ENVIRONMENTAL INFLUENCE ON METABOLISM OF RUMINANTS

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Heat stress negatively impacts a variety of dairy parameters including milk yield and reproduction and therefore is a significant financial burden (~$900 million/year in the USA; St. Pierre et al., 2003) in many dairy-producing areas of the world. Advances in management (i.e. cooling systems) and nutritional strategies have alleviated some of the negative impact of thermal stress on dairy cattle, but production continues to decrease during the summer. Accurately identifying heat stressed cows and understanding the biological mechanism(s) by which thermal stress reduces milk synthesis and reproductive indices is critical for developing novel approaches (i.e. genetic, managerial and nutritional) to maintain production or minimize the reduction in dairy cow productivity during stressful summer months.

IDENTIFYING HEAT STRESS

The effect of ambient heat on dairy cattle maintenance and milk production is well known and furthermore heavily influenced by relative humidity. A combination of the two variables (temperature-humidity index; THI) is a better predictor of whether or not cows are "stressed" (Armstrong et al., 1993; Armstrong, 1994). As an example, the THI in southern Minnesota (an area of relatively high humidity) during the 2006 Memorial Day weekend was in the mid 90's but only in the low 80's in Phoenix Arizona (an area of low humidity).

A THI > 72 is the point at which a dairy cow starts to decrease productivity (Armstrong et al., 1993; Armstrong, 1994). A THI of 72 can be achieved at moderate temperatures if relative humidity is high. Unabated heat stress can decrease feed intake more than 35%. Even on well-managed and well-cooled dairies, heat stress decreases feed intake by 10 to 15% (Collier and Beede, 1985; Armstrong, 1994; West, 2003). Another easily recognized factor of heat stress is a significant reduction in milk yield. Even in well-cooled dairies, heat stress typically decreases milk yield by 10-15% and in non-cooled management systems milk yield can decrease by 40-50% during severe conditions (Collier and Beede, 1985; Armstrong, 1994; West, 2003). In addition to the immediate effects (milk yield and feed intake), cows will typically lose body weight and condition during prolong periods of heat stress. Furthermore, the negative effects of heat stress on reproduction indices are not only immediately obvious, but linger/persist well into the fall months, even after cows have returned to more comfortable environmental conditions (Fuquay, 1981; Armstrong, 1994; Roth et al., 2004).

The basic thermoregulatory strategy of a dairy cow is to maintain a core body temperature higher than ambient temperature to allow heat to flow out from the core via four basic routes of heat exchange (conduction, convection, radiation and evaporation). When ambient temperature conditions approach body temperature the only viable route of heat loss is through evaporation and if ambient conditions exceed body temperature heat flow will reverse and an animal will become a heat sink. Therefore, accurately estimating the thermal environment around animals is necessary to understanding their cooling needs. Because the typical location of cooling equipment and the variable locations cows can physically be in, there are a wide variety of microenvironments present within a facility. As a consequence, accurately determining the degree of heat stress a cow is experiencing over time is challenging.

Traditionally, respiration rate (RR; breathes/minute) has been used as a tool to measure the severity of heat stress on an animal. Although RR will vary with body weight and milk yield, it is a relatively accurate tool for determining the degree of heat stress. Recently, cattle housed in the Animal Research Complex (ARC; The University of Arizona, Tucson, AZ) environmental facility under thermal neutral conditions (18.8˚C; 63.5 THI) for 48 hrs followed by heat stress (36.7˚C; 79.6 THI) for 16 out of 24 hrs/d for 3 d had RR of 50 during thermal neutral and 71 during heat stress conditions, respectively.

If the skin surface temperature of a dairy cow is below 35˚C the temperature gradient between the core and skin is large enough for an animal to effectively use all four routes of heat exchange. Infrared thermography guns have been shown to be a low cost approach to estimate actual skin surface temperature of animals. However, because of variability in skin surface moisture at a given point in time, the accuracy of infrared guns to predict an animals heat load may be limited. For example, if an animal recently walked under a shade, but previously was in the sun (solar radiation) the infrared measurement of skin will not be reflective of cows under the shade that were not recently exposed to the sun.

