Galactopoiesis, Seasonal Effects

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This article is a revision of the previous edition article by R. J. Collier and D. Romagnolo, Volume 3, pp 1465–1470, © 2002, Elsevier Ltd.

Introduction

Enhancing established lactation is referred to as galactopoiesis (from Greek, *gala*, milk, *poiesis*, production). In dairy production, the capacity for mammary tissue to synthesize and secrete milk components is maximal at peak lactation and declines linearly thereafter. The slope of the decline in milk yield following peak lactation is referred to as the persistency of lactation. Lactation persistency is a result of maintaining mammary epithelial cell (MEC) number and cellular secretory activity. Cellular dynamics from early postpartum stages to peak lactation can be characterized by an increase in secretory capacity of MEC rather than gland growth via MEC proliferation. Enhancing established lactation has major economic benefits to dairy producers. Hence, the factors that regulate MEC turnover and secretion rate together with mechanisms mediating mammary nutrient uptake and milk synthesis or secretion have been the major foci of research and are discussed relative to galactopoiesis. Factors affecting yield are reviewed first, followed by issues affecting milk component synthesis.

Galactopoietic Factors

Three management methods consistently increase milk yields in lactating dairy cows during established lactation: the administration of exogenous bovine somatotropin (bST), increased milking frequency, and increased photoperiod. Two of these methods, increased photoperiod and bST, also alter persistency, while the third, increased milking frequency, alters peak milk yield but has little effect on persistency.

Bovine Somatotropin

The galactopoietic response of ruminants to recombinant bST has stimulated much research into its role in nutrient partitioning. Milk yield increases in a dose responsive manner to exogenous bST and the enhancement is influenced by parity, stage of lactation and degree of negative energy balance. Bovine somatotropin stimulates hepatic tissue insulin-like growth factor I (IGF-I) synthesis and secretion, which may act on the mammary gland through an endocrine mode of action in concert with circulating and local IGF-I binding proteins. However, a direct role of IGF-I on galactopoiesis in mammary tissue has not been concretely established. In general, bST coordinates metabolism to alter the delivery of nutrients to the mammary gland. This action of bST is homeorhetic in nature because metabolism is coordinated to favor the flow of nutrients for a specific and dominant physiological function, namely increased milk yield. It carries out this action without creating a metabolic imbalance and thus does not cause physiological problems.

The response to bST is remarkably consistent and increases lactation yields by approximately 900 kg over a 300-day lactation. Typically, treatment begins following peak lactation and is continued until dry-off. The milk yield response is partly influenced by the stage of lactation, and this is primarily because of differences in body condition. For example, more fat is partitioned to the mammary gland in cows receiving bST during early lactation at the expense of lipid synthesis in adipose tissue. During the first 8 weeks of treatment, exogenous bST promotes an increase in milk energy yield; while dry matter intake and digestibility are not affected, the rate of peripheral glucose oxidation is reduced. Treatment with bST increases the circulating concentration and the oxidation rate of nonesterified fatty acids, which suggests that fatty acids are mobilized from adipose tissue to compensate for the decreased energy balance due to the higher milk energy output. There is a concomitant accumulation of fat in milk, predominantly long-chain fatty acids at the expense of *de novo* fatty acid synthesis. These changes apparently occur in the absence of fluctuations in the concentration of circulating insulin or glucose, although, in some studies, administration of bST was accompanied by a hyperglycemic response. Treatment with bST increased mammary uptake of glucose at the expense of that of nonmammary tissue. Glycerol appears to contribute to the synthesis of glucose via gluconeogenesis, whereas the contribution from glycogen, amino acids, and proprionate seem to be negligible. After 8 weeks of treatment, dry matter intake increases, thus compensating for increased milk output in the absence of effects on milk fat content. The exact causes of the increase in milk output are not known, but proposed mechanisms include increased rate of synthesis per cell, reduced rate of cell loss, and an increase in the number of cells actively secreting at any one time. Cumulative evidence to date suggests that increased rate of synthesis per cell and an increase in the number of cells actively secreting are the primary mechanisms because milk yield returns to baseline values when bST treatment ceases, or in other words, there is no carryover effect on milk yield.

