessed animal fat	L	−1.23	0.38	−1.99 to	−0.47	0.01
Hydrogenated fat	L	−0.26	0.47	−1.20 to	0.68	0.57
Ca-PFA[3]	L	−2.52	0.51	−3.54 to	−1.50	<0.0001
CP		0.42	0.23	−0.04 to	0.88	0.07
Restricted data file						
Mean		112.4	4.2	104.0 to	120.8	<0.0001
Oilseeds	L	−7.96	2.89	−13.74 to	−2.18	0.01
	Q	1.36	0.63	0.10 to	2.62	0.04
Unprocessed animal fat	L	−3.55	1.13	−5.81 to	−1.29	0.01
Hydrogenated fat	L	−8.19	3.54	−15.27 to	−1.11	0.02
	Q	1.73	0.80	0.13 to	3.33	0.04
Ca-PFA	L	−5.01	1.23	−7.47 to	−2.55	<0.0001
FA content of control diet		−1.38	0.71	−2.80 to	0.04	0.06

[1]L = Linear effect of added FA.

[2]Q = Quadratic effect of added FA.

[3]Ca-PFA = Calcium salts of palm FA.

reduce FA digestibility (83) and added unsaturated FA can result in decreased fiber digestibility in the RR (201). Unfortunately, effects of fat category on digestible energy intake could not be evaluated because only two experiments were found that reported means and standard errors for digestible energy intake with supplemental fat. For one experiment, substitution of yellow grease for grain at 4% of diet DM had no effect on digestible energy intake of lactating cows (34). For the other, an interaction between fat addition and the NSC content of the diet was found, with fat decreasing digestible energy intake in high NSC diets and increasing digestible energy intake in low NSC diets (86). Only about one half of the studies in the data file reported digestibility of DM and fewer reported digestibility of FA. Although statistical significance or measures of variation in treatment means were not reported, digestible energy intake was calculated from gross energy intake and energy digestibility for two other experiments. Addition of Ca-PFA to diets of lactating cows at approximately 3% of diet DM had no effect on digestible energy intake in a study reported by Andrew et al. (5) but resulted in approximately 6% lower digestible energy intake compared to control in a study reported by Erickson et al. (89). Although energy utilization is more efficient for digested fat than digested carbohydrate (5), it is clear that addition of fat to the diet does not always result in increased net energy intake and that reduction in DMI is one of the primary reasons. Differences in hypophagic effects of fat categories observed in Figure 7 could be caused by differences in

their acceptability and physical and chemical characteristics as discussed below.

Acceptability

Differences in acceptability of fat sources can contribute to differences in their hypophagic effects. Fat supplements were found to vary in acceptability when fed alone or top-dressed, with lower acceptability for the Ca-PFA, than for tallow, sodium alginate encapsulated dry tallow, or prilled long chain fatty acids (**LCFA**) (119). Differences among fat supplements decreased when they were mixed with grain and, except for Ca-PFA, acceptability of fat increased following an adaptation period. The effects of fat source on acceptability of diets when fat is included in TMR are not known, but are probably small unless inclusion rates are very high.

