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FAT IN DAIRY CATTLE RATIONS

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INTRODUCTION

History

During the past decade, fat has gained much attention as a feed ingredient for high-producing cows. Even though we have expended a great deal of effort on investigation of the feeding and metabolism of fat in dairy cows over the last 20 years (Palmquist, 1984), research on this topic goes back at least to the beginning of the century. Kellner (1907) concluded from European research that supplemental fat provided no advantage for lactation. Maynard and associates (Loosli et al., 1944) conducted extensive studies on fat supplements for lactation and their metabolism. In the first edition of his classic textbook Maynard (1937) showed that ether-extracted concentrates supported lower milk yield than a concentrate which contained 5.8 % fat (Fig. 1). He concluded that milk yield was not reduced unless cows consumed less fat than the amount secreted in the milk, and he remarked on the phenomenon that it was the yield of the milk, rather than milk fat percent, which was affected by limiting dietary fat.

In the 1960's there was a great surge of interest in the mechanisms regulating milk fat synthesis (Bauman and Davis, 1974), stimulated in some degree, no doubt, by the emergence of the gas-liquid chromatograph, which greatly simplified and speeded the determination of milk fat composition. However, lessons from Maynard et al. seem to have been forgotten, and attention was focused on the role of adipose tissue and liver-synthesized lipoproteins in supplying long-chain fatty acids for milk fat synthesis (Van Soest, 1963; Griel and McCarthy, 1969; Davis and Brown, 1970). To be sure, even though Maynard et al. early showed advantages for fat feeding, most cows had not reached production levels where supplemental fat was critical, corn was cheap (and contained a significant amount of fat), and a feed-fat industry had not developed.

By 1960 milk production potential of cows was increasing to the point that some dairymen were feeding amounts of cereals that exceeded physiological limits of cows, resulting in off-feed, rumen acidosis, fat cow syndrome, and low milk fat percent (Van Soest, 1963; Kesler and Spahr, 1964; Davis and Brown, 1970). Linkage of fat cow syndrome with low milk fat percent contributed to the prevalent idea that adipose tissue was a primary source of long-chain fatty acid for milk fat synthesis.

In 1967 we initiated studies with isotope tracers to attempt to define the relative importance of diet and adipose tissue as sources of long chain fatty acids for milk fat synthesis. (We previously defined the roles of acetate and ß-hydroxybutyrate as contributing approximately 40-50% and 8-10%, respectively, to milk fat carbon; Palmquist et al., 1969). Those studies showed that 90% of long-chain fatty acids in milk were derived directly from the diet (Palmquist and Conrad, 1971), an estimate which we later confirmed independently (Palmquist and Mattos, 1978). Studies using protected polyunsaturated fats showed that milk fat composition became highly unsaturated within 24-48 hours of initiating the new diets (Plowman et al., 1972), consistent with the important role of diet in supplying fatty acids for milk fat synthesis.

With the important role of dietary fat in milk fat synthesis clearly established, we initiated feeding studies to evaluate optimal types and amounts of fats in lactation diets, and to develop feeding management strategies. Important findings in those studies (Palmquist and Conrad, 1978, 1980) included: 1) adding 3% fat to dairy rations increased milk yield 6 to 15%; 2) milk fat percent was not compromised; 3) fat did not decrease digestibility of fiber; 4) digestibility of fat decreased at higher fat intakes; 5) calcium addition had a positive effect on digestibility of dry matter and fiber; 6) fat tended to be more efficiently utilized in higher protein diets; 7) hydrolyzed animal-vegetable blend and tallow were equally well-utilized at 3% of feed dry matter; 8) substituting fat for starch in the ration improved rumen fermentation and increased milk fat percent without compromising energy intake or milk yield; 9) substituting fat for starch prevented excessive fattening of cows.