Core body temperature (CBT) has been shown to decrease in cooled cows compared to non-cooled cows. Recently, cattle housed in the ARC environmental facility under thermal neutral conditions (18.8˚C; 63.5 THI) for 48 hrs followed by heat stress (36.7˚C; 79.6 THI) for 16 out of 24 hrs/d for 3 d had vaginal temperatures of 37˚C during thermal neutral and 38.8˚C during heat stress conditions, respectively. Our group has measured CBT using intravaginal probes attached to blank CIDRs (as applicators only) to determine where and/or when cows are getting hot and/or remaining the coolest. These devices are inserted and remain inside the cow's vagina measuring CBT every 60 seconds for up to 6 d. Such technology allows cows CBT to be monitored and recorded 24 hrs/d as they move throughout a facility. Specifically, a holding pen (designed to allow 15 square ft/cow), without proper cooling, is an area where dairy cows may experience severe heat stress, however, if properly cooled vaginal temperature will be reduced (VanBaale et al., 2005).

Utilizing a CBT probe to continuously monitor vaginal (core body) temperature allows a producer to accurately determine where and when a cow is experiencing the most heat stress. As a consequence, management decisions can be made to improve cooling and reduce heat stress thus, improving cow performance. In addition, parlor exit sprinklers have demonstrated that when a cow enters a corral with a wet body surface the moisture will evaporate thus cooling the cow for an additional period of time depending on weather conditions. The effects of barn and cooling system design are important factors in determining the efficacy of cooling on dairy facilities. Factors critical to the correct design and cooling system are obviously dependent on the geographic location of the dairy (daily average high and low temperature, annual rainfall, humidity and prevailing winds).

BIOLOGICAL CONSEQUENCES OF HEAT STRESS

The biological mechanism by which heat stress impacts production and reproduction is partly explained by reduced feed intake, but also includes altered endocrine status, reduction in rumination and nutrient absorption, and increased maintenance requirements (Collier and Beede, 1985; Collier et al., 2005) resulting in a net decrease in nutrient/energy availability for production. This decrease in energy results in a reduction in energy balance (EBAL), and explains why cows lose significant amounts of body weight when subjected to heat stress.

Reductions in energy intake during heat stress result in a majority of lactating cows entering into negative energy balance (NEBAL), and this is likely stage of lactation independent. Essentially, because of reduced feed and energy intake the dairy cow is putting herself in a bioenergetic state, similar (but not to the same extent) to the NEBAL observed in early lactation. The NEBAL associated with the early postpartum period is coupled with increased risk of metabolic disorders and health problems (Goff and Horst, 1997; Drackley, 1999), decreased milk yield and reduced reproductive performance (Lucy et al., 1992; Beam and Butler, 1999; Baumgard et al., 2002; 2006). It is likely that many of the negative effects of heat stress on production, animal health and reproduction indices are mediated by the reduction in EBAL (similar to the way it is during the transition period). However, it is not clear how much of the reduction in performance (yield and reproduction) can be attributed or accounted for by the biological parameters affected by heat stress (i.e. reduced feed intake vs. increased maintenance).

Effect of Heat Stress on Rumen Health

Heat stress has long been known to adversely affect rumen health. One way cows dissipate heat is via panting and this increased respiration rate results in enhanced CO_2 (carbon dioxide) being exhaled. In order to be an effective blood pH buffering system, the body needs to maintain a 20:1 HCO_3^- (bicarbonate) to CO_2 ratio. Due to the hyperventilation induced decrease in blood CO_2, the kidney secretes HCO_3^- to maintain this ratio. This reduces the amount of HCO_3^- that can be used (via saliva) to buffer and maintain a healthy rumen pH. In addition, panting cows increase drool which reduces the quantity of saliva that would have normally been deposited in the rumen. The reductions in saliva HCO_3^- content and the decreased amount of saliva entering the rumen make the heat stressed cow much more susceptible to sub-clinical and acute rumen acidosis.

Due to the reduced feed intake caused by heat stress and the heat associated with fermenting forages, nutritionists typically increase the energy density of the ration. This is typically accomplished with extra concentrates and reductions in forages. However, this needs to be conducted with care as this type of diet can be associated with a lower rumen pH. The combination of a "hotter" ration and the cows reduced ability to neutralize the rumen (because of the reduced saliva HCO_3^- content and increased drooling) directly increases the risks of rumen acidosis and indirectly enhances the risk of negative side effects of a unhealthy rumen (i.e. laminitis, milk fat depression, etc.)