Chain Length

Fat fed to lactating cows varies greatly in the ratio of C_{16} to C_{18} FA. Palm oil has approximately 47% palmitic acid (84), which is higher than most other sources of fat fed to dairy cows. However, greater hypophagic effects of Ca-PFA are probably not related to higher palmitic acid content because there is no evidence that C_{16} FA is more hypophagic than C_{18} FA. Abomasal infusions of soy oil and high palmitate soy oil with ratios of C_{16} to C_{18} FA of 0.10 and 0.68, respectively, resulted in similar reductions in DMI by lactating cows (30). Also, regression analysis of pooled data reported in the
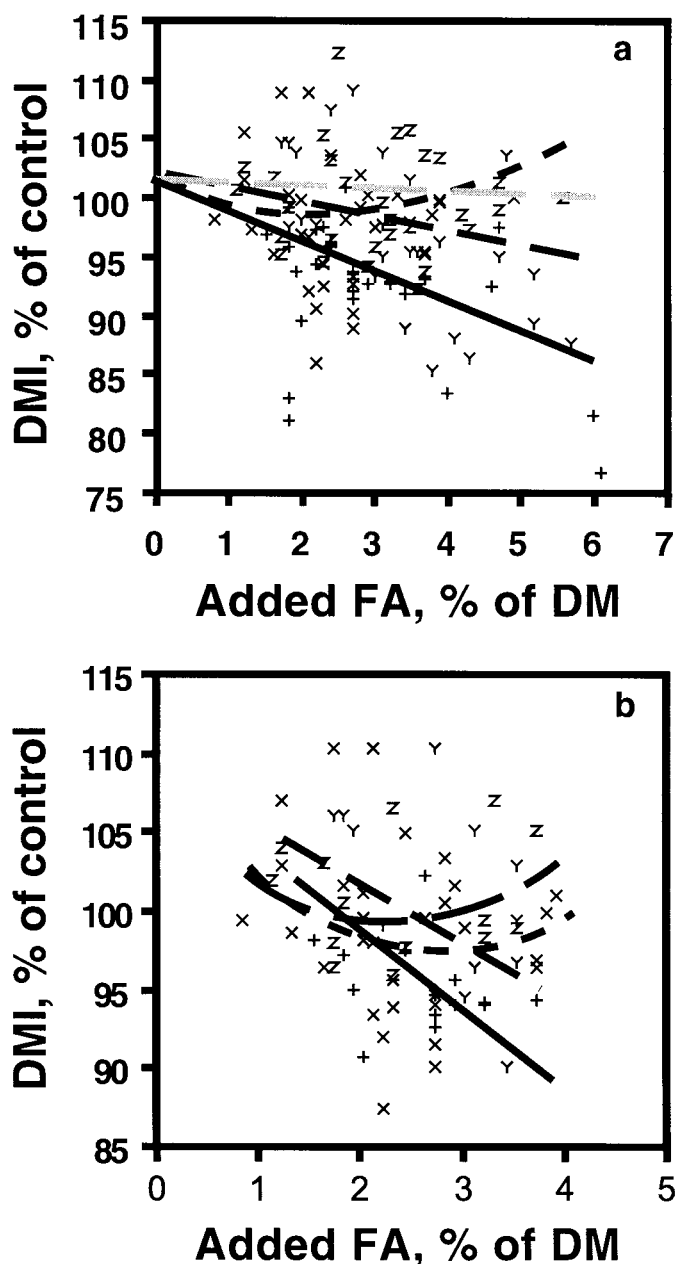
Figure 7. Relationship between added fatty acids (FA) and DMI by lactating cows using the data file described in Table 1 (a) and a subset of the data file which includes treatment means with dietary FA content of 6% of DM or less (b). Categories of fat include oilseeds (x), unprocessed animal fat (y), hydrogenated TG and FA (z), and calcium salts of palm FA (+). Regressions lines are plotted for each category: oilseeds (short dashed line), unprocessed animal fat (medium dashed line), hydrogenated fat (long dashed line line), and Ca-PFA (solid line), using regression results in Table 2 and mean values for CP and FA content of control diets for each category of fat. Black regression lines signify a significant effect and gray regression lines signify a nonsignificant effect of added FA on DMI for each category of fat.

literature did not detect a significant effect of C_{16} to C_{18} FA ratio on DMI of lactating cows (94). In addition, feed intake of lactating cows decreased with increasing chain length of LCFA infused into the abomasum (76), although the effects of chain length were confounded with percent saturation.

Saturation

Hypophagic effects of added fat increase with proportion of unsaturated FA (136, 203, 204). Elliott et al. (84) reported that DMI tended ($P < 0.12$) to be depressed 5.5% by addition of 6.1% Ca-PFA compared with addition of similar concentrations of hydrogenated palm FA that were either prilled or flaked. However, digestibility of total FA were higher for the Ca-PFA, and no differences were observed for digestible energy intake. Firkins and Eastridge (94) evaluated treatment means from 11 experiments and reported that DMI and FCM decreased as degree of unsaturation of LCFA increased. They suggested that the greater hypophagic effect of unsaturated FA is from a reduction of ruminal fiber digestion increasing distension in the RR, or from metabolic regulation of DMI because of the greater absorption of unsaturated compared with saturated LCFA. As previously mentioned, increased distention in the RR from reduced fiber digestion from added fat has not been demonstrated experimentally. Also, metabolic regulation from increased FA absorption is inconsistent with the observation that DMI was not reduced by increasing dietary concentrations of oilseed or hydrogenated fat (Figure 6).