We then focused on studying what seemed to be the most limiting factor for using fats routinely in dairy rations - namely the inhibition of fiber digestion by ruminal microorganisms (Palmquist and Jenkins, 1980). As calcium was known to be an important factor in fat utilization (White et al., 1958; Davison and Woods, 1963; Galbraith et al., 1971; El Hag and Miller, 1972; Galbraith and Miller, 1973; Palmquist and Conrad, 1980), we chose to examine in detail the interaction of calcium and fatty acids in ruminal content and their effects on microbial digestion of fiber (Jenkins and Palmquist, 1982). We found that, although calcium and fatty acids reacted in the rumen to form insoluble calcium soaps, there was a time lag which allowed fatty acids to interact with ruminal microorganisms (Jenkins and Palmquist, 1982; Palmquist et al., 1986). These studies led to the discovery that calcium soaps of long-chain fatty acids were both inert toward ruminal bacteria (thus microbial inhibition was prevented) and were digested by the cow (Palmquist and Jenkins, 1982; Jenkins and Palmquist, 1984; Palmquist, 1991). These results, combined with feeding studies of others, have led us to develop feeding guidelines outlined in Table 1.

FEEDING RECOMMENDATIONS

Maximum Forage

No feeding program is optimal without normal rumen function. The feeding program should be built on this principle, consistent with forage availability and energy needs of the cow. Forage stimulates ruminal motility, rumination, and salivation, and stabilizes ruminal microbial activity. Fatty acids in the rumen associate with forage particles, preventing their inhibition of ruminal microbial activity.

Calcium and Magnesium

At low intake fatty acid digestibility is greater than 80% (Palmquist, 1991). As intake of fatty acids exceeds 4-5%, their digestibility declines (Figure 2). Unabsorbed fatty acid combines with calcium and magnesium in the lower intestine (Body and Grace, 1983) decreasing digestibility of these essential minerals. Fortifying calcium and magnesium prevents hypocalcemia (Palmquist and Conrad, 1980; Steele, 1983), and hypomagnesemia (Kemp et al., 1966; Steele, 1983).

Balancing Carbohydrate and Protein

A most important function of ruminants is to maximize the fermentation potential of the rumen. Optimum balance of rumen-available (degradable) protein and rapidly fermentable carbohydrate (non-structural carbohydrate, NSC) is a key part of maximizing microbial protein synthesis (Hoover and Stokes, 1991). Using fat in the ration provides flexibility to optimize fiber and NSC content without compromising high energy intake. One must also consider increasing rumen undegradable protein content of the diet when fat is added, to balance energy:protein ratio of the diet. Whenever a ration is changed by adding fat, the ration should be totally rebalanced to optimize all nutrients.

How Much Fat to Feed?

As noted above, Maynard (1937) suggested that the optimum amount of fat in the diet approximated that produced in the milk. Fifty years later, we arrived at the same recommendation, based on a more complete understanding of fat metabolism in the cow. Assuming that adipose metabolism is in zero balance, the proper amount to feed is determined by the digestibility of fat (20% of intake lost in feces; Palmquist, 1991), and the proportion of absorbed fat secreted into milk (76%; Palmquist and Mattos, 1978). These two estimates account for 80% of dietary fat. The remaining 20% may be oxidized; although oxidation of fat increases as plasma fatty acid concentration increases, it usually represents only about 5% of total oxidative energy. Therefore, as 60% of dietary fat is taken up by mammary gland (80% absorbed x 76% uptake), and long-chain fatty acids make up about 60% of the weight of milk fat in fat-supplemented diets, the recommended feeding amount approximates that secreted in milk.

It should be recognized that the recommended amount of fat to feed needs to be adjusted to allow for changes in energy balance. Thus, when adipose tissue is being mobilized, the estimated amount of mobilization must be subtracted from the recommended fat feeding allowance. In one study we measured a loss in body condition score (BCS) of .75 (scale: 1 = thin; 5 = fat) during the first month of lactation. Ferguson and Otto (1989) estimated 1 BCS = 400 Mcal of net energy. Therefore, .75 x 400 = 300 Mcal loss in 30 days or 10 Mcal/day. This equals 10 Mcal day^{-1}/6 Mcal NE_ℓ (kg $fat)^{-1}$ = 1.67 kg body fat lost per day. Under such severe conditions one would not recommend feeding more fat. We usually assume a more moderate loss of 500 g body fat/day during the first month of lactation (3.5 Mcal NE_ℓ). If a cow is gaining considerable body weight, as in late lactation, one could add more fat in the diet, if it were desirable to increase fattening.