Milking Frequency

Increasing the number of times milk is removed from the mammary gland increases milk yield in dairy animals. For example, increasing the milking frequency from 2 to 3 times daily increases milk yield from 15 to 20%. Further increases in milk yield (>20%) have been reported when milking frequency was increased from 3 times (38.5 kg day^{-1}) to 6 times (46.8 kg day^{-1}). However, on commercial dairies, this further increase is more difficult to achieve as time away from feed may adversely affect the response because of large distances to and from the housing barn to the milking parlor. Research indicates that the transition from 3 times to 6 times daily milking was accompanied by an increase in the circulating levels of oxytocin, growth hormone, IGF-I, prolactin, dry matter intake, and nonesterified fatty acids and a decrease in circulating insulin, whereas glucose levels were unaffected. There is also a stage-of-lactation effect on the response to increased milking frequency. Initiating 3 times daily milking at the beginning of lactation results in much greater responses than initiating 3 times daily milking after peak lactation. Furthermore, some reports suggest a positive carryover effect on milk yield if cows are milked 3 times daily beginning immediately after calving but returned to twice a day milking after peak lactation. Increased milking frequency increases mammary growth, and this effect is most pronounced in early lactation when the gland is still growing. Mammary gland DNA continues to increase with a 26% mammary growth for rats during early lactation. Furthermore, it is interesting to note that without a suckling stimulus, the growth in early lactation does not occur for this species.

As milk yield per cow has steadily increased, the percentage increase in milk yield to increased milking frequency has declined. The current US Department of Agriculture adjustments for 3 times daily milking over 2 times milking for lactation records are a 12% increase for the first lactation and 14% for second and later lactations. Increased milking frequency is additive to the increase in milk yield associated with the use of bST, and the increase in milk production associated with increased photoperiod. When utilizing bST and increased milking frequency concomitantly, milk yield is increased in an additive manner. Studies demonstrating the additive effects of milking frequency and bST also show that they work through different mechanisms. A study that utilized midlactation heifers in which udder halves were milked either 2 or 4 times daily and subsequently treated with bST and saline demonstrated clear additive effects. Milk yield was increased by 12.8% by 4 times daily milking over 2 times daily milking, 14% by bST, and 28.5% when 4 times daily milking was combined with bST. These scientists also utilized mammary biopsies to determine which galactopoietic agent (agents) enhances (enhance) mammary growth. Mammary epithelial size tended to increase in glands milked 4 times daily but no effects were detected for bST or the combined treatment (bST and 4 times daily milking).

Photoperiod

Photoperiod is a galactopoietic management tool utilized by dairy producers to increase milk yield. Natural photoperiod is greatly influenced by latitude, and near the equator, there is little variation in photoperiod. However, at latitudes greater than 30° north and south the range in photoperiod is much more pronounced. Increasing photoperiod to 16 h of light and 8 h of darkness from 12 h of light and 12 h of darkness increases milk yield by 8–10%. This response is associated with increased feed intake and increased plasma prolactin concentration and sometimes an increase in plasma IGF-I levels. There appears to be no stage-of-lactation difference in the response to photoperiod, and there is no evidence that increased photoperiod alters mammary growth during lactation or pregnancy. Milk component concentration is generally not affected by long-day photoperiod, although some studies have reported both increased and decreased milk fat percentages. When cattle are exposed to continuous lighting, there is a change in milk yield, and this is hypothesized to be a result of desynchronization of the cows' biological rhythm. The increase in milk yield following increased photoperiod has been shown to be additive to increased milk yields because of exogenous bST and increased milking frequency. This suggests that the three management methods increase milk yields through differing mechanisms. Studies evaluating photoperiod effects during the dry period on milk yield in the subsequent lactation do not show any positive effect of long-day photoperiod. On the contrary, short-day photoperiod treatment of pregnant dry cows resulted in higher milk yields in the subsequent lactation. However, there was no further increase in milk yield by extending photoperiod in the same cows during lactation. In other words, the dairy producer can use either short photoperiods during late gestation or long photoperiods during lactation to achieve the increase in milk yield. Interestingly, during short-day photoperiod of late pregnant goats, there was no increase of IGF-I or prolactin during treatment associated with greater milk yields during lactation.