While reduction in fiber digestion and increased FA digestibility cannot be ruled out as potential mechanisms responsible for the hypophagic effects of fat, additional mechanisms are involved. Potential ruminal effects were avoided in experiments that infused LCFA post-ruminally in lactating cows. Greater hypophagic effects of LCFA with increased degree of unsaturation were observed when LCFA were infused into the abomasum, with no effects of fat source on total tract FA digestibility (30, 43, 76). Drackley et al. (76) suggested that unsaturated LCFA reaching the small intestine of dairy cows affects gastrointestinal motility and DMI. Differences in hypophagic effects for unsaturated C_{18} FA have not been clearly determined and await affordable sources of pure $C_{18:1}$ and $C_{18:2}$ FA (30).

Biohydrogenation of FA

Extensive biohydrogenation of FA occur in the RR (61, 257), which should reduce the hypophagic effects of some unsaturated fat sources. Although biohydrogenation can be as high as 90% (29), degree of biohydro-

genation is affected by characteristics of the fat source, and retention time and characteristics of the microbial population in the RR. Biohydrogenation increases with degree of unsaturation of C_{18} FA (143, 269) and is reduced as amount of added unsaturated fat increases (42). Oils supplemented in diets appear to be highly biohydrogenated in the RR. Biohydrogenation of sunflower oil fed to lactating cows has been reported to be approximately 80% (143) and saturation of total FA in the RR of nonlactating cows exceeded 75% when soybean oil was added up to 8% of dietary DM (17). Extent of biohydrogenation of FA in oilseeds is probably affected by retention time in the RR and accessibility of oil which is affected by grinding, extrusion, and chewing. Greater biohydrogenation for liquified triglycerides from choice white grease compared to prilled FA fed to steers (81) suggests that prilling decreases release and biohydrogenation of FA in the RR. Also, similar biohydrogenation of LCFA for TG compared with a mixture of TG and FA fed to steers (81) suggests that TG containing unsaturated FA are readily hydrolyzed in the RR since remaining esterified FA are not biohydrogenated in the RR (135). Ruminal lipolysis of dietary TG decreased linearly as the degree of saturation increased (83). Fat supplementation of oleamide, but not canola oil, decreased DMI of lactating cows, which could be because oleamide is resistant to biohydrogenation in the RR (138). Biohydrogenation of total FA in diets containing Ca-PFA was 57% which was much lower than the 87% reported for FA in diets containing animal vegetable fat blend (269). Net biohydrogenation of unsaturated C_{18} FA in Ca-PFA was estimated to be 33% in an experiment with lactating cows (148).

Although the different effects of source of FA on DMI observed in Figures 6 and 7 cannot be explained by differences in saturation of FA of the supplements, differences in biohydrogenation of unsaturated fats has a direct effect on the amount of unsaturated FA reaching the duodenum. For the categories of fat shown in Figures 6 and 7, the degree of saturation is as follows: hydrogenated fat > Ca-PFA > tallow and grease > oilseeds. However, the reverse order is likely for biohydrogenation of FA, which could result in greater amounts of unsaturated fat reaching the duodenum for Ca-PFA and tallow compared to oilseeds and hydrogenated fats. The effects of fat sources on DMI shown in Figure 7 could be consistent with the hypothesis proposed by Drackley et al. (76) that DMI is affected by the amount of unsaturated fat reaching the duodenum. Greater hypophagic effects as amount of unsaturated FA reaching the duodenum increases might be from greater release of CCK stimulated by unsaturated compared to saturated FA. In addition, unsaturated FA might be absorbed and oxidized in the liver more quickly, generating reducing equivalents and satiety faster than saturated FA. Future research should determine the effects of fat source and other factors such as DMI and fermentability of diets on amounts of unsaturated FA reaching the duodenum. In addition, the effects of saturation of FA reaching the small intestine on CCK release and rate of FA absorption and oxidation by the liver should be determined for lactating dairy cows.

Esterification

No differences have been observed between TG and FA on DMI of lactating cows (78) or steers (81, 83). However, supplemental fat did not decrease DMI in these experiments, so differences in effects of esterification on DMI cannot be expected. Esterification decreased digestibility of FA entering the small intestine in one experiment (83) but not in others (78, 81).