A second factor in determining the optimum amount of fat to feed considers metabolic efficiency. It has been estimated that the optimum efficiency of metabolism occurs when 15-20% of the metabolizable energy (ME) is supplied from fat (Kronfeld, 1976; Brumby et al., 1978). Much of this has to do with the very high metabolic efficiency of directly depositing dietary fatty acids into product (milk fat), as compared to *de novo* synthesis. Figure 3 shows the contribution of dietary fat to ME when it is fed in an amount equal to milk fat yield over the range of 10-50 kg/d of 3.5% milk produced by a 600 kg cow. At low yield, fat provides a lower percentage of ME because maintenance energy contributes a large proportion of the total energy requirement. At higher production levels, the recommended amount of fat approximates the range of maximum metabolic efficiency. This is an important consideration at high production levels, because disposal of metabolic heat constrains feed intake and yield of high-producing cows. The more efficiently nutrients are utilized, the less waste heat is produced. Note in the legend to Figure 3 that the efficiency of utilization of energy for lactation of the total diet (k_ℓ) is .62, whereas for fat it is .84. Thus, the waste heat produced from metabolizing 1 Mcal of fat is 1/2 that of metabolizing 1 Mcal of energy from carbohydrates (1 - .82 = .18) vs. (1 - .62 = .38).

How To Use Fats

As shown in Table 2, several fat sources may be used to formulate dairy rations. Consider first the fatty acid (not ether extract) concentration in the basal feed ingredients. In corn-based diets, this may be as high as 3% of feed dry matter. In barley, wheat, or milo-based diets, it will be less. Forages contribute relatively little fatty acid. Next use economical fat sources that fit the feeding management conditions, such as tallow, hydrolyzed animal-vegetable (A-V) blend, and whole oil seeds. The combination of basal and these supplemental fats should not exceed 5-6% of feed dry matter. The maximum will depend on amount and quality of forages, saturation of fat, and feeding management. More fat can be used in high alfalfa diets than in high corn silage diets, for example. These limits are imposed so that normal functioning of ruminal microorganisms will not be compromised. If more than 6% fat is needed in the diet to meet recommended amounts (according to milk fat yield), then a quality rumen-inert fat should be used in order to maintain normal rumen function.

When To Feed Fat

As can be deduced from Figure 3, one would not expect to feed fat to cows producing less than 600 g milk fat/day. Nevertheless, we have observed a milk yield response of about 10% in late-lactation cows producing 20 kg milk/d. This would not be anticipated, as feed intake should not be limiting in such cows. It probably represents a shift in metabolic efficiency. There is clear-cut evidence that when fat is included in dairy rations after the peak of lactation that persistency of lactation is improved (Ferguson et al., 1988; Jerred et al., 1990), and the effect on persistency may be even greater in first lactation cows (Ferguson et al., 1988).

Although it has long been believed that the greatest need for fat is during the first 100-120 days of lactation, cows often demonstrate a lag in dry matter intake and delayed lactation peak when fat is included in rations in early lactation (Ruegsegger and Schultz, 1985; Driver et al., 1990; Jerred et al., 1990). Baysingar et al., (1989) reported that higher milk yield of cows fed a basal ration containing 15% whole cottonseed responded to additional fat (450 g/d poultry fat) only after 80 days of lactation. Indeed, milk yield of cows less than 40 days in lactation was 10% lower than controls (Figure 4). L. H. Schultz (personal communication) observed that cows do not respond to supplemental dietary fat before 5 - 6 weeks of lactation.

Interactions between mobilization of body fat, dry matter intake, and the role of dietary fat in regulating dry matter intake remain to be worked out. Although there is reason to be cautious about feeding high amounts of fat early in lactation, current thought is to have cows calve in thinner condition (BCS not greater than 3.5 on 1 - 5 scale) and use some fat in the early lactation diet, rather than to have cows calve fatter and risk metabolic problems, such as fatty liver and ketosis (Jones and Garnsworthy, 1989; Garnsworthy, 1990).

Finally, it may be useful to use small amounts of fat prior to calving. In the last few days before parturition, cows often go off feed which leads to mobilization of adipose tissue and development of fatty liver (Skaar et al., 1989). Grummer and Carroll (1991) suggested that dietary fat may prevent this response, as dietary fat is metabolized by extrahepatic tissues, thus lowering the risk of fat infiltration of the liver.

