INTRODUCTION

The genetic trend for increasing milk yield in the dairy cow population is impressive evidence of the application of genetic principles in dairy cattle selection. Walton (31) recently predicted that by the year 2000, individual cow records will approach 31,800 kg of milk per year and 1,360 kg of milk fat. Top individual herd averages will be nearly 16,000 kg of milk and 635 kg of milk fat. If these predictions are close, the subject of energy nutrition and metabolism will remain a relevant topic for many years. It will be a continuing challenge to design feeding systems and diet formulations that support this high production. An appropriate question is what high genetic merit for milk production means to a nutritionist or physiologist. To me it means the physical capacity and the physiological drive for cows to eat large volumes of energy-dense feeds, to assume negative energy balance through much of the first trimester of lactation, and to partition most of the feed energy plus energy from body stores into milk energy.

I will sketch a broad picture of energy nutrition and metabolism in the lactating cow and identify those areas in knowledge and understanding that constrain dairy scientists from assisting cows of superior genetic merit to produce milk more efficiently. I see five areas for potential improvement in use of energy by lactating cows: a) increased production, b) increased energy consumption, c) increased digestive efficiency, d) increased metabolic efficiency, and e) changed energy flow to partition more dietary energy to milk and less to body reserves for a longer period during lactation. I will attempt to relate the symposium speakers’ presentations to some of these areas.

DISCUSSION

Increased Production

Geneticists have contributed to more efficient energy utilization by sire selection programs that result in cows that produce more and eat more. It has been estimated that genetic trend has been responsible for 30% of the increase in milk yield during the last 25 years (R. L. Powell, US Department of Agriculture, personal communication). The well-recognized phenomenon of greater energy consumption diluting the maintenance requirement has been one of the most effective ways to move to higher feed efficiency. This is also the reason that income over feed cost (IOFC) continues to increase when larger amounts of concentrates are fed to responsive cows. Smith (21) showed that for high-potential cows, IOFC continues to increase with feeding up to 2,500 kg concentrate dry matter (DM)/yr to the point where milk fat depression becomes a problem. Even with relatively high feed costs, it is profitable to feed high-potential cows large volumes of energy-dense feed. The relationship of high peak production to lactation yields was shown by Broster (4) and Smith (22) to be about 250 to 1; i.e., each kilogram of higher production at the peak was reflected in about 250 kg more milk in the total lactation. Peak yields are determined primarily by the genetic impetus to withdraw large reserves of body energy, to consume large volumes of feed energy, and to direct both sources to milk energy.

Increased Intake of Net Energy

Despite being offered high energy diets ad libitum, most healthy dairy cows assume a period of negative energy balance (NEB) for much of the first trimester of lactation, which has both desirable and undesirable features (Figure 1). The process allows much higher production, but it may induce ketosis, and it seems antagonistic to early return to estrus. The lag in feed DM intake, in which
maximum plateaus are often reached about 12 to 15 wk postpartum compared to peak milk at about 5 to 8 wk, is widely acknowledged but the reasons are largely unexplained. Some of this lag may be the result of inappropriate nutritional management near parturition. However, better techniques to induce greater energy consumption earlier will probably not diminish the magnitude of NEB but will likely stimulate higher peak production. Without selection for a larger cow, physical capacity will continue to be a primary constraint to greater feed intake, and unless something distinctly new is learned about achieving greater energy intake, magnitude of NEB can be expected to increase.

Maximum benefit from additional concentrate appears to be ca. 60 to 65% of the diet. The best option for additional benefit at this time seems to be added fat, as shown in the data of Palmquist and Conrad (17). In their study, cows were assigned at parturition to control, high-fat, or isoenergetic diets for two lactations. Fatty acid content of the three diets was 2.5, 7.4, and 5.7%, dry basis. Ad-libitum intake of digestible energy (DE) during early lactation (the first 140 d) averaged 3.29, 3.49, and 3.28 multiples of maintenance, respectively. Concentration of DE (Mcal/kg of DM) in early lactation was 3.05, 3.32, and 3.13 for the three diets. As noted later, it is very likely that the differences in net energy (NE) among the three diets were greater because of the low heat increment of fat. Similar DM intakes with either extruded soybeans or whole cottonseed substitutions have also resulted in higher energy intakes in early lactation (24).