Metabolic Adaptations to Reduced Nutrient Intake

A prerequisite of understanding the metabolic adaptations which occur with heat stress, is an appreciation of the physiological and metabolic adaptations to thermal-neutral NEBAL (i.e. underfeeding or during the transition period).

Cows in early lactation are classic examples of when nutrient intake is less than necessary to meet maintenance and milk production costs and animals typically enter negative energy balance (Moore et al., 2005a). Negative energy balance is associated with a variety of metabolic changes that are implemented to support the dominant physiological condition of lactation (Bauman and Currie, 1980). Marked alterations in both carbohydrate and lipid metabolism ensure partitioning of dietary derived and tissue originating nutrients towards the mammary gland, and not surprisingly many of these changes are mediated by endogenous somatotropin which is naturally increased during periods of NEBAL (Bauman and Currie, 1980). One classic response is a reduction in circulating insulin coupled with a reduction in systemic insulin sensitivity. The reduction in insulin action allows for adipose lipolysis and mobilization of non-esterified fatty acids (NEFA; Bauman and Currie, 1980). Increased circulating NEFA are typical in "transitioning" cows and represent a significant source of energy (and precursor for milk fat synthesis) for cows in NEBAL. Post-absorptive carbohydrate metabolism is also altered by the reduced insulin action during NEBAL with the net effect of reduced glucose uptake by systemic tissues (i.e. muscle and adipose). The reduced nutrient uptake coupled with the net release of nutrients (i.e. amino acids and NEFA) by systemic tissues are key homeorhetic (an acclimated response vs. an acute/homeostatic response) mechanisms implemented by cows in NEBAL to support lactation (Bauman and Currie, 1980).

Production Adaptations to Heat Stress

Heat stress reduces both feed intake and milk yield and the decline in nutrient intake has been identified as a major cause of reduced milk synthesis (Faquay, 1981). However, the exact contribution of declining feed intake to the overall reduced milk yield remains unknown. To evaluate this question, we utilized a group of thermal neutral pair-fed animals to eliminate the confounding effects of nutrient intake. Lactating Holstein cows in mid-lactation were either cyclically heat stressed (THI = ~80 for 16 hrs/d) for 9 days or remained in constant thermal neutral conditions (THI = ~ 64 for 24 hrs/d) but pair-fed with heat stressed cows to maintain similar nutrient intake. Cows were housed at the University of Arizona's ARC facility and individually fed ad libitum a TMR consisting primarily of alfalfa hay and steam flaked corn to meet or exceed nutrient requirements (NRC, 2001). Heat stressed cows had an average rectal temperature of ~105° F during the afternoons of the treatment implementation. Heat stressed cows had an immediate reduction (~5 kg/d) in dry matter intake (DMI) with the decrease reaching nadir at ~ day 4 and remaining stable thereafter (Figure 1). As expected and by design, thermal-neutral pair fed cows had a feed intake pattern similar to heat stressed cows (Figure 1). Heat stress reduced milk yield by ~14 kg/d with production steadily declining for the first 7 days and then reaching a plateau (Figure 2). Thermal neutral pair-fed cows also had a reduction in milk yield of approximately 6 kg/d, but milk production reached its nadir at day 2 and remained relatively stable thereafter (Figure 2). This indicates the reduction in DMI can only account for

~40-50% of the decrease in production when cows are heat stressed and that ~50-60% can be explained by other heat stressed induced changes.