DIETARY FAT AND MILK COMPOSITION

Milk Fat Concentration

The effect of dietary fat on milk fat percent is variable, depending on feeding management and type of fat fed. Unsaturated oils invariably reduce milk fat percent due to interference with rumen metabolism and fiber digestion (Palmquist and Jenkins, 1980). Whole oilseeds, tallow, animal-vegetable blend, and inert fats may increase milk fat percent. We summarized (unpublished) 50 literature studies in which optimal fat feeding management was reported, and found a positive relationship of .172 milk fat percentage units per pound of fat supplemented (.38 percent per kg fat supplemented). Feeding calcium soaps (.45 kg/d) increased fat percent .05 in 8 University trials and .066 in 7 field trials (Church and Dwight Co. Research Summary, 1988). Hansen and Knudsen (1987a,b,) presented evidence in cellular studies that palmitic acid (16:0) stimulated synthesis and incorporation of fatty acids into milk fat by promoting initiation of fatty acid esterification, whereas oleic acid inhibited synthesis of all fatty acids except butyric. Although this idea has not been tested rigorously in feeding trials, it is consistent with the data of Noble et al. (1969) who observed higher daily milk fat yields with 10% palmitic acid than with 10% stearic acid in the diet. Finally, increased *trans* 18:1 absorption, either from diet or ruminal synthesis, may specifically inhibit mammary synthesis of short chain milk fatty acids (Selner and Schultz, 1980; Banks et al., 1984, 1990; Teter et al., 1990).

Milk Fat Composition

Changes in milk fat composition caused by feeding fat have been known and researched for a century (Smith, 1916). Responses are of 2 general types: 1) increased mammary uptake of long chain fatty acids from diet inhibits *de novo* synthesis of short chain fatty acids in the mammary tissue, and 2) the long chain fatty acids of milk fat change in composition. Milk fat produced on a low fat diet will have rather high 16:0 content from *de novo* synthesis. Most supplemented fats are high in 18-carbon fatty acids which become saturated in the rumen and are absorbed mainly as stearic acid (18:0). This is desaturated to oleic acid (18:1) by the intestinal and mammary tissues and substitutes for 16:0 and shorter chain fatty acids. Generally, the content of long chain fatty acids in milk fat reflects the relative amounts of 16- and 18-carbon fatty acids in the diet.

Milk Protein Concentration

Milk nitrogen is composed of casein, whey, and non-protein (NPN) fractions. On average, true protein is 95.1% of total N; the major part of NPN is urea-N. Casein is 77.9% of total N (casein number) or 82.0% of true protein.

Feeding practice has measurable, significant effects on milk N content and distribution (Emery, 1978; Thomas, 1980). Increasing feed protein above requirements increases milk N, but this is primarily in the NPN fraction. Underfeeding protein decreases protein yield more than milk protein percent. Milk protein content increases .015 units per unit of NE_ℓ intake (Mcal/d) when the increased energy source is carbohydrate (Emery, 1978), or .0125 units for all energy sources (Spörndly, 1989). Alternatively, increasing energy from fat decreases milk protein content - .154 units per kg supplemental fat (Palmquist, unpublished).

The physiological or metabolic basis for the negative relationship between dietary fat intake and milk protein content has not been determined. Various postulates include decreased protein absorption due to decreased ruminal protein synthesis, fat-induced insulin resistance which may affect mammary amino acid uptake (Palmquist and Moser, 1981), fat-induced somatotropin deficiency (Casper and Schingoethe, 1989), altered mammary blood flow with reduced uptake of amino acids (DePeters, ADSA, 1990), and altered mammary metabolism (Cant et al., 1991).

Though there is little support for a protein deficiency concept, no hypotheses have been rigorously tested. Evidence is stronger, however, that amino acid uptake by the mammary gland is compromised in some way, and that milk protein content can be increased by raising the plasma concentration of all or limiting amino acids. This increases uptake and milk protein synthesis by processes independent of the dietary fat effect. This can be accomplished by supplementing certain rumen-protected amino acids (Chow et al., 1990; Canale et al., 1990), or high quality proteins, such as animal by-products, fish meal, or intestinally-infused casein (Cant et al., 1991). Niacin has been suggested to increase milk protein, but the response has been inconsistent.