Factors Affecting Milk Component Yields

Milk protein

After parturition, developmental and hormonal signals induce a number of ontological events that lead to enhanced expression of milk protein genes. Specifically, the lactogenic hormone, prolactin, and glucocorticoids contribute to the activation of expression of caseins and whey proteins. The transfer of amino acids into the mammary gland is primarily from plasma. Although red blood cells contribute modest amounts of amino acids, they account for approximately 14% of the total mammary uptake of methionine. Approximately 15–30% of the mammary uptake of aspartic acid and proline is concentrated in red blood cells as they pass through the mammary gland. The partition of amino acids into milk protein synthesis is influenced by several factors, including the availability of amino acids in the arterial blood, mammary blood flow rate, and the efficiency with which amino acids are extracted by the mammary gland and used for protein synthesis or intracellular metabolism. The efficiency of converting extracted amino acids into milk protein can be expressed by the following equation:

$$K = \left(\frac{\mathrm{AV}}{\mathrm{AC}}\right) \times \mathrm{BF} \times E$$

where K is the fractional use for milk protein synthesis, AV the arteriovenous concentration difference divided by the arterial concentration AC, BF the flood flow rate ($\mathrm{l\,h^{-1}}$), and E the efficiency of utilization of the extracted amino acid.

Total protein synthesis exceeds by approximately twofold the rate of protein secretion, thus suggesting, a high rate of protein turnover by mammary tissue. Protein degradation affects both newly synthesized and mature caseins and contributes to maintaining an intermediary pool of available amino acids at the sites of protein synthesis.

Amino acids, including leucine, valine, isoleucine, arginine, threonine, and histidine, are typically extracted in excess of their milk output, suggesting that the mammary gland may metabolize these amino acids to balance milk protein requirements. In contrast, when maize silage–based diets are fed, amounts of nonessential amino acids and lysine and methionine available for uptake rarely exceed milk output. For example, supplementation of increasing amounts of soybean meal as protein supplement further decreased the absorbable methionine. Duodenal infusion of lysine at peak of lactation (∼5 weeks postpartum) and fed a 70:30 maize silage:concentrate ratio increased the blood extraction rates of amino acids and secretion of milk protein. In contrast, lysine infusion had no effects on milk yield beyond week 8, suggesting that lactational response to supplemental amino acids is influenced by stage of lactation.

Amino acids limiting milk yield and composition vary depending on the type of forage and protein supplements in the basal diet. The pool of amino acids available to the mammary gland is influenced by the profile of the absorbed amino acids and metabolism by nonmammary tissues. For example, approximately 20–30% of absorbed total essential amino acids are metabolized by the portal-drained viscera and liver, and this results in deviations from the absorbed amino acid composition. The amino acids lysine and methionine are the most likely to be limiting in metabolizable protein for milk protein synthesis in diets based on maize silage, whereas histidine has been identified as first-limiting for milk yield of cows fed a grass silage and cereal diet. However, methionine deficiencies seem to influence milk fat more effectively than protein synthesis, whereas lysine may be more important in mammary gland amino acid metabolism. Supplementing maize silage and grass silage diets with ruminally protected methionine effectively increased milk fat content. A possible explanation is that, in mammary tissue, methionine may serve as a methyl donor in the transmethylation reaction of lipid biosynthesis. Therefore, amino acids may influence milk composition beyond their expected role of precursors for protein synthesis.