Hyperphagic Effects of Added Fat

Supplementation of fat has resulted in higher DMI in several studies (Figure 6). Substitution of fat for grain can reduce the hypophagic effects of propionate by reducing its flux to the liver. In addition, dietary fat has a lower heat increment per unit of energy than other energy sources and its inclusion in diets has been advocated as a means of reducing heat stress, possibly increasing DMI of lactating cows (23, 183). Thermostatic control of feed intake was demonstrated by Bhattacharya and Warner (28) who reported that feed intake by heifers was significantly increased 24% compared to control by infusion of cold water (5°C) into the RR and decreased by 9% (not significant) compared to control with infusion of warm water. Skaar et al. (242) reported that DMI was significantly increased 7% in the warm season and was 5% lower (not significant) in the cool season for cows consuming diets with added fat compared with diets without added fat. However, experiments with lactating cows housed in heat stress or thermoneutral environments and fed diets with and without supplemental fat, reported no interaction of diet and environment for feed intake (151, 180).

Supplemental fat could prevent hypophagic effects of other fuels. For instance, Langhans et al. (158) reported that subcutaneous injections of lactate and pyruvate decreased feed intake in rats fed a high starch diet but had no hypophagic effects for rats fed a high fat diet. Lactate must be converted to pyruvate to be metabolized and high fat diets have been found to decrease activity of pyruvate dehydrogenase in rats (24), which should inhibit pyruvate oxidation in favor of carboxylation to oxaloacetate. Although no interaction was observed for fat supplementation and source of carbohy-

drate for two experiments (167, 240), hyperphagic effects of fat could be from similar mechanisms.

TEMPORAL EFFECTS OF DIGESTION AND ABSORPTION ON SATIETY

Fermentation patterns in the RR probably affect feeding behavior, but little research has been done in this area. The rate of increase in osmolality in the RR and the flux of propionate and other fuels to the liver is determined by rate of eating during meals and rate of fermentation of OM in the RR. Factors affecting production of fermentation acids and their removal from the RR influence pH and rate of absorption of VFA from the RR (3). Thus, meal size could be smaller when rapidly fermented carbohydrates such as processed barley or wheat are included in the diet and when high grain diets that result in lower ruminal pH are fed. Possible effects on DMI would depend, in part, on effects of diet on length of inter-meal interval determined by hunger. Similarly, factors affecting absorption of FA from the small intestine likely affect meal patterns. Future investigations of the effects of diet characteristics related to rate of digestion and absorption on meal patterns should help us understand mechanisms affecting hunger and satiety.

INTEGRATION OF SATIETY SIGNALS

Evidence shows that DMI is regulated by more than one mechanism and that these mechanisms are not mutually exclusive but interact to affect satiety (100, 133). This is supported by several observations. Effects of ruminal infusion of Na acetate and portal infusion of Na propionate depressed DMI of a pelleted diet 60% by sheep, which was approximately additive; DMI depression was 44% for Na acetate and 19% for Na propionate alone (1). Ruminal distension by inflation of a balloon and intra-ruminal infusions of Na acetate and Na propionate failed to significantly reduce DMI of lactating cows individually, but distension plus infusion of VFA together depressed DMI (171). Although the ruminal infusion rate of Na acetate required for a statistically significant reduction in DMI of lactating cows was higher than the rate at which acetate is normally produced in the RR (103), lower levels could have reduced DMI under other conditions by additive effects of other stimuli. Additivity was also reported for the effects of increased diet NDF content and ruminal VFA infusions on reduction of DMI by lactating cows (39).

Integration of effects might be in brain satiety centers or peripherally such as the prevention of hypophagic effects of lactate by supplemental fat reported for rats (158). Another example of an integrative mechanism is the synergistic effects of inhibition of FA oxidation combined with inhibition of glycolysis on increasing DMI of rats (105). In that experiment, administration of methyl palmoxirate, a specific inhibitor of FA oxidation at the mitochondrial transport level, and injection of 2-deoxyglucose, an inhibitor of glycolysis, had no effect on feed intake by rats when given alone but combined treatment resulted in a pronounced increase in feed intake.