Composition of Milk Protein

Many investigators have failed to observe an effect of fat on milk protein content. Early reports suggested that casein content was reduced. Often milk NPN is increased in fat feeding. When milk N is measured by Kjeldahl, only total N is measured, and a change in composition would not be observed. On the other hand, infrared instruments measure true protein, but do not pick up changes in milk NPN. Thus, only studies which determine milk protein fractions can define the effect of fat, if any.

Dietary Fat and Reproduction

High producing cows in negative energy balance are difficult to rebreed, because cycling is delayed. It has been postulated that feeding fat in early lactation should improve energy balance and return to cycling. As noted above, this is compromised if fat causes feed intake to be lower in early lactation. Some data suggest that fat feeding causes energy balance to be more sharply negative in early lactation, but the return to positive energy balance may be shortened (Skaar et al., 1989). Obviously, this is dependent on feeding management.

As reproductive status is influenced by steroid hormones, considerable interest has been generated concerning the idea that because feeding fat increases blood cholesterol, steroid hormone synthesis should be enhanced (Lucy et al., 1991). Indeed, this has some validity. Sklan et al. (1991) have reported increased pregnancy rate and reduced days open in cows fed high fat diets in Israel. However, Pate (Personal communication) has shown that insulin is a permissive factor in overall ovarian function, and feeding fat tends to depress circulating insulin levels, especially in early lactation. Determination of feeding and management effects on reproductive performance requires large numbers of animals to establish confidence in measures. As concepts of fat effects are only now being concisely formulated, it will be some time before specific recommendations for using fat to enhance reproductive performance can be formulated.

SUMMARY

Feeding supplemental fat in dairy rations clearly enhances lactation performance. The appropriate amount of fat in the diet approximates that produced in the milk. Sound feeding and management practices will assure success of fat utilization. Some effects of fat on metabolic function in dairy cows, such as regulation of feed intake, effects on milk protein synthesis, and role in reproductive performance, remain to be determined.

Table 1. Feeding guidelines for maximizing use of fat in dairy rations.

- Maximize forage content of the ration (minimum 21% ADF).
- Keep calcium and magnesium contents of the diet at minimum of 0.9 and 0.3% of the dry matter, respectively.
- Balance ration for rumen-degradable and -undegradable intake protein, and for non-structural carbohydrate intake.

Table 2. Guidelines for adding fat to dairy rations

- Feed as much fat (total fatty acid) as the cow secretes in her milk.
- Add fat in the following order:

Fatty acid, % of dry matter[1]	Source
0 - 3	Basal diet ingredients
3 - 6	Tallow, A-V blend, whole seeds[2]
> 6	Rumen-inert fat

[1] Actual percentages will be influenced by feeding conditions.

[2] Choice dictated by user; maximum of this range will be influenced by feeding conditions; i.e., lower if fat is more unsaturated, or if forage is limiting.