**Increased Digestive Efficiency**

In the mid-1960's, Moe et al. (14) and Tyrrell and Moe (27) showed marked depression in digestibility of mixed diets with increasing intake by high-producing cows averaging about 4% per multiple of maintenance [Figure 2 (27)]. There has been some controversy over the magnitude of the depression and the conditions under which it occurred. However, depression has been shown to be real under most conditions and perhaps due to faster rate of passage and preferential use of soluble carbohydrate by rumen microbes in cows fed high-grain diets. The depression was first thought to occur primarily in the cell wall fraction of the plant, but Purdue workers (32) showed that, in diets based on corn, a significant part could be due to starch passage.

Davis and Clark (8) emphasized managing the rumen to promote growth of microorganisms to allow them to perform those functions most valuable to the host. In particular,
control of pH can favor the fiber digesters whose role is highly valued. Ideally rumen microbes ought to digest most of the fiber but allow most of the starch and high quality protein to escape for digestion in the small intestine where efficiency is greater. As Sutton (25) pointed out, 75% of postruminal starch digestion occurs before the terminal ileum with both barley and corn diets. However, in one study with dry cows, 23 to 60% of starch disappearance in the intestine was due to fermentation in the proximal ileum. Consequently, not all starch disappearing in the small intestine is being absorbed as glucose. The caecum appears to be a secondary fermentation compartment in which both starch and fiber are partially fermented before excretion. Starch, which at low intakes is 95% or greater digestible, represents a major carbohydrate loss at high intakes, particularly from corn-based diets. Steam-flaking would increase tureen digestion of corn starch but would probably depress fat test. The solution to starch indigestibility remains elusive. Part of the differences seen in the effects of limestone buffers on the digestibility of starch may be in the reactivity and particle size of the limestones used (11). The value of starch hydrolysis and absorption as glucose in the small intestine is apparent, particularly for the cow in NEB who is often hypoglycemic. In terms of digestive efficiency and rumen fermentation it is desirable to retain all desirable attributes of the rumen but to be able to provide escape mechanisms for some of the protein, carbohydrate, and lipid.

Jackson (10) noted that by 1900, Kellner and Kohler showed that pressure cooking of straws in dilute sodium hydroxide solutions, followed by washing with water, sharply increased straw digestibility. There is much recent interest in this process using sodium hydroxide or ammonium hydroxide. Most of the benefit of treatment is with products of low digestibility; however, anhydrous ammonia and ammonia solutions have been used successfully on whole plant corn at ensiling for many years, but primarily to add nonprotein nitrogen. Alkali treatment of roughages results in some solubilization of the lignin, silica, and hemicellulose but not the cellulose (10). Buetttner and others (5) observed an increase in DM digestibility from 39.4 to 57.4% with ammoniation of tall fescue hay at 30 g of ammonia/kg hay. Even larger increases in digestion coefficients for hemicellulose and cellulose were noted. An examination of possible modes of action of ammonia showed a sharply lowered ester bond absorbance index, perhaps from cleavage of ester bonds. It was suggested that the breakage of ester bonds between lignin and polysaccharides may be the mechanism of increased fiber digestion by ammoniation. Because of its advantages as a preservative and an economical NPN source, and because of its favorable effect on fiber digestibility, ammonia warrants much greater research attention.

Flatt (9) showed that, under some conditions, partial compensation for the depression in energy digestibility with increasing intake occurs by decreased losses in combustible gasses and urine. This means that the metabolizable energy (ME) of rations does not decline as much as the DE and under some conditions does not decline at all with the higher intakes achieved by increasing amount and proportion of concentrate in the ration. More recent work suggests this compensation is not related to the amount and degradability of the protein (28). Declines in gaseous and urine energy seem to be more the result of a higher percentage concentrate at intakes of three to four times maintenance than the effect of conscious diet manipulation. Although the magnitude of these losses is not large compared with fecal energy (FE) and heat production (HE) (Figure 3), their reduction can add significantly to energy conversion efficiency. Tyrrell (29) has described factors that affect digestive losses, in particular, physical form plus the amount and degradability of protein. The major effect of protein seems to be on digestibility and intake rather than on digestive or metabolic efficiency (28). The ultimate value in knowing or being able to predict this compensation is to define more precisely the ME of individual feeds and complete rations at producing levels of consumption. Increased Metabolic Efficiency