Short-term regulation of feed intake is complex and our knowledge is far from complete. Mechanistic modeling efforts have been inhibited by lack of knowledge of control mechanisms, particularly pertaining to metabolic regulation. Variation in thresholds caused by additivity and interactions are particularly difficult to model. Attempts to model dietary effects on DMI have been directed mainly at physical regulation (132). A few simple models have integrated physical and metabolic control, but specific mechanisms were not addressed and the models have not been validated extensively (96, 98, 176). Efforts to develop mechanistic models of short-term regulation of DMI are encouraged because the complexity of the problem can be reduced by mathematical representation. However, mechanistic models that accurately predict DMI are probably far in the future. In the meantime, a greater understanding of the main factors affecting DMI and their interactions can be used to better formulate diets for lactating cows although careful monitoring and evaluation of animal response is required.

STRATEGIES TO MAXIMIZE ENERGY INTAKE

Prices and availability of feed ingredients vary by geographic region, which greatly affects the diets fed. Regardless of geographic region, energy intake is often a primary limitation for milk yield and although available feeds can be quite different, diet formulation strategies to increase energy intake should be similar. For example, consideration should be given to the hypophagic effects from distension in the RR, direct or indirect effects of hypertonicity in the RR, flux of absorbed propionate, and hypophagic effects of fat. Distension in the RR can be reduced by decreasing the forage NDF content of the diet and including forages with highly digestible NDF. Distension might also be reduced by substitution of NFFS for forage NDF, particularly when dietary NDF content is high. Minimizing the filling effect of the feed becomes more important as the effects of distension on DMI increase as milk yield increases. Forages with greater NDF digestibility should be allocated to the highest producing cows on the farm. Hypertonicity in the RR and absorbed propionate flux can be reduced by decreasing the amount of fermentable starch

consumed. This might result in large increases in DMI for cows consuming highly fermentable diets as shown in Figure 4. However, when DMI is not limited by effects of fermentation acids, reducing ruminal starch fermentation could result in lower milk yield because of reduced microbial protein yield and possibly lower whole tract starch digestibility. Although site of starch digestion can be altered readily by substitution of starch sources, we are not currently able to accurately predict it for different starch sources fed to lactating cows in widely ranging diets. In addition, the threshold at which fermentation acids limit DMI is not known and must vary by cow and with physiological state of cows over time. Therefore, careful evaluation of animal response in DMI is required after diets are formulated and fed. Reducing the fermentable starch consumed can be accomplished by substituting a less fermentable starch source, NFFS, or forage in the diet for the highly fermentable starch source. Substitution of a less fermentable starch source with high whole tract digestibility is preferable because this should have the least effect on distension in the RR compared with substitution of forage or NFFS. In addition, more slowly fermentable starch sources could allow increased meal size and possibly DMI by reducing rate of increase in osmolality in the RR and absorbed propionate flux to the liver following initiation of meals. Decreasing ruminal fermentation of starch should also increase ruminal pH, which can increase energy intake further by increasing NDF digestibility.

Inadequate protein can limit energy intake although effects are small for the range of CP content of diets typical for high producing cows. Fat can be supplemented to increase energy intake further but inclusion of fat does not always increase energy intake and choice of supplement can have important effects. Ruminally active fat sources, primarily oils, can reduce fiber digestibility in the RR, unsaturated fat reaching the duodenum can reduce DMI, and saturated TG are poorly digested, all of which can alter the effect of supplemental fat on energy intake.

When cows are not fed individually, grouping strategies must be considered. Higher energy intake and more efficient utilization of nutrients can be attained by feeding different diets to smaller groups of cows that have similar energy requirements. Distension is a greater limitation on DMI for high producing cows, and diets for these cows should be formulated with lower forage NDF content and include forages with higher NDF digestibility, compared with diets for cows with lower milk yield. Variation in DM and NDF of silage can result in large changes in diet composition of TMR containing a large quantity of the silage. This necessitates feeding higher NDF diets to manage the risk of acidosis,

but that will lower DMI when it is limited by distension. Careful attention to reducing variation in DM and NDF of silages when filling silos should benefit energy intake.

Dietary factors can have a large effect on DMI of lactating cows. Although accurate predictive models for DMI do not currently exist for lactating cows, formulation of diets to maximize DMI while maintaining or increasing energy digestibility and careful evaluation of animal response to dietary changes can increase energy intake substantially. Increased understanding of mechanisms affecting satiety and hunger will increase the success of this process.

ACKNOWLEDGMENTS

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