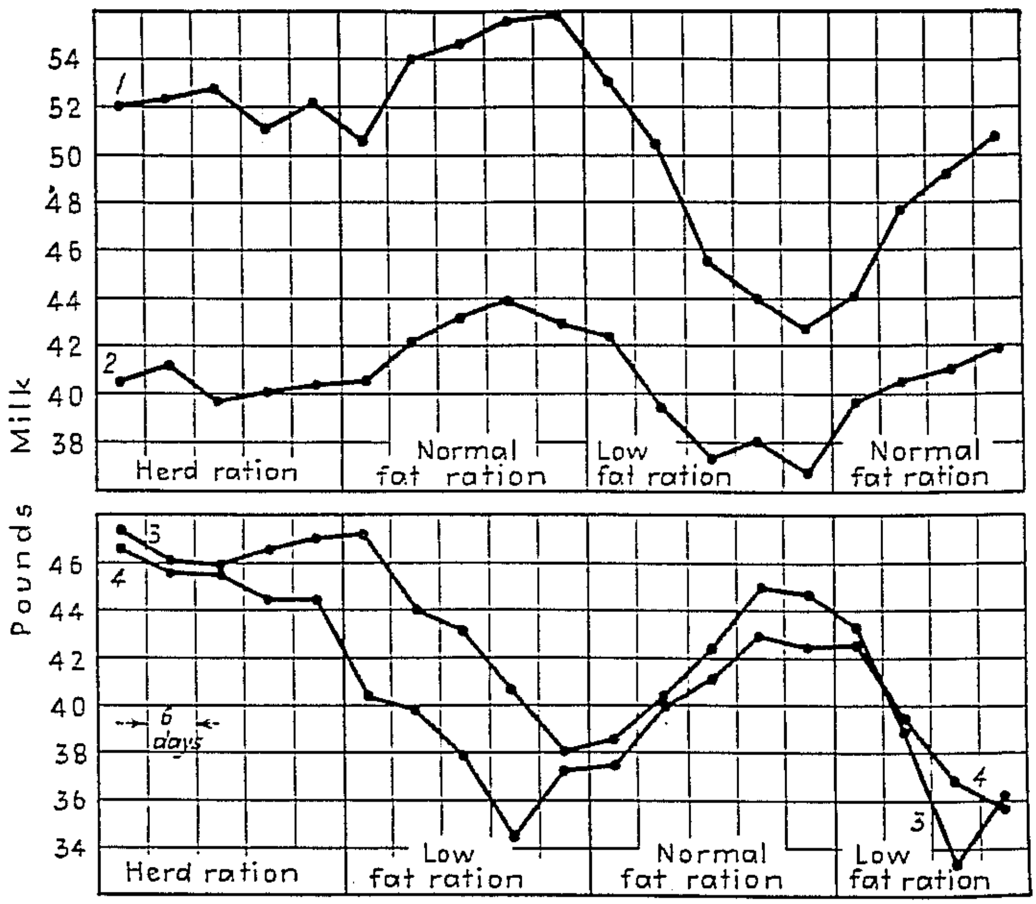

Figure 1. The influence of a ration low in fat on milk yield. Figure from Maynard's textbook, Animal Nutrition (1937), showing milk yield of cows fed low or high fat diets. (Maynard and McCay).