Energy distribution in the lactating cow (Figure 3) shows HE as the second largest category, nearly equal to FE in a high-producing cow. For the relatively inactive cow in a
thermoneutral environment, HE can be factored into heat associated with maintenance, and heat increment (HiE), the heat associated with ingestion of feed. In turn, HiE can be further divided into heat of product formation, heat of digestion, heat of waste formation and excretion, and heat of fermentation (Figure 4). The primary question is whether there are mechanisms that would allow reduction in any of these fractions of HE while maintaining or increasing NE intake. Under heat stress, there are two advantages to reducing HE: 1) an increase in metabolic efficiency, and 2) less heat to be dissipated. A cow’s tendency to reduce feed intake under heat stress is a protective mechanism, but cows in early lactation that continue to mobilize large amounts of body energy more easily sustain their milk production, because heat production associated with metabolism of body energy stores results in half the HE of direct conversion of dietary ME to milk. That is, an efficiency of 82 vs. 64% for the two conversions is the same as a comparative heat production of 18 vs. 36% of the ME used.

Maynard and Loosli (12) note that, “the greater than expected value of fat as a source of energy can be explained on the basis that, with isocaloric diets, increasing the fat component decreases the heat increment.” (p. 74). Chalupa (7) adapted data from two sources to show protected fat consumption of 1.3 to 3.3 kg/d increased partial efficiency from 65 to 74 and 71%, respectively. Both milk yield and milk fat percentage were increased by supplemental fat. This increased efficiency also suggests that added fat would be more valuable in hot weather than cold. As predicted, Moody (16) reported less heat stress as indicated by lower body temperatures in cows fed whole cottonseed in Arizona. The degree that added fats or ingredients with high fat decrease HiE, they are undervalued by current feed evaluation systems (total digestible nutrients or net energy for lactation) when they are fed within or above
the zone of thermal neutrality. These observations on the effect of supplemental fat on HiE need verification with total energy balance studies.

Miller (13) recently pointed out the importance of amino acid balance, particularly the need to avoid excess amino acids in reducing the HiE of poultry diets during hot weather. Buttery and Boorman (6) note that the energy cost of protein deposition is nearly twice the energy of the peptide bond synthesis plus the energy in the protein deposited. They attribute this difference to cost of protein turnover, excretion cost of excess nitrogen, and the improbability of providing a completely balanced supply of amino acids. In ruminant nutrition, protein requirements cannot be defined yet in terms of amino acids delivered to the small intestine. When this is possible, a considerable reduction of HE may occur. Ames et al. (1) showed with both sheep and cattle that protein intake could be reduced in proportion to expected reduction in daily gain as a function of thermal stress without affecting gain. Thus, efficiency of protein use was increased. These results occurred because of the increase in maintenance that results from thermal stress.

Baldwin et al. (3) suggest that manipulations of ion transport and protein turnover could yield maximum benefits of 10 to 30% in terms of energy costs for basal maintenance. Another possibility pointed out by this group was that by adjustment of patterns of nutrient utilization to an optimum pattern, decreases in HiE of production in growing animals of up to 50% might be possible. These authors also noted that two futile cycles have a particularly large influence on maintenance requirements: a) sodium (Na+)/potassium (K+) transport (20 to 30%) and b) protein turnover (10 to 15%). There was no suggestion that these cycles could be eliminated, but a reduction in their cost would improve energetic efficiency. The recent emphasis in poultry nutrition concerning electrolyte balance, suggests progress in this context in that species. Mongin (15) found optimum gain in chicks when the sum of (Na+ + K)/chlorine was 25 (in milliequivalents/100 g of diet).

Change Partitioning

The priority that healthy lactating cows of high genetic merit give to ME changes with advancing lactation (Figure 5). This assumes 2× milking and immature cows. In early lactation, a high percentage of feed ME is directed to milk, as is a large amount of body energy. But the priority of lactation is less with succeeding trimesters of lactation. The conventional term is persistency, which seems to be partially under genetic control. Outside influences have little effect except to lower the priority of lactation sooner through nutritional mismanagement. Van Soest (30) suggested that diets that tend to depress milk fat lower the priority of lactation and raise the priority of body fat deposition.

Baldwin et al. (2) think the potential for changing energy partitioning is relatively large. Recent work by Bauman's group (18, 19) with injections of exogenous bovine growth hormone (bGH) showed that 51.5 IU/d resulted in sharp increases in milk yield (3.9 to 4.3 kg/d), in all major milk components, and in milk energy (3.3 to 3.4 Mcal/d), which were similar in early and late lactation. Ad libitum intakes of a complete ration declined by 3 to 16% in early and late lactation, respectively. Because of the short period (10 d), the intake effect may have been a temporary adjustment that will lessen with physiological adjustment to longer periods of bGH administration.