Modulation of protein synthesis

Milk protein content is relatively constant, although substrate availability may influence, at least in part, protein synthesis by the mammary gland. For example, fat supplementation has been reported to depress protein synthesis because of reduced mammary blood flow. A potential explanation for this phenomenon is that increased levels of circulating fatty acids have a sparing effect on oxidation of acetate, thereby increasing the efficiency of lactose synthesis from glucose. However, the increased availability of glucose and higher milk yields are not paralleled by an increase in amino acid uptake, resulting in a reduction of protein in milk. In contrast, feeding of diets containing a high percentage (70–80%) of concentrate increases the supply of amino acids to mammary tissue or the extraction from blood of amino acids, which sustain increased synthesis of milk proteins.

In general, milk protein production is highly correlated to energy in the diet. Enhanced microbial protein, which is influenced by energy availability, accounts for the largest component of intestinal protein flow. Approximately 11% of adenosine triphosphate (ATP) generated within the mammary gland is utilized for milk protein synthesis.

Studies of the endocrine regulation of milk protein synthesis have reported that treatment with bST increased the yield but not the concentration of milk components. On the other hand, hyperinsulinemia, under conditions of euglycemia markedly increases protein percentage (from 3.13 to 3.44%) in milk from cows fed an alfalfa hay-maize-based diet and receiving an abomasal casein infusion. These data suggest that mammary protein synthesis is endocrine regulated. Consequently, it appears there is approximately 25% additional protein synthetic capacity in bovine mammary tissue that is not presently being utilized.

Milk caseins are subjected to partial hydrolysis during mammary gland involution, whereas the whey proteins α-lactalbumin and β-lactoglobulin are relatively resistant to plasmin digestion. This process probably involved hydrolysis by plasmin and other proteases. The accumulation of milk components at dry-off is one of the factors that contributes to increasing susceptibility to mastitis. Digestion of milk protein leads to the production of biologically active peptides that may be involved in mammary gland involution. Lactoferrin, an important antimicrobial protein found in mammary secretions during involution, may also be a substrate for degradation by plasmin. Digestion products of lactoferrin, lactofericins, have a broad-spectrum antimicrobial activity.

Phagocytosis by leukocytes that invade the mammary gland during involution contribute to clearance of milk components.

Lactose

Lactose is the major osmotic determinant of milk and therefore factors that increase lactose synthesis also increase milk yield. Treating lactating dairy cows with bST increases availability of glucose and rate of synthesis of lactose, leading to an increase in milk yield. However, the increase in milk yield is proportional to the increase in lactose synthesis, resulting in no change in milk lactose content. Likewise, increase milking frequency and increased photoperiod, which also increase milk yield, do not alter milk lactose concentration. Recent information on the feedback regulation of milk synthesis indicates that serotonin, a neurotransmitter is also synthesized in mammary tissue and the expression of its synthesis appears to be under partial control by prolactin. Serotonin downregulates expression of the gene coding for α-lactalbumin, the rate-limiting enzyme for lactose synthesis. Thus, increasing amounts of serotonin in milk due to delayed milking acts to downregulate lactose synthesis, which leads to reduced milk synthetic rate.

Milk fat

Milk from Holstein dairy cows fed standard diets based on maize or grass silage and alfalfa hay contains approximately 35–40 $\mathrm{g\,l^{-1}}$ of fat. Fat content is typically highest immediately following parturition and lowest during peak milk yield. Acetate and β-hydroxybutyrate (rumen-derived volatile fatty acids) are important carbon sources for *de novo* fatty acid synthesis by mammary tissue. Approximately 50% of butyric acid is derived from circulating β-hydroxybutyrate, whereas the remaining fraction is originated by condensation of acetyl units.