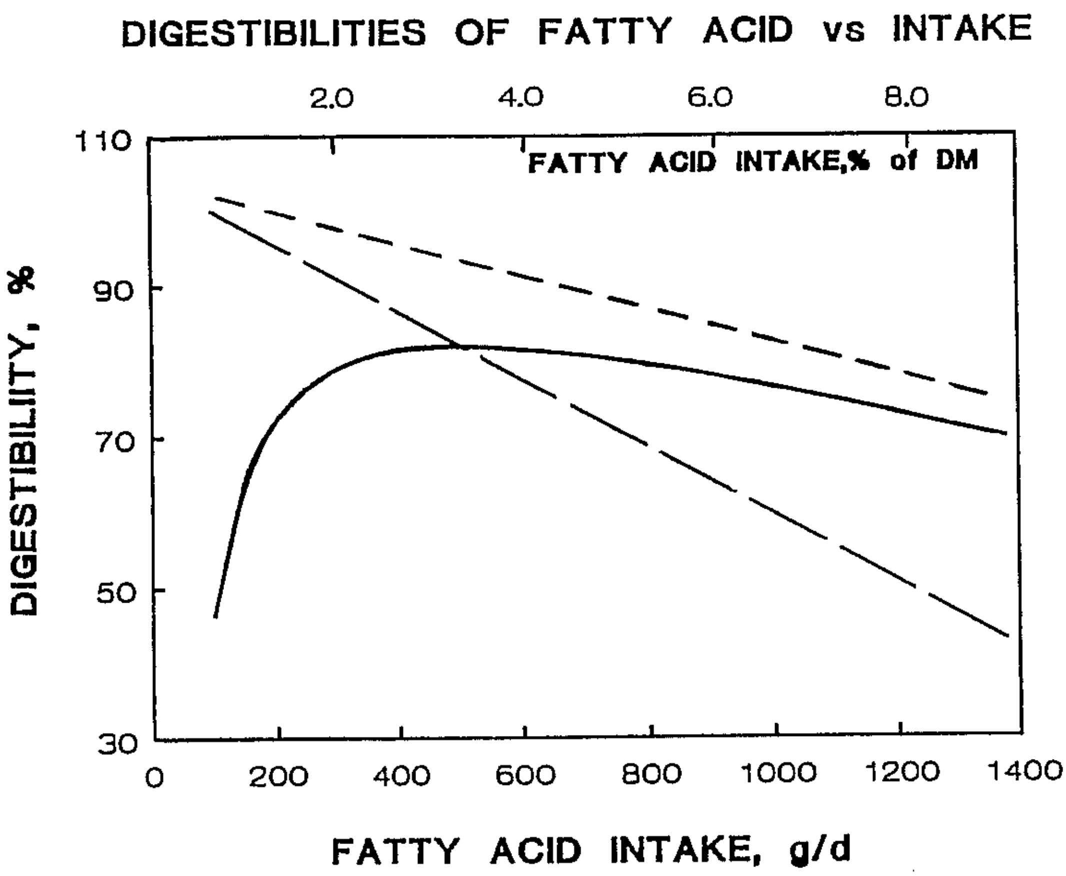

Figure 2. Apparent (—), true (---), and marginal true (– –) digestibilities of fatty acids by dairy cows. Computed from the regression: Fatty acid absorbed (g/d) = $-55.9 + 1.044x - .0002224x^2$; $r^2 = .837$; $n = 72$; $P < .001$. (Palmquist, 1991).

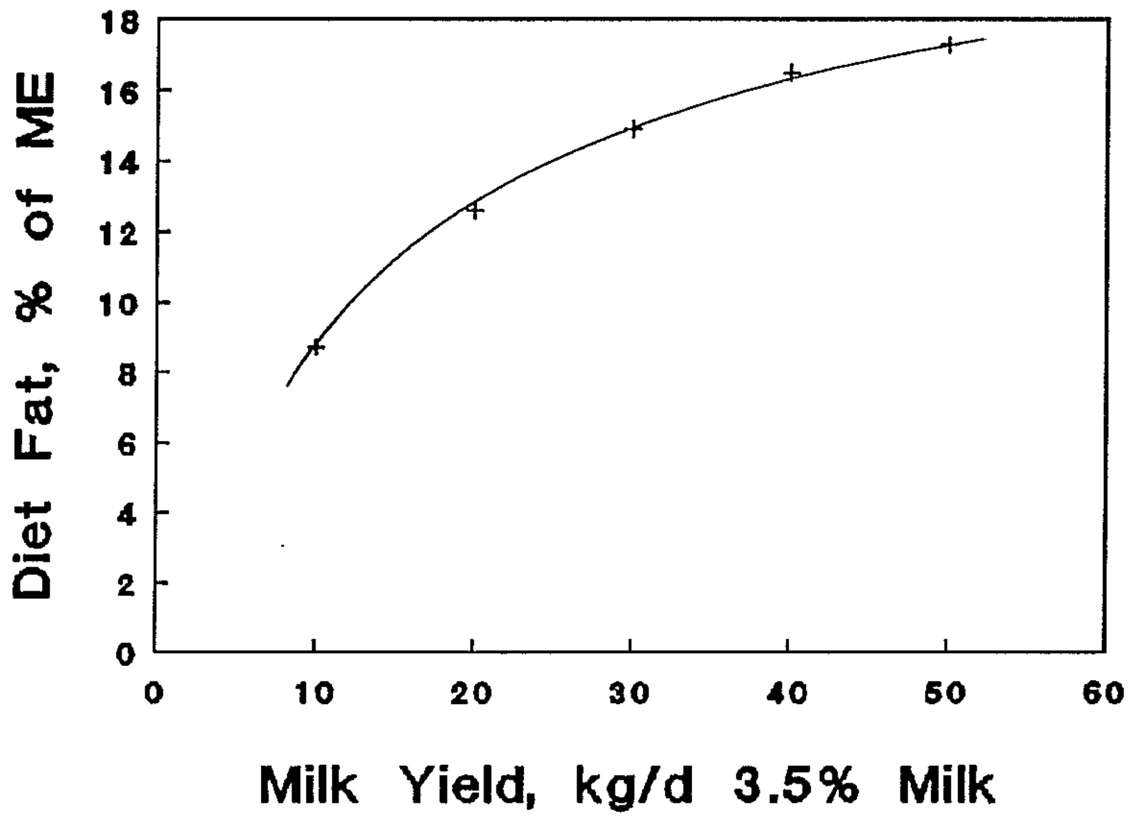

Figure 3. Dietary fat, percent of ME requirement vs. milk yield, kg/d of 3.5% milk by a 600 kg cow when the amount of fat fed equals that produced in milk. Energy requirement for maintenance + milk is from NRC, Rev. 1989, Table 6-4. Diet ME = $NE_{\ell}/.62$. Fat ME, MCal/kg = 6.0/.84. See text.