The report by Tyrrell and others (26) in which lactating cows were injected with bGH during total metabolism measurements revealed that the action of bGH did not change either digestive or metabolic efficiency. This means that bGH changed the flow of feed ME from milk plus tissue to predominantly milk and in late lactation may have resulted in a resumption of NEB. Because no change in efficiency occurred with the injections of bGH, and the supply of body reserves is obviously limited, a very careful balance in dose-response would be

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<th>TRIMESTER</th>
<th>LACTATION &gt; REPRODUCTION &gt; GROWTH &gt; MAINTENANCE</th>
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Figure 5. Physiological priorities for metabolizable energy by immature lactating dairy cows milked twice daily.
TABLE 1. Effect of milking frequency (3X vs. 2X) on intake, production, and body weight change (23).

<table>
<thead>
<tr>
<th>Older cows</th>
<th>Production Milk (kg)</th>
<th>Fat (kg)</th>
<th>DM1 Intake Total (kg)</th>
<th>% Avg weight</th>
<th>Body weight Begin (kg)</th>
<th>End (kg)</th>
<th>Change (kg)</th>
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<tr>
<td>2X</td>
<td>7,502</td>
<td>258</td>
<td>5,977</td>
<td>3.09</td>
<td>634.2</td>
<td>697.3</td>
<td>63.1</td>
</tr>
<tr>
<td>3X-A 📌</td>
<td>8,972</td>
<td>301</td>
<td>6,153</td>
<td>3.19</td>
<td>665.1</td>
<td>671.9</td>
<td>6.8</td>
</tr>
<tr>
<td>3X-B 📌</td>
<td>8,779</td>
<td>303</td>
<td>6,289</td>
<td>3.12</td>
<td>683.3</td>
<td>711.4</td>
<td>28.1</td>
</tr>
</tbody>
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1 Dry matter.

2 Switched to medium and low energy diets at 28 and 23 kg milk/d.

3 Switched to medium and low energy diets at 31 and 25 kg milk/d.

essential if bGH were to be effectively administered over an extended period. It appears that under usual conditions, cows do not (cannot) reassume a posture of negative energy balance beyond about midlactation nor, until the growth hormone work, has a mechanism been available to induce such a redirection of ME.

A recent full-lactation study of 3X vs. 2X milking (23) suggests that 3X milking may induce the cow to continue directing feed ME to milk plus maintenance without the usual restoration of body energy stores in mid and late lactation (Table 1, Figure 6). Older cows milked 3X had 3 to 5% greater feed intake but an 18% greater milk yield than cows milked 2X. Change in weight during the lactation showed that cows milked 3X did not regain body weight during the lactation as did cows milked 2X (Table 1). Similar results were evident in the weight gain of first lactation cows. Obviously cows milked 3X must regain body energy during the dry period if they are to have a successful succeeding lactation. Even though we now recognize it is more efficient metabolically to regain body energy concurrent with lactation, it may be more economical to restore that energy during the dry period, particularly if forage is relatively inexpensive. One mechanism by which 3X milking results in greater energy efficiency is to sustain the flow of feed ME to milk, and prevent the partition of feed ME to body stores in late lactation.

Conclusions

Genetic merit for high milk production is widespread in the dairy cow population and is increasing. Developing technology, including embryo transfer, embryo freezing, and sexing of embryos will contribute to this genetic progress. It will be a rigorous challenge to provide feeding systems and diet formulations to support this high production. The best strategy to increase energy eaten in the near postpartum is to add fat or ingredients with high fat content. This presumes a forage to concentrate ratio in the order of 40:60, dry basis.

Depressions in digestibility of mixed diets at production intakes reflect greater passage of undigested cell walls and starch. Ammoniation
increases digestion of cell walls in forages of low digestibility and may help in higher quality forages. Starch indigestibility and escape remain an enigma, but the loss is clear and the topic warrants much effort. Some compensation for lower digestibility occurs by lower energy losses in methane and urine. These are relatively small but important. Added fat is our best present ingredient to increase efficiency of ME use, but total energy measurements are needed to validate this assertion. Future ways to reduce HiE will probably include adjustments in electrolytes and more precise amino acid nutrition.

Cows change their priorities for use of ME as lactation advances; milk fat-depressing diets seem to lower the priority of milk relative to stores of depot energy. Three times per day milking seems to sustain lactation in rank order for use of ME through much of lactation. Growth hormone holds promise as another mechanism to induce the cow to direct more ME to milk.

REFERENCES

30 Van Soest, P. J. 1963. Ruminant fat metabolism