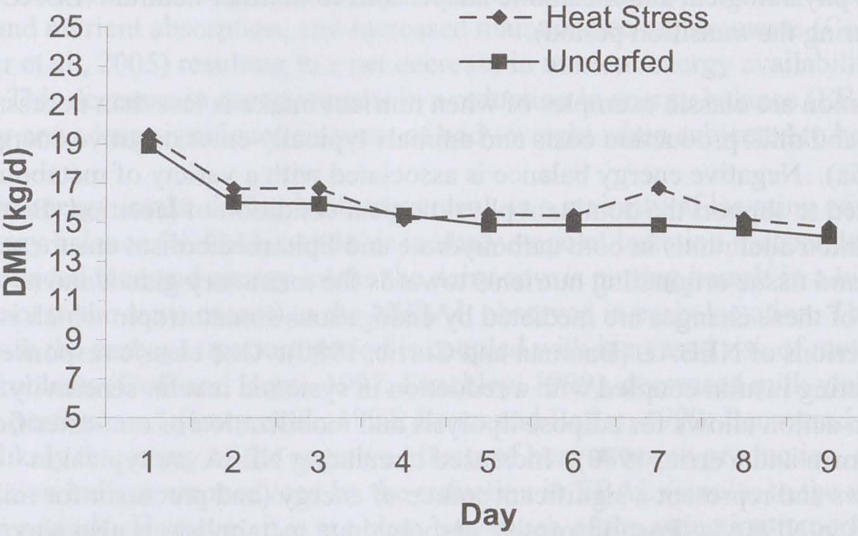

Figure 1. Effects of heat stress and pair-feeding thermal neutral lactating Holstein cows on dry matter intake. Rhoads and Baumgard, unpublished.

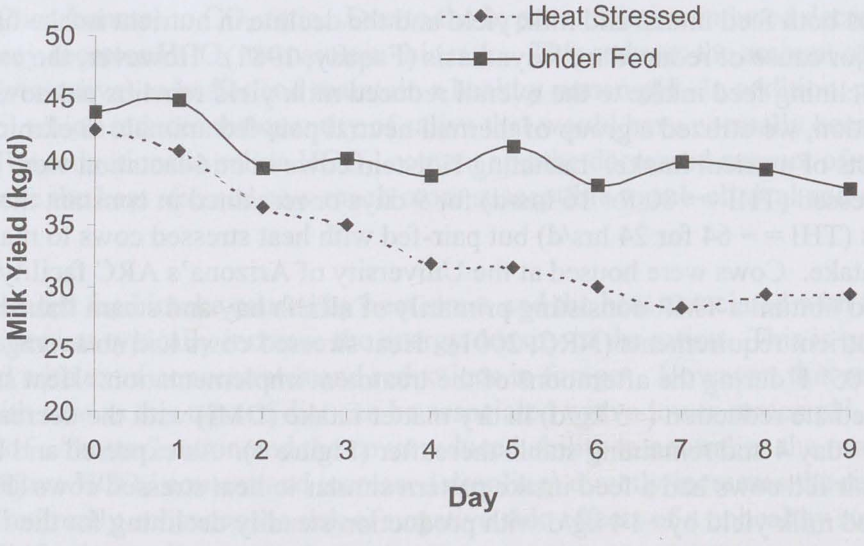

Figure 2. Effects of heat stress and pair-feeding thermal neutral conditions on milk yield in lactating Holstein cows. Rhoads and Baumgard, unpublished.

Metabolic Adaptations to Heat Stress

Due to the reductions in feed intake and increased maintenance costs, and despite the decrease in milk yield heat stressed cows enter into a state NEBAL (Moore et al., 2005b). In a similar trial to the one described above, heat-stressed cows entered into and remained in NEBAL (~4-5 Mcal/d) for the entire duration of heat stress (Figure 3; Wheelock et al., 2006). However, unlike NEBAL in thermal neutral conditions, heat stressed induced NEBAL doesn't result in elevated plasma NEFA (Figure 4). This was surprising as circulating NEFA are thought to closely reflect calculated EBAL (Bauman et al., 1988). In addition, using a glucose tolerance test, we demonstrated that glucose disposal (rate of cellular glucose entry) is greater in heat stressed compared to thermal neutral pair-fed cows (Figure 5; Wheelock et al., 2006). Furthermore, heat-stressed cows have a much greater insulin response to a glucose challenge when compared to underfed cows (data not presented). Both the aforementioned changes in plasma NEFA and metabolic and hormonal adjustments in response to a glucose challenge can be explained by increased insulin effectiveness. Insulin is a potent antilipolytic signal (blocks fat break down) and the primary driver of cellular glucose entry. Therefore, it appears the heat stressed cow becomes hypersensitive to insulin.

