Effect of Milking Frequency on Mammary Functioning and Shape of the Lactation Curve

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ABSTRACT

Milk yield is a function of the number of mammary secretory cells and their metabolic activity. Both are not static, but change during the course of lactation. The rate at which they change may be influenced by farm management practices, such as feeding, photoperiod, hormonal treatment (e.g., bovine somatotropin), and milking frequency. By applying such practices, or a combination thereof, at any time during lactation, the farmer has tools to alter the shape of the lactation curve. These practices could be applied after peak lactation to increase milk yield and perhaps slow down the rate of postpeak decline in milk yield, but can also be used to promote mammary involution near drying-off. The present review focuses on milking frequency. Compared with twice-daily milking, milking three times a day or more often (robotic milking) will increase milk yield by 18%, whereas once-daily milking decreases milk output by 20%. Although frequent milking is practiced more often than once daily, the once-daily milked gland provides an excellent model to study functional changes related to milking frequency. The effects of increasing and decreasing milking frequency on mammary functioning are discussed, with emphasis on functional changes in the once-daily milked gland with regard to processes such as changing cell number or activity, feedback inhibition, tight junction leakiness, apoptosis, and cisternal-alveolar milk storage.

(Key words: mammary gland, milking frequency, mammary functioning, tight junction)

Abbreviation key: ACC = acetyl CoA carboxylase, FAS = fatty acid synthetase, FIL = feedback inhibitor of lactation, GST = galactosyltransferase, PTHrP = parathyroid hormone-related peptide, TJ = tight junction, X = number of milkings per day

INTRODUCTION

Milk provides a complete diet with all the essential nutrients for the newborn calf, which initially is unable to collect, chew, or ingest solid foods. As such, milk is essential to the calf’s survival. However, as a result of selection, controlled breeding programs, proper nutrition, and management the milk yield of the modern dairy cow is many times that needed for its offspring. Indeed, milk has become a valuable commodity to man, both in nutritional and economical sense (Stelwagen et al., 1992a).

The level of milk output per cow is a key factor in the economic survival of the modern dairy farm. Whether this requires maximizing milk yield per cow or optimizing milk output is a valid but separate discussion and will not be part of this paper. Instead, the aim of the present paper is to discuss a number of tools available to the farmer that can be used to manipulate milk yield per cow, with major emphasis on milking frequency and how it affects mammary functioning and possibly the shape of the lactation curve.

TOOLS TO MANIPULATE MILK PRODUCTION

Controlled breeding programs and proper, well-balanced nutrition programs have been very important tools for reaching the production level of the dairy cow to date. However, today’s dairy farmer has also other tools available to directly manipulate milk production, either during the entire lactation or only part thereof, such as photoperiod, hormonal treatment, and milking frequency.

The beneficial effects of longer photoperiod on milk production have been known for some time. Peters et al. (1981) reported a 6.7% increase in milk yield of cows exposed to a regimen of 16 h of light and 8 h of darkness, compared with cows exposed to ambient light (9 to 12 h/d). Similarly, Dahl et al. (1997) showed more recently that compared with ambient light (≤13 h) cows exposed to a long photoperiod (18 h) produced 6.5% more milk per day. The exact mechanism by which extended photoperiods act to increase milk yield is not fully understood. Although increasing the amount of light reduces melatonin concentrations and increases prolactin levels (Stanisiewski et al., 1988), there still is no clear evidence linking these endocrine changes to enhanced milk secretion. Results of a recent study showing that levels of IGF-I increase with an extended photoperiod (Dahl et al., 1997) are therefore very interesting, because it is commonly accepted that IGF-I is an important mediator of the galactopoietic effects of bST.

Selective use of bST is one of the best examples of hormonal treatment as a management tool to increase milk production. Although the galactopoietic effects of bST were already known early in the last century (Asimov and Krouze, 1937), research into the use of bST as a tool to increase milk production suddenly accelerated after it became possible in the early 1980s to produce recombinant bST in large and pure quantities. Bauman et al. (1982) were the first to show that recombinant bST increased milk yield significantly. Since
then, numerous studies carried out under many different management conditions have confirmed these early results, showing an average increase in milk production of 15 to 20% (Chilliard, 1989; McBride et al., 1988). Since the mid 1990s, bST has been commercially available to dairy farmers in the United States. Alternatively, bST may also be used to stimulate milk production indirectly, through enhancing mammogenesis. In heifers and lambs treated with bST during the last trimester of gestation, subsequent milk yield was significantly enhanced (Stelwagen et al., 1992b, 1993).

Generally cows are milked twice daily (2X), but increasing milking frequency to three times a day (3X) or even more often increases milk yield by 10 to 20% (Erdman and Varner, 1995; Jurjanz et al., 1993; Van der Iest and Hilerton, 1989). More frequent milking is commonly practiced to increase milk yield on commercial dairy farms and with the number of farms with robotic milking systems rapidly increasing (Lind et al., 2000), it may become the standard practice rather than the exception. On the other hand, in low-cost and low-input dairy systems, such as in New Zealand and Ireland, once daily milking (1X) during the entire or part of the lactation can also provide an effective management tool (Davis et al., 1999).

Although each of these tools can be used to manipulate milk production, a combination of tools may be even more effective. Miller et al. (1999) showed that an extended photoperiod (18 vs. 9.5 to 14.5 h of ambient daylight) and bST each increased milk yield in cows, but that a combination of treatments resulted in the highest milk yield. Similarly, in a study in which cows were treated with or without bST and had udder halves milked four times a day (4X) or 2X, the 4X and bST treatments resulted in, respectively, 14 and 13% more milk, but the combined treatments again resulted in the highest milk yield (28.5%; Knight et al., 1992). In both experiments the effects of the different treatments were additive rather than synergistic. Moreover, the adverse effects of 1X on milk production may be overcome by the use of bST (Carruthers et al., 1991; Stelwagen et al., 1994a).

In the following sections, the effects of milking frequency on mammary functioning will be discussed in more detail. However, first the difference between milking frequency and milking interval needs to be emphasized.

### MILKING FREQUENCY AND MILKING INTERVAL

The terms milking frequency and milking interval are often used interchangeably. However, although closely related, they cannot be used synonymously. If milking frequency within a given time frame, commonly a 24-h period, increases, then it often follows that the milking interval decreases, and vice versa. However, this does not necessarily have to be the case. For example, with 3X milking one could imagine two short intervals of only a few hours and a very long interval. Research has shown, however, that the milking interval has to be less than 18 h to avoid adverse effects on milk yield and milk quality (Stelwagen and Lacey-Hulbert, 1996; Stelwagen et al., 1997).

For the current discussion, milking frequency refers to the number of milkings in a 24-h period. Further, unless specified otherwise, resulting milking intervals are assumed to be relatively similar between milkings.

#### Table 1. Effect of milking frequency on milk yield in different species, using half-udder experiments (change expressed as a percentage of the 2X-milked control gland).¹

<table>
<thead>
<tr>
<th>Species</th>
<th>1X</th>
<th>3X</th>
<th>4X</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cow (early lactation)</td>
<td>–38</td>
<td></td>
<td></td>
<td>Stelwagen and Knight, 1997</td>
</tr>
<tr>
<td>Cow (late lactation)</td>
<td>–28</td>
<td></td>
<td></td>
<td>Stelwagen and Knight, 1997</td>
</tr>
<tr>
<td>Cow</td>
<td>+14</td>
<td></td>
<td></td>
<td>Knight et al., 1992</td>
</tr>
<tr>
<td>Cow</td>
<td>+7</td>
<td></td>
<td></td>
<td>Morag, 1973</td>
</tr>
<tr>
<td>Cow</td>
<td>+32</td>
<td></td>
<td></td>
<td>Cash and Yapp, 1950</td>
</tr>
<tr>
<td>Sheep</td>
<td>–19</td>
<td></td>
<td></td>
<td>Morag, 1968</td>
</tr>
<tr>
<td>Goat</td>
<td>+10</td>
<td></td>
<td></td>
<td>Knight, 1992</td>
</tr>
<tr>
<td>Goat</td>
<td>+14</td>
<td></td>
<td></td>
<td>Knight et al., 1990</td>
</tr>
<tr>
<td>Goat</td>
<td>+20</td>
<td></td>
<td></td>
<td>Wilde et al., 1987</td>
</tr>
<tr>
<td>Goat</td>
<td>–26</td>
<td></td>
<td></td>
<td>Wilde and Knight, 1990</td>
</tr>
</tbody>
</table>

¹ Differences in response within a certain milking frequency may depend on differences in stage of lactation, production level, breed, duration of the milking regimen, and individual udder characteristics.