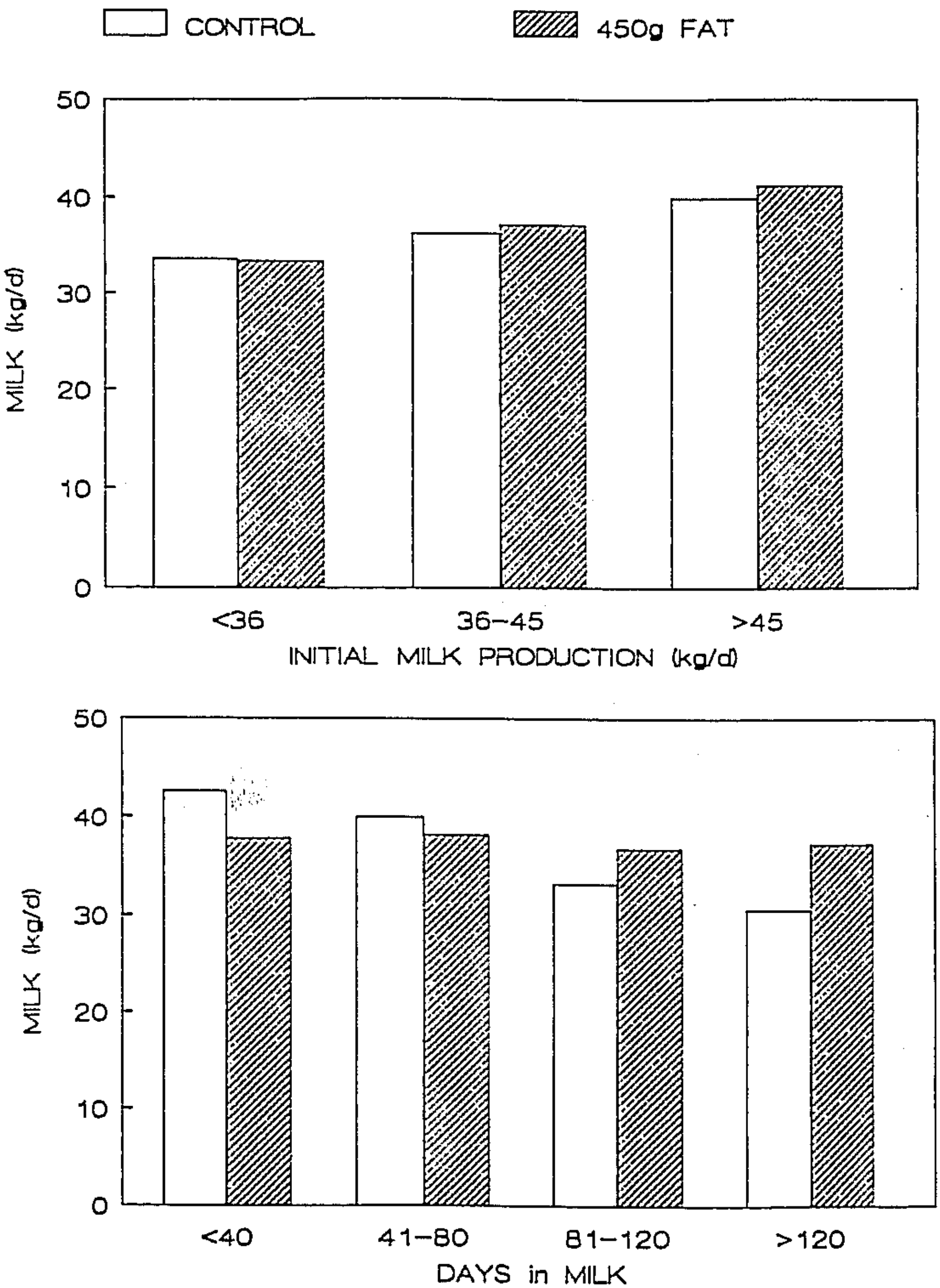

Figure 4. Effect of level of milk yield and stage of lactation on milk yield response to supplementing poultry fat (450 g/d). Control diet (DM): alfalfa silage, .35; barley, .35; whole cottonseed, .15; supplement, .15. (Baysingar et al., 1989).

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