Ruminants typically consume a diet rich in polyunsaturated fatty acids, yet milk and other dairy products tend to have higher saturated fatty acid content. This is primarily because unsaturated fatty acids tend to be toxic to rumen microflora and therefore biohydrogenated by rumen microbes. Intermediates of biohydrogenation include fatty acids containing a *trans* double bond, and these (including the saturated end product) are incorporated into ruminant lipids. Dietary fatty acids are packaged and transported via chylomicrons and very low-density lipoproteins (repackaged hepatic triglycerides), and their triglyceride core is hydrolyzed by lipoprotein lipase in mammary capillary beds. Long-chain fatty acids (50% of $C_{16:0}$ and longer) represent approximately 50–60% of the total milk fatty acid pool by weight and 40–50% of the total milk fatty acid pool on a molar basis. Short- and medium-chain fatty acids ($C_{4:0}$ to $C_{14:0}$ and 50% of $C_{16:0}$) are synthesized *de novo* and represent the difference on a weight and molar basis, respectively. Fatty acids containing 18 carbons and less constitute a large majority, but over 400 different fatty acids are found in milk fat. Blood and *de novo*-derived fatty acids (both saturated and unsaturated) can be desaturated by sterol CoA desaturase and along with unique rumen-derived fatty acids (odd, even, and branched chained) contribute to the assortment and variation found in typical milk fat. Fatty acids are esterified onto a glycerol backbone, and the positioning of specific fatty acids within the triglyceride contributes to the physical (fluidity characteristics) and organoleptic qualities (taste, smell, etc.) of milk and milk products.

Modulation of milk fat synthesis

Compared with the relative consistency of milk protein and lactose concentrations, milk fat levels can vary markedly and are heavily influenced by nutrition and environment. Rumen microbial carbohydrate fermentation contributes the precursors (primarily acetate) for milk fat synthesis. Therefore, modifications of the rumen environment can manipulate the mammary supply of milk fat building blocks. Certain dietary situations cause milk fat levels to decline, and this low milk fat syndrome is commonly referred to as milk fat depression (MFD). MFD can be described briefly as milk that contains a reduced fat concentration and thus decreased yield of total milk fat. Milk has traditionally been, in large part, priced on the basis of milk fat content, and, consequently, MFD has been an economic concern for dairy producers for over a century. Many feeding regimes such as high-concentrate, low-fiber diets, or diets that contain high amounts of plant oils, cause MFD.

When cows experience MFD the milk fat content of *trans*-$C_{18:1}$ increases and these unique fatty acids are 100% rumen derived. Detailed analysis of the *trans* fatty acid pattern reveals that diet-induced MFD is specifically associated with an increase in *trans*-10 $C_{18:1}$. The association between increased *trans*-10 $C_{18:1}$ and MFD has now been observed in a number of situations. However, whether or not specific *trans* $C_{18:1}$ monoenes actually cause MFD is still not clear. The putative origin of *trans*-10 $C_{18:1}$ is the hydrogenation of *trans*-10, *cis*-12 conjugated linoleic acid (CLA), and this rumen-derived unique fatty acid markedly reduces milk fat synthesis. However, *cis*-9, *trans*-11 CLA, the primary CLA isomer found in milk fat does not induce MFD. In fact, a variety of CLA isomers have been tested and most of them do not cause MFD. Only the aforementioned CLA isomer and *trans*-9, *cis*-11 CLA and *cis*-10, *trans*-12 CLA negatively affect milk fat synthesis. The CLA isomers that do reduce milk fat levels do it by primarily inhibiting *de novo* milk fatty acid synthesis, although during extensive MFD, preformed fatty acids contribution to milk fat is also reduced.

CLA and human health

Theoretically, a number of CLA isomers that differ in the positions of the double bond pairs (7–9, 8–10, 9–11, 10–12, etc.) are possible. Additional differences can exist in the geometric configuration of the double bond so that *cis–trans*, *trans–cis*, *cis–cis,* or *trans–trans* configurations are possible. Fatty acids with conjugated double bonds were first demonstrated in ruminant food products over 65 years ago and later shown to consist of primarily *cis*-9, *trans*-11 CLA. CLA has been shown to have a 'functional food' role because a variety of CLA isomers possess anticarcinogenic properties in a variety of models (mammary, skin, stomach, intestinal, lung and prostate cancers). Subsequent work has identified additional beneficial health effects and consequently milk CLA has received considerable attention from not only the medical community and human nutritionists but also animal scientists. In general, potential beneficial health effects have been identified using biomedical studies with animal models and utilizing chemically synthesized supplements containing a variety of CLA isomers.

CLA synthesis

Traditionally, *cis*-9, *trans*-11 CLA was thought to originate only from ruminal production. However, the dynamics of rumen biohydrogenation are such that CLA are only transient intermediates, and the reduced products of CLA (*trans*-$C_{18:1}$ isomers) accumulate. Therefore, it was hypothesized that this particular CLA isomer was produced by an additional route. In support of this hypothesis, it has been demonstrated recently that at least 64% of *cis*-9, *trans*-11 CLA originates by endogenous synthesis involving sterol CoA desaturase in the mammary gland. Presumably, desaturation of *trans*-7 $C_{18:1}$ (and other *trans* isomers produced from rumen biohydrogenation) within the mammary gland is also the source of *trans*-7, *cis*-9 CLA, the second most abundant CLA isomer found in ruminant fat. Vaccenic acid (*trans*-11 $C_{18:1}$) is typically the most abundant trans 18:1 monoene in ruminant milk fat, and this isomer is also desaturated by sterol CoA desaturase in human tissues. Consequently, human lipid *cis*-9, *trans*-11 CLA is derived from consuming both *cis*-9, *trans*-11 CLA and vaccenic acid (both of which are unique to ruminant-derived food products).

Seasonal Effects

Pronounced seasonal patterns of milk yield and composition are evident in cattle. These seasonal patterns are largely induced by climatologic variables, breed effects, and management factors, such as feed quality and reproductive management. Month of parturition has a pronounced impact on subsequent milk yield and composition. Highest yields occur following January and February parturition, whereas lowest yields occur following August and September calvings (see **Figure 1**).

This results in correction factors that are used to adjust milk yields to remove effects of season on breeding considerations. The seasonal pattern in milk yield is related to the direct and indirect effects of environment on milk production. Direct effects are related to the effects of elevated temperature on milk yield; indirect effects are a result of photoperiod effects and the negative impact of heat stress, during late pregnancy on maternal and fetal metabolism, and circulating plasma endocrine patterns that are altered by the stress. As is apparent from **Figure 1**, there is also a seasonal pattern in milk protein that parallels the seasonal pattern in milk yield. Interestingly, the milk protein yield pattern appears to be more directly affected by temperature as the nadir occurs during the hottest part of the summer, while the milk yield curve displays some of the carryover effects related to indirect effects on pregnancy and metabolic state of the cow.

The majority of studies published on climatic effects on milk composition and yield have evaluated effects of temperature. Dairy cattle are sensitive to heat stress because of the high metabolic heat production feed intake associated with rumen fermentation and milk yield. Likewise, for the same reasons, dairy cattle are relatively resistant to cold stress. Heat stress in cattle is characterized by increased rectal temperature, elevated respiration rates, and decreased feed intake that subsequently, decreases milk yield. The environmental temperature range from −5 to 23.9 °C has little impact on milk yield and composition and is referred to as the thermoneutral zone for the lactating dairy cow. However, temperatures above 23.9 °C are known to decrease solids-not-fat (SNF), protein, lactose, and fat percentage of milk. Because of its