### MAMMARY FUNCTIONING AND MILKING FREQUENCY

#### Local Effects

Both the effects of increasing and decreasing milking frequency on milk yield appear to be caused by local, intramammary factors. The evidence for this comes from half-udder experiments, in which the treatment (e.g., 1X or 3X) is applied to one half of the udder, whereas the contralateral half, milked 2X, is used as a control. With cows, diagonally opposed glands are often paired. Because treatments are applied within animal with this experimental approach, both halves of the udder are exposed to the same systemic factors. Hence, any treatment difference must be solely due to intramammary factors. The intramammary effects of milking frequency on milk yield range from −38% with 1X to +32% with more frequent milking regimens (Table 1). Moreover, Table 1 also demonstrates that these local, intramammary effects are not species specific.

In particular, in cases in which less frequent milking (i.e., 1X) is compared with 2X, a small compensatory increase in milk yield in the 2X-glands may initially be observed (Stelwagen and Knight, 1997). This increase may be related to greater sudden substrate availability to the 2X glands. However, such compensatory effects can be accounted for by expressing the yield as the relative milk yield quotient (Linzell and Peaker, 1971), allowing the extent of the local, intramammary effects of altered milking frequency on milk yield to be determined.

#### Mammary Cell Number and Cell Activity

To understand how these intramammary mechanisms function, it is important to understand that ultimately milk yield is a function of the number of secretory cells present in the udder and the metabolic activity of these cells. Both of these processes, alone or in combination, determine the milk
yield potential of the mammary gland. In the normal lactating goat, mammary gland postpeak milk yield appears to be largely a function of the number of cells present, whereas before peak yield cell activity also plays an important role in determining milk yield (Knight and Wilde, 1987). On the other hand, in rodents, cell number may play a more important role in early lactation (Knight and Wilde, 1987).

Changes in mammary cell activity are often measured as changes in the activity of several key mammary enzymes, such as acetyl CoA carboxylase (ACC), fatty acid synthetase (FAS), and galactosyltransferase (GT). Travers and Barber (1993) showed that in goats increasing milking frequency from 2X to 3X increased mammary cell activity. Both the amount of RNA per cell (general cell activity) and the activities ACC and FAS (specific cell activity) were increased. Others have also demonstrated increased enzyme activity with 3X milking in goats (Wilde et al., 1985, 1987; Wilde and Knight, 1990) and 4X milking in cows (Hillerton et al., 1990; Knight et al., 1992) compared with the 2X-milked contralateral glands. If increasing milking frequency increases mammary cell activity relative to the activity in 2X-milked tissue, one would expect to see a decrease in cellular activity in glands that are milked less frequently. Only a few studies have compared enzyme activities in udder halves milked 1X compared with 2X. In cows milked 1X or 2X unilaterally, the activities of ACC, FAS, and GT were indeed significantly lower in the 1X tissue (Farr et al., 1995b). A goat study also showed a trend toward decreased enzyme activity with 1X milking (Wilde and Peaker, 1990), and Stelwagen and Knight (1997) showed a reduction in milk secretion efficiency (i.e., milk per unit udder-half volume) in 1X compared with 2X-milked udder halves of cows.

In most of these experiments, mammary cell activity has been measured after a relatively short treatment period, weeks rather than months. Interestingly, there is evidence from goats to suggest that during long-term (i.e., months) 3X milking the increased cellular activity is not maintained, despite a persistently higher milk yield (Wilde et al., 1985). This implies that over the longer term, the higher milk yield is maintained by factors other than increased cellular activity. Consistent with this notion, the same group found that long-term (i.e., 9 mo) 3X milking resulted in more mammary parenchyma (Henderson et al., 1985), suggesting an increase in mammary cell number. Although, it cannot be ruled out that the increase in parenchyma was due to hypertrophy and was not a result of hyperplasia, the same group reported in a subsequent study that after 37 wk the 3X-milked glands contained more secretory cells than the 2X-milked glands (Wilde et al., 1987).

Collectively, these data suggest that short-term effects (i.e., weeks) on milk secretion as a result of a change in milking frequency are mediated via an up or down regulation of cellular activity, whereas the long-term (i.e., months) effects are more likely related to changes in cell number. However, the effects of altered milking frequency are almost immediate, and there are a number of important processes happening during the first 24 h after the change in milking frequency. It would seem pertinent therefore to distinguish an “acute phase” during the first 24 h of change after which changes in cell activity and cell number occur. The following sections will highlight the main processes occurring during the first 24 h. The 1X-milked gland will be used as a model, because it represents an “extreme” situation and therefore emphasizes the acute changes in mammary functioning.

**Feedback Inhibitor of Lactation**

In the early 1970s, Linzell and Peaker (1971) already mentioned the possibility of milk yield being regulated by a chemical in the milk that acts as a feedback inhibitor of lactation (FIL). Since then, several experiments have been conducted in which a crude milk fraction, purported to contain the FIL-fraction, decreased casein and lactose synthesis in mammary explant cultures and decreased milk yield in vivo when administered via the teat in goats (Wilde et al., 1995). To date, numerous review papers have been written about FIL and its proposed mode of action (Knight et al., 1998; Peaker et al., 1997; Wilde and Hurley, 1996; Wilde and Peaker, 1990; Wilde et al., 1997). One such mode of action is that it accumulates in milk until it reaches a certain critical concentration, at which time it acts as a negative feedback inhibitor. Another potential mode of action is that FIL is always present in milk but is shielded from its receptor until milk that accumulates in an alveolus stretches its surface enough to exposes potential receptors for FIL. However, in an experiment with cows that were milked 1X but had also infused an intramammary solution of sucrose and lactose equal to “five hours worth” of milk, milk secretion was inhibited to a greater extent then in the control cows milked 1X (Stelwagen et al., 1998). Yet, in this case the concentration of FIL would have been diluted and also the intramammary volume would have been sufficient to stretch the alveolar surface and expose potential FIL receptors. Instead, mammary tight junctions (TJ) became leaky much earlier than after the usual 18 h observed with 1X milking (Stelwagen et al., 1997, 1998). Elucidating the exact mode of action of FIL will be greatly facilitated if the gene for FIL can be isolated and when it becomes possible to measure FIL concentrations in milk and thus establish its kinetics in relation to milking frequency.

**Tight Junction Permeability**

The tight junction, or zonula occludens, is the most apical member of the junctional complex between epithelial or endothelial cells, and it serves a dual function. In its “fence” function, it separates the cell membrane in apical and basolateral domains, each of distinct composition. However, it is the “barrier” function that allows the TJ to restrict the passage of ions and (or) small molecules between adjacent cells (Schneeberger and Lynch, 1992). This is not a passive process; TJ are actively involved in regulation of paracellular transport (Madara, 1988; Schneeberger and Lynch, 1992). The observation in goats that TJ of the mammary epithelium became leaky during a 24-h milking interval and that the moment they became leaky (after approximately 20 h) coincided with the moment the rate of milk secretion began to decline, suggested that TJ play a role in the milk loss with 1X milking (Stelwagen et al., 1994b). This has since been confirmed in studies with cows milked 1X, showing that TJ become leaky after approximately 17 to 18 h of milk accumulation (Stelwagen et al., 1997, 1998a, 1998b), which coincides with the rate of milk secretion starting to decline at that stage (Davis et al., 1998). Evidence of a more direct link between milk secretion and TJ is coming from experiments with induced leakiness of TJ (Allen, 1990; Stelwagen et al., 1995). In a “half-udder” experiment with goats in which TJ-
leakiness was artificially induced unilaterally, induced glands yielded approximately 15% less milk than the contralateral control glands (Stelwagen et al., 1995). Interestingly, the magnitude of this milk loss is of the same order as that observed with 1X milking.

The exact mechanism through which leaky TJ affect milk production remains elusive, but a proposed mechanism is presented in Figure 1a. Starting with a reduction in milking frequency, e.g., going from 2X to 1X, two processes are initiated: a reduction in prolactin secretion and cell stretching. There is good evidence from studies with rodents that preventing milk removal inhibits prolactin release (Lee et al., 1989; Yamamuro and Sensui, 1994) and expression of the long form of the prolactin receptor (Kim et al., 1997). Moreover, it was recently demonstrated that prolactin has a direct effect on the expression of occludin, one of the major TJ proteins (Stelwagen et al., 1999). Although the role of prolactin in ruminants is less clear than in rodents (Knight, 1993), its exact role in ruminants warrants revisiting. Cell stretch or flattening is related to pressure building inside the alveolus as a result of its filling (Figure 2). It is expected that these are very subtle pressure changes, which can not easily be measured in vivo and which are quite different from the intramammary pressure changes measured at cessation of milking (Peaker, 1980). This hypothesis is supported by a study with cows in which two glands were catheter-drained once after 24 h, whereas the contralateral glands were continuously drained via a catheter. In the latter glands, the continuous drainage would have prevented intra-alveolar pressure build-up. As predicted, milk secretion from these glands was significantly higher than that from the once-drained glands (Stelwagen et al., 1996). The substantial differences in cell shape before (i.e., flattened cells) and after (i.e., elongated cells) milking were quite nicely shown in early electron micrographs by Richardson (1947). Changes in cell shape have been shown to induce mechanotransduction in lung, uterine, and bladder tissues (Daifotis et al., 1992; Wirtz and Dobbs, 1990; Yamamoto et al., 1992) and have been proposed in 1X mammary tissue (Stelwagen et al., 1997). Mechanotransduction is the process by which physical stimuli, such as pressure, induce intracellular signaling events that culminate in gene expression events. Further, both prolactin and cell stretch or mechanotransduction have been shown to regulate parathyroid hormone-related peptide (PTHrP) secretion (Daifotis et al., 1992; Thiede, 1989; Wirtz and Dobbs, 1990; Yamamoto et al., 1992). Thus, in the proposed model (Figure 1a), both the decrease in prolactin and the increase in cell stretch would lead to a down regulation of PTHrP, which in turn would block apical calcium channels (Bacskai and Friedman, 1990) and prevent replenishing of intracellular calcium stores, which are important for maintenance of TJ (Jovov et al., 1994). In agreement with this theory, PTHrP secretion into milk declines with 1X milking compared with 3X milking (Thompson et al., 1994) or after weaning of pups in rats (Yamamuro and Sensui, 1994). Moreover, preliminary data show a direct effect of PTHrP on TJ formation in vitro in mouse mammary epithelial cells (Stelwagen and Callaghan, 2000, unpublished data). Because TJ are closely inter-linked with the cytoskeleton of the cell, any perturbation of TJ will induce cytoskeletal changes that in turn interfere with milk secretion (Guerin and Loizzi, 1978; Patton, 1976a, 1976b; Nickerson et al., 1980). Alternatively, the proposed mechanism of action also holds up with increased milking frequency (Figure 1b), except that the effects may be less pronounced given that 3X milking represents a less extreme scenario than 1X milking. Unfortunately, little information is available on the effects of frequent milking on mammary TJ. However, plasma...
concentrations of the milk protein α-lactalbumin, which is a good indicator of TJ leakiness (Stelwagen et al., 1997), were significantly lowered in 3X compared with 2X-milked cows (McFadden et al., 1987), suggesting that mammary TJ were tighter with increased milking frequency.

Apoptosis

Apoptosis is the process of programmed or controlled cell death and occurs in many different tissues and at all stages of development. It is one of the body’s ways of ridding itself of unwanted cells without causing an inflammatory reaction, as would have been the case with any necrotic process. The mammary tissue is no exception, and Walker et al. (1989) and Strange et al. (1992) were the first to show that apoptosis is part of the normal tissue remodeling process during mammary involution in rodents.

Weaning or cessation of milk removal causes a drop in lactogenic hormones, which leads to involution of the mammary glands. The process of mammary involution remains reversible during approximately the first 30 to 36 h, after which the process becomes irreversible (Jaggi et al., 1996). Nevertheless, important changes occur within 24 h of weaning. Protein kinase A activity and DNA-binding activity of the activator protein-1 transcription factor complex increase, and expression of the early response genes c-Fos, junD, c-Jun, sulfated glycoprotein-2, bcl-x, and bax is up-regulated (Strange et al., 1992; Heermeier et al., 1996; Jaggi et al., 1996; Li et al., 1997). All these events are associated with the initiation of mammary apoptosis. Although it may be dangerous to extrapolate directly from the rodent mammary gland to the ruminant udder, apoptosis has also been demonstrated to occur in the caprine and bovine mammary glands during involution (Quarrie et al., 1994, Wilde et al., 1997b). It is therefore tempting to speculate that during the extended milking interval in the 1X-milked cow the process of apoptosis (i.e., early involution) is initiated every time and that the galactopoietic process is “rescued” each time when the gland is milked after 24 h. This scenario of changes during milk accumulation fits well with other changes such as TJ leakiness, reduced mammary blood flow, and milk secretion starting after approximately 18 to 20 h of milk accumulation in cows and goats (Stelwagen et al. 1994b, 1997). Moreover, the plasmin system is also implicated in the onset of involution (Politis, 1996) and increases in plasmin, plasminogen, and plasminogen activator activity observed in milk of 1X-milked cows are consistent with the above-noted preapoptotic changes in gene activity (Kelly et al., 1998; Knutson et al., 1993; Stelwagen et al., 1994c).

In extending this scenario to the frequently milked gland, one would assume that with increased milking frequency, the galactopoietic process is “rescued” (i.e., milk is removed) often enough that the early apoptosis-associated events are prevented. Although data to support or deny this contention are lacking, limited information on milk plasmin activity in relation to frequent milking are supportive. Milk plasmin did not increase with 3X compared with 2X milking (Klei et al., 1997), and very frequent milk removal (i.e., every 2 h) resulted in even a reduction of plasmin activity in milk (Kaartinen et al., 1990).

Alveolar and Cisternal Milk Storage

The processes discussed so far occur at a cellular or intercellular level, but anatomical differences at the whole gland level also appear to be important in mediating the effects of milking frequency, in particular with 1X milking. Cows that store a relatively small proportion of the milk in the cistern benefit most from 3X milking (Dewhurst and Knight, 1992). On the other hand, cows that store a bigger proportion of the milk in the gland cistern show less of a decline in milk yield with 1X than cows that do not (Knight and Dewhurst, 1994). Others have also confirmed an inverse relationship between the proportion of milk stored in the cistern or total udder capacity and milk yield loss with 1X milking (Davis et al., 1987; Stelwagen and Knight, 1997), although some have found a much weaker relationship (Carruthers et al., 1993). In a study in which udder halves of cows were catheterized and milk from one gland was drained after 24 h (1X) and milk from the opposing glands was drained continuously during a 24-h period, milk yield from the latter, representing cisterns with infinite capacity, was significantly higher (Stelwagen et al., 1996). This study demonstrates that milk loss with 1X is related to cistern capacity and is consistent with the proposed model in Figure 2a.

Relating cisternal milk storage capacity to milk loss with 1X milking may be too simplistic. The ability of milk to drain freely from the alveoli into the cistern also appears to be important in determining the extent of milk loss with 1X milking. Although in the cow the alveolar and cisternal compartments both start to fill shortly after milking (Stelwagen et al., 1996), the former is filled to capacity approximately 16 h after milking (Davis et al., 1999). This time agrees well with the time after which TJ become leaky in the udder (Stelwagen et al., 1997). Obviously, if milk continues to drain freely from the alveoli at this stage, such negative intramammary changes may be averted for a longer period of time or, in other words, the gland would be more tolerant to 1X milking. Data from cows (Farr et al., 1995a) and denervated mammary glands in rats (Grosvenor and Findlay, 1968) and sheep (Labussière et al., 1978) demonstrate the importance of ductal drainage in the mammary gland.

MILKING FREQUENCY AND REGULATION OF MILK SECRETION

Attempting to provide a detailed summary of the complex regulatory processes underlying the changes in milk production induced by altering milking frequency is nearly impossible. However, Knight et al. (1988) proposed to distinguish three phases through which the mammary gland evolves in adapting to increased or decreased milking frequency: an acute phase (one to several days), a short to medium-term phase (days to weeks), and a long-term phase of adaptation (weeks to months). It is tempting to limit the acute phase to only 24 h. This phase is characterized by acute regulatory mechanisms such as feedback inhibition of lactation, TJ leakiness, and the onset of apoptosis. During the short- to medium-term phase, the gland adapts to a state of lower or higher cellular activity (e.g., enzyme activity). Finally, during the long-term phase, changes in mammary parenchyma or cell number are proposed to occur. In addition, gland anatomy appears to be involved in determining the extent of changes in milk yield in response to altered milking frequency. Therefore, the regulation of milk secretion is likely
The dairy farmer has a number of tools to directly manipulate milk production. Changing milking frequency is one such tool. Increasing or decreasing milking frequency impacts the processes involved in mammary functioning. These processes seem to be continually geared at cessation of milk synthesis, which becomes particularly obvious with less frequent milking, such as with 1X milking, when during the course of a 24-h milking interval, several events leading to cessation of milk synthesis are initiated, but where each time these events are reversed by milking after 24 h, thus rescuing lactation. Alternatively, increasing milking frequency (2X) will prevent the onset of these events and may even stimulate mammary cell activity (>2X), resulting in an increased milk production. The milking frequency to maximize the milk yield response is between 3X and 4X. Short-term alteration of milking frequency can transiently lower or increase milk yield, whereas long-term changes in milking frequency may lead to sustained changes in milk yield as a result of changes in the amount of secretory tissue present in the udder. In both instances, it will allow the farmer to use milking frequency to change the shape of the lactation curve.

CONCLUSIONS

The short answer is: yes. More or less frequent milking will, respectively, increase or decrease milk output and thus lead to changes in the shape of the milking curve. Moreover, full lactation studies have shown that these changes in milk secretion can be sustained throughout lactation (DePeters et al., 1985; Holmes et al., 1992).

Of greater interest is, however, the question: do changes in mammary functioning that are a result of altered milking frequency cause any changes in lactational persistency? In other words, will increased or decreased milking frequency, respectively, decrease or increase the rate at which milk yield declines following peak production. The answer to this question is less apparent. Most of the work elucidating the effects of milking frequency on mammary functioning is based on short-term experiments ranging in length from days to several weeks, and it is therefore difficult to deduce any permanent effects on mammary functioning from such experiments.

There is evidence that long-term 3X milking increased the amount of mammary parenchyma in goats (Henderson et al., 1985). In cows, when milking frequency was reduced from 3X to 2X (Poole, 1982) or from 6X to 3X (Bar-Peled et al., 1995) partway through lactation, milk yield, although lowered, remained above the levels in the control groups, suggesting that frequent milking caused an increase in mammary parenchyma. Given that the amount of secretory tissue is an important determinant of milk yield, one might expect that the increased amount of parenchyma would result in a more persistent lactation curve. However, this appears not to be substantiated by a study of DePeters et al. (1985), in which 3X cows produced more milk than those milked 2X, but the rate of decline of postpeak milk yield was the same for both groups. However, there is some evidence to suggest that 1X milking enhances mammary regression (Carruthers et al., 1993), and also continued incomplete milking of cows hastened mammary regression and resulted in a short lactation (Davis et al., 1985, Ziesack et al., 1986).

SHAPE OF THE LACTATION CURVE

In the preceding sections, a number of processes essential to the proper functioning of the mammary gland have been described in relation to milking frequency. The question now is: will milking frequency-induced changes in these processes culminate into a change in the shape of the lactation curve? The short answer is: yes. More or less frequent milking will, respectively, increase or decrease milk output and thus lead to changes in the shape of the lactation curve.
REFERENCES