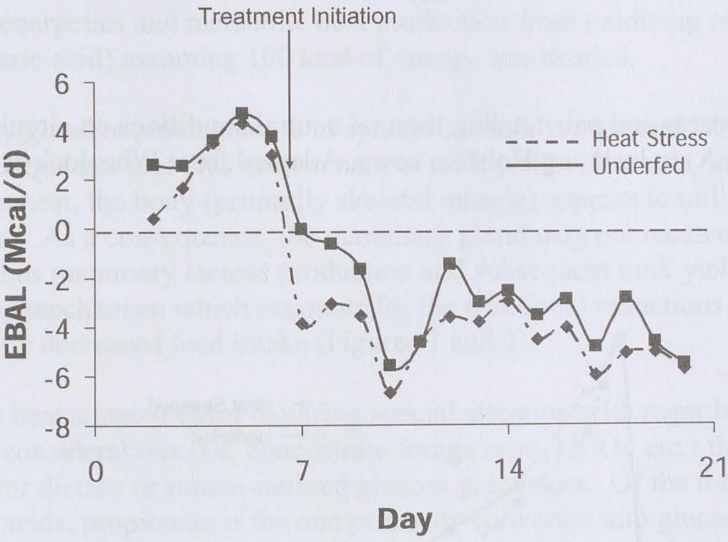

Figure 3. Effects of heat stress and pair-feeding thermal neutral conditions on calculated net energy balance in lactating Holstein cows. Adapted from Wheelock et al., 2006.

Well-fed ruminants primarily oxidize (burn) acetate (a rumen produced VFA) as their principal energy source. However, during NEBAL cows also largely depend on NEFA for energy. Therefore, it appears the post-absorptive metabolism of the heat-stressed cow markedly differs from that a thermal-neutral cow, even though they are in a similar negative energetic state. The apparent switch in metabolism and the increase in insulin sensitivity is probably a mechanism by which cows decrease metabolic heat production. Despite having a much greater energy content, oxidizing fatty acids generates more metabolic heat (~2 kcal/g or 13% on an energetic basis) compared to glucose (Figure 6). Therefore, during heat stress, preventing or blocking adipose mobilization/breakdown and increasing glucose "burning" is a presumably a strategy to minimize metabolic heat production.

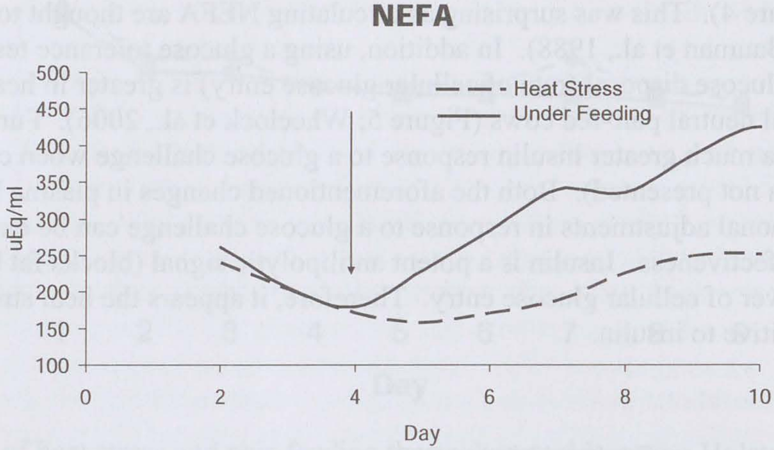

Figure 4. Effects of heat stress and pair-feeding thermal neutral conditions on circulating non-esterified fatty acids (NEFA) in lactating Holstein cows. Adapted from Wheelock et al., 2006.