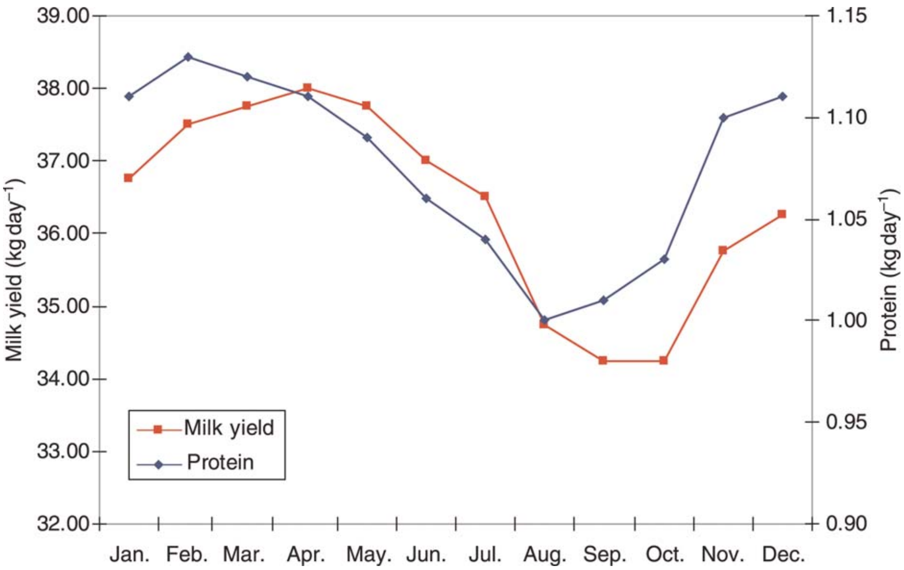

Figure 1 Effect of month of year on milk and protein yield of lactating dairy cows. Adapted from Barash H, Silanikove N, Shamay A, and Ezra E (2001) Interrelationships among ambient temperature, day length, and milk yield in dairy cows under a Mediterranean climate. *Journal of Dairy Science* 84: 2314.

involvement in osmotic regulation of milk, the impact of temperature on lactose and mineral content of milk is much less than that of temperature on protein and fat yields. Generally, in temperate regions, the fat content may average 0.4% lower and the protein content 0.2% lower in summer than in winter months. An alternative approach to evaluating cooling needs in cattle is to use the Temperature Humidity Index (THI). This combined measure of both ambient temperature and relative humidity has been shown to be more effective in evaluating environmental effects on lactating cattle than temperature alone. The original upper limit for cow comfort was established as a THI of 72, using cows producing at or less than 15 kg day^{-1}. Recent data indicate that increasing milk yields of dairy cows to or above 35 kg day^{-1} lowers the upper THI limit to 68.

A final component of milk that displays strong seasonal trends is milk somatic cell content. Milk somatic cell content rises during warm summer months related to increases in pathogen populations in the environment during summer months, decreased disease resistance in cattle associated with prolonged effects of thermal stress, and behavior of the animals that results in animals seeking wet environments with high pathogen populations.

As stated earlier, heat stress is a major contributor to the seasonal pattern of milk yield due to the negative effects of elevated temperature on feed intake and subsequently on milk yield. There is a demonstrated genotype – environment interaction both across and within breeds, indicating that genetic selection for increased heat tolerance is feasible. Furthermore, some traits, such as increased sweat gland number, hair coat characteristics, and increased skin surface area, could be altered without adversely affecting milk yields. However, the time required for achieving a higher level of heat resistance is lengthy. Therefore, the greatest opportunity for increasing milk yield during periods of environmental heat stress has been in the management of the environment surrounding the cow. Dairies in warm climates use a variety of cooling systems, including protection from solar radiation (shades), fans, combinations of fans and misters, and evaporative cooling to produce an environment around the cow, which is preferably in the thermoneutral zone (−5 to 23.9 °C) or a THI below 68.

See also: **Lactation**: Galactopoiesis, Effect of Treatment with Bovine Somatotropin; Galactopoiesis, Effects of Hormones and Growth Factors; Lactogenesis. **Stress in Dairy Animals**: Heat Stress: Effects on Milk Production and Composition.

Further Reading

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