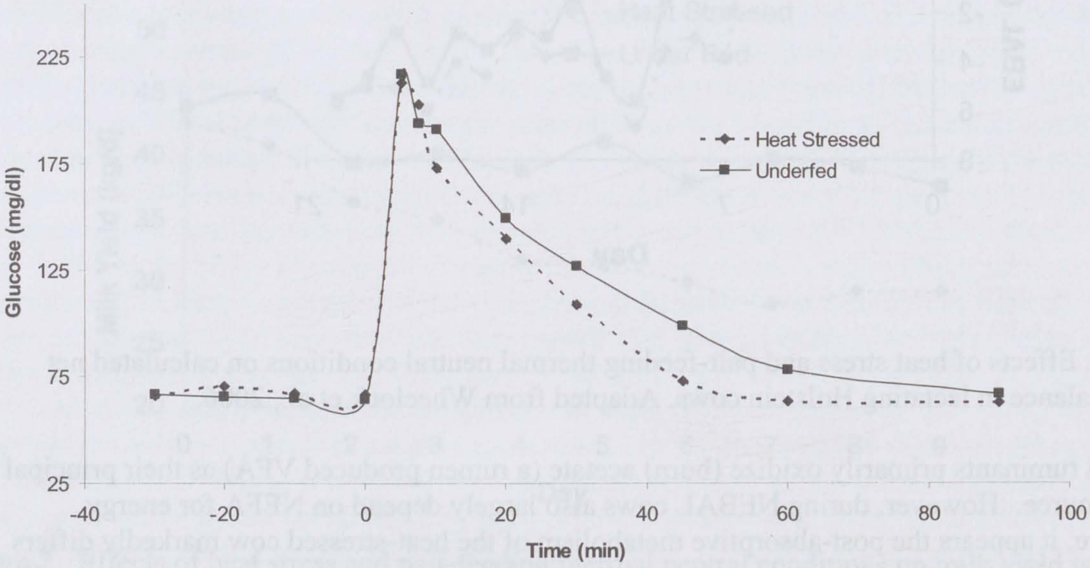

Figure 5. Effects of heat stress and pair-feeding thermal neutral conditions on plasma glucose response to a glucose challenge. Adapted from Wheelock et al., 2006.

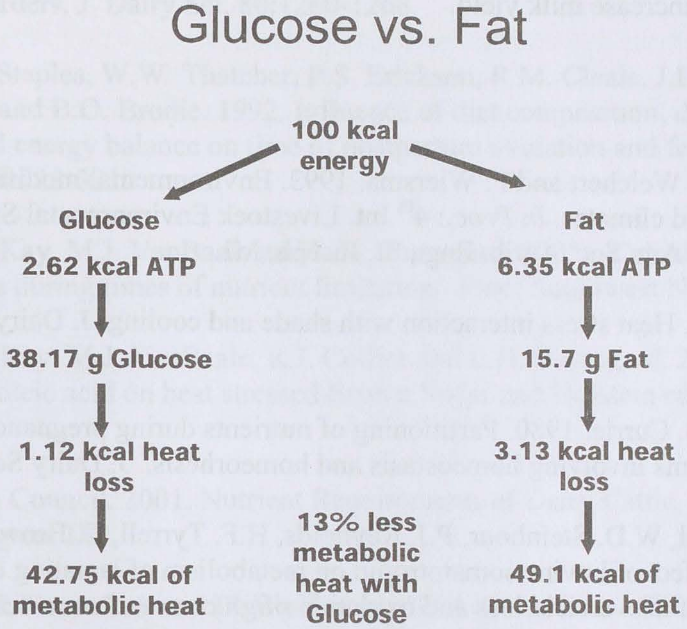

Figure 6. Bioenergetics and metabolic heat production from oxidizing either glucose or fatty acids (i.e. stearic acid) assuming 100 kcal of energy was needed.

The mammary gland requires glucose to synthesize milk lactose and lactose production is the primary osmoregulator and thus determinant of milk yield. However, in an attempt to generate less metabolic heat, the body (primarily skeletal muscle) appears to utilize glucose at an increasing rate. As a consequence, the mammary gland may not receive adequate amounts of glucose and thus mammary lactose production and subsequent milk yield is reduced. This may be the primary mechanism which accounts for the additional reductions in milk yield that can not be explained by decreased feed intake (Figures 1 and 2).

In addition to heat stressed cows requiring special attention with regards to heat abatement and other dietary considerations (i.e. concentrate:forage ratio, HCO_3^- etc.) they also have an extra requirement for dietary or rumen-derived glucose precursors. Of the three main rumen produced volatile fatty acids, propionate is the one primarily converted into glucose by the liver. Highly fermentable starches such as grains increase rumen propionate production, and although propionate is the primary glucose precursor, feeding additional grains can be risky as heat stressed cows are already susceptible to rumen acidosis.

TAKE HOME MESSAGE

Clearly the heat-stressed cow implements a variety of post-absorptive changes in both carbohydrate and lipid metabolism that wouldn't be predicted based upon their energetic state. The primary end result of this altered metabolic condition is that the heat-stressed lactating dairy cow has an extra need for glucose (due to its preferential oxidization by extra-mammary tissue). Therefore, any dietary component that increases propionate production (the primary precursor to hepatic glucose production), without reducing rumen pH, will probably increase milk yield. In addition, reducing systemic insulin sensitivity will increase glucose availability to the mammary and thus also probably increase milk yield